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Perceived Velocity of Luminance, Chromatic and Non-Fourier Stimuli: Influence of Contrast and Temporal Frequency

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We measured perceived velocity as a function of contrast for luminance and isoluminant sinusoidal gratings, luminance and isoluminant plaids, and second-order, amplitude-modulated, drift-balanced stimuli. For all types of stimuli perceived velocity was contrast-invariant for fast moving patterns at or above 4 deg/sec. For slowly moving stimuli the log of perceived velocity was a linear function of the log of the contrast. The slope of this perceived velocity-vs-contrast line (velocity gain) was relatively shallow for luminance gratings and luminance plaids, but was steep for isoluminant gratings and isoluminant plaids, as well as for drift-balanced stimuli. Independent variation of spatial and temporal frequency showed that these variables, and not velocity alone, determine the velocity gain. Overall, the results indicate that slow moving stimuli defined by chromaticity or by second-order statistics are processed in a different manner from luminance defined stimuli. We propose that there are a number of independent mechanisms processing motion targets and it is the interplay of these mechanisms that is responsible for the final percept.

Color   Isoluminance   Motion   Velocity

INTRODUCTION

Velocity judgments are important for many visual tasks: perception and tracking of objects moving in the environment, perception of three-dimensional structure from motion (parallax information) and for the initiation and control of eye, head and body movements. Human observers can judge the velocity of objects defined by luminance borders in one and two dimensions, chromatic borders and borders defined by second-order components such as drift-balanced stimuli (Chubb & Sperling, 1988) or illusory borders. We have measured the effect of contrast on relative perceived velocity for selected stimuli from each of these groups in an attempt to determine if there are any similarities or differences between stimulus configurations that would allow us to draw conclusions about the underlying motion mechanisms.

Since Ramachandran and Gregory (1978) reported loss of apparent motion at isoluminance, there have been numerous reports that indicate motion perception is compromised at or near isoluminance; isoluminant stimuli appear to move more slowly than luminance stimuli of the same physical velocity (Cavanagh et al., 1984; Cavanagh & Farreau, 1985; Derrington & Badcock, 1985; Troscianko & Fahle, 1988; Cavanagh & Anstis, 1991; Kooi & DeValois, 1992; Mullen & Boulton, 1992). It has also been shown that even for one-dimensional luminance borders, e.g. gratings, perceived velocity is not invariant with changes in luminance contrast (Thompson, 1982; Stone & Thompson, 1992). Because of the large overlap in the absorption spectra of the L- and M-cones the maximum contrast at the input to the visual system is greatly reduced at isoluminance as compared to luminance modulations (MacLeod & Boynton, 1979; Gegenfurtner & Kiper, 1992). Therefore, the question arises whether isoluminance stimuli simply act as low contrast luminance stimuli or if they induce responses that are qualitatively different from those elicited by low contrast luminance stimuli? We have recently shown that the relationship between perceived velocity and contrast is different for luminance and isoluminant stimuli at slow velocities, but not at fast ones (Hawken et al., 1994). Therefore, at least at slow velocities, isoluminant moving gratings are not simply behaving like low contrast luminance gratings. The idea of more than one motion pathway is consistent with other recent reports suggesting two different motion pathways for slow and fast moving patterns (Gorea et al.,

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1993). Here we investigate the temporal properties of these two pathways.

We extended the paradigm to investigate the properties of two-dimensional plaid patterns to see whether the contrast dependence of the perceived velocity of plaids could be predicted from that of the component gratings. In the luminance domain the motion of two-dimensional patterns such as plaids, formed by pairs of gratings at different orientations, appears to move in a direction and with a velocity determined to a large degree by the constraints the individual motion vectors impose on the global motion (Adelson & Movshon, 1982). More recently it has been shown that the direction and velocity predictions need to take into account the contrast dependency of the perceived velocity of the components (Stone et al., 1990; Derrington & Suero, 1991). The effects of contrast on the perceived velocity of luminance gratings predict the perceived velocity of luminance plaid patterns (Stone & Thompson, 1992), although when the contrasts of the components are different the perceived direction tends to be dominated by the higher contrast component (Kooi et al., 1992). There is also some evidence for an important role of temporal frequency in the perception of plaids. Two-dimensional plaid patterns formed by pairs of gratings selected from different cardinal directions in color space moving at 1 deg/sec do not cohere (Krauskopf & Farell, 1990). For a plaid with luminance and red–green isoluminant components moving at 3 deg/sec, there is partial coherence and plaid direction is partially predicted by applying the intersection of constraints using the perceived velocity of the components (Kooi & DeValois, 1992). There is still considerable debate as to whether plaid motion is due to a mechanism working on the outputs of motion energy detectors for the component motions (Welch, 1989; Derrington & Suero, 1991; Kooi & DeValois, 1992; Derrington & Colombo, 1993; Kim & Wilson, 1993), or whether it is due to a feature mechanism that tracks the grating intersection points (Ferrera & Wilson, 1991; Rubin & Hochstein, 1993; Sinha, 1993). We have investigated the characteristics of the contrast dependence of velocity judgments for luminance and chromatic plaids. If a component process determines plaid motion, we should get a velocity gain at low velocities, similar to the one for luminance gratings. If a feature tracking mechanism is active, we might expect to observe a different velocity gain for the plaid when compared to the component gratings.

Motion of non-Fourier targets is seen under a variety of conditions. There is some controversy as to whether the mechanism responsible for signaling the movement of non-Fourier target motion is similar to, or the same as the mechanism that signals Fourier target motion. The difference in the mechanisms is assumed to appear before the motion stages; the difference in the two classes of stimuli lies in the processing of their spatial attributes rather than their motion (Chubb & Sperling, 1988; Wilson et al., 1992; Wilson & Kim, 1994). The results of comparisons of the perceived velocity of non-Fourier and Fourier (luminance) targets have been controversial (Ledgeway & Smith, 1994; Werkhoven & Boulton, 1994; Witt et al., 1994) and, in at least one study, the effects of varying contrast indicate that Fourier and non-Fourier motion stimuli behave in the same way (Ledgeway & Smith, 1994). We wished to determine if the similarity between Fourier and non-Fourier motion targets was independent of temporal frequency. If the motion of the non-Fourier target is processed by the same mechanism as first-order luminance-defined gratings, then we would expect to see the performance for non-Fourier motion match the luminance gratings' behavior at all temporal frequencies. On the other hand, if there are different processes operating across different temporal frequency ranges then we might expect to see these differences reflected in the velocity matches.

METHODS

Equipment

Stimuli were displayed on a Barco RGB monitor (CCID 7351B) by a True-Vision Vista graphics board with a refresh rate of 128 Hz interlaced. Each gun of the CRT was linearized by a look-up table to give 8-bit intensity resolution. A Photo Research Model 703-PC spectroradiometer was used to calibrate the display screen. The display was 21 × 15 deg at the viewing distance of 71 cm and had a mean luminance of 14.4 cd m^{-2} for the grating and plaid stimuli, and 34 cd m^{-2} for the drift-balanced stimuli. Each pixel subtended 2.12 min arc. Subjects were seated with their chins resting on a chin rest and they viewed the display binocularly through natural pupils.

Subjects

Overall, five subjects participated in different parts of this study. The two authors (KG and MH) and three experienced psychophysical observers were tested. All subjects had normal or corrected-to-normal visual acuity and showed normal color vision as tested with the Ishihara color plates and Farnsworth–Munsell 100 Hue-test.

Stimuli

Three classes of stimuli were used; sinewave gratings, plaids and amplitude-modulated, drift-balanced gratings. One c/deg sinewave gratings were vertically oriented and drifted horizontally either to the left or right. Plaid stimuli were constructed by the superposition of two sinusoidal gratings of identical spatial frequency, temporal frequency and contrast but oriented 90 deg apart, either at 45 and 315 deg to give rightward horizontal pattern motion or at 135 and 225 deg to give leftward pattern motion. The amplitude-modulated, second-order stimuli consisted of a random noise field, where the amplitude of each noise pixel was modulated by a moving square-wave grating. This type of stimulus has equal amounts of motion energy in both directions, and its motion is
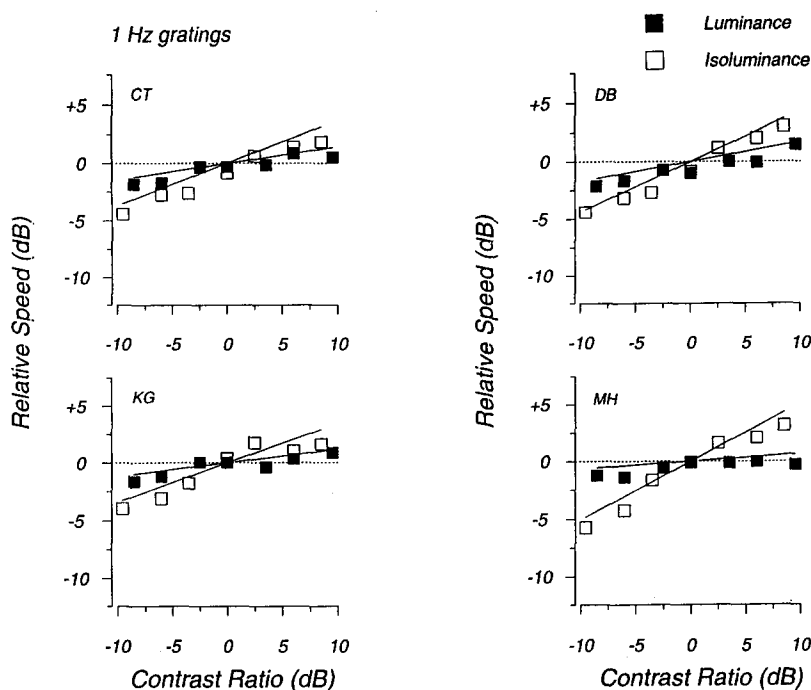
FIGURE 1. Effect of contrast on the perceived velocity of gratings moving at 1 Hz. Each graph presents results for a different observer, identified by their initials in the upper-left corner of each graph. The x-axis represents the contrast of the comparison grating relative to the contrast of the standard grating. The y-axis indicates the relative change in velocity of the comparison that was required so that the observer judged the velocity of the comparison to be equal to that of the standard grating. The temporal frequency of the standard grating was fixed at 1 Hz. For convenience, negative values mean that an increase in velocity of the comparison was required to produce the match. In both conditions the grating had a spatial frequency of 1 c/deg so the velocity was 1 deg/sec. For all observers the relative perceived velocity of the red–green isoluminant gratings was more dependent on relative contrast than the velocity of achromatic gratings.

therefore invisible to motion energy detectors (Chubb & Sperling, 1988).

The luminance modulation of the sinusoids making up gratings and plaids was around a yellow background with the CIE xyY coordinates (0.46, 0.47, 14.4). For the drift-balanced stimuli we modulated around a white point with xyY coordinates (0.33, 0.33, 34). The red–green isoluminant axis that was used to modulate gratings and plaids was from red (0.61, 0.35, 14.4) to green (0.31, 0.59, 14.4) through the yellow background defined above. This red–green axis differentially excites the second-stage mechanism defined by opponent L- and M-cone inputs (MacLeod & Boynton, 1979; Krauskopf et al., 1982; Derrington et al., 1984).

Procedure

The objective of the experiments was to determine the velocity required for observers to make a perceptual match between a comparison stimulus and a standard stimulus. On each trial the observer's task was to judge which of two simultaneously presented targets moved faster. Each stimulus presentation consisted of two windows, one above and the other below the fixation point. Each window was 18 deg wide × 4.5 deg high. For each trial one window contained the standard target which always had a fixed velocity. The other window contained the comparison target; the velocity of the comparison was determined using a staircase procedure. Changes in velocity were achieved by changing the

temporal frequency only, spatial frequency remained constant. The central horizontal border of each window was positioned at 0.5 deg from a central black fixation square (2 × 2 min arc). Stimulus duration was 1 sec and inter-stimulus interval between 0.5 and 1 sec. In order to avoid systematic bias of velocity judgments by motion aftereffects, which can occur for both luminance and chromatic gratings (Derrington & Badcock, 1985) we randomly assigned the direction (left or right) and the position (upper or lower window) of the standard. The two gratings always moved in opposite directions to minimize following eye movements. One disadvantage of this procedure was that on a few occasions the lowest contrast comparison stimulus might follow the presentation of the highest contrast stimulus. Therefore any short-term adaptation effects were averaged but not eliminated by this procedure.

The spatial, two-alternative, forced-choice procedure was used to drive a staircase. Using a one-up, one-down rule the staircase adjusted the velocity of the comparison stimulus to obtain the point where the perceived velocity of the comparison matched that of the standard. Six reversals were obtained for each staircase and two staircases were interleaved for each comparison stimulus (Wetherill & Levitt, 1965). Seven comparison stimuli were interleaved in one session and six sessions were run for each experiment. The average perceived velocity of each comparison was taken as the mean across the six sessions. The contrast of the comparison stimuli was
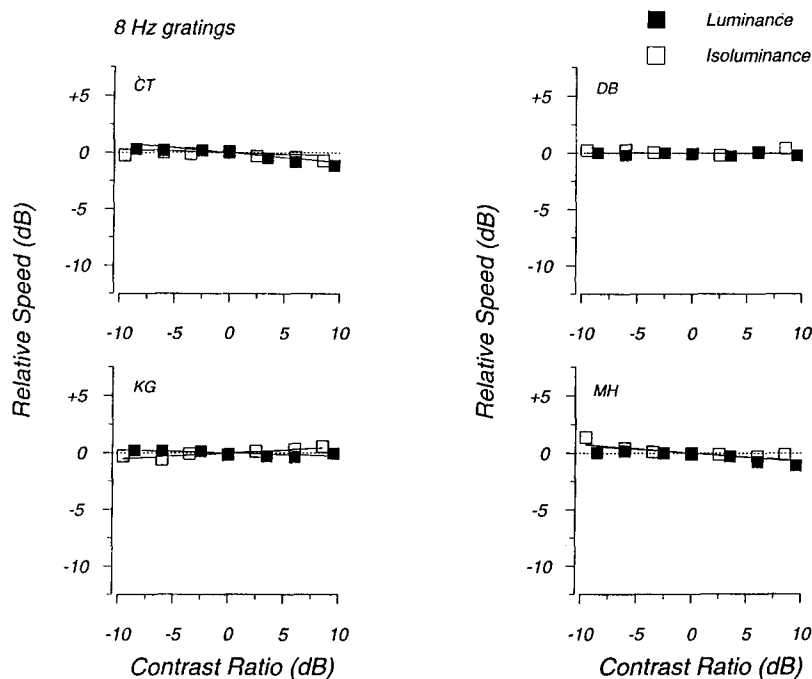
FIGURE 2. Effect of contrast on the perceived velocity of gratings moving at 8 Hz for the same observers whose data is shown in Fig. 1. Other details are given in the legend to Fig. 1. For all four observers there is very little dependence of relative velocity on stimulus contrast, either for achromatic luminance modulation or for red–green isoluminant targets.

varied both above and below the contrast of the standard, usually in half octave steps. The spatial frequency and chromaticity of the standard and all the comparisons were the same within each session of the experiment.

RESULTS

Luminance and isoluminant gratings

Under certain conditions the perceived velocity of a grating target depends on its contrast (Thompson, 1982; Stone & Thompson, 1992). We recently showed (Hawken et al., 1994) that perceived velocity is related to stimulus contrast by a power function. In our previous experiments we reported that the slope of the line relating log perceived velocity to log contrast, which we have termed velocity gain, was independent of the absolute contrast of the standard. By definition the velocity gain is also invariant under linear transformations of the contrast scale, since these transformations only change the intercept but not the slope of the line. The use of velocity gain allows us to compare slopes for isoluminant and luminance gratings, even though the absolute values of contrast for luminance and isoluminance are generally not comparable.

Figure 1 shows the perceived velocity of luminance and isoluminant gratings moving at 1 Hz. The contrast of the luminance standard was 4%. The cone contrasts for the isoluminant standard were 12% in the M-cones and 5% in the L-cones. The perceived velocity of these two stimuli approximately matched each other, which was confirmed in control experiments using a luminance standard and isoluminant comparison gratings. The straight lines through the origin are the linear regressions

fitted to the data, the slope of the lines indicating the velocity gain. The slope for the luminance condition was lower for all four observers than the slope for isoluminance.

Figure 2 shows results for the same four observers at a temporal frequency of 8 Hz. This time perceived velocity was contrast-invariant for both luminance and isoluminant stimuli.

These data show that isoluminant gratings do not simply act as low contrast luminance gratings. The velocity gains of luminance and isoluminant gratings are different at 1 Hz. At some point, isoluminant and luminance gratings must pass through different neural pathways. At 8 Hz the relative velocity gains for luminance and isoluminant gratings are equal. In addition, when the standard was an 8 Hz drifting luminance grating and the comparisons were isoluminant gratings we found that the velocity gain function was flat, just as in the luminance–luminance and isoluminance–isoluminance conditions. While the difference in velocity gain is quite clear between isoluminant gratings drifting at 1 and 8 Hz, it is not obvious what happens at intermediate temporal frequencies. Figure 3 shows relative velocity judgments as a function of contrast for temporal frequencies from 1 to 16 Hz for one observer. We have summarized the slopes of the regression lines from Fig. 3(A, B) as relative velocity gain in Fig. 3(C). The relative velocity gain is about five times greater for the isoluminant condition [Fig. 3(C), □] at the two slowest temporal frequencies that we tested, 1 and 2 Hz. At 4 Hz the effect of contrast is much reduced and for the two highest temporal frequencies (8 and 16 Hz) the relative velocity gain is low and similar to the gain for the
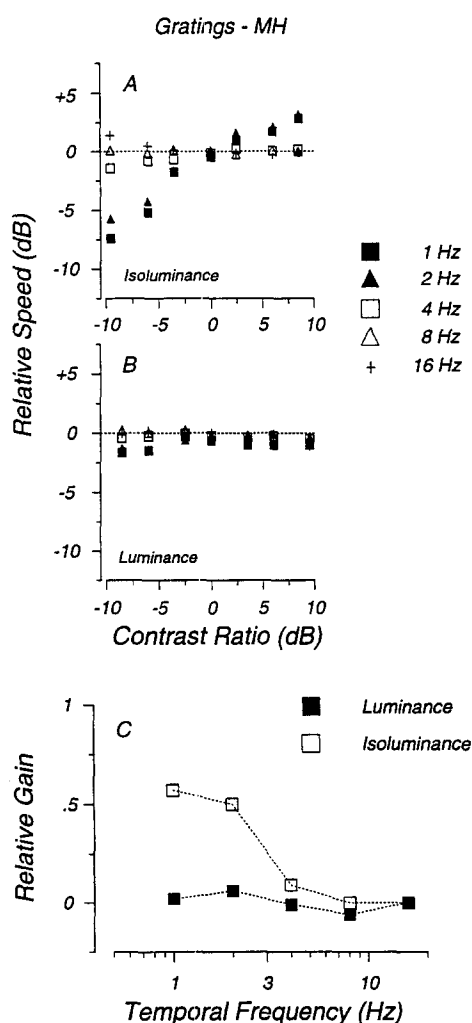
FIGURE 3. Effect of contrast on perceived velocity for red–green isoluminant (A) and yellow/black luminance (B) 1 c/deg gratings moving at temporal frequencies from 1 to 16 Hz. Other details are the same as those given for Fig. 1. Observer MH. The slopes of the regressions are summarized in (C). For achromatic gratings (■) the slopes are close to zero for all temporal frequencies indicating a very weak dependency of perceived velocity on contrast. For slowly moving red–green isoluminant gratings (□) there is relatively steep slope at low temporal frequencies which becomes flatter at temporal frequencies at or above 4 Hz.

luminance condition. The transition between 2 and 4 Hz is very sharp.

Close inspection of the data for the 1 and 2 Hz conditions in Fig. 3(A) suggests that the actual slope is even steeper than the regression when values of contrast lower than the standard are considered in isolation. This is mainly evident for the isoluminant conditions. At contrast levels greater than the standard there tends to be some saturation, as indicated by a shallower slope.

For red–green isoluminant gratings the threshold for detection is lower than the threshold for identification of the direction of motion at low temporal frequencies (Metha et al., 1994; Gegenfurtner & Hawken, 1995; Stromeyer et al., 1995). In the present experiments the contrasts of the isoluminant gratings were clearly above threshold for direction of motion, therefore the results

cannot be attributed to a failure to identify the motion direction per se but rather an inability to match the rate of temporal modulation.

Luminance and isoluminant plaids

We tested whether the perceived velocity of isoluminant and luminance plaid patterns is dependent on contrast across the same range of velocities that were used for the grating experiments. The plaid components were always of equal spatio-temporal frequency and contrast (type I), so that the resultant pattern is always perceived as rigid and coherent moving leftward or rightward. Figure 4 shows data for two observers over a range of component temporal frequencies from 0.5 to 16 Hz. For the luminance plaid the contrast of the components making up the standard was 4%. As was seen for the luminance gratings there was little effect of contrast at 4 Hz or above, and there was a small effect (relative slowing) at low temporal frequencies for the two lowest contrasts [Fig. 4(B, D)]. Isoluminant plaids were dependent on contrast in a manner predicted by the perceived velocity of their component gratings [Fig. 4(A, C)]. Another feature of the results was that observer MH showed a saturation at contrasts above the standard while KG tended to be more linear across the whole range of comparison contrasts. Marked individual differences in direction biases for isoluminant plaids are quite common (Kooi & DeValois, 1992) and the difference in tendency to saturate at higher values of isoluminant contrasts that we found for our two subjects may be within the range of individual variation.

Drift-balanced targets

Recently, Chubb and Sperling (1988) described a motion mechanism sensitive to targets with only second-order motion information. One form of Chubb and Sperling's second-order or non-Fourier stimulus is called amplitude-modulated; a field of spatially random black and white dots whose amplitude is modulated between 0 and 1 by a moving envelope. In our experiments we used a square-wave envelope with a spatial frequency of 1 c/deg. The other details were exactly the same as for the one-dimensional grating stimuli. When the temporal frequencies of the envelope was low (1–2 Hz) then there was a significant contrast effect on relative perceived velocity [Fig. 5(A, B) solid symbols]. At 4 Hz there was still a small positive relative velocity gain for subject MH. By 8 Hz, the highest velocity for which either observer could do the task, there was almost no effect of contrast on perceived velocity. Figure 5(C) summarizes the results: the form of the relative velocity gain as a function of contrast was remarkably similar to the isoluminant grating and plaid results.

Velocity vs temporal frequency

All the above experiments were done at a spatial frequency of 1 c/deg, mostly to avoid potential artifacts caused by chromatic aberration with isoluminant stimuli of higher spatial frequencies (Thibos et al., 1990;
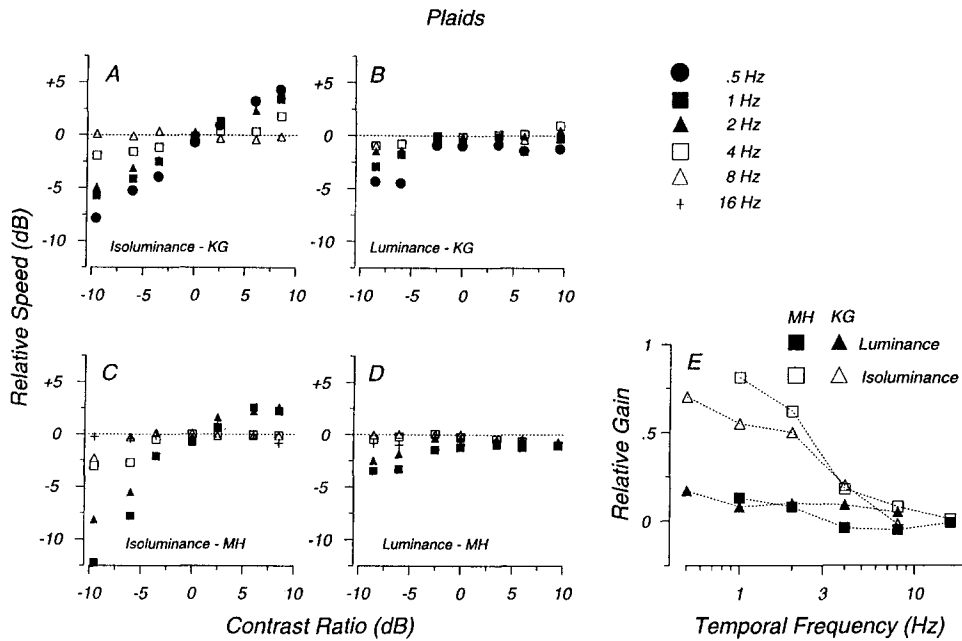
FIGURE 4. The effects of contrast on the perceived velocity of red–green isoluminant (A, C) plaids and of luminance plaids (B, D) for two observers [KG (A, B) and MH (C, D)]. Six standard temporal frequencies between 0.5 and 16 Hz were tested. For luminance plaids there is only a small effect of contrast, just as there was for one-dimensional gratings; velocity judgments are almost contrast invariant. On the other hand for red–green isoluminant gratings there is a very pronounced effect of contrast on velocity judgments at the lowest temporal frequencies. Spatial frequency 1 c/deg; modulation around a yellow background as in Fig. 3. Plaid components were at 45 and 315 deg so that the coherent plaid appeared to move horizontally. (E) Summary of results showing relative velocity gain derived from the slope of the regressions fitted to the data in (A)–(D) plotted against temporal frequency.

Cavanagh & Anstis, 1991). Only temporal frequency was varied in these experiments. We wished to determine whether the relative velocity gain showed the same slope when the velocity of the standard was kept constant at 4 deg/sec but was produced by different spatial and temporal frequency combinations. Stone and Thompson (1992) found little effect on the relative velocity gain when they varied temporal frequency by a factor of nearly 3 while keeping velocity approximately constant. However, their experiments used temporal frequencies from about 3 to 8 Hz, which is the range of temporal frequencies where the effect of contrast on perceived velocity is relatively small. We kept the velocity constant at 4 deg/sec but used two temporal frequencies, 1 and 4 Hz, which is a range that showed more pronounced differences in slope in our experiments.

We determined the effects of co-varying the spatial and temporal frequency to keep the velocity constant. The standard contrast was 12% for all conditions while the comparison contrast was varied between 3 and 50%. All the experiments were conducted with one-dimensional luminance gratings. Figure 6 shows the results for two observers. On the left [Fig. 6(A, C)] are the velocity gain functions where the velocity of 4 deg/sec was produced by gratings with a spatial frequency of 1 c/deg drifting at 4 Hz. As seen earlier, perceived velocity becomes contrast invariant under these conditions. On the right [Fig. 6(B, D)] we show the velocity gain functions for the same velocity, but this time generated by drifting a 0.25 c/deg grating at 1 Hz. We observe that there is a

contrast dependence and that the slope is even steeper than with 1 c/deg and 1Hz gratings (Fig. 1). Therefore velocity cannot be the sole factor determining the velocity gain—spatial and temporal frequency clearly interact to have an effect. Both lower spatial and lower temporal frequencies seem to cause higher velocity gains, but for a comprehensive assessment of the relationship it will be necessary to examine the whole spatio-temporal response surface.

DISCUSSION

In velocity matching experiments Thompson (1982) showed that the perceived velocity of a comparison stimulus depends on its contrast relative to the test stimulus at low temporal frequencies but not at high temporal frequencies. In our present study we extended the range of stimulus conditions to include one-dimensional gratings and two-dimensional plaids modulated in chromaticity along a red–green axis in the isoluminant plane and to amplitude-modulated, drift-balanced stimuli. The experiments were designed to determine whether motion in chromatic and non-Fourier targets is processed in the same manner as luminance motion over a range of temporal frequencies. We found that at low temporal frequencies the effect of contrast on perceived velocity was much more pronounced for chromatically modulated stimuli and for non-Fourier stimuli than for luminance-defined Fourier stimuli. At higher temporal frequencies all classes of stimuli tended to behave in a similar
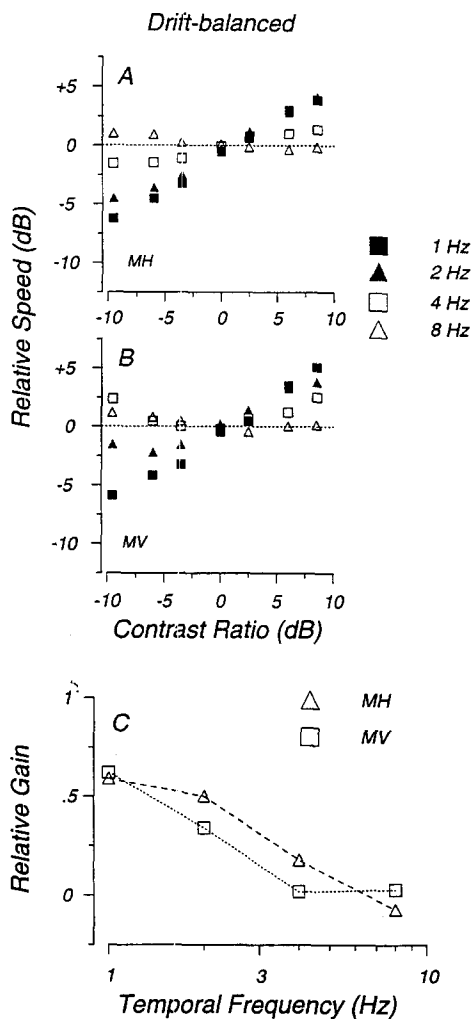
FIGURE 5. (A, B) The effect of contrast on the perceived velocity for drift-balanced targets. The standard stimulus was always of a fixed contrast (25%) and moved at a constant velocity. In this figure the results of experiments with four standard velocities are shown. When the velocity is low, 1 or 2 Hz, there is a substantial effect of contrast, both above and below the standard contrast. As the velocity of the standard is increased then the effect of contrast diminishes until between 2 and 4 Hz there is no effect of contrast. (C) Relative gain as a function of temporal frequency for the two observers, which summarizes the slopes of the regressions to the data in (A) and (B).

manner, and perceived velocity judgments were invariant with contrast.

In order to account for the differences in velocity gain as a function of temporal frequency, we proposed that there was a single pathway that handled motion processing of luminance and chromatic targets at high temporal frequencies and separate pathways for luminance and chromatic stimuli at low temporal frequencies (Hawken et al., 1994). The current results reinforce the notion that there is a single pathway for motion processing at moderate to high temporal frequencies. In previous experiments we showed that one-dimensional chromatic gratings and luminance gratings moving at temporal frequencies of 4 Hz or greater have almost flat velocity gain functions. In this study we have shown that two-dimensional isoluminant plaids and non-Fourier stimuli also show relatively flat velocity gain functions

when moving at high temporal frequencies. At low velocities we showed that chromatic gratings and plaids as well as non-Fourier stimuli have higher velocity gains than luminance gratings and plaids. Therefore, more than one pathway is required to account for the processing of all types of slow-moving targets.

Mechanisms for motion processing

The main question that we have addressed in this study is whether it is necessary to invoke separate mechanisms for processing of different types of motion stimuli, i.e. luminance, chromatic and non-Fourier. There seems to be general agreement that there are at least two broadly tuned, temporal frequency channels that provide the low-level input to the luminance motion pathway (Anderson & Burr, 1985; Hess & Snowden, 1992). And, although it is generally agreed that local motion processing is accomplished via a set of spatio-temporal energy filters (Adelson & Bergen, 1985; Watson & Ahumada, 1985; van Santen & Sperling, 1985) the nature of the process encoding image velocity is not so well established (Heeger, 1987; Smith & Edgar, 1994). It is quite clear that velocity perception is carried out by a distributed system, because there is little evidence that there are detectors tuned specifically to stimulus velocity.

Next, we consider whether the mechanisms that are responsible for encoding the direction and speed of luminance stimuli could also provide a signal that is adequate to account for the velocity judgments of color and non-Fourier stimuli. It seems likely that fast moving, relatively low spatial frequency luminance stimuli are signaled by the local motion energy mechanism. There is some recent evidence that indicates that non-Fourier stimuli are processed in a similar manner to Fourier gratings at 4 Hz and above (Smith et al., 1994). Fourier and non-Fourier components tend to cohere to form a plaid when the temporal frequency is around 3 Hz (Stoner & Albright, 1992) supporting the idea that there is a common motion mechanism (Chubb & Sperling, 1988; Wilson & Kim, 1994). Our findings that perceived velocity judgments for non-Fourier targets with the modulator drifting at 4 or 8 Hz are contrast invariant (Fig. 5) and have the same velocity gain as first-order luminance and chromatic targets gives further weight to the idea of a common motion mechanism. In the chromatic domain there is evidence that thresholds for detection and identification of the direction of moving gratings are identical at high temporal frequencies (Gegenfurtner & Hawken, 1995). Furthermore the observation that the chromatic contours for detection and direction of motion are almost identical at high temporal frequencies (Gegenfurtner & Hawken, 1995) is additional evidence that supports the idea of a common, magnocellularly dominated, mechanism for detection and identification of direction of motion. Chichilnisky, Heeger and Wandell (1993) similarly found that a single univariate mechanism could account for their results in a motion nulling task. In our current work at temporal frequencies of 4 Hz and above, chromatically modulated
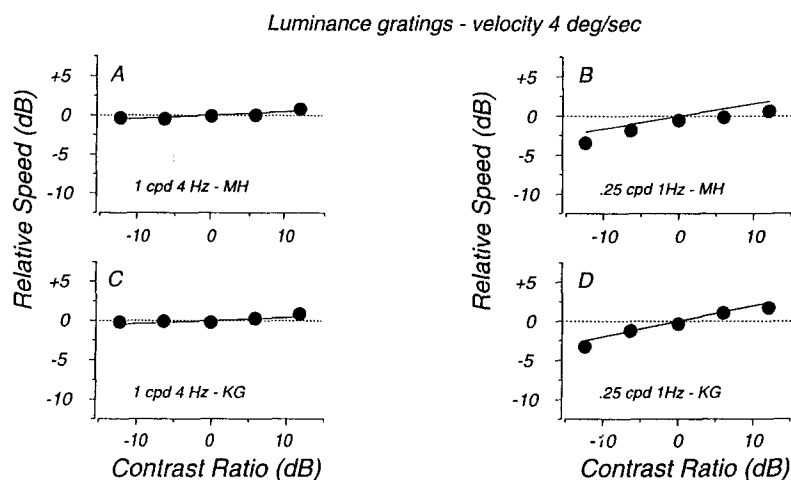
Luminance gratings - velocity 4 deg/sec

FIGURE 6. The effect of contrast on perceived velocity when the standard is moving at 4 deg/sec. Although the velocity is constant the spatial and temporal frequencies are different by a factor of 4 in the two columns. Contrast dependence is a function of both the spatial and temporal frequency of the grating and not just of the velocity.

one-dimensional gratings (Figs 2 and 3) and plaids (Fig. 4) produce similar performance to that seen with luminance gratings and plaids, indicating a common mechanism operating for luminance and color. In an earlier series of experiments we measured the latency and initial acceleration of pursuit eye movements for luminance and isoluminant red–green chromatic targets moving at relatively fast velocities (Hawken et al., 1991). There was very little difference in the initial acceleration and visual latency between these two stimulus conditions supporting the notion of a common, low-level motion mechanism for luminance and color. The mechanism provides signals for perceptual judgments of velocity and relays signals to the oculomotor system for control of eye movements. Our view is that the present evidence argues for a single mechanism in the mid to high range of velocities, which offers a veridical estimate of velocity and is relatively invariant to changes in contrast, chromaticity or spatial form (Albright, 1992).

At low velocities, an argument in favor of a single channel comes from studies that show a significant motion aftereffect for chromatic gratings can be induced by either luminance or chromatic adaptation (Cavanagh & Favreau, 1985; Derrington & Badcock, 1985). Derrington and Badcock have argued that "it is difficult to see how cross-adaptation between motion and colour could occur unless both are processed by the same system". But at low velocities there seem to be additional processes operating. We recently proposed that two mechanisms were required to account for the substantial differences in contrast dependency for color and achromatic targets; one sensitive to chromatic motion at low velocities and the other sensitive to achromatic motion. Cavanagh et al. (1984) put forward the proposal that "the perceived velocity is derived from a weighted sum of the separate color and luminance analyses of the stimulus, the analysis of color signaling a much lower velocity". If we assume that their proposal relates only to low velocities, then two minor modifications of their proposal

will account for many of the results at low velocities. We will concentrate on chromatic targets in the next part of the discussion and then incorporate non-Fourier targets in the following section.

At low chromatic contrast, observers can detect an isoluminant target but not identify its direction of motion (Lindsey & Teller, 1990; Cavanagh & Anstis, 1991; Palmer et al., 1993; Metha et al., 1994; Gegenfurtner & Hawken, 1995; Stromeyer et al., 1995). At the lowest chromatic contrasts in our experiments, even though the observers could reliably determine the motion direction, they consistently judged the velocity of the low contrast chromatic gratings to be much lower than the higher contrast chromatic standard (Figs 1, 3 and 5). Consider three independent mechanisms operating. One that is a chromatic detection mechanism, which does not give a motion signal. The second mechanism is motion sensitive to chromatic contrasts above threshold for direction of motion and is akin to the long-range motion mechanism (Braddick, 1980; Cavanagh & Mather, 1989). The third is the conventional short-range motion sensitive mechanism which is sensitive to luminance contrast and to higher levels of chromatic contrast. The observer's judgment is made on the basis of a weighted combination of the signals provided by these mechanisms. Low color contrasts at or just above threshold for direction of motion give rise to two sets of signals that are inconsistent, one set of signals is provided by the non-directional chromatic detection mechanism and the other set of signals is for a moving object provided by the long-range motion mechanism. The perception of a slowly moving target is derived from the weighted interaction between these two mechanisms. At high chromatic contrasts the conventional short-range motion mechanism begins to respond. As chromatic contrast increases, the perceived velocity is determined by the weights provided to three mechanisms and a combination rule. The lower velocity gain for the low velocity standards at the highest chromatic contrasts seen in Figs 1, 3 and 4 is

consistent with the proposal that the conventional short-range motion mechanism begins to give significant weight at higher chromatic contrasts. Individual differences in gain and local slope might be due to different weights that are given to the various signals. The idea here is akin to cue combination where several cues give rise to signals for the same percept, such as in depth judgments (Landy et al., 1995).

The contrast dependency of slow moving non-Fourier stimuli (Fig. 5) is much like the contrast dependency shown by isoluminant gratings and plaids (Figs 1, 3 and 4). Therefore our initial supposition that non-Fourier stimuli would be processed by the same motion mechanism as first-order patterns is not correct. The most likely hypothesis is that slow moving non-Fourier stimuli are processed by a long-range mechanism which is separate from the conventional luminance motion mechanism (Cavanagh & Mather, 1989). Victor and Conte (1992) showed that at low velocities plaids made of Fourier and non-Fourier grating components never cohere. They suggested that there must be a high level interpretation. There seems to be little residual sensitivity of the luminance sensitive mechanism to our non-Fourier motion targets as there is little or no evidence of saturation of the velocity–contrast functions (Fig. 5) even at the highest contrasts.

Pathways

There are two principal proposals put forward to account for the color input to motion. One is that the motion pathway is not color blind and receives a weak chromatic input (Cavanagh et al., 1984; Cavanagh & Favreau, 1985; Troscianko & Fahle, 1988; Kooi & DeValois, 1992). The second proposal suggests that the color pathway possesses motion sensitivity that is independent of the luminance-based motion system (Derrington & Badcock, 1985; Krauskopf & Farell, 1990). Human subjects will attend to whatever signals that are available to them, hence when the velocity of either one- or two-dimensional targets is intermediate between the sensitivity of two mechanisms, as might be the case for a 3 deg/sec stimuli, then the decision will be based on the relative strengths of the conflicting cues.

For moderate to fast moving targets the current evidence suggests a common motion mechanism that is sensitive to both luminance, chromatic and non-Fourier stimuli in both one and two dimensions. Gegenfurtner et al., (1994) determined that single cells in macaque monkey area MT were relatively more sensitive to isoluminant gratings at high temporal frequencies than at low temporal frequencies, in addition to their sensitivity for achromatic targets. A pathway that includes magno-cellular neurons, cells in layers 4B and 6 of V1 and direction selective cells in MT is most likely to underlie at least part of the neural substrate for motion perception of moderate to fast movement. Lesion studies in the macaque monkey tend to support the idea that the magnocellular pathway is primarily concerned with low spatial frequency, high temporal frequency components

at low and intermediate levels of contrast (Merigan & Maunsell, 1990; Merigan et al., 1991a).

At present the neural substrate which provides a motion signal for slow moving chromatic targets at low contrasts is not known. It is likely that the signals are initially relayed via the parvocellular input to the cortex (Merigan et al., 1991b) but the neurons that provide the motion signal have not been identified. Gegenfurtner et al. (1994) showed that at low velocities the sensitivity of MT cells for isoluminant gratings is about five times lower than required to support perceptual motion sensitivity for isoluminant gratings of the behaving monkey observer. Thus residual sensitivity of MT cells to isoluminant stimuli is unlikely to account for the behavioral results. There is evidence that there is a motion signal for non-Fourier stimuli among the cells of MT (Albright, 1992) and preliminary evidence that the motion signal for non-Fourier targets appears as early as V1 (Albright & Chaudhuri, 1989). If the signal for low temporal frequency non-Fourier motion stimuli is due to a long-range motion process (Braddick, 1980) it may not be associated with single direction selective neurons in V1, but rely on the combined responses over a spatially distributed population.

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