The chromatic input to global motion perception

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Abstract
For over 30 years there has been a controversy over whether color-defined motion can be perceived by the human visual system. Some results suggest that there is no chromatic motion mechanism at all, whereas others do find evidence for a purely chromatic motion mechanism. Here we examine the chromatic input to global motion processing for a range of color directions in the photopic luminance range. We measure contrast thresholds for global motion identification and simple detection using sparse random-dot kinematograms. The results show a discrepancy between the two chromatic axes: whereas it is possible for observers to perform the global motion task for stimuli modulated along the red–green axis, we could not assess the contrast threshold required for stimuli modulated along the yellowish-violet axis. The contrast required for detection for both axes, however, are well below the contrasts required for global motion identification. We conclude that there is a significant red–green input to global motion processing providing further evidence for the involvement of the parvocellular pathway. The lack of S-cone input to global motion processing suggests that the koniocellular pathway mediates the detection but not the processing of complex motion for our parameter range.

Keywords: Motion, Random-dot kinematogram, Color, Isoluminance, Parvocellular, Koniocellular, Cone-opponent mechanisms

Introduction
For over 30 years, scientists have been debating whether color-defined motion can be perceived by the human visual system. Some results suggest that there is no chromatic motion mechanism at all (Ramachandran & Gregory, 1978), whereas others do find evidence for a purely chromatic motion mechanism (Cavanagh & Favreau, 1985; Derrington & Badcock, 1985; Mullen & Baker, 1985; Cropper & Derrington, 1996; Dougherty et al., 1999; Seidemann et al., 1999; Wandell et al., 1999). It is now clear that there are differences in the way the motion system processes luminance and chromatic information. Depending on the temporal and spatial parameters and the task, either luminance or chromatic information is more effective for motion processing.

An often cited piece of evidence for the existence of different motion mechanisms for luminance and color is the observation that, for chromatic stimuli, the motion system requires a greater contrast to discriminate the direction of motion than it does for simple detection (Levinson & Sekuler, 1975; Watson et al., 1980; Lindsey & Teller, 1990). The ratio between detection threshold and motion discrimination contrast threshold is close to 1 for luminance modulations, whereas it is higher for chromatic modulations (Lindsey & Teller, 1990; Cavanagh & Anstis, 1991; Kooi & De Valois, 1992; Mullen & Boulton, 1992a,b; Derrington & Henning, 1993; Palmer et al., 1993; Metha et al., 1994; Metha & Mullen, 1998). For low temporal frequencies, there is a discrepancy between the contrast required for detection and that required for discrimination of stimuli modulated along the L–M- and the S-cone axis (Metha et al., 1994; Gegenfurtner & Hawken, 1995; Stromeyer et al., 1995). In conjunction with data on perceived speed and adaptation, this result suggests that two different mechanisms discriminate motion at slow (<4–8 Hz) and fast speeds for chromatic stimuli (Hawken et al., 1994; Gegenfurtner & Hawken, 1995, 1996; Metha & Mullen, 1997). Another factor that affects the detection-to-discrimination ratio is stimulus duration; shorter stimulus durations require higher contrasts for motion discrimination thresholds compared with detection thresholds (Cropper & Derrington, 1994, 1996). Detection thresholds increase more rapidly for chromatic than for achromatic stimuli with increasing eccentricity (Mullen, 1985, 1991; Metha et al., 1994). Bilodeau and Faubert (1997) measured color contrast thresholds for direction discrimination as a function of retinal position, and found a dramatic fall-off in comparison to the detection performance. Hence, foveal (<4 deg) stimuli presented under photopic conditions (>30 cd/m^2) will favor the chromatic motion mechanism.

The studies discussed above investigate the chromatic and luminance input to local or component motion for a range of spatial and temporal parameters. In the present study, we are concerned with global motion (“pattern motion”) rather than with local motion (“component motion”) processing. Studies investigating the dependence of global motion perception and integration on chromatic information have mainly focussed on the interaction between the luminance and the chromatic motion signals and the role of chromatic information in aiding segmentation of the image.
before local motion signals are combined (Ramachandran & Gregory, 1978; Ramachandran, 1987; Edwards & Badecock, 1996; Croner & Albright, 1997; Moller & Hurlbert, 1997a,b; Britten, 1999; Snowden & Edmunds, 1999; Li & Kingdom, 2001). To investigate global motion processing, random-dot kinematograms (RDK) are generally used (Ramachandran & Gregory, 1978; Braddick, 1980; Newsome & Pare, 1988). The task for the observer is to indicate the direction of motion in a display of many elements. To discriminate the direction of the pattern motion, the system has to integrate local motion vectors and extract the prevailing motion direction in the display. RDKs are described by their coherence level, which is the percentage of elements that share the same motion direction (“Signal Dots”).

Bilodeau and Faubert (1999) studied the chromatic input for a global motion task by comparing performance for luminance and isoluminant RDKs. When stimuli were equated in L- and M-cone contrast, the relative coherence required to identify the direction of motion was twice as high for the isoluminant stimuli. In some cases observers could not identify the motion even for a coherence level of 100%. These experiments were run at a mean luminance of 10 cd/m² and only one color direction (red–green) was measured. The present study examines the chromatic input to global motion processing for slowly moving and foveally presented stimuli for a range of color directions in the isoluminant plane. Our stimuli are in the photopic luminance range (50 cd/m²) and we compare chromatic with luminance input.

**Methods**

**Apparatus**

Our experiments were run on a standard PC with a VSG2/5 graphics card (32-MB memory, Cambridge Research Systems, Ltd., Kent, UK). The stimulus presentation was controlled with Matlab (Mathworks®, Cambridge, UK) and the stimuli were presented on a 21-inch CRT-monitor (SONY GDM-F500, Berkshire, UK). The chromatic and luminance output of the monitor were calibrated with a spectroradiometer (Photo Research PR650, Glen Spectra Ltd., Middlesex, UK). The monitor had been switched on a button box (CT3, Cambridge Research Systems, Ltd., Kent, UK) and were seated 200 cm from the screen in an otherwise dark cubicle.

All participants had normal or corrected-to-normal vision. We tested participants’ color vision with the Cambridge Colour Test (Cambridge Research System, Ltd., Kent, UK). Participants were informed about the objective of the study and gave their signed consent.

**Stimuli**

We used sparse random-dot kinematograms (RDKs) with 300 colored Gaussian blobs. The diameter of a single Gaussian blob at its base was 20 pixels, which corresponded to 0.22 deg of visual angle. The blobs moved at a speed of 1 deg/s and the array of the RDK was 5.1 deg × 4 deg on an otherwise grey background of 1024 × 768 pixels. The monitor refresh rate was 120 Hz and we allocated seven video pages for a motion interval that lasted 233 ms. We limited the duration to 233 ms to minimize eye movements. Each individual blob moved along a trajectory during such an interval and did not have a limited lifetime. A new RDK was generated for each interval. The coherence level, that is, the proportion of the Gaussian blobs sharing a common motion direction, was 40% in our RDKs. The background had a luminance of 50 cd/m².

**Procedure**

We used a two-interval forced-choice (2IFC) design in which participants had to decide whether the first or the second interval contained coherent motion irrespective of its direction. In one interval the direction of coherent motion was either leftward or rightward; in the other interval all dots moved randomly. A trial started with a fixation cross for 500 ms, presented in the center of the screen, then the first motion interval was displayed for 233 ms, followed by another fixation cross for 500 ms, and finally the second motion interval appeared for 233 ms. Participants were required to respond after the second motion interval, by pressing a button to indicate the interval in which they thought coherent motion had appeared. The next trial started after the participant had responded. Participants were instructed to give a correct answer, not a fast answer, and they were provided with acoustic feedback. The participant’s responses guided a staircase adjustment of the signal (Levitt, 1971): three correct responses decreased contrast and one false response increased it.

To estimate the contrast threshold from the relative frequency of a correct response, we fitted a Weibull function of the following type:

\[
 f(x) = A - (A - B) \cdot e^{-(kx)^b},
\]

where \( x \) corresponds to the stimulus level (contrast), \( A \) and \( B \) denote the upper and lower performance limits, and \( b \) the slope of the function. In a 2IFC paradigm, chance performance is always 0.5 and for large stimulus contrasts we expect the asymptotic performance to be 1. Therefore, we fix \( A = 1 \) and \( B = 0.5 \) when fitting the function to the data. The resulting 1/k-value indicates the threshold for 81% performance. Each threshold was measured twice for each of the five participants (four naive observers and one author).

**Color space**

To establish the contrast thresholds for a global motion integration task, we used the DKL-color space (Derrington et al., 1984; Brainard, 1996) which is an extension of the MacLeod-Boynton chromaticity diagram (MacLeod & Boynton, 1979). The stimuli were modulated along three different axes: along one axis, the achromatic axis, all three cone classes (L, M, & S) are modulated such that the contrast in all three cone classes is identical, that is, \( \Delta L/\Delta B_L = \Delta M/\Delta B_M = \Delta S/\Delta B_S \), where \( \Delta L, \Delta M, \) and \( \Delta S \) denote the incremental cone excitations in three cone classes, respectively. \( L_B, M_B, \) and \( S_B \) indicate the L-, M-, and S-cone excitations of the background (WP in Fig. 1). The maximum contrast that can be achieved in each cone class is 1 if stimuli are modulated along the achromatic direction. The second direction refers to a modulation along a red–green axis; modulations in this direction leave the excitation of the S-cones constant (i.e. \( \Delta S = 0 \)), and the excitation of the L- and M-cones covaries as to keep their sum constant. Therefore, this axis is referred to as “Constant S-Cone Axis” (Kaiser & Boyton, 1996, p. 306) or a “red–green isoluminant” axis (Brainard, 1996). Along the third axis, only the S-cones are modulated, and \( \Delta L = \Delta M = 0 \). Therefore, this axis is referred to...
as a “Constant L & M cone” axis (Kaiser & Boyton, 1996, p. 306) or as an “S-cone isoluminant” axis (Brainard, 1996). Instead of defining the chromatic properties of the stimuli by their respective L, M, and S cone modulations, the stimuli can be defined in terms of the responses of a set of hypothesized mechanisms (Derrington et al., 1984; Brainard, 1996; Eskew et al., 1999; Wuerger et al., 2002). In the following figures, we characterize the chromatic properties of our stimuli by the responses of the underlying mechanisms rather than by the cone coordinates of the stimuli that isolate these mechanisms. The three corresponding mechanisms are two cone-opponent color mechanisms and a luminance mechanism. One of the two cone-opponent mechanisms is a red–green mechanism that takes the weighted difference between the differential S- and the L-cone excitations. The second cone-opponent mechanism is a yellowish-violet mechanism that takes the weighted difference between the differential M- and L-cone excitations. The luminance mechanism sums the weighted differential M- and L-cone signals. For the sake of simplicity, these mechanisms are referred to as “L” and “M”, “S+(M+L)” (Derrington et al., 1984). These directions are linear transformations of cone space and the precise mapping can be found in Brainard (1996).

We selected the nominal isoluminant plane at 50 cd/m² and all colors in this plane have the same luminance. Luminance is defined by the luminous efficiency function proposed by the CIE and modified by Judd (1951) (Wyszecki & Stiles, 2000, p. 395). This definition is based on heterochromatic flicker photometry. The CIE coordinates of the grey background (indicated by WP in Fig. 1) are as follows: x = 0.292, y = 0.306, and Lum = 50 cd/m². The corresponding cone coordinates are: L = 32.42, M = 17.58, and S = 1.055. The color modulations that can be produced on a monitor are limited by the three phosphors. We adjusted the range of colors such that the modulations around the white point are symmetric along the “M-L” and the “S-(L+M)” axis.

Fig. 1 shows the DKL-color space, the selected isoluminant plane, and the endpoints of the two color directions: 0 and 180 refer to the endpoints of the “M-L” direction. Green is indicated by 0 deg and a radius (r) of 1 and its absolute cone coordinates are: L = 30.39, M = 19.61, and S = 1.05; 180 deg and r = 1 refers to the red endpoint (L = 34.45, M = 15.55, and S = 1.05). The maximum contrast achievable in the L- and M-cones in the “L-M” direction are 0.06 and 0.11, respectively, and is indicated by a radius of 1 in all figures. 90 deg and 270 deg refer to the endpoints along the “S-(M+L)” direction: 90 deg and r = 1 represents violet (L = 32.42, M = 17.58, and S = 1.8), and 270 deg and r = 1 indicates the yellowish endpoint (L = 32.42, M = 17.58, and S = 0.31). The maximum available S-cone contrast for our monitor is 0.84 and a radius of 1 in the “S-(M+L)” direction corresponds to an S-cone contrast of 0.706.

**Observer isoluminance**

To adjust for observers’ individual point of isoluminance, the nominal isoluminant color plane needs to be tilted with respect to the luminance axis. This means that, for example, a red stimulus of a given contrast has to be of lower luminance than a green stimulus to be perceived isoluminant by the observer. Although there is a standard observer model behind the concept of isoluminance (see Color Space), it is known that there are significant deviations from the model in the population (Wyszecki & Stiles, 2000, p. 396). We express the deviation from the nominal isoluminant color plane in percent luminance deviation from our chosen luminance level of 50 cd/m²; for example, if the observer perceives a red of 47 cd/m² as isoluminant, this would correspond to a deviation of +6% [(53 – 50)/50 × 100]. Similarly, if green had to be of less luminance than red to be perceived isoluminant, the deviation would be negative.

**Heterochromatic flicker photometry (HCFP)**

To determine observers’ point of isoluminance, we used heterochromatic flicker photometry (Walsh, 1958). In this paradigm, the display alters between a red and a green stimulus at a certain temporal frequency. By varying the luminance of red and green in opposite directions, one can find a setting for which the perception of flicker is minimal. HCFP utilizes the fact that the chromatic system is too slow to follow fast temporal changes but the luminance system is able to detect the fast changing luminance differ-
ences between red and green. Therefore, if the perception of flicker is minimized the luminance difference is minimized as well. Since temporal and spatial factors may affect the individual isoluminant point, we used stimuli as similar as possible to the temporal and spatial layout of our global motion task, that is, we used the RDK stimuli (a screen with 300 Gaussian blobs and same display settings as described in Stimuli) and altered the color between red and green at 20 Hz. Participants were asked to change the luminance settings of red and green to minimize flicker. All observers reported that they could find a setting where the flicker disappeared. Each observer repeated this selection five times reliably and the average was taken.

Experiments 1a and 1b

We determined chromatic contrast thresholds (81% correct) for global motion detection in the isoluminant color plane \([S-(M+L)] vs. M-L\) for 12 different colors. Observers had to distinguish between an interval with random motion and an interval in which 40% of the blobs moved either left or right (2IFC). All blobs had the same color contrast in a given trial and were presented on a grey background.

In Experiment 1a, all colors had the same nominal luminance of 50 cd/m². Since it is known that there are individual differences in the luminance \((V(\lambda))\) mechanisms (Wyszecki & Stiles, 2000) which may result in a small luminance signal being present in the nominally isoluminant chromatic signals, we determined isoluminance for each observer individually by HCFP in Experiment 1b. Experiment 1a and 1b were conducted with the same observers. We present both sets of data to show that even if the display suffers from luminance artefacts the results do not change, that is, the main input to the motion integration process is the chromatic signal.

Results

In Fig. 2, the color contrast thresholds for global motion integration are plotted. The top row shows the results for nominal isoluminance (Experiment 1a), and the bottom row shows the results for individual observer’s isoluminance setting (Experiment 1b). Each data point in this plot is defined by the angle and its distance from the origin (the white point). The angle \((\phi, \text{ see Fig. 1})\) indicates the color, and the radius reflects the contrast (which is loosely related to saturation).

Fig. 2 shows that all observers can use the chromatic signal along the “M–L” axis to extract motion. More importantly, the results do not change when accounting for the individual point of isoluminance. The thresholds (expressed as radius) along the “M–L” axis vary from 0.37 for observer JCSF to 0.82 for observer CXVF. The thresholds are roughly symmetric around the white point indicating that increments and decrements in both L- and the M-cones are equally effective in this motion task. The results along the yellowish-violet axis (270 deg and 90 deg) are different: we could not produce a contrast at which the participants were able to respond reliably. When debriefing, the participants stated independently that the stimuli were visible but they were not able to see any coherent movement for isoluminant yellowish or violet colors and therefore guessed in which interval coherent motion appeared.

Fig. 2 also shows that the thresholds in the intermediate isoluminant color directions are limited by their projection onto the “M–L” axis. This is indicated by the dotted line, which represents the mean of the projections of the thresholds onto the “M–L” axis.

Fig. 2. Experiments 1a and 1b. Color contrast thresholds (●) for global motion integration for nominal isoluminance (50 cd/m²; top row) and for individual settings of isoluminance for the same five observers (bottom row; ●). Observers’ average deviations from the nominal isoluminance point (at 50 cd/m²) were derived by heterochromatic flicker photometry and are given in percent; positive deviations indicate a higher sensitivity to red. AIRF: +7.3%; CXVF: +4.7%; JCSF: +4.0%; BRIM: +4.0%; WGMM: +3.2%. Experiment 2. Simple detection thresholds (bottom row; ▲) in the isoluminant plane based on individual heterochromatic flicker photometry for the same observers as in Experiments 1a and 1b.
We also measured luminance thresholds of two of our five observers. The task was exactly the same as in Experiments 1a and 1b, and we established thresholds for luminance increments and decrements. To compare the luminance with the red–green thresholds, we converted them into cone contrast and averaged them. Cone contrast for a specific stimulus $w$, $r$ is defined as follows:

$$C_L = \frac{\Delta L}{L_{BG}} = \frac{(L_{w,r} - L_{BG})}{L_{BG}},$$

(2)

and likewise $C_M$, where BG stands for background. The average is defined as

$$C_M + C_L = \frac{\Delta M}{M_{BG}} + \frac{\Delta L}{L_{BG}}.$$

(3)

When expressed in averaged LM-cone contrast, the luminance (0.068, S.D. ± 0.014) and the red–green thresholds (0.034, S.D. ± 0.003) were similar for observer AIRF. Observer CXVF, however, showed a larger cone-contrast variation in the luminance thresholds (0.1867, S.D. ± 0.1101) than in the red–green thresholds (0.0731, S.D. ± 0.0124).

Experiments 1a and 1b show that there is a strong input of the red–green mechanism to global motion processing. The adjustment for the individual points of isoluminance (Experiment 1b) does not change qualitatively the results from Experiment 1a; in our parameter range, the yellowish-violet mechanism does not contribute to global motion and the thresholds for the other colors are determined by their projection onto the “M–L” axis.

Experiment 1c: Adding luminance noise

Another source of luminance artefacts in the stimulus display is in the variation of the isoluminant point with temporal frequency (Cavanagh et al., 1987; Stromeyer et al., 1995; Metha & Mullen, 1996), or in a temporal phase lag between L- and M-cone signals (Swanson et al., 1987; Stromeyer et al., 1995, 1997; Tsujimura et al., 1999, 2000). A method to exclude the possible contamination of the stimulus with luminance artefacts is to superimpose luminance noise over the chromatic stimulus, because the luminance noise will affect the detection of luminance contrast but not the detection of isoluminant stimuli (Gegenfurtner & Kiper, 1992; Losada & Mullen, 1995; Sankeralli & Mullen, 1997). This method has been used successfully for assessing chromatic motion mechanisms (Baker et al., 1998; Yoshizawa et al., 2000).

Dynamic (two-dimensional) luminance noise was superimposed onto our stimuli; noise amplitude was quantified as RMS contrast. We first measured motion discrimination thresholds for achromatic stimuli with varying levels of RMS noise contrast and different pixel sizes of the masking noise dots for three observers, including a condition without any added luminance noise. The latter served as a baseline and represents the minimum luminance contrast that is necessary to perform our task at threshold (81% correct). From the underlying psychometric functions for each masking condition, we selected that masking condition for which its psychometric function passed through the 50% performance point (chance performance) for the baseline threshold (without added luminance noise). This condition was met by a $3 \times 3$ pixel noise with an RMS noise contrast of 19.5% for all three observers; the motion threshold for this added luminance noise was twice the threshold for the baseline condition. Noise with these parameters was added to our displays, and the motion discrimination thresholds for chromatic stimuli were measured for three observers.

Results

The thresholds with and without added luminance noise are plotted in Fig. 3. In some directions, the thresholds for the added-noise conditions are slightly higher than for the baseline condition, but even with this luminance noise, the red–green modulations can be used for our motion task. Superimposing luminance noise onto our chromatic motion displays does not change our previous results. We conclude that our results in Experiments 1a and 1b are not due to luminance artefacts and that there is genuine red–green input to global motion processing.

![Fig. 3. Added luminance noise. Color contrast thresholds for global motion integration of three observers with (●) and without (○) added luminance noise (Isoluminance was determined by heterochromatic flicker photometry; RMS noise contrast for all three observers was 19.5%, noise pixel size: 3 × 3 pixels.)](image-url)
The previous experiment showed that stimuli modulated along an isoluminant red–green axis provide input to a global motion mechanism. For our parameter range, stimuli that isolate the yellowish–violet mechanism do not allow the observer to extract motion. To evaluate whether the absence of the S-cone input is specific to the motion mechanism, we measured simple detection thresholds using the same stimuli as in Experiment 1b. We measured color contrast detection thresholds (81% correct) in the cone-opponent color space [“M–L” vs. “S–(M–L)”] for eight different colors (see Fig. 1). We used again a 2IFC paradigm: one interval contained the RDK, whereas the other interval contained the grey background only. Participants had to indicate which interval contained the RDK as the color contrast was changed according to an adaptive procedure (see Procedure). This experiment was run at observer’s isoluminance.

**Results**

Detection thresholds are plotted as “>” symbols in Fig. 2. For all color directions in the isoluminant plane, participants were able to detect the stimuli at much lower color contrasts than required for the global motion task. This is particularly striking for the stimuli that isolate the “S–(L+M)” mechanism. For these stimuli, global motion thresholds could not be measured at all but the detection thresholds are low (about 0.14 S-cone contrast). In Fig. 4, the global motion contrast threshold to detection contrast threshold ratio is plotted as a function of the angle in the isoluminant plane; 0 deg and 180 deg refer to the “M–L” axis, and 90 deg and 270 deg refer to the “S–(L+M)” axis. Since global motion thresholds for S-cone stimuli (90 deg and 270 deg) could not be measured, it can be assumed that the necessary cone contrast has to be at least ±0.84 (maximum S-cone contrast that could be produced along the 90/270 deg axis). The ratio of global motion to detection contrast threshold at these values is therefore at least 12. In general, the ratio of global motion threshold to detection threshold increases when one approaches the “S–(L+M)” axis. It is striking that these S-cone stimuli can be detected at a rather low contrast but we could not generate a contrast that allows the visual system to extract global motion. We conclude that different mechanisms must mediate global motion processing and detection of the chromatic stimuli. The lack of S-cone input to global motion processing for a wide range of parameters confirms previous results by Wuerger and Landy (1993) who showed that stimuli that isolate the “S–(L+M)” mechanisms were not effective in a structure-from-motion task (SFM), whereas stimuli modulated along the “M–L” axis at a moderate contrast provided input to the SFM mechanism.

**Discussion**

**Global motion mediated by a red–green mechanism**

We measured contrast thresholds in a global motion task for stimuli that isolate either the luminance (“L+M”), the red–green (“M–L”), or the yellowish–violet (“S–(L+M)”) mechanism and various intermediate isoluminant color directions. Our results suggest that, in the isoluminant plane, only a red–green mechanism mediates global motion processing; the largest S-cone contrast we could generate (i.e. 0.84) did not suffice to elicit any significant motion input of the “S–(L+M)” mechanism. We excluded the possibility that residual luminance contrast was used in the motion task by assessing the contrast thresholds at each individual observer’s point of isoluminance defined by HCFP with the same stimulus pattern as in the motion task. Furthermore, we ran a control experiment where we added luminance noise to the chromatic motion stimulus to mask a potential luminance component. If the performance for red–green modulations had been due to a residual luminance component, then observers should not be able to extract motion when luminance noise was added. Our results show that red–green modulations can be used to extract global motion even in the presence of luminance noise.

These results confirm previous findings reported by Wuerger and Landy (1993). They showed that there is a significant red–green input to the mechanism that extracts structure from motion, which is a global motion task. The current experiments corroborate these findings by showing that stimuli that isolate an “M–L” mechanism can also be used for pattern motion which is probably computed in extrastriate areas MT or MST (Dougherty et al., 1999; Seidemann et al., 1999; Wandell et al., 1999). Isoluminant red–green stimuli are most likely processed by the parvocellular pathway, which traditionally has not been associated with motion processing (Moutoussis & Zeki, 1997). Together with recent findings (Anderson et al., 1995; Willis & Anderson, 1998, 2002), our experiments provide further evidence that the parvocellular pathway is involved in motion processing.

Lu et al. (1995, 1999) have developed a theory of the functional architecture for human motion processing. Their results suggest that there is no significant red–green input into a mechanism that computes motion energy and that motion energy computation relies entirely on a luminance input. Zaidi and DeBonet (2000), on the other hand, find evidence for a red–green input to motion computation mechanism. Apart from different calibration procedures, the stimuli used in these two studies also had different temporal parameters, which might be a significant factor in explaining this discrepancy. The present study suggests that there is a significant red–green input for global motion perception but it did not attempt to characterize the precise level of this chromatic contribution.

**Detection vs. motion coherence performance**

To evaluate whether the same mechanism mediates the detection and the extraction of global motion, we measured contrast thresholds for both tasks. The discrepancy between detection and discrimination thresholds for chromatic motion stimuli has been established for stimuli modulated along an “L–M” axis (Lindsey & Teller, 1990; Cavanagh & Anstis, 1991; Kooi & De Valois, 1992; Mullen & Boulton, 1992a,b; Derrington & Henning, 1993; Palmer et al., 1993; Metha et al., 1994; Gegenfurtner & Hawken, 1995; Metha & Mullen, 1998). Fig. 4 shows that the ratio of global motion threshold to detection threshold increases when the stimulus gets closer to the “S–(L+M)” axis (90 deg and 270 deg). In the isoluminant plane, global motion threshold to detection threshold ratios are smallest for stimuli isolating the “M–L” mechanism and converge to large values for stimuli isolating the “S–(L+M)” axis. In comparison to the “M–L” mechanism, the S-cones feed effectively into a detection mechanism but are poor in driving global motion processing. These findings corroborate conclusions drawn by Stromeyer and colleagues (Stromeyer et al., 1995). They found that along a chromatic (however, not necessarily isoluminant) axis two mechanisms operate at thresh-
old, one tuned to detect the presence and the hue of a stimulus, the other tuned to discriminate its motion.

The lack of S-cone input to global motion processing

We investigated the input of the S-cones to global motion processing using a set of Gaussian blobs with a diameter of 0.22 deg moving at a slow speed (1 deg/s). Under these conditions, isoluminant S-cone stimuli do not feed into a global motion mechanism. The lack of the “S-(L+M)” mechanism in mediating global motion confirms previous results by Wuerger and Landy (1993) who showed that, for a similar range of spatial and temporal parameters, the S-cone input for a structure-from-motion task is negligible.

Studies by Curcio et al. (1991) show that the S-cone spacing in the human fovea is about 10 arc min, and in our RDK each Gaussian blob (with a diameter of 12 arc min) moved about 14 arc min. Therefore each blob was on average “seen” by at least two S-cones. These calculations are in agreement with psychophysical studies by Barbur and Saunders (1985), who found for foveal presentation that a displacement of 6–7 arc min is enough for reliable motion detection when stimulating the yellowish-violet pathway. Our Gaussian blobs correspond to a spatial frequency of about 2 cycles/deg, which is within the foveal resolution limit based on the small bistratified ganglion cell density (Dacey, 1993; Dacey & Lee, 1994). Recent findings support the idea that resolution is limited by the blue–yellow ganglion cell sampling, directly relating to short-wavelength-driven ganglion cell density (Metha & Lennie, 2001; Anderson et al., 2002).

These results together with the detection performance suggest that the lack of S-cone input to global motion processing is due to postreceptor processing and might be specific to the extraction of global motion. Isoluminant S-cone targets are likely to stimulate the koniocellular pathway (De Valois et al., 2000). Rabin and colleagues (Rabin et al., 1992) found that visibility of isoluminant S-cone stimuli predicts performance in a form-perception task, which is different from our findings using global motion stimuli. We speculate that the koniocellular pathway is more effective in mediating form than motion processing.

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