Form and motion processing of second-order stimuli in color vision

Luis Garcia-Suarez
McGill Vision Research, Department of Ophthalmology, McGill University, Montreal, Quebec, Canada

Kathy T. Mullen
McGill Vision Research, Department of Ophthalmology, McGill University, Montreal, Quebec, Canada

We investigate whether there are second-order form and motion mechanisms in human color vision. Second-order stimuli are contrast modulations of a noise carrier. The contrast envelopes are static Gabors of different spatial frequencies (0.125–1 cycles/°) or drifting Gabors of different temporal frequencies (0.25 cycles/°, 0.5–4 Hz). Stimuli are isoluminant red-green or achromatic. Second-order form processing is measured using a simultaneous 2IFC (two-interval forced-choice) detection and orientation identification task, and direction identification is used for second-order motion processing. We find that for simple detection thresholds, chromatic performance is as good or better than achromatic performance, whereas for both motion and form tasks, chromatic performance is poorer than achromatic. Chromatic second-order form perception is very poor across all spatial and temporal frequencies measured and has a lowpass contrast modulation sensitivity function with a spatial cutoff of 1 cycle/° and temporal cutoff of 4 Hz. Chromatic second-order motion sensitivity is even poorer than for form and typically is limited to 1–2 Hz. To determine whether this residual motion processing might be based on feature tracking, we used the pedestal paradigm of Lu and Sperling (1995). We find that adding a static pedestal of the same spatial frequency as the drifting Gabor envelope, with its contrast set to 1–2 times its detection threshold, impairs motion direction performance for the chromatic stimuli but not the achromatic. This suggests that the motion of second-order chromatic stimuli is not processed by a second-order system but by a third-order, feature-tracking system, although a genuine second-order motion system exists for achromatic stimuli.

Introduction

The visual system not only uses first-order information, defined as spatio-temporal variations in luminance and/or color, but also extracts second-order information based on spatio-temporal variations in contrast or texture (Cavanagh & Mather, 1989; Chubb & Sperling, 1988). Many studies have shown that second-order information is used in achromatic vision both to define form (Schofield & Georgeson, 1999, 2003; Scott-Samuel & Georgeson, 1999; Sutter, Sperling, & Chubb, 1995) and motion (Baker, 1999; Chubb & Sperling, 1988, 1989; Ledgeway & Smith, 1994; Lu & Sperling, 1995, 2001; Nishida, Ledgeway, & Edwards, 1997; Nishida, 2004; Pavan, Campana, Guerreschi, Manassi, & Casco, 2009; Schofield & Georgeson, 1999, 2003; Smith & Ledgeway, 1997), and as a cue to stereopsis (Wilcox & Hess, 1997). Here we aim to determine whether color vision can support second-order form and/or motion processing and define its spatio-temporal sensitivity.

Although there was early doubt about whether color vision could support first-order form perception at isoluminance, a range of studies have since revealed a prominent role of color vision in extracting first-order shape and form, with direct evidence for contour and shape processing (Mandelli & Kiper, 2005; Mullen, Beaudot, & Ivanov, 2011; Mullen, Beaudot, & McIlhagga, 2000), bandpass spatial frequency tuning (Losada & Mullen, 1994, 1995), and orientation discrimination (Beaudot & Mullen, 2005; Webster, De Valois, & Switkes, 1990). In comparison, relatively little is known about the role of color vision in second-order form processing. While one study has measured the spatial properties for the detection of contrast-modulated chromatic stimuli using beat patterns (Cropper, 2006), there are none that have measured directly the spatial properties of second-order color processing. For achromatic contrast, this has typically been done using an orientation identification task to ensure that stimulus detection is based on form identification rather than global contrast increment discrimination

Citation: Garcia-Suarez, L., & Mullen, K. T. (2013). Form and motion processing of second-order stimuli in color vision. *Journal of Vision*, *13*(7):10, 1–14, http://www.journalofvision.org/content/13/7/10, doi:10.1167/13.7.10.

doi: 10.1167/13.7.10 Received April 5, 2013; published June 17, 2013 ISSN 1534-7362

(Hutchinson & Ledgeway, 2006; Ledgeway & Hutchinson, 2005; Ledgeway & Smith, 1994; Smith & Ledgeway, 1997, 1998). In the first part of this study, we measure stimulus orientation identification as compared to stimulus detection for second-order Gabor stimuli over a range of envelope spatial and temporal frequencies in order to define the spatio-temporal contrast modulation sensitivity function (CMSF) for form in color vision.

Genuine first-order motion is thought to be absent in color vision. Although there is evidence that subjects can perform on first-order motion tasks at isoluminance, it is thought that this is mediated by other mechanisms. First, performance on first-order chromatic motion tasks has been shown to be mediated by responses in a luminance-based pathway rather than by a dedicated color mechanism because chromatic motion performance is selectively eliminated by a superimposed luminance noise mask, whereas the same mask has no effect on chromatic stimulus detection (Baker & Hess, 1998; Mullen, Yoshizawa, & Baker, 2003; Yoshizawa, Mullen, & Baker, 2000, 2003). We note, however, that a few studies suggest that color vision can support first-order motion under specific stimulus configurations (Cropper, 2005, 2006; Cropper & Wuerger, 2005). Second, Lu and Sperling (1995) used a pedestal paradigm to study the nature of the mechanism for first-order motion processing in color vision. They found that adding a static pedestal to first-order contrast-modulated chromatic stimuli brings the observers' performance level to chance, suggesting that motion from first-order stimuli in color vision is actually analyzed by a third-order motion or feature-tracking system, particularly under slow temporal frequency conditions.

There have not been many studies that have selectively assessed second-order motion processing in color vision using second-order stimuli (Cropper & Derrington, 1996; Cropper & Johnston, 2001). Instead, studies on higher-order color motion have used contrast-modulated stimuli, such as random Gabor kinematograms (RGK), with superimposed luminance noise masks to remove any first-order responses (Cropper, 2005; Mullen et al., 2003; Yoshizawa et al., 2000, 2003). The motion performance based on the chromatic contrast envelope has been found to be immune to the addition of luminance noise, suggesting that the higher-order motion in these stimuli can be processed by a genuine color system (Mullen et al., 2003; Yoshizawa et al., 2000, 2003). An issue that remains unresolved, however, is whether the motion was analyzed by a second-order motion system, which extracts the contrast modulation, or a third-order, feature-tracking motion system. In a recent study, we investigated whether there are mechanisms in color vision that support second-order global motion (Garcia-Suarez & Mullen, 2010). We used limited-lifetime stimuli to minimize the tracking of the second-order RDKs and to avoid the use of the third-order, feature-tracking motion system. We found that the global motion performance for chromatic stimuli was null even when second-order RDKs were at 100% motion coherence. We concluded that the chromatic input to global motion processing for second-order stimuli is very limited or nonexistent under our stimulus configuration. This might be due, however, to failure of global motion processing for color vision at the level of area MT (medial temporal) or an impairment of second-order processing of the motion of the individual elements, arising at a lower cortical stage.

We address this issue in the second part of this study, in which we investigate the motion processing of contrast-modulated stimuli based on second-order cues. We measure thresholds for the identification of motion direction for second-order Gabor stimuli over a range of envelope temporal frequencies, presented at an optimal spatial frequency. We then test whether these chromatic thresholds are determined by a second-order motion mechanism or by a third-order (feature-tracking) motion mechanism by using a similar pedestal paradigm to Lu, Lesmes, and Sperling (1999).

In summary, the present study aims to characterize the spatio-temporal properties of both form and motion processing for second-order chromatic Gabor stimuli based on the contrast modulation of a spatially band-passed noise carrier. Contrast modulation sensitivity functions for second-order static and moving chromatic stimuli are measured using a detection task, a form identification task, and a motion identification task, and are compared to the same results obtained for second-order achromatic stimuli. The role of feature-tracking in the second-order task is then compared for chromatic and achromatic stimuli.

Methods

Material and observers

Stimuli were displayed on a CRT monitor (Sony Trinitron GDM-500PST, Sony Corporation, Tokyo, Japan) with a spatial resolution of 1024 × 768 pixels and a temporal refresh rate of 120 Hz. A 14-bit per channel graphics card, ViSaGe (Cambridge Research Systems, Kent, UK) programmed using Matlab (Mathwork version 2008b), was used to generate all stimuli. We used the OptiCal photometer (CRS) in combination with the VSG calibration routine to gamma correct our CRT display monitor. The spectral emissions of the red, green, and blue phosphors were measured using a Spectrophotometer SpectraScan PR-

645 (Photo Research Inc., Chatsworth, CA, USA). The mean luminance (white point) used in all experiments was set to half of the maximum luminance output of the monitor and was 50 cd/m^2.

Four observers, three naive (IVI, NN, and MM) and one author (LG), participated in the study. All have normal or corrected-to-normal acuity and normal color vision assessed with the Farnsworth-Munsell 100-hue test. Subjects were seated 55 cm away from the screen. They viewed the stimuli binocularly in a darkened room and recorded their response after each trial using a response box (CB6 from CRS). Feedback was given, unless otherwise noted.

Stimuli

All stimuli were designed to stimulate second-order mechanisms and consisted of a static or drifting contrast modulation of a static, bandpass-filtered noise carrier. In all experiments, except for observer NN, we used the same noise carrier, which consisted of a flat spectrum noise spatially bandpassed. The bandpass filter was made by coupling a lowpass and a highpass Butterworth digital filter. The lower and upper cutoff frequencies of the filters were set to 0.25 and 2 cycles/°, respectively, and the filter reduced amplitude by 40dB at 4 cycles/°. We used a 2 cycles/° upper cutoff frequency for the filter for two main reasons: to reduce or eliminate the presence of chromatic aberrations that may induce luminance artifacts at high frequencies (Flitcroft, 1989) and to match the lowpass nature of human color vision (Mullen, 1985). The lower cutoff frequency boundary was set to minimize luminance artifacts that may arise from the use of large pixel size noise carrier (Smith & Ledgeway, 1997), although in a previous work we show no luminance artifact intrusion when using a lowpass-filtered noise without the lower cutoff frequency (Garcia-Suarez & Mullen, 2010). In this study, we used such a lowpass-filtered noise carrier only with observer NN, who shows similar results to the other three observers. The noise carrier had a squared shape subtending 17°. The contrast envelope of the stimuli consisted of either a static Gabor (sigma = 5°) of different spatial frequencies from 0.125 to 1 cycles/°, or a drifting Gabor set to an optimal spatial frequency (0.25 cycles/°) with temporal frequencies from 0.5 to 4 Hz. The orientation of the Gabor was either 45° or 135°. The contrast modulation of the carrier was obtained by multiplying the Gabor by the noise carrier. Figure 1 shows examples of the stimuli used.

The achromatic noise carrier contrast was set to a clearly visible contrast, 10 times individual detection noise carrier threshold, as determined in a preliminary experiment using a two-interval forced-choice task (2IFC) with a staircase method. The contrast of the chromatic noise carrier was determined using a visibility-matching experiment with a method of constant stimuli. This method has been shown to provide accurate and consistent contrast-matching results between achromatic and chromatic stimuli (Switkes, 2008; Switkes & Crognale, 1999). For the contrast matching, we used as a reference stimulus the achromatic carrier noise, and the test stimuli were a range of red-green carriers of six different contrast levels. The observer's task was to determine which interval contained the stimulus with the more visible contrast in a 2IFC task. A Weibull psychometric function was fitted to the data (a minimum of 40 trials per contrast levels) using the psignifit toolbox, version 2.5.6 (Wichmann & Hill, 2001), yielding a 50% performance level to define the matching contrast between the test and the reference stimulus. The duration of the stimulus presentation was 1 s and the stimulus was presented within a Gaussian temporal envelope (sigma = 250 ms) to avoid transient responses at the onset and offset of the stimulus presentation. The interstimulus interval duration in temporal 2IFC tasks was 500 ms, and each stimulus interval was preceded and ended by a uniform gray screen of the mean luminance with a fixation dot.

Color space

Second-order stimuli were designed to isolate the achromatic and red-green (L / M) postreceptoral mechanisms. A three-dimensional cone contrast space was used to represent stimulus contrast (vector length) and chromaticity (vector direction), as previously described (Garcia-Suarez & Mullen, 2010). Each axis represents the quantal catch of the L-, M-, or S-cone types normalized with respect to the white background (Cole, Hine, & McIlhagga, 1993; Sankeralli & Mullen, 1996, 1997). The luminance cardinal stimulus had a direction in this space of L + M + S (the achromatic direction), and the cardinal red-green isoluminant stimulus had a direction determined for each subject. A minimum perceived motion technique was used to determine isoluminance; the observer varied the ratio of L- and M-cone contrast with the method of adjustment in order to find the minimal perceived motion of a vertical Gabor of stationary envelope and drifting (3 Hz) sinewave carrier (1 cycle/°). Ten measurements were obtained for each eye and 10 from binocular measurements. Since no significant differences were found between monocular and binocular isoluminant points for each observer, the average of the 30 measurements were taken as the individual isoluminant point. The isoluminant points (the ratios of M-cone weight relative to L) were: −1.95 for observer IVI,

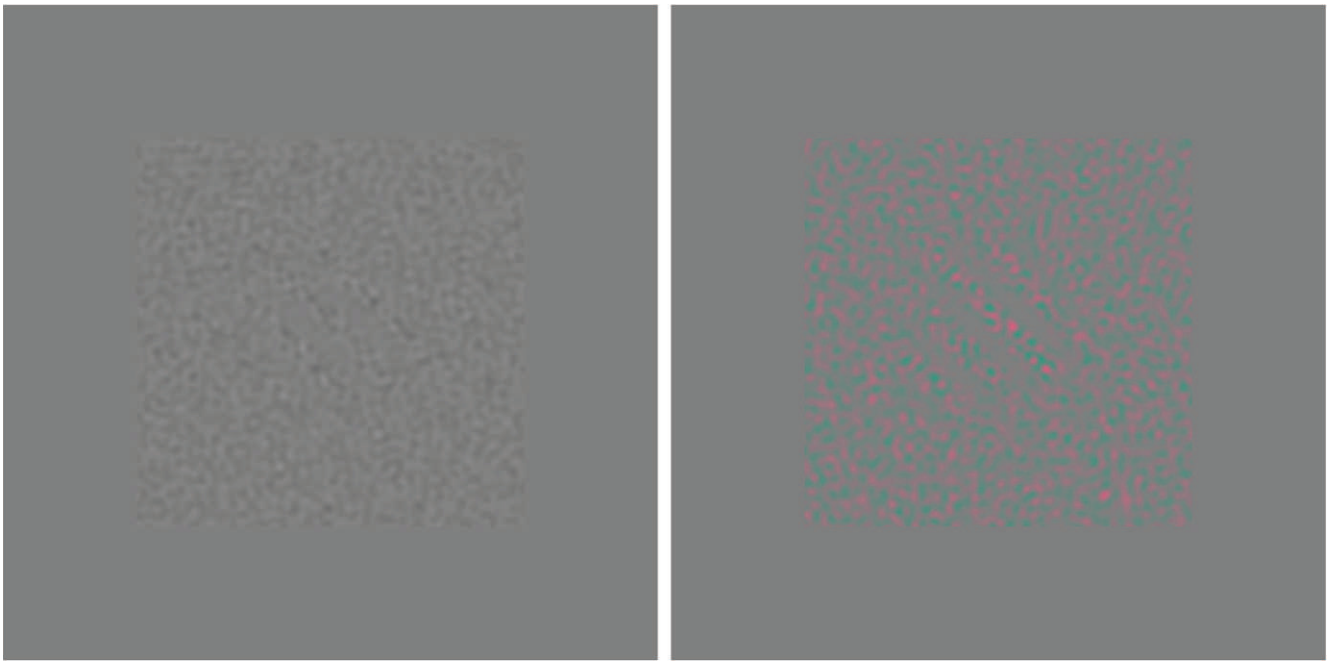

Figure 1. Example of one frame of the second-order achromatic (left) and isoluminant red-green (right) stimuli. In this example, the orientation of the contrast modulation is 135°. The red-green stimulus is for illustration purposes only.

−4.3 for NN, 1 for MM, and −1.77 for LG, which are all within the normal range.

Procedure

The present study has four main experiments: The first three provide measurements of the second-order contrast-modulation sensitivity functions for form and motion thresholds, and the last is a pedestal experiment. The first three experiments all use the same paradigm: a 2IFC simultaneous detection/identification task with a method of constant stimuli. After each presentation, the observers had to indicate which interval contained the test stimulus (detection task) and, depending on the experimental condition, which orientation (oblique right or oblique left) or motion direction (oblique right or oblique left) the stimulus had (identification task). The other interval contained an unmodulated noise carrier. A new noise carrier was drawn in the buffer for each interval presentation. The stimulus interval and the two possible stimulus orientations or motion directions were randomized for each trial. We collected a minimum of 40 trials per data point and a minimum of six data points per condition, and these were used to fit the Weibull psychometric function with the psignifit toolbox. We used the 81.6%-correct performance level to define the threshold. Error bars (±1 *SD*) were determined using bootstrap analysis (1,999 bootstrap simulations).

For the pedestal experiment, we followed the paradigm of Lu and Sperling (1995). According to this paradigm, if there is a dedicated motion system for second-order stimuli, performance for the motion task will be immune to the addition of a pedestal of similar spatial frequency to the drifting envelope but its contrast set to once or twice the motion detection threshold, but should be disrupted if the visual system uses a third-order motion system (the stimuli will appear to "wobble" or oscillate). In the present pedestal experiment, the contrast modulation levels of the pedestals were set as multiples of detection threshold (MDT) of the static second-order results from the first experiment. We used 1.1, 1.5, 1.25, and 1.75 MDT for observers IVI, NN, MM, and LG, respectively. The pedestal and the moving test had the same spatial frequency and temporal parameters as in the motion experiment described above. We used a one-interval 2IFC task with the method of constant stimuli. At each stimulus interval, the phase and the orientation of the pedestal and the motion direction of the test stimulus was chosen randomly, the test orientation being set to the same orientation as the pedestal. The observers' task was to identify the motion direction of the test stimulus (oblique right or left). We collected a minimum of 40 trials per data point, and similar psychometric function fitting and bootstrap analysis procedures were used as described above whenever data results allowed it. In this pedestal experiment, no feedback was given in order to minimize the learning of motion cues (Lu & Sperling, 1995).

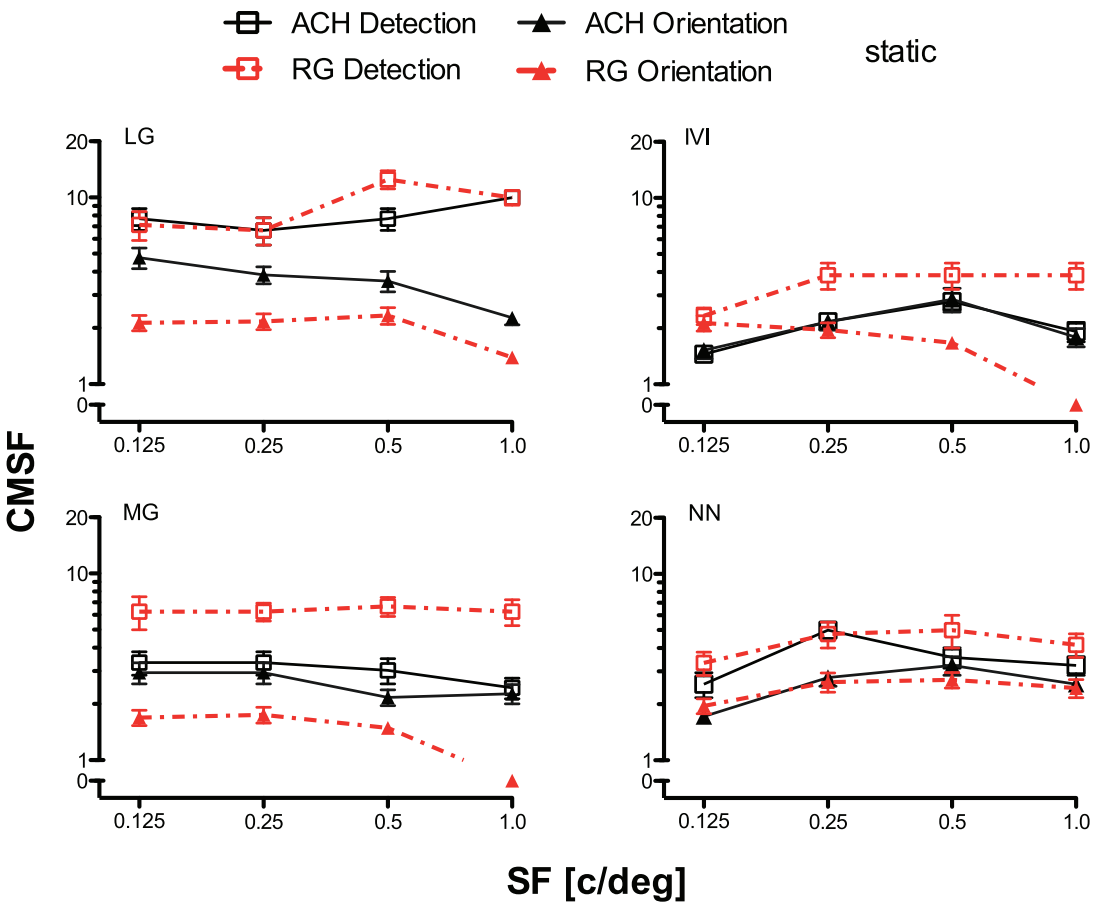

Figure 2. CMSFs for four observers plotted as a function of the spatial frequency of the envelope (0.125–1 cycles/°) for static stimuli. Squares show the inverse of CM (contrast modulation) detection thresholds and triangles show orientation direction identification thresholds. Black and red symbols with lines are for achromatic (ACH) and isoluminant red-green (RG) stimuli, respectively. Data points on the zero *x*-axis indicate that we were not able to measure any performance. Error bars represent ±1 *SD* from the bootstrap analysis.

Results

In the first two experiments, we determined the sensitivity of the visual system for second-order detection and form identification across spatial and temporal frequency, respectively. We first used a static, second-order stimulus and measured detection thresholds and thresholds for the identification of the orientation of second-order static stimuli (form task) as a function of spatial frequency. We then extended these measurements across temporal frequency using a spatial frequency within the range of optimal sensitivity. The CMSFs were defined as the inverse of the contrast modulation thresholds for the detection or orientation identification of the second-order stimuli, plotted as a function of spatial or temporal frequency.

In Figure 2, we plot the CMSFs for the spatial frequency of the Gabor envelope for static achromatic (black line) and chromatic (red dashed line) conditions. Results are for four observers, and functions based on the results averaged across all observers are shown in Figure 6a. We observe from Figures 2 and 6a that contrast modulation sensitivity is generally very low (below 10) for all conditions. For the detection task (square symbols), the average CMSFs are flat for both the achromatic and color stimuli. The orientation identification task (triangles), however, shows a decline in sensitivity at the highest spatial frequency used that is more marked in the color condition. This is in agreement with previous studies using achromatic second-order stimuli (Dakin & Mareschal, 2000; Schofield & Georgeson, 1999, 2003; Sutter et al., 1995). For both detection and orientation identification there are differences between the chromatic and achromatic thresholds that depend on the type of task (detection vs. form identification). A two-way ANOVA with factors of threshold type (achromatic detection, achromatic identification, chromatic detection, and chromatic identification) and spatial frequency shows that, while the factor of spatial frequency is not significant, $F(3, 9) = 0.53$, $p = 0.25$, there is a significant main effect

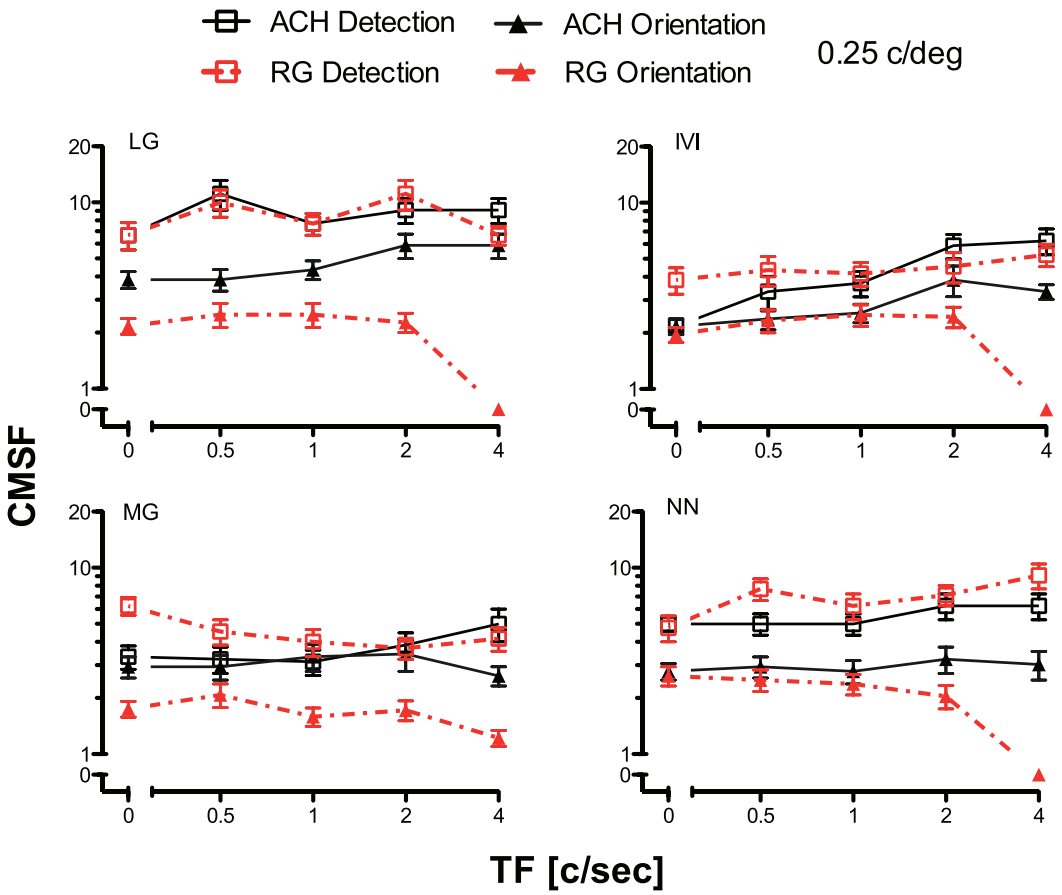

Figure 3. CMSFs for detection and orientation identification of drifting second-order stimuli for four observers. Squares show the inverse of CM detection thresholds and triangles show orientation direction identification thresholds as a function of the temporal frequency of the drifting envelope set at a spatial frequency in the region of the optimal spatial frequency (0.25 cycles/°). Black and red symbols are for achromatic (ACH) and red-green (RG) conditions, respectively. Data points on the zero *x*-axis indicate that we were not able to measure any performance. Error bars represent ±1 *SD* from the bootstrap analysis.

of threshold type, $F(3, 9) = 0.53$, $p < 0.0001$, with no significant interactions between the two factors, $F(3, 9) = 0.20$, $p = 0.84$. A one-way ANOVA on the collapsed averaged data across observers and spatial frequencies (Figure 6a) shows a significant difference between thresholds types, $F(3, 9) = 38.65$, $p < 0.0001$. The post-hoc Bonferroni pairwise t test shows that color detection is significantly better than achromatic detection (Bonferroni pairwise t test, $t = 4.06$, $p < 0.05$). Chromatic form identification, although worse than the achromatic, is not significantly different from it (Bonferroni airways t test, $t = 2.32$). In addition, the form identification of chromatic contrast modulation is significantly worse than detection (Bonferroni pairwise t test, $t = 10.05$, $p < 0.05$), which can be seen in Figures 2 and 6a by the larger gap between detection and identification thresholds in the chromatic condition compared to the achromatic condition, where the two are closer (Figure 6a) but still significantly different (Bonferroni pairwise t test, $t = 3.66$, $p < 0.05$).

We next measured the contrast modulation sensitivity functions for drifting envelope stimuli to assess the temporal properties of the visual system for form processing. Spatial frequency was set to 0.25 cycles/°, within the optimal range. We measured thresholds for detecting and identifying the orientation of the envelope as a function of drift rate using the same tasks as before, with results shown in Figure 3 for four individual subjects and their average in Figure 6b. The average detection thresholds are relatively flat as a function of temporal frequency for both the chromatic and achromatic conditions. Achromatic form identification thresholds also remain relatively flat with sensitivity maintained at 4 Hz. On the other hand, the average sensitivity for chromatic form identification has a lowpass shape with a cutoff in sensitivity at 4 Hz, above which chromatic form could no longer be detected, revealing a distinct difference from the achromatic function. A one-way ANOVA performed on the average data across observers (Figure 6b) shows a significant difference between threshold types, $F(3, 9)$

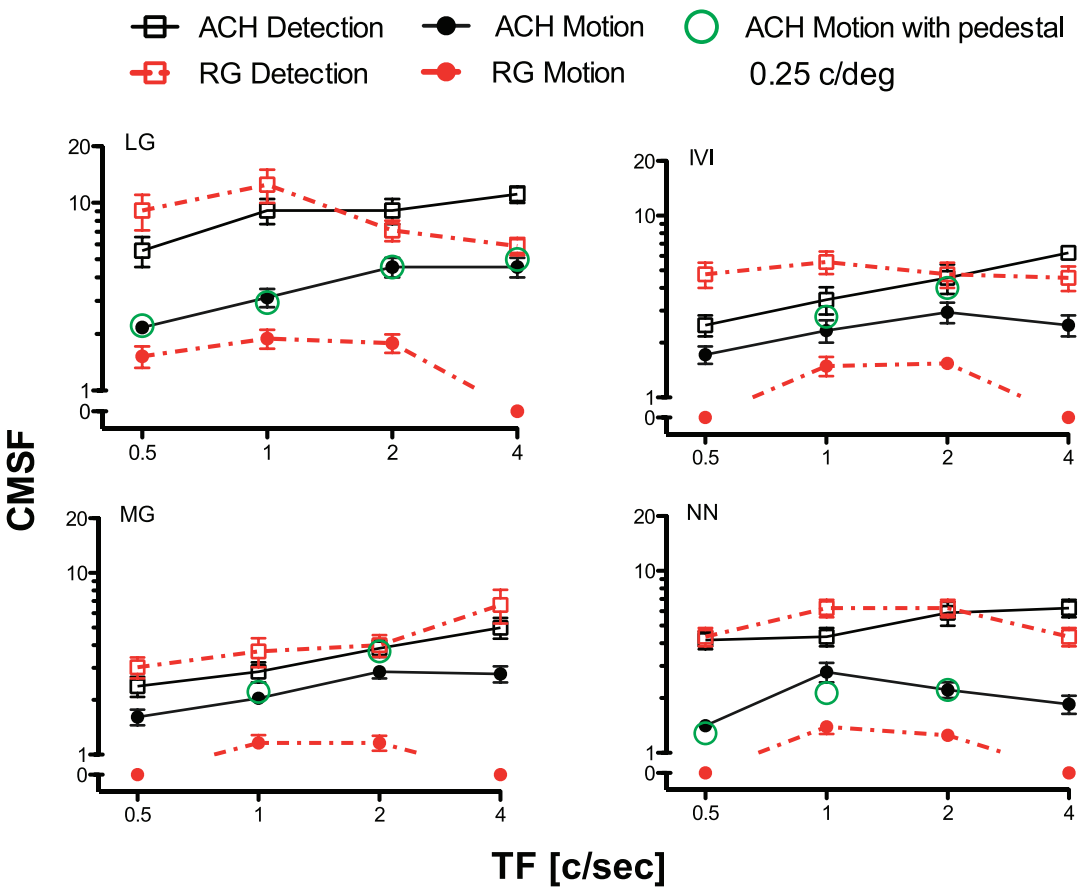

Figure 4. CMSFs for detection and motion identification of drifting second-order stimuli for four observers. Squares show the inverse of CM detection thresholds and circles show motion direction identification thresholds as a function of the temporal frequency of the drifting envelope set at a spatial frequency in the region of the optimal spatial frequency (0.25 cycles/°). Black and red symbols are for achromatic (ACH) and red-green (RG) conditions, respectively. Green symbols are the CMSFs (motion identification) for the achromatic pedestal condition (pedestal experiment described in the text). Data points on the zero *x*-axis indicate that we were not able to measure any performance. Error bars represent ±1 *SD* from the bootstrap analysis.

$= 30.66$, $p < 0.0001$. The Bonferroni-corrected pairwise *t*-test analysis shows no significant difference between chromatic and achromatic detection thresholds ($t = 1.1$, $p < 0.05$), but it shows that chromatic orientation identification thresholds are significantly worse than the achromatic ones ($t = 3.22$, $p < 0.05$). Analysis also shows that orientation identification thresholds are worse than detection thresholds for the chromatic and the achromatic stimuli (Bonferroni pairwise *t* tests: $t = 8.76$, $p < 0.05$ and $t = 4.34$, $p < 0.05$, respectively).

In the next experiment, we investigated contrast modulation sensitivity for second-order motion. Results for detection and motion identification are plotted as a function of drift rate in Figure 4 for individual observers with their average shown in Figure 6c. The CMSFs for the detection of chromatic and achromatic stimuli are similar and are fairly flat across the temporal frequency range assessed. In both achromatic and chromatic conditions, the thresholds for motion identification are consistently poorer than for stimulus detection, with a one-way ANOVA performed on the average data across observers showing a significant difference, $F(3, 9) = 30.45$, $p < 0.0001$. We also observe a much bigger gap between detection and motion performance for the chromatic compared to the achromatic stimuli. Bonferroni-corrected pairwise *t* tests show a significant difference between the detection and motion thresholds for chromatic stimuli (Bonferroni pairwise *t* test, $t = 8.24$, $p < 0.05$) and for the achromatic stimuli (Bonferroni pairwise *t* test, $t = 4.56$, $p < 0.05$). Although the average thresholds for color and luminance detection are not significantly different (Bonferroni pairwise *t* test, $t = 0.66$), the motion identification thresholds for the chromatic stimuli are significantly poorer than for achromatic stimuli (Bonferroni pairwise *t* test, $t = 3.57$, $p < 0.05$). It is the significantly greater deficit in chromatic compared to achromatic motion identification that creates the larger gap between detection and identification thresholds in the chromatic compared to achromatic function. The

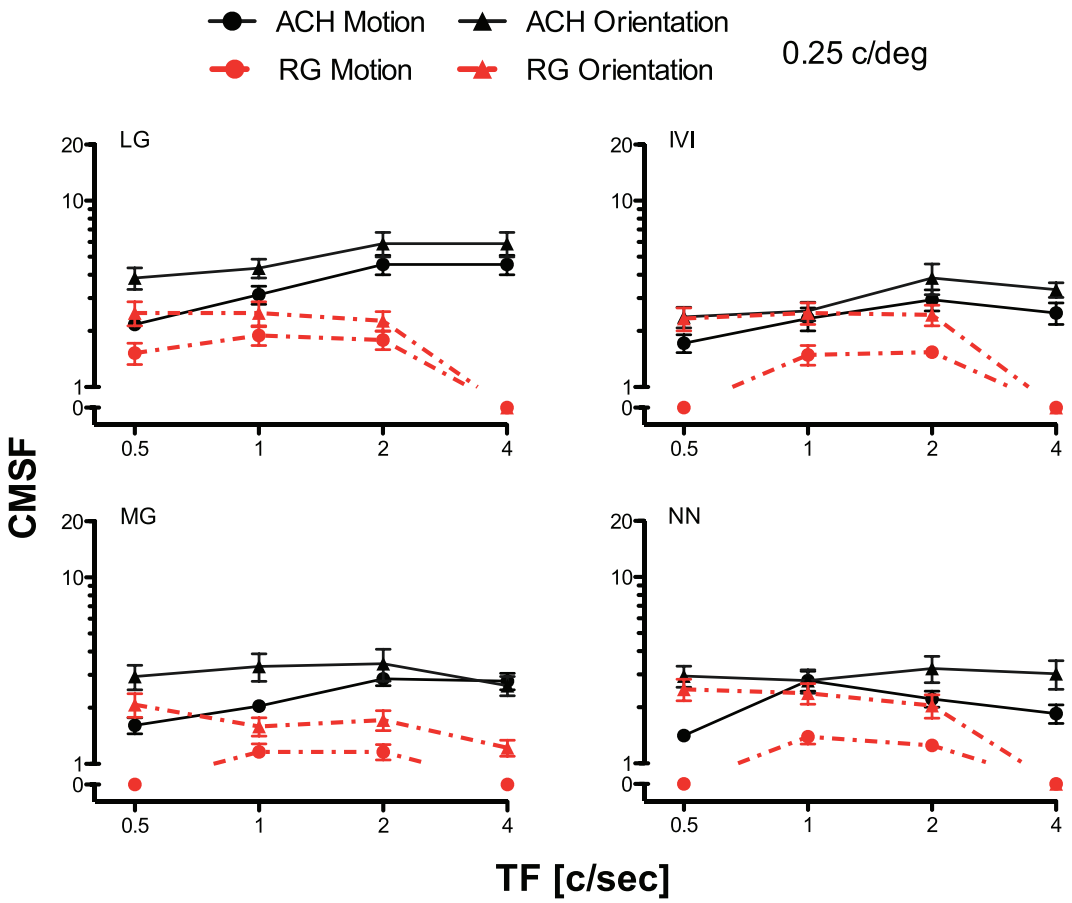

Figure 5. CMSFs for motion and orientation identification of drifting second-order stimuli. Squares show the inverse of CM motion direction identification thresholds and triangles show orientation direction identification thresholds as a function of the temporal frequency of the drifting envelope set at a spatial frequency in the region of the optimal spatial frequency (0.25 cycles/°). Black and red symbols are for achromatic (ACH) and red-green (RG) conditions, respectively. Data points on the zero *x*-axis indicate that we were unable to measure any performance. Error bars represent ±1 *SD* from the bootstrap analysis.

differences between detection, orientation, and motion direction identification thresholds in the achromatic condition are in agreement with previous second-order achromatic studies and seem to be a signature of second-order vision (Hutchinson & Ledgeway, 2006; Ledgeway & Hutchinson, 2005; Ledgeway & Smith, 1994; Smith & Ledgeway, 1997, 1998).

In Figures 5 and 6d, we replot the CMSFs for identifying motion direction and orientation so the differences between form and motion performance can be compared. These results reveal a clear difference between the processing of chromatic and achromatic second-order stimuli both in terms of their sensitivities and in their temporal properties. The average CMSFs in the chromatic condition for both the form and motion tasks are significantly lower in sensitivity than for the achromatic stimuli (Bonferroni pairwise *t* tests, $t = 3.32$, $p < 0.05$ for the form condition and $t = 3.57$, $p < 0.05$ for the motion condition), indicating that color vision is significantly poorer than luminance vision at second-order form and motion tasks. This difference becomes most apparent as temporal frequency increases (above 2 Hz) and, in color vision, both the form and motion thresholds are extinct by 4 Hz. This gives the chromatic form task a clear lowpass shape as sensitivity is maintained for low temporal frequencies and static stimuli, but the motion task has a bandpass shape as performance deteriorates at both high and low temporal frequencies. In the achromatic condition, the CMSFs have highpass shapes for both the motion task and orientation task as sensitivity improves with temporal frequency.

In our next experiment we addressed the question of whether our second-order stimuli are processed by a genuine second-order motion system or by a third-order motion system that uses feature-tracking (Lu et al., 1999; Lu & Sperling, 1995). We measured motion direction identification thresholds with the presence of a pedestal using Lu and Sperling's (1995) pedestal paradigm (see the Methods sections). In the chromatic condition, we were initially not able to measure the performance with the pedestal because of the limitation

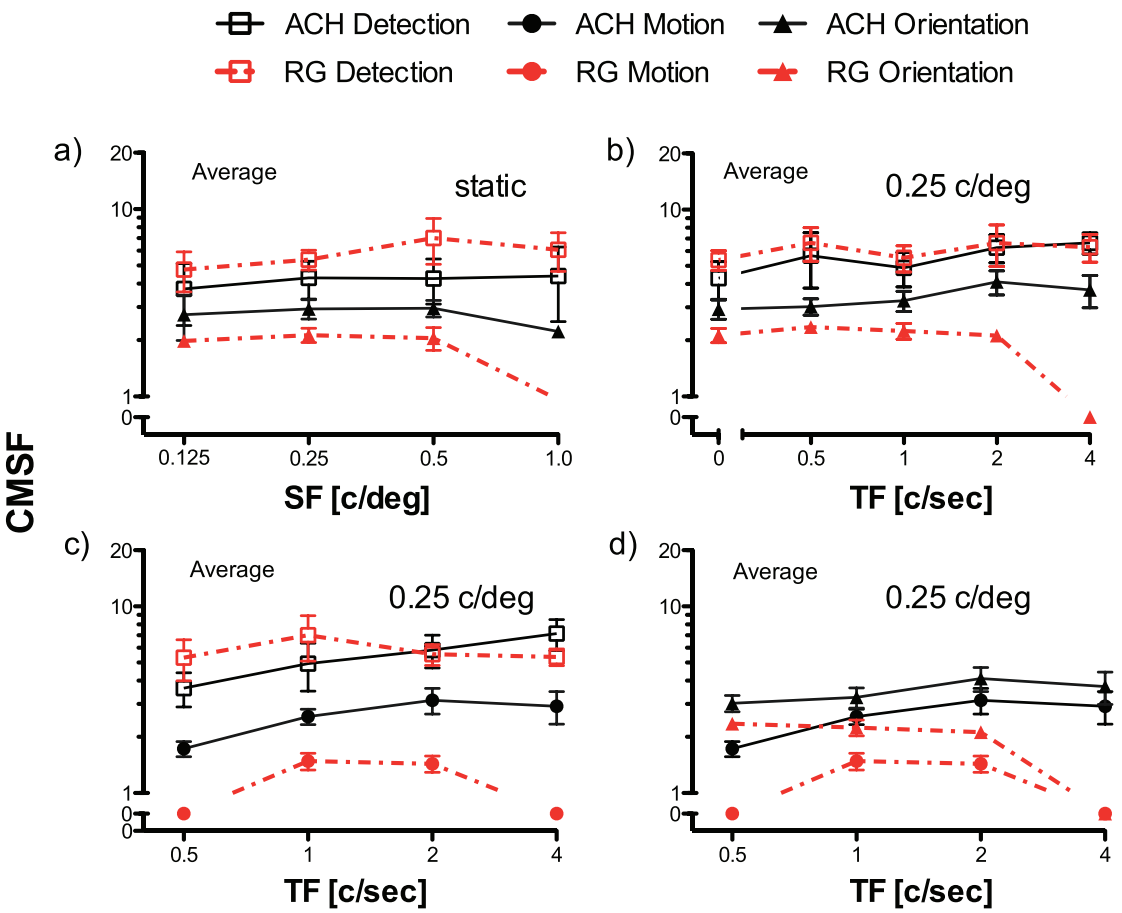

Figure 6. Average CMSFs for four observers: (a) for the detection and form task in the static condition (Figure 2), (b) for the detection and form tasks in the drifting stimulus condition (Figure 3), (c) for the detection and motion direction identification tasks in the drifting stimulus condition (Figure 4), and (d) for the form versus motion comparison (Figure 5). Black and red symbols are for achromatic (ACH) and red-green (RG) conditions respectively. Data points on the zero *x*-axis indicate that we were not able to measure any performance. Error bars represent ±1 *SE* of the mean of four observers.

of the color gamut of the monitor. In order to increase its color gamut and to be able to measure higher thresholds, we switched to using a yellow rather than a white background. This has the additional effects of slightly decreasing the mean luminance of the background and changing the color of the gray background to yellow. Isoluminant points were remeasured for each observer and motion direction thresholds were measured for the new chromatic configuration. Due to the poor sensitivity to color motion and to the high difficulty in identifying the motion direction of the envelope (performance in the nonpedestal condition does not reach 100% correct), we only represent in Figure 7 the performance in percent correct for high contrast modulation levels set to just above the performance level (81.6%). In Figure 4, we show the achromatic results with green circles. In the achromatic pedestal condition, we only represented for comparison purposes the data points that were measurable in the equivalent chromatic conditions. We can observe from Figure 4 that the achromatic results with and without the pedestal are similar and that the thresholds with a pedestal are not impaired. Figure 7 shows the percent correct responses for the chromatic motion task with pedestal (shaded striped column) and without pedestal (empty column) for contrast modulation levels set just above performance level for the nonpedestal condition and for the temporal frequencies of the drifting envelope set to 1 Hz. The results for one observer (MG) were excluded due to her very poor sensitivity to second-order chromatic form and motion stimuli. We find that performance in the pedestal condition is impaired for the chromatic stimuli but not for the achromatic stimuli. Again Figures 4 and 7 show a substantial difference in the results between achromatic and chromatic conditions, indicating a difference in the underlying mechanisms of the visual system for processing chromatic and achromatic second-order motion stimuli. These results suggest that second-order chromatic stimuli are processed by a third-order (feature-tracking) motion system, but achromatic

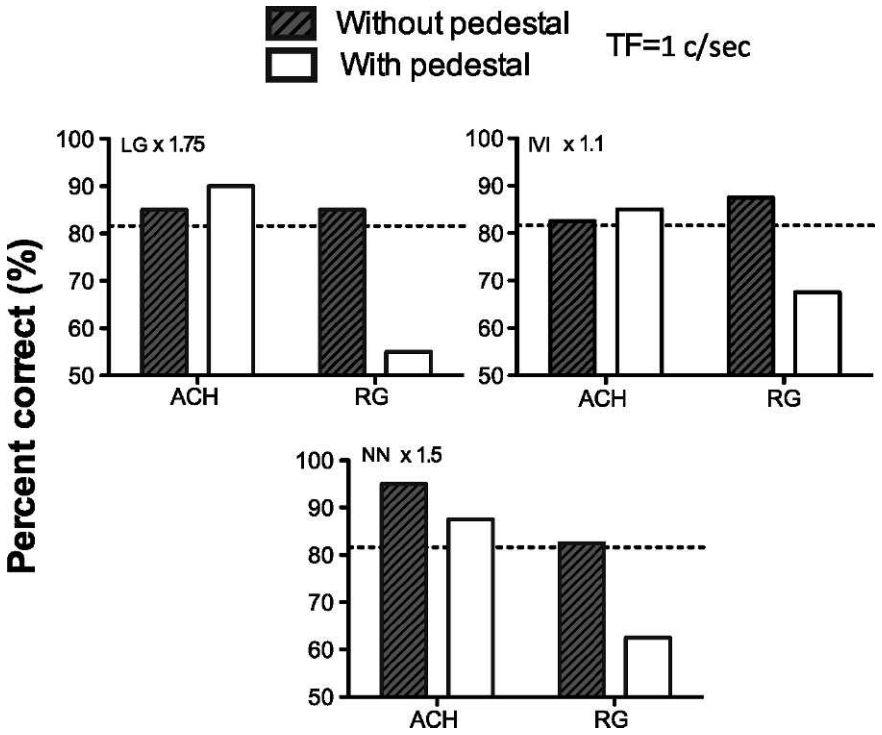

Figure 7. Performance (in percent correct) at identifying the motion of the drifting envelope (TF [temporal frequency] = 1 Hz) with (dashed column) and without the pedestal (empty column). Results are shown for one contrast modulation level (indicated on the *x*-axis) set just above performance level (horizontal dash line) of the nonpedestal condition. Results are for three observers (observer MG was excluded due to her very poor sensitivity to chromatic contrast modulations) and for the achromatic (ACH) and the chromatic (RG) conditions. The numbers next to the observers' initials represent the contrast modulation levels of the pedestals expressed as multiples of detection threshold (MDT) of the static second-order results from Figure 2.

stimuli are processed by a genuine second-order motion system.

Discussion

We have studied form and motion processing of second-order stimuli in color vision. Previous studies in second-order color vision have used beat stimuli (superimposed gratings of different spatial frequencies; Cropper & Derrington, 1996) or contrast modulation of a noise carrier as second-order stimuli (Cropper & Johnston, 2001). In the present study, we used the contrast modulation of a noise carrier. In the form task, we measured the detection and orientation identification thresholds of stimuli with a static envelope and in the motion task the detection, orientation identification, and motion direction thresholds of stimuli with drifting envelopes. Our main findings are that, in color vision, form and motion processing of second-order stimuli are very poor and have a low temporal resolution, with performance on both falling significantly below that for achromatic stimuli. Using the pedestal paradigm described by Lu and Sperling (1995), we have found that chromatic motion thresholds are based on a tracking mechanism (third-order motion mechanism) rather than on a genuine second-order motion mechanism in color vision.

In the second-order form task, performance is less sensitive for chromatic than achromatic stimuli and is more spatially lowpass. The form sensitivity deficit is found for static stimuli and across a range of temporal frequencies. Within the range of temporal frequencies assessed (up to 4 Hz), performance in the achromatic condition is flat and in agreement with previous studies (Hutchinson & Ledgeway, 2006; Ledgeway & Hutchinson, 2005; Smith & Ledgeway, 1998), whereas the chromatic performance is temporally lowpass with a low temporal resolution. Interestingly, stereopsis has been reported to fail for second-order but not first-order chromatic stimuli (Simmons & Kingdom, 2002), and this may be a function of the very poor form processing ability of second-order color vision.

We also found that performance on the motion task is significantly less sensitive for color vision than for luminance vision with thresholds only measurable for 1 and 2 Hz in color vision: Motion performance is clearly bandpass for the chromatic condition and highpass for the achromatic condition. The shallow decline in sensitivity at low temporal frequencies can be explained

by the limitation in the visibility of the motion due to the temporal window being truncated from using a low spatial frequency with the lowest temporal frequency. Taking this into account, the achromatic motion performance is quite flat within the range of temporal frequency assessed, whereas the chromatic motion performance has a clear upper frequency fall-off (low temporal resolution). These results, in conjunction with the pedestal experiment showing no impairment in the results in the presence of a pedestal stimulus, suggest that the mechanism for identifying the motion direction of achromatic second-order stimuli is a genuine second-order mechanism. For second-order chromatic stimuli, however, the evidence indicates that the mechanism for motion discrimination is based on a third-order or feature-tracking mechanism; first, we just noted a low temporal resolution in the chromatic condition that is a typical finding for stimuli processed by a third-order system (Lu et al., 1999; Lu & Sperling, 1995, 2001) and second, in the chromatic condition, observers were unable to identify the direction of the envelope motion when using the pedestal condition.

Comparing the detection versus form identification, we found for static chromatic stimuli that form identification is much poorer than simple detection. This difference in performance was smaller with achromatic stimuli, with performance closer or overlapping for some subjects. In the detection task, observers may use the root mean square (rms) contrast cue to detect the contrast-modulated stimulus interval, due to the higher rms contrast in the stimulus interval than in the nonmodulated interval. Instead, in the form identification task, both possible orientations of the stimulus have the same rms contrast, and observers cannot use the rms contrast cue; their poor performance indicates a genuine deficiency in the orientation task. This implies that the visual system is good at detecting second-order chromatic contrast changes or rms contrast changes, but the processing of form for second-order chromatic stimuli is very poor. For achromatic stimuli, however, some observers seem to use contrast cues to detect second-order stimuli and others not (overlapping in detection/form performance). Schofield and Georgeson (1999) found no difference in the detection and form performance using similar static, second-order stimuli. Their results, however, were based on one observer. Here, we found some intersubject variability, with some subjects that may use contrast cues and others not. The shapes of the sensitivity functions are broadly bandpass and lowpass for both achromatic and chromatic conditions as similarly found in previous studies with stationary second-order achromatic stimuli (Schofield & Georgeson, 1999, 2003; Sutter et al., 1995). This spatially lowpass nature of second-order vision supports the idea that the second stage filters of the filter–rectify–filter model are tuned to a low spatial frequency envelope and prefer a noise carrier tuned to a higher spatial frequency than the envelope (Dakin & Mareschal, 2000; Schofield & Georgeson, 1999, 2003; Sutter et al., 1995).

Comparing performance on the detection, form, and motion performance, the results show that detection performance is better than form or motion performance, and motion performance is worse than form performance in the achromatic condition and more markedly so in the chromatic condition. These results agree with previous studies in achromatic second-order motion vision that support separate functional mechanisms for first- and second-order motion (Hutchinson & Ledgeway, 2006; Ledgeway & Hutchinson, 2005; Ledgeway & Smith, 1994; Smith & Ledgeway, 1997, 1998): This difference between form and motion direction identification performance seems to be characteristic of second- or higher-order vision.

Summarizing, our results suggest that color supports second-order form processing of static and moving envelope stimuli, although performance is significantly worse than for the equivalent achromatic stimuli. We do not know why second-order form processing is so poor in color vision. Some have argued that the nonlinear contrast responses supporting second-order form sensitivity originate in subcortical neural populations (Rosenberg, Husson, & Issa, 2010). In this case, a possible physiological origin of the second-order form effect in color vision might lie in the P cell responses. Physiological recordings of primate P cells in the lateral geniculate nucleus (LGN) show relatively linear responses to red-green color contrast compared to the nonlinear contrast responses of the M cell population (Kaplan & Shapley, 1986; Lennie & Movshon, 2005; Przybyszewski, Gaska, Foote, & Pollen, 2000; Solomon & Lennie, 2005). This P cell response linearity might explain the very poor sensitivity of color vision to second-order modulations.

We find that, although we can measure some response to direction in second-order motion, this is likely to be a tracking mechanism, and hence we argue that second-order motion processing is to be highly deficient or absent in color vision. We found in a previous study (Garcia-Suarez & Mullen, 2010), using a global motion task that taps higher-level areas of motion processing, that there was no measurable second-order global motion in color vision. The results of the present and previous study together suggest that there is no genuine contribution of color to either local or global motion processing, implying a deficit of the dorsal pathway for second-order color at both levels of motion processing. Altogether, these results suggest that the division between the ventral and dorsal pathways is maintained for second-order color processing, demonstrated by a weak contribution of color

form to the ventral pathway but with no measureable contribution of pure chromatic motion to the dorsal pathway.

Conclusions

We investigated how second-order processing in color contributes to form and motion-based tasks. We found that form processing of second-order stimuli (contrast modulation of a spatially bandpassed carrier) is very poor in color vision and worse than in achromatic vision. There appears to be no dedicated second-order mechanism for motion in color vision, while there is in achromatic vision. The low temporal resolution in the chromatic sensitivity functions in conjunction with the impairment of the motion direction performance when using a pedestal suggest that the second-order chromatic stimuli are analyzed by a third-order (feature-tracking) system.

Keywords: second-order, form, motion, psychophysics, color vision, contrast modulation

Acknowledgments

We wish to thank Iliya Ivanov, Mina Gheiratmand, and Niia Nikolova for their participation as observers and Dr. Yeon Jin Kim for her assistance. This research was supported by a Canadian NSERC Grant (RGPIN 183625-05) to KTM.

Commercial relationships: none.
Corresponding author: Kathy T. Mullen.
Email: kathy.mullen@mcgill.ca.
Address: McGill Vision Research, Department of Ophthalmology, McGill University, Montreal, Quebec, Canada.

References

Baker, C. L., Jr. (1999). Central neural mechanisms for detecting second-order motion. *Current Opinion in Neurobiology*, *9*, 461–466.

Baker, C. L., Jr., & Hess, R. F. (1998). Two mechanisms underlie processing of stochastic motion stimuli. *Vision Research*, *38*(9), 1211–1222.

Beaudot, W. H., & Mullen, K. T. (2005). Orientation selectivity in luminance and color vision assessed using 2-d band-pass filtered spatial noise. *Vision Research*, *45*, 687–696.

Cavanagh, P., & Mather, G. (1989). Motion: The long and short of it. *Spatial Vision*, *4*, 103–129.

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*, 1986–2007.

Chubb, C., & Sperling, G. (1989). Two motion perception mechanisms revealed by distance driven reversal of apparent motion. *Proceedings of the National Academy of Sciences, USA*, *86*, 2985–2989.

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 A*, *10*(1), 38–51.

Cropper, S. (2005). The detection of motion in chromatic stimuli: First-order and second-order spatial structure. *Vision Research*, *45*, 865–880.

Cropper, S. (2006). The detection of motion in chromatic stimuli: Pedestals and masks. *Vision Research*, *46*, 724–738.

Cropper, S. J., & Derrington, A. M. (1996). Detection and motion detection in chromatic and luminance beats. *Journal of the Optical Society of America A*, *13*, 401–407.

Cropper, S. J., & Johnston, A. (2001). Motion of contrast envelopes: Peace and noise. *Journal of the Optical Society of America A*, *18*(9), 2237–2254.

Cropper, S. J., & Wuerger, S. M. (2005). The perception of motion in chromatic stimuli. *Behavioral & Cognitive Neuroscience Reviews*, *4*(3), 192–217.

Dakin, S. C., & Mareschal, I. (2000). Sensitivity to contrast modulation depends on carrier spatial frequency and orientation. *Vision Research*, *40*, 311–329.

Flitcroft, D. L. (1989). The interactions between chromatic aberration, defocus and stimulus chromaticity: Implications for visual physiology and colorimetry. *Vision Research*, *29*(3), 349–360.

Garcia-Suarez, L., & Mullen, K. T. (2010). Global motion processing in human color vision: a deficit for second-order stimuli. *Journal of Vision*, *10*(14): 20, 1–11, http://www.journalofvision.org/content/10/14/20, doi:10.1167/10.14.20. [PubMed] [Article]

Hutchinson, C. V., & Ledgeway, T. (2006). Sensitivity to spatial and temporal modulations of first-order and second-order motion. *Vision Research*, *46*, 324–335.

Kaplan, E., & Shapley, R. M. (1986). The primate retina contains two types of ganglion cells, with high and low contrast sensitivity. *Proceedings of the National Academy of Sciences, USA*, *83*, 2755–2757.

Ledgeway, T., & Hutchinson, C. V. (2005). The influence of spatial and temporal noise on the detection of first-order and second-order orientation and motion direction. *Vision Research*, *45*, 2081–2094.

Ledgeway, T., & Smith, A. T. (1994). Evidence for separate motion detecting mechanisms for first- and second-order motion in human vision. *Vision Research*, *34*(20), 2727–2740.

Lennie, P., & Movshon, J. A. (2005). Coding of color and form in the geniculostriate visual pathway. *Journal of the Optical Society of America A*, *22*, 2013–2033.

Losada, M. A., & Mullen, K. T. (1994). The spatial tuning of chromatic mechanisms identified by simultaneous masking. *Vision Research*, *34*(3), 331–341.

Losada, M. A., & Mullen, K. T. (1995). Color and luminance spatial tuning estimated by noise masking in the absence of off-frequency looking. *Journal of the Optical Society of America A*, *12*(2), 250–260.

Lu, Z.-L., Lesmes, L. A., & Sperling, G. (1999). The mechanism of isoluminant chromatic motion perception. *Proceedings of the National Academy of Sciences, USA*, *96*, 8289–8294.

Lu, Z.-L., & Sperling, G. (1995). The functional architecture of human visual motion perception. *Vision Research*, *35*(19), 2697–2722.

Lu, Z.-L., & Sperling, G. (2001). Three-systems theory of human visual motion perception: Review and update. *Journal of the Optical Society of America A*, *18*(9), 2331–2370.

Mandelli, M. J., & Kiper, D. C. (2005). The local and global processing of chromatic Glass patterns. *Journal of Vision*, *5*(5):2, 405–416, http://www.journalofvision.org/content/5/5/2, doi:10.1167/5.5.2. [PubMed] [Article]

Mullen, K. T. (1985). The contrast sensitivity of human colour vision to red-green and blue-yellow chromatic gratings. *Journal of Physiology*, *359*, 381–400.

Mullen, K. T., Beaudot, W. H., & Ivanov, I. V. (2011). Evidence that global processing does not limit thresholds for RF shape discrimination. *Journal of Vision*, *11*(3):6, 1–21, http://www.journalofvision.org/content/11/3/6, doi:10.1167/11.3.6. [PubMed] [Article]

Mullen, K. T., Beaudot, W. H., & McIlhagga, W. H. (2000). Contour integration in color vision: A common process for the blue-yellow, red-green and luminance mechanisms? *Vision Research*, *40*(6), 639–655.

Mullen, K. T., Yoshizawa, T., & Baker, C. L., Jr. (2003). Luminance mechanisms mediate the motion of red-green isoluminant gratings: The role of "temporal chromatic aberration." *Vision Research*, *43*, 1237–1247.

Nishida, S., Ledgeway, T., & Edwards, M. (1997). Dual multiple-scale processing for motion in the human visual system. *Vision Research*, *37*, 2685–2698.

Nishida, S. Y. (2004). Motion-based analysis of spatial patterns by the human visual system. *Current Biology*, *14*, 830–839.

Pavan, A., Campana, G., Guerreschi, M., Manassi, M., & Casco, C. (2009). Separate motion-detecting mechanisms for first- and second-order patterns revealed by rapid forms of visual motion priming and motion aftereffect. *Journal of Vision*, *9*(11):27, 1–16, http://www.journalofvision.org/content/9/11/27, doi:10.1167/9.11.27. [PubMed] [Article]

Przybyszewski, A., Gaska, J., Foote, W., & Pollen, D. (2000). Striate cortex increases contrast gain of macaque LGN neurons. *Visual Neuroscience*, *17*, 485–494.

Rosenberg, A., Husson, T. R., & Issa, N. P. (2010). Subcortical representation of non-Fourier image features. *Journal of Neuroscience*, *30*, 1985–1993.

Sankeralli, M. J., & Mullen, K. T. (1996). Estimation of the L-, M-, and S-cone weights of the postreceptoral detection mechanisms. *Journal of the Optical Society of America A*, *13*(5), 906–915.

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

Schofield, A. J., & Georgeson, M. A. (1999). Sensitivity to modulations of luminance and contrast in visual white noise: separate mechanisms with similar behaviour. *Vision Research*, *39*, 2697–2716.

Schofield, A. J., & Georgeson, M. A. (2003). Sensitivity to contrast modulation: The spatial frequency dependence of second-order vision. *Vision Research*, *43*, 243–259.

Scott-Samuel, N. E., & Georgeson, M. A. (1999). Feature matching and segmentation inmotion perception. *Proceedings of the Royal Society of London B: Biological Sciences*, *266*, 2289–2294.

Simmons, D. R., & Kingdom, F. A. (2002). Interactions between chromatic- and luminance-contrast-sensitive stereopsis mechanisms. *Vision Research*, *42*, 1535–1545.

Smith, A. T., & Ledgeway, T. (1997). Separate detection of moving luminance and contrast

modulations: Fact or artifact? *Vision Research*, *37*(1), 45–62.

Smith, A. T., & Ledgeway, T. (1998). Sensitivity to second-order motion as a function of temporal frequency and eccentricity. *Vision Research*, *38*(3), 403–410.

Solomon, J. A., & Lennie, P. (2005). Chromatic gain controls in visual cortical neurons. *Journal of Neuroscience*, *25*(19), 4779–4792.

Sutter, A., Sperling, G., & Chubb, C. (1995). Measuring the spatial frequency selectivity of second-order texture mechanisms. *Vision Research*, *35*(7), 915–924.

Switkes, E. (2008). Contrast salience across three-dimensional chromoluminance space. *Vision Research*, *48*, 1812–1819.

Switkes, E., & Crognale, M. A. (1999). Comparison of color and luminance contrast: Apples versus oranges? *Vision Research*, *39*, 1823–1831.

Webster, M. A., De Valois, K. K., & Switkes, E. (1990). Orientation and spatial-frequency discrimination for luminance and chromatic gratings. *Journal of the Optical Society of America A*, *7*(6), 1034–1049.

Wichmann, F. A., & Hill, N. J. (2001). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception & Psychophysics*, *63*(8), 1293–1313.

Wilcox, L. M., & Hess, R. F. (1997). Scale selection for second-order (non-linear) stereopsis. *Vision Research*, *37*, 2981–2992.

Yoshizawa, T., Mullen, K. T., & Baker, C. L., Jr. (2000). Absence of a chromatic linear motion mechanism in human vision. *Vision Research*, *40*, 1993–2010.

Yoshizawa, T., Mullen, K. T., & Baker, C. L., Jr. (2003). Failure of signed chromatic apparent motion with luminance masking. *Vision Research*, *43*, 751–759.