Failure of direction discrimination at detection threshold for both fast and slow chromatic motion

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Separate pathways have recently been proposed for "fast" and "slow" motion, whose properties differ in the way that color contrast is processed [see Nature (London) **367**, 268 (1994); Trends Neurosci. **19**, 394 (1966); and Vision Res. **36**, 1281 (1996) and **35**, 1547 (1995)]. One reported difference is that for slow motion the direction of chromatic stimuli cannot be determined at detection threshold, whereas at higher temporal rates detection and direction discrimination threshold coincide. Using a carefully designed psychophysical procedure, we measured simultaneously the thresholds for detection, direction discrimination, and color identification for isoluminant red–green and achromatic Gabor patches (1.5 cpd), over the range of visible temporal frequencies (1–16 Hz). We find that the color of both the red–green and the achromatic targets can be identified at detection threshold, indicating effective isolation of the luminance and the red–green mechanisms at all stimulus speeds. For the achromatic mechanism, direction discrimination thresholds are significantly greater than detection thresholds at all stimulus speeds. This result calls into question models of chromatic motion processing that are dichotomized along the lines of stimulus speed. © 1998 Optical Society of America [S0740-3232(98)01012-6]

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1. INTRODUCTION

It has recently been proposed that the processing of motion information at slow speeds and fast speeds is mediated by separate and distinct mechanisms, whose properties differ with respect to the way that color information is processed.¹⁻⁴ These authors posit a "fast" motion pathway that codes the velocity of quickly moving patterns (>4 Hz) of any chromaticity, but that may not explicitly signal the color of such patterns, and a second "slow" pathway with a high sensitivity to chromatic targets that signals the direction of slowly moving patterns (<4 Hz) but does not veridically encode velocity. There are two pieces of psychophysical evidence favoring this position. First, it has been found that contrast dependencies for speed perception are different under the fast and slow conditions and that this difference is particularly apparent for drifting isoluminant red-green (RG) stimuli. For slowly moving targets the perceived speed of isoluminant RG stimuli is highly dependent on contrast, whereas it is only moderately contrast dependent for achromatic targets. A different pattern of results arose for fast speeds, for which the speeds of both RG and achromatic targets were found to be perceived almost veridically at all contrast levels.³

The second psychophysical result marshalled in support of this speed-based motion-processing dichotomy is based on the well-established finding that at slow speeds, the contrast thresholds for detecting and identifying the direction of RG targets do not coincide.⁴⁻¹³ There is a threshold gap arising from the fact that low-contrast isoluminant drifting patterns can be detected while their direction of motion is confused. This is not the case for equivalent achromatic patterns drifting at the same speed.

Some of the above authors, however, have noted that at higher speeds the threshold gap disappears for RG targets, signifying correct direction discrimination at detection threshold.^{4,8} This has been taken as evidence for a fundamental difference in the processing of chromatic motion information at high and low speeds, thus supporting a speed-based dichotomy in which there is no independent chromatic motion mechanism operating at high speeds. However, the literature offers many conflicting reports about this point. Some studies have reported that the threshold difference between detection and direction discrimination for foveal RG targets remains significant even at fast drift rates,^{7,9,14} yet others find no threshold difference for foveally presented isoluminant targets at any drift rate.¹⁵ The lack of concordance among these results presumably stems from procedural differences among the studies with respect to stimulus size and eccentricity, the exact nature and timing of the detection and direction discrimination threshold tasks, and the accuracy of the determination of isoluminance.

In light of the uncertainty in the literature over this issue and because of the theoretical significance for models of motion processing attached to the results, we undertook to determine carefully and explicitly the relationship between detection and direction discrimination thresholds for foveally viewed RG chromatic stimuli as a function of drift rate. In the experiments, we used procedures ensuring that the detection and direction discrimination threshold data could be validly compared over a wide range of drift rates and that the RG stimuli effectively isolated the red-green chromatic mechanism. First, we used a multiple-judgment paradigm to measure detection and direction discrimination thresholds simultaneously, instead of assessing them in separate runs during the course of which the two different task thresholds might vary independently. Second, we block randomized the order of stimulus speeds measured, so that data were collected evenly over time for different speeds in an interleaved fashion. Third, we did not rely on photometric measures of isoluminance to isolate the RG channel but rather determined RG isoluminance by a minimum-motion paradigm separately for each observer at each drift rate tested.

Last, and most important, we added a third question to the multiple-judgment task that required the observer to identify the color of the stimulus being presented (redgreen versus black-white), which allowed us to ensure that the RG chromatic and luminance mechanisms had been properly isolated during the measurements of the detection and direction discrimination thresholds.

2. METHODS

The stimuli were foveally presented 1.5 cycles per degree (cpd) Gabor patches viewed monocularly at 180 cm on a Barco Calibrator monitor. This was driven with gammacorrected 12-bit accuracy (per gun) by a Cambridge Research Systems VSG 2/2 video card at a frame rate of 120 The time and space average chromaticity (x)Hz. = 0.3377, y = 0.3184) and luminance (66.2 cd m⁻²) of the entire screen was constant. Stimulus contrast was ramped on and off in a raised-cosine manner with total duration of 1 s. The sinusoidal carrier drifted inside a stationary Gaussian envelope (standard deviation = 0.66°) at six different rates (1, 2, 4, 8, 11.3, or 16 Hz). Fixation was aided by a 2-mm spot centered on the CRT screen. The Gaussian envelope diameter was truncated at 2.6°, corresponding to four spatial periods of the sinusoidal carrier.

The two authors and a third subject, näive about the aims of the experiment, served as observers. Using a minimum-motion task, we first determined for each observer and each drift rate the isoluminant conditions required for isolating the RG chromatic mechanism. The suprathreshold stimulus is described by a vector specifying a direction in the LM plane of cone-contrast space (Scone contrast was zero). This vector was rotated in 2.5° steps while the cone-contrast magnitude was adjusted so as to maintain a constant projection in the L-M direction, thus maintaining constant excitation of the RG mechanism at approximately twice the RG direction discrimination threshold while varying stimulation of the luminance mechanism. At these low contrasts, when the stimulus significantly modulates the luminance mechanism, it appears to drift quickly; but as the cone-contrast vector is rotated through the isoluminance point, the salience and perceived speed of motion decreases, subsequently increasing again as the vector moves to the other side of the isoluminance point. The angle that results in the weak-



Fig. 1. Input cone-contrast ratios for the luminance mechanism as a function of temporal frequency (TF). Each point represents the average and standard deviation of 10–20 minimum-motion settings. The gray curves drawn through the data are best-fitting power functions to these data: PM (circles), L:M = $5.265 \times \text{TF}^{-0.240}$; KTM (triangles), L:M = $4.913 \times \text{TF}^{-0.124}$; ABM (squares), L:M = $1.884 \times \text{TF}^{0.178}$).

est motion percept is our estimate of the RG isoluminance point.

From randomized starting positions, subjects used the computer mouse to make 10-20 isoluminance settings at each drift rate in random order. These data were averaged for each drift rate, and the luminance L:M input ratio was computed; it is plotted in Fig. 1. All observers reported the task easy to perform and set repeatable end points, as indicated by the small error bars in Fig. 1. The systematic increases in the error bar size with luminance L:M ratio are a reflection of the closeness of the isoluminance angle to the M-cone-contrast axis and do not imply that observers PM or KTM had any more variability than ABM in making minimum-motion settings; in terms of the color angle of the stimulus in cone-contrast space, all observers showed approximately the same variance. The curves shown in Fig. 1 are the best-fitting power functions to these data. In agreement with previous studies, there is a systematic variation of these L:M ratios, for each observer with different observers showing different patterns of variation as a function of temporal frequency.^{4,14,16,17} It has also recently been shown by Stromeyer III et al.^{13,18} that the average adapting-screen chromaticity plays an important role in determining how the luminance L:M ratio varies with temporal frequency. Stromeyer III et al. point out that for any observer, it is possible to select an adapting-screen color for which the luminance L:M ratio is constant with temporal frequency. We did not seek to find such a condition, but by using RG stimuli in the main experiment with L:M ratios defined by the fitted curves in Fig. 1 for each temporal frequency, we were able to isolate the RG mechanism under the adaptive conditions of our experiment. That RG isolation was successful is borne out by the color naming results of the main experiment (see below). To isolate the luminance mechanism, we used a stimulus that excites all three cone classes equally, resulting in an achromatic stimulus whose chromaticity is not different from that of the adapting background.

In the main experiment, thresholds were determined by using a blocked 3×2 -interval forced-choice method of constant stimuli. Observers were presented with two successive intervals marked by tones and separated by 500 ms. One interval contained a stimulus of a certain drift rate, which was either RG or achromatic and drifted either up or down. Observers sequentially indicated the following by button presses:

1. The interval in which the stimulus appeared (the detection task),

2. The color of the stimulus (the color identification task, i.e., to discriminate RG versus luminance),

3. The drift direction of the stimulus (the direction discrimination task).

After an initial training period, all observers found this multiple-judgment task easy to do. To ensure that variation in the results for the 6 different drift rates could not be attributed to any systematic variation in sensitivity over time, the complete experiment was pseudorandomly divided into 30 smaller blocks within which drift rate was held constant. Within each block (i.e., at each drift rate), achromatic and RG isolating stimuli as determined above were presented eight times at six different contrast levels spanning detection threshold in 0.15-log₁₀-unit steps. Immediately before the main experiment, initial threshold estimates were made by interleaved staircases, in order to allow appropriate contrast levels to be selected for the psychometric function measurements. The blocks were repeated in pseudorandom fashion 5 times, resulting in 40 trials at each contrast level for each condition, from which the different psychometric functions for detection, direction discrimination, and color identification were constructed and analyzed.

3. RESULTS

Figure 2 shows thresholds for detection and direction discrimination plotted as RMS cone contrast sensitivity as a function of temporal frequency, for all three observers. The 75% performance thresholds were determined by simultaneously fitting the RG and the achromatic psychometric functions for each task with base 2 Weibull functions, using a least-chi-square metric and binomial estimates for the variance at each contrast datum. The guess rates for RG and achromatic color-identification psychometric functions were free to covary in a complementary manner in order to account for the potential for bias in the color identification task (see Metha and $Mullen^{19}$ for details). The error bars in Fig. 2 show the estimated standard deviation of thresholds calculated by this procedure. The top panels show that detection and direction discrimination sensitivity are similar in shape for the chromatic RG stimuli and peak at lower temporal frequencies (1-2 Hz), in contrast to the achromatic sensi-



Fig. 2. Detection (open symbols) and direction discrimination (filled symbols) thresholds plotted as RMS cone-contrast sensitivity as a function of temporal frequency for all three observers. The top and bottom panels show performance with isoluminant RG and achromatic targets, respectively.



Fig. 3. Threshold gaps for all observers expressed in \log_{10} units for average color identification (triangles), and direction discrimination for RG (circles) and achromatic (squares) targets as a function of stimulus drift speed. We use the average of the RG and achromatic color identification threshold gaps in this plot to compensate for the potential bias in identifying stimulus color, as explained in the text. Unconnected points on the right present the average threshold gaps across all speeds tested. Error bars represent the estimated standard deviations for these calculations.

tivities (bottom panels) for these tasks, which peak at 4-8 Hz. In cone-contrast terms, RG detection sensitivity exceeds achromatic sensitivity at low temporal frequencies, but the reverse is true for frequencies above 4 Hz. The important aspect of these data, however, is that the RG detection and direction discrimination sensitivity functions are relatively displaced vertically at all temporal frequencies, in contrast to the achromatic curves, which overlay each other.

The relationships between these different thresholds are highlighted in Fig. 3, which shows the ratio of direction discrimination to detection thresholds in \log_{10} units for RG and achromatic stimuli as a function of temporal frequency, as well as the threshold ratio of color identification thresholds to detection thresholds. The error bars in Fig. 3 are the propagated standard deviations of these ratios, calculated by using Gaussian arithmetic and based on the estimated standard deviations of the absolute thresholds in each case. For achromatic stimuli there is no threshold gap at any stimulus speed; when stimulus contrast is increased to a point that allows correct detection of achromatic targets, motion direction can also be reliably reported. The same is true for the average color identification thresholds. As soon as either the achromatic or the isoluminant RG stimuli are detected, their color can also be reliably reported. This is a very important control finding, for it implies that the mechanisms responsible for detection in each case are labeled for color and that our stimuli have effectively isolated the luminance and RG chromatic pathways at all temporal frequencies tested. Finally, Fig. 3 also shows that for RG targets there is a consistent and reliable gap between the direction discrimination and detection thresholds that remains across all temporal frequencies up to the 16-Hz limit of our measurements. While for one observer (PM) the gap becomes noticeably larger at lower temporal frequencies (1-2 Hz), for all observers the RG threshold gap never approaches the small values measured for the luminance-defined stimuli, at any temporal frequency. The average RG threshold gap across all temporal frequencies (unconnected points on the right-hand side in Fig. 3) ranged between 0.26 and 0.44 \log_{10} unit, or roughly a factor of 2.

This does not necessarily imply that the RG direction discrimination thresholds are subserved by a different RG mechanism that mediates detection, but the main point of this paper is that for these RG isolating stimuli, direction discrimination is not possible at detection threshold at any of the drift rates tested: The chromatic motion system is thus behaving in a distinctly different manner in comparison with the achromatic motion system, for which direction discrimination is possible at detection threshold. The results are parsimoniously explained by postulating that both fast and slow chromatic motion signals are processed by a common RG motion mechanism that, unlike the achromatic system, can operate reliably only at contrast levels significantly above detection thresholds.

4. DISCUSSION

This study shows that while detection and direction discrimination threshold for our achromatic stimuli are the same for all speeds, there is a clear threshold difference for these tasks when stimuli isolate the RG chromatic mechanism, and this difference persists as speed increases up to our limit of 16 Hz.

These conclusions are in line with the findings of Mullen and Boulton,⁹ who reported small but significant ratios of direction discrimination thresholds to detection thresholds for RG isoluminant stimuli for a range of spatial (0.3-2.1 cpd) and temporal (0.4-12.8 Hz) frequencies.

These authors used a multiple-judgment task similar to that used in the present experiment and also adjusted the isoluminant point for all conditions. Our results here are also consistent with the findings of Cavanagh and Anstis,⁷ who found significant threshold gaps (0.2–0.5 \log_{10} unit) for 0.5- and 1.0-cpd RG isoluminant gratings drifting at 2, 4, and 8 Hz. Metha¹⁴ also reported that red–green isoluminant direction discrimination and detection threshold ratios remain well separated for foveally presented 1.0-cpd gratings drifting at 1, 8, and 16 Hz.

However, not all studies that explored a range of temporal frequencies have come to the same conclusion. Derrington and Henning¹⁵ reported that for similar foveally viewed 1-cpd grating particles, detection and direction discrimination thresholds coincided at drift rates from 1 to 16 Hz. Unlike in the present experiment, Derrington and Henning used separate runs to determine the detection and direction discrimination thresholds for each condition they tested. They argued that in multiplejudgment tasks, the observer must divide attention between the tasks in some unknown manner. While this may be true, we feel that the power of the threshold comparison can become severely compromised by not collecting the different task-threshold data in the same period of time. Furthermore, all observers reported that the task was easy after training, and there is no reason to suppose that any division of attention for the two tasks would be along stimulus chromaticity lines. Of further concern regarding the Derrington and Henning¹⁵ study is that the stimulus presentation conditions for the two tasks were quite different: In the detection task only one interval contained a stimulus, whereas in the direction discrimination task, both intervals did. Under these conditions, signal detection theory predicts that discrimination performance for orthogonal labeled detectors should be better than detection performance by as much as a factor of $\sqrt{2}$, or up to 0.15 log₁₀ unit.^{14,20} This reason, along with the potential for relative sensitivity drifts for the two tasks, may account for the many data points in their Fig. 4 that indicate that direction discrimination thresholds actually fall below detection thresholds, especially for luminance-defined stimuli.

Gegenfurtner and Hawken⁴ also performed experiments concerning the threshold difference between direction discrimination and detection for RG stimuli as a function of temporal frequency and arrival at conclusions different from those of the present study. The same criticisms as those mentioned in the previous paragraph, however, also apply to their study. For their foveally presented stimuli, the two tasks differed in fundamental ways: The detection task consisted of two intervals, whereas the direction discrimination task used only one interval. Also, detection and direction discriminations were measured separately, and speed was constant for any one session, meaning that long periods of time could elapse between the collection of data for the two tasks and between different speeds.

To explore parafoveal stimuli, Gegenfurtner and Hawken⁴ changed the nature of their task to one in which detection and direction discrimination were measured simultaneously, and they found that the threshold difference for red–green stimuli extended to higher temporal

Although in both the foveal and the frequencies. parafoveal studies complete cone-contrast threshold contours were generated, these authors chose to calculate the red-green threshold differences by using stimuli that were photometrically isoluminant, even though their threshold data and curve-fitting analysis elegantly indicated that the isoluminance conditions change as a function of stimulus temporal frequency. At higher drift rates the cone-contrast threshold contours become increasingly elongated in the direction favoring the luminance mechanism. While this makes it possible to define the inputs to the luminance mechanism more accurately, it also makes it critically important to specify the isoluminant angle very exactly. Close inspection of the data of Gegenfurtner and Hawken⁴ (e.g., their Fig. 3C) reveals significant foveal red-green threshold gaps at functional isoluminance ($\sim 0.1 \log_{10}$ unit in this case) that at the photopically defined isoluminance point recede to zero. We suspect that such photopically defined, nominally isoluminant stimuli do not isolate the RG chromatic channel and are in fact detected by the relatively more sensitive luminance channel at high drift rates, subsequently behaving like luminance stimuli.

The superior sensitivity of the RG mechanism at low speeds guarantees that slowly drifting RG patterns are not detected by any intruding achromatic mechanism that sums L- and M-cone inputs. At higher speeds, however, the sensitivity relationships of the RG and the achromatic mechanisms are reversed, and it becomes possible that nominally isoluminant stimuli may stimulate a cone additive mechanism at high contrasts, despite RG isolation at detection threshold. Stromeyer et al.¹⁸ show that on strongly colored backgrounds this may well be the case; they model such effects by assuming that L- and Mcone signals are phase shifted relative to one another as they form the receptive-field surround of cone additive retinal ganglion cells. There are several reasons why it is unlikely that our RG direction discrimination results reflect the action of some intruding achromatic mechanism and not a cone-opponent motion mechanism. First, the neutral gray that we used as the adapting background color is very close to the neutral condition for which Stromeyer et al. found that relative phase shifts were minimal. Second, Fig. 2 shows that the shape of the RG direction discrimination contrast-sensitivity function is essentially the same as the RG detection contrastsensitivity function and is not shallow at the hightemporal-frequency limb as would be expected if the achromatic mechanism were determining threshold direction discrimination performance. The RG threshold gap, while significant, is nevertheless small and constant over the entire temporal frequency range. Third, in determining the isoluminant point, observers found that for lowcontrast stimuli, the angle in cone-contrast coordinates does alter the perceptual saliency and speed of motion. Indeed it is this phenomenon that allows the isoluminant point to be found. If the achromatic mechanism were active at these contrasts, we would not expect the speed and salience to change as the effective luminance contrast was altered.

The notion that the RG mechanism can operate independently to determine motion performance for hightemporal-frequency chromatic stimuli is also supported by the experiments of Cropper and Derrington,²¹ who found evidence for a distinct RG mechanism responsible for mediating direction discrimination for very quickly (17 ms) presented RG stimuli. That this fast RG motion mechanism is independent of the achromatic mechanism was revealed by the finding that achromatic masks did not alter the performance of direction tasks for RG targets but severely interfered with the same tasks when achromatic stimuli were used.

In summary, the present results suggest that any differences in the properties of chromatic motion processing as a function of speed are not as clear as previously suggested, thus calling into question the assertion of two motion mechanisms dichotomized along the lines of stimulus speed. In addition, recent modeling shows how, in principle, different contrast dependencies for speed perception can arise from consideration of the contrast-transduction properties of early temporal filters in both the chromatic and the luminance cases.^{19,22} Different dependencies of perceived speed on stimulus contrast for fast- and slowdrifting RG and achromatic stimuli need not necessarily reflect the operation of distinct motion-processing systems operating over different speed regimes.

5. CONCLUSION

These experiments were designed to determine carefully and explicitly the relationship between detection and direction discrimination thresholds for foveally presented RG and achromatic stimuli over a range of temporal frequencies, while ensuring mechanism isolation in each case. For stimuli that isolate the RG channel, we find a similar threshold difference at all temporal frequencies, which is important because it reveals that for this particular aspect of chromatic motion processing, there are no major differences along the dimension of stimulus speed.

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