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Human Speed Perception is Contrast Dependent

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When two parallel gratings moving at the same speed are presented simultaneously, the lower-contrast grating appears slower. This misperception is evident across a wide range of contrasts (2.5–50%) and does not appear to saturate (e.g. a 50% contrast grating appears slower than a 70% contrast grating moving at the same speed). On average, a 70% contrast grating must be slowed by 35% to match a 10% contrast grating moving at 2°/sec ($N = 6$). Furthermore, the effect is largely independent of the absolute contrast level and is a quasilinear function of log contrast ratio. A preliminary parametric study shows that, although spatial frequency has little effect, relative orientation is important. Finally, the misperception of relative speed appears lessened when the stimuli to be matched are presented sequentially.

Motion perception Speed discrimination Direction discrimination Contrast Motion energy Gratings Plaids

INTRODUCTION

The coding of speed and direction within the visual system has long been a focus of research for visual neuroscientists. Impressive progress has been made in our understanding of direction coding, but speed coding remains largely a mystery. The generally accepted picture is as follows. Direction information is retained using a place code with the direction of stimulus motion given by *which* cell is firing most vigorously within an ensemble of neurons. Each neuron acts as a detector labeled for a particular direction of motion within a spatial map of all possible directions. This is strongly supported by the finding of an organized array of direction columns within the middle temporal cortex (MT), an area of monkey visual cortex known to be involved in motion perception (Albright, Desimone & Gross, 1984; Newsome, Wurtz, Dursteler & Mikami, 1985; Newsome, Britten & Movshon, 1989; Salzman, Britten & Newsome, 1990). Since no such spatial organization has ever been found for speed-tuning, one possibility is that speed information is encoded by the neuronal firing rate. However, because the firing rate of individual visual cortical neurons is not uniquely related to speed (for a review, see Maunsell & Newsome, 1987), stimulus speed would have to be encoded by the collective firing rate of an ensemble of neurons. The details of such a scheme, however, have yet to be worked out.

Physiological studies have shown that the response of most neurons within the visual cortex increases monotonically with increasing stimulus contrast (e.g. Albrecht & Hamilton, 1982; Sclar, Maunsell & Lennie, 1990). This contrast response is not a problem for a direction-coding scheme that uses the peak response within a population of neurons to determine direction, as long as the neurons have similar contrast sensitivities. However, contrast variations present a significant obstacle to any speed-coding scheme that uses neuronal firing rate to encode speed information. Any such scheme must include a mechanism to disambiguate speed and contrast information.

The basic problem of how to distinguish neuronal responses related to contrast from those related to speed has been a major concern of both physiologists and modelers. Various elegant mechanisms have been proposed by which this could be achieved (e.g. Watson & Ahumada, 1985; Adelson & Bergen, 1986; Heeger, 1987; Grzywacz & Yuille, 1990). However, an early study of the effect of contrast on the perceived speed of moving gratings showed that perceived speed is in fact affected by contrast. Using the method of adjustment and magnitude estimation, Thompson (1982) found that, at least below 8 Hz, a lower-contrast grating appears to move more slowly than a higher-contrast grating moving at the same speed. Unfortunately, he only examined a limited range of contrasts (at and below 17.8%). In apparent conflict with this result, a study of grating-speed discrimination found no effect of random trial-by-trial variations (from 5 to 82%) in contrast (McKee, Silverman & Nakayama, 1986). This second result suggested that speed is veridically coded and cleanly disambiguated from contrast variations. The issue was revived by a recent finding that the direction of a moving plaid (the sum of two sinusoidal gratings of different orientation)

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whose components have different contrasts is biased by up to 20° in the direction of motion of the higher-contrast component (Stone, Watson & Mulligan, 1990b). This bias can be explained if component speed is misperceived as predicted by Thompson (1982). To reconcile these discrepancies, we reexamined the effect of contrast on the perceived speed of moving gratings over a wide range of contrasts using a two-alternative forced-choice paradigm. Preliminary reports have appeared elsewhere (Stone, Thompson & Watson, 1990a; Thompson & Stone, 1990).

GENERAL METHODS

Experimental paradigms

Subjects were asked to perform two types of psychophysical judgments: speed-matching and direction-discrimination. In the first task, we measured the perceived relative speed of two grating patches of identical spatial frequency but of different contrast. In the second task, we measured the perceived direction of a moving plaid (the sum of two sinusoidal gratings of different orientation) whose component gratings were of identical spatial frequency but different contrasts.

We used 8 observers (6 of whom were naive with respect to the purpose of the experiment) aged between 16 and 40. Subjects viewed the screen binocularly through natural pupils from a distance of 273 cm. The image subtended 5.4 × 5.4° (20 pixels/cm). The mean luminance of the image was 75 cd/m^2.

Data analysis

The staircase method yielded typical psychometric curves (Fig. 1). We fit the data for each condition (24 trials per staircase with 2 interleaved staircases per condition) with a cumulative Gaussian using a weighted least-squares procedure (Mulligan & MacLeod, 1988) based on Probit analysis (Finney, 1971). For the speed-matching task, the location of the inflection point represents a bias which we refer to as the *speed match* (the test grating speed that is perceived equal to that of the standard) expressed as a percentage of the standard speed. We define the *speed error* as the percent error of the speed match compared to the standard speed. The standard deviation of the best fitting cumulative Gaussian is a measure of the precision in the observer's judgments. We use this fact to plot *speed uncertainty*, calculated by taking the ratio of the standard deviation of the psychometric curve to the speed of the standard and dividing it by $\sqrt{2}$ because we assume that the test and standard contribute equally to the variance. For the direction-discrimination task, the location of the inflection point (bias) is the direction of plaid motion that is perceived as straight upward. This bias, obtained by manipulating the speed ratio, is the exact negative of the *direction error* perceived when the plaid is actually moving straight upward, assuming that the direction error is indeed caused by an underlying inequality in the perceived component speeds (Stone *et al.*, 1990b).

Stimulus generation

We generated the drifting grating patches and plaids on a Mitsubishi 19-in. high-resolution monochrome monitor (model M-6950) using an Adage RDS 3000 image display system. The luminance output of the monitor was linearized using a lookup table procedure described elsewhere (Watson, Nielsen, Poirson, Fitzhugh, Bilson, Nguyen & Ahumada, 1986). A 10-bit "color" lookup table and 10-bit DACs provided approx. 9 bits of gray-scale resolution after the linearization process. With our animation technique, this allowed a contrast resolution of better than 0.5%. A detailed analysis of our animation procedure can be found in Mulligan and Stone (1989) and the procedure has been used previously to generate moving plaids (Stone *et al.*, 1990b).

Briefly, the stimulus was a 512 × 512 pixel image created using both locally developed programs and the HIPS image-processing software package (Landy, Cohen & Sperling, 1984). In some experiments (for all plaids and gratings with 20 and 40% test contrasts), four 2-D sinusoidal gratings were generated (sine- and cosine-phase components for each grating patch). These four images were multiplied by a two-dimensional Gaussian to provide windowing without sharp edges. The images were then halftoned using a modified error-diffusion method (Floyd & Steinberg, 1975; Mulligan, 1986). The resulting four bit-mapped images were loaded into the four lower-order bit-planes of the 8-bit framebuffer. A 3 × 3 pixel white fixation cross was drawn into a fifth bit-plane in the center of the image. The remaining three bit-planes were blank. The image could be loaded into the framebuffer within a few seconds. Then, by varying the lookup table on a frame by frame basis (at 60 Hz), we modulated the contrast of the sine- and cosine-phase components of each grating in temporal quadrature so that they appeared as a single drifting grating. Using this method, we had complete control over the speed and contrast of both gratings without having to load new images into the framebuffer. Furthermore, the initial spatial phase of each grating was randomized so that position cues would be difficult to use to assess motion. A different base image was necessary for each spatial-frequency and relative orientation.

In some experiments (70% test contrast), we used a modified procedure for two reasons: because, at high contrast, halftoning at 1 bit/pixel produces visible noise and because the method described above does not allow the generation of a total contrast (sum of both grating contrasts) above 71%. To reduce the halftoning noise and increase contrast resolution, we halftoned each individual grating image down to 2 bits/pixel using the same error-diffusion algorithm. To increase the maximum attainable contrast, we constructed two half-images so that each could be as high as 71%. Two 4-bit half-images (256 × 512) were generated each containing two 2-bit halftoned sine- and cosine-phase components of a grating patch. The two upper and lower half-images were combined to generate a 512 × 512 image. A 1-bit mask was put into the fifth bit-plane of one half of the image to allow separate animation of the upper and lower patches. A fixation cross was put into the sixth plane at the center of the image. Animation was again achieved by modifying the lookup table on a frame-by-frame basis. The principles behind these modifications are described in detail in Mulligan and Stone (1989).

Control for size and duration

All stimulus intervals were 500 msec. The contrast rose with a Gaussian time–course reaching full contrast after 50 msec, stayed at full contrast for 400 msec, then fell with the same Gaussian time–course over the final 50 msec. Because the spatial and temporal windowing ties changes in stimulus contrast to changes in perceived stimulus size and duration, we repeated some of the experiments in two subjects (including one naive) using sharp circular spatial windows and sharp temporal onset and offset. The results were qualitatively unchanged. The contrast manipulations *per se* and not the concomitant small changes in size and duration were responsible for the speed-matching errors of these two subjects. Therefore, it is unlikely that the effects described for the other subjects and for the other experiments are due to the apparent size or duration changes associated with our contrast manipulations.

RESULTS

Experiment 1: Contrast-Induced Misperception in Relative Speed

Methods

In this first set of experiments (Figs 1–5), we measured the perceived relative speed of two *simultaneously* presented horizontally oriented drifting gratings. The stimulus consisted of two horizontally elongated, Gaussian-windowed grating patches centered either 1.3° above or below the fixation cross at the center of the image. For the 70% test-contrast experiments, the x and y standard deviations of the Gaussian window were 0.71 and 0.36°, respectively. For 20 and 40% test-contrast experiments, the x and y standard deviations were 0.95 and 0.48°. Subjects were presented with a single stimulus interval during which both gratings drifted upward. They were asked to ignore contrast, to fixate the center cross, and to determine in a two-alternative forced-choice which of the two (top or bottom) gratings appeared faster. The standard moved at 2°/sec (1.5 c/deg at 3 Hz) except in the parametric study presented in Fig. 5. The speed of the test was changed by varying temporal frequency within two interleaved up–down staircases. The test was randomly located in either the upper or lower position.

Results

When two drifting grating patches are presented one above the other, the lower-contrast grating appears to move more slowly than an otherwise identical higher-contrast grating moving at the same actual speed. Figure 1 plots typical raw psychometric curves for one subject under three different stimulus conditions. The center curve was generated in response to stimulus presentations in which both gratings were 70% contrast (solid squares). The leftmost curve was generated with a 70% contrast test grating and a 10% standard grating (open squares). The rightmost curve was generated with a 10% test grating and a 70% standard grating (open circles). In all three cases, the standard moved at 2°/sec. Note that when the contrasts were identical, the subject made veridical matches with the point of subjective equality (inflection point) being at 1.97°/sec yielding a speed match of 98.5% or a speed error of 1.5%. However, when the contrast of the test was higher (leftmost curve), the inflection point was at 1.71°/sec (85.5% speed match, 14.5% error). Conversely, when the contrast of the test was lower (rightmost curve), the inflection point was at 2.34°/sec (117% speed match, 17% error).

Contrast produced a consistent effect on the speed-matching performance of five out of the six subjects tested with simultaneously presented pairs of moving parallel gratings. Figure 2 plots the speed match for the six subjects as a function of the contrast ratio in dB (20 $\log_{10}$ of the ratio of the standard contrast to the test contrast). For the four leftmost points, the test grating was 70% contrast and the standards were 10, 30, 50, and 70% contrast, starting from the left. When the standard had 10% contrast, the test needed to be slowed by as much as 45% to appear to drift at the same rate as the standard. Furthermore, the upward arrows indicate that, for all but one subject, the 70% test needed to be slowed even to match the 50% contrast standard with the perceived speed difference significant for four subjects ($P < 0.05$ in one-tailed t-test). This result suggests that the effect occurs over the entire range of contrasts. When the standard and test were both 70%, all six subjects made veridical matches. For the rightmost point, the test was 10% and the standard was 70% contrast. In this case,

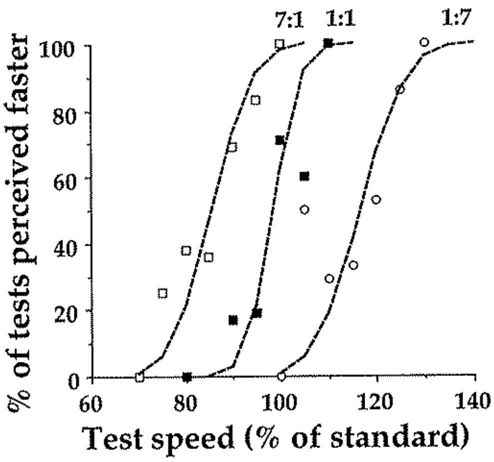

FIGURE 1. Raw psychometric curves for one subject at three contrast ratios. The data are plotted as the percent of trials in which the test grating was perceived faster than a 2°/sec standard as a function of the actual speed of the test for three different contrast ratios. All gratings were 1.5 c/deg unless otherwise stated. The dashed lines are integrals of Gaussians fitted using Probit analysis, a weighted least-square method that weights each point according to the number of trials at the test speed and according to the binomial distribution of the underlying probability.

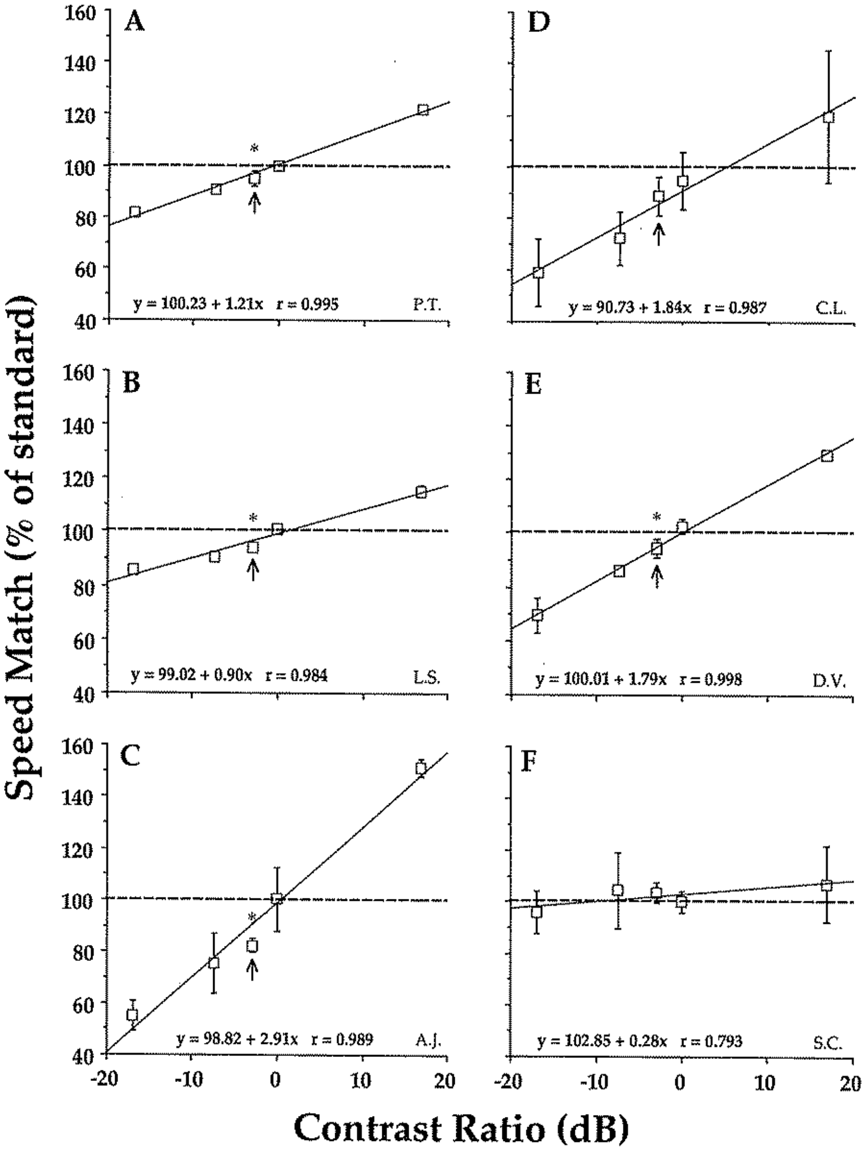

FIGURE 2. Speed matches for six subjects tested with 70 and 10% contrast tests. The mean inflection points of the fitted Gaussians (see Fig. 1) are plotted as a function of the contrast ratio. Error bars are standard deviations over three or four sessions. The dashed line represents veridical matching. The asterisks indicate that four subjects made significant mismatches ($P < 0.05$; one-tailed t-test) when the 70% contrast test was matched to the 50% contrast standard. The solid lines, whose equations appear at the bottom of each panel, were fit to the data using simple linear regression. For each of five subjects, the linear trend was highly significant (one-way ANOVA, $P < 0.001$) while for the remaining subject (SC), the linear trend was not significant (one-way ANOVA, $P > 0.05$).

the same five subjects matched speeds when the test was up to 51% faster than the standard. This indicates that the two symmetric methods for measuring the effect, slowing the higher contrast grating or speeding up the lower contrast grating, yielded similar results.

The effect on perceived speed appears quasilinear in log contrast. On average, the six subjects mismatched speed by 30% when matching 70 and 10% contrast gratings. Furthermore, the data in Fig. 2 are fit remarkably well by straight lines for all subjects (mean slope, 1.5% bias/dB; mean intercept, 98.6%; mean correlation coefficient, 0.958). Even for the one subject for whom the effect appears weak or non-existent (SC), the correct trend is still present (i.e. positive slope).

Speed discrimination, the ability to distinguish small differences in speed, is not systematically affected by contrast under the same conditions that produce matching-errors. Note that although the three curves in Fig. 1 are shifted with respect to each other, they have similar slopes. The speed uncertainties are 4.5, 7.0, and 7.5%, for the center, leftmost, and rightmost curves, respectively. Figure 3 plots speed uncertainty as a function of contrast ratio for the same six subjects and the same stimuli. Although for some subjects there was a slight tendency for higher uncertainty when the contrasts were more unequal, averaged over all subjects, there is only a weak linear trend between the precision of the match and the absolute value of log contrast ratio (slope, 0.18% increase in uncertainty per dB). Therefore, although subjects are consistently mismatching speed by up to 50% when the contrasts are different, they are doing so with similar levels of uncertainty regardless of the relative contrast.

Speed-matching errors were not affected by changing the absolute contrast level. Three subjects (one of whom

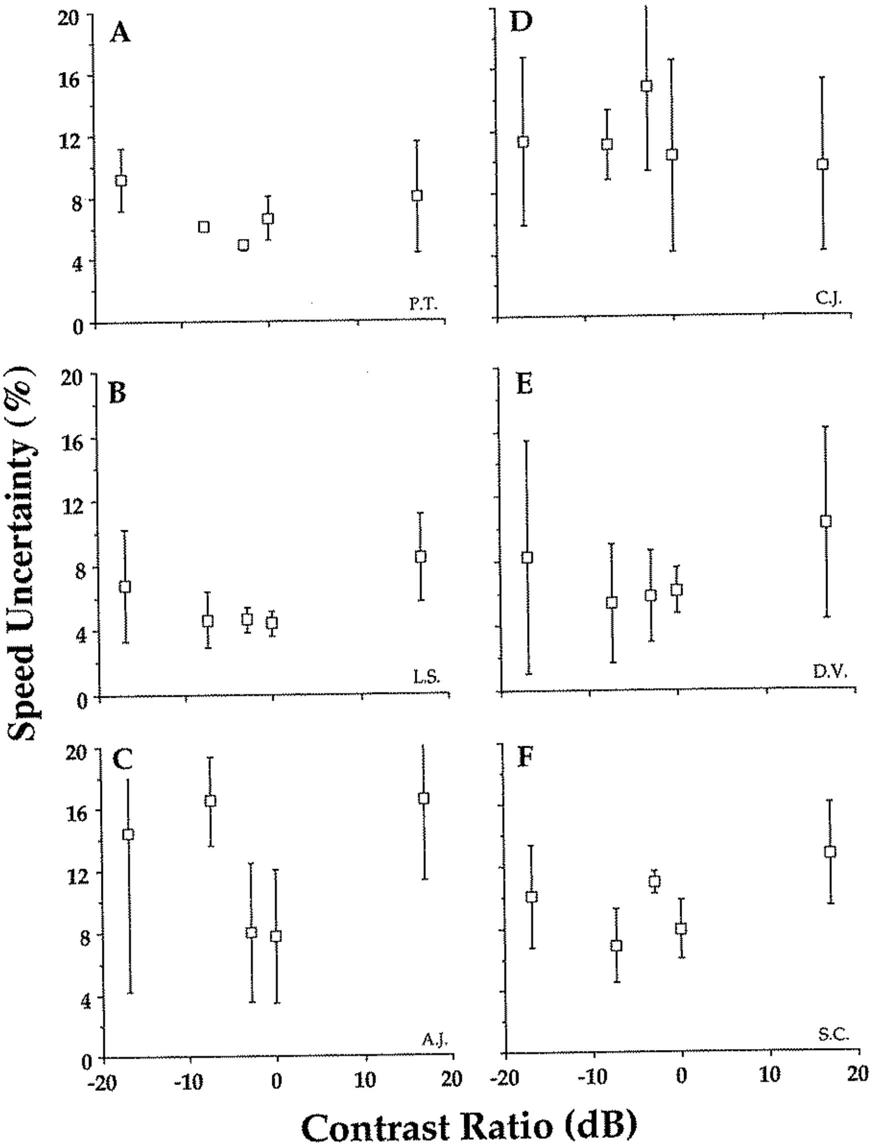

FIGURE 3. Speed discrimination for the same six subjects and the same task as in Fig. 2. Speed uncertainty was calculated by taking the ratio of the standard deviation of the fitted Gaussian to the standard speed and dividing it by $\sqrt{2}$ because the variance in performance is assumed to be the sum of two equal variances produced by the uncertainty in both the test and standard speeds. The mean uncertainty is plotted as a function of the contrast ratio. Error bars are standard deviations over three or four sessions. For only two of the subjects (PT and LS), there was a significant (one-way ANOVA, $P < 0.05$) linear trend between uncertainty and the absolute value of the log contrast ratio. However, averaged over all subjects, the linear trend was borderline significant ($P \approx 0.05$).

was naive) were tested with more than one test contrast. The lefthand panels of Fig. 4 plot results when 70, 40, and 20% contrast test gratings were slowed to match lower contrast gratings. Note that, for all three subjects, the data nearly superimpose. The righthand panels of Fig. 4 plot results when 10 and 2.5% contrast test gratings were increased in speed to match higher contrast gratings. For all three subjects, the speed-error data point for the 10% test is nearly identical to the corresponding points in the lefthand panels. However, at 2.5% test contrast, for all three subjects, the speed errors appear larger at a given contrast ratio than those in the lefthand panels. These data indicate that, at least for test contrasts at and above 10%, the contrast-induced speed-matching error is a function of the contrast ratio alone and is largely insensitive to differences in absolute contrast. At and below a 2.5% test contrast, the effect may be larger.

Speed-matching errors were not sensitive to small changes in temporal and spatial frequencies. The same subjects as in the previous figure were tested at two different spatial and temporal frequencies as well (Fig. 5). For all three subjects, the effect is remarkably similar for a 1.5 c/deg standard moving at 2°/sec (3 Hz) and for a 3 c/deg standard moving at 2.75°/sec (8.25 Hz). These data show that a 2-fold change in spatial frequency and a nearly 3-fold change in temporal frequency have little effect on the contrast-induced errors in perceived relative speed. Even higher temporal frequencies were tested with two subjects. One subject (PT) continued to show the contrast-induced errors even at 10 Hz (3 c/deg at 3.33°/sec) while a second subject (LS) could

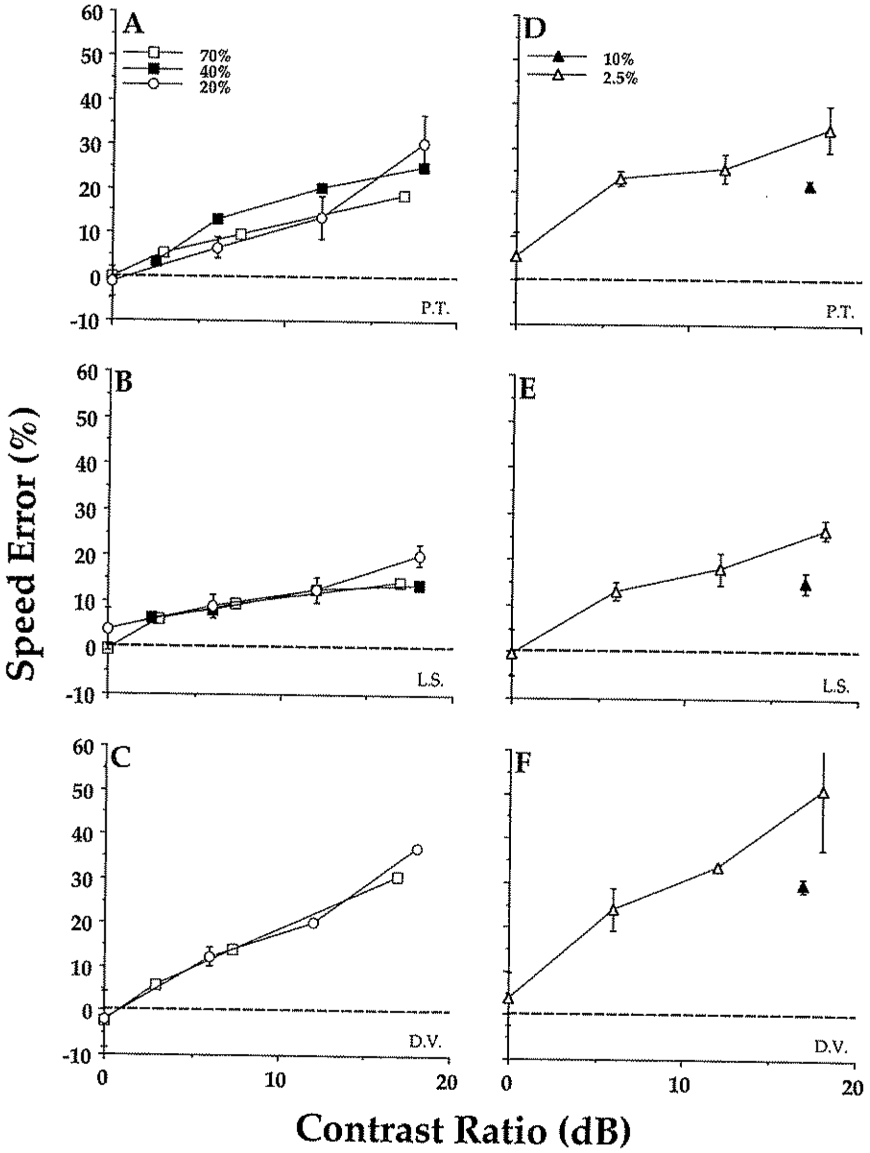

FIGURE 4. Contrast-induced speed errors are independent of absolute contrast. Mean speed error over three sessions is plotted as a function of the contrast ratio for high-contrast tests matched to lower contrast standards (A), (B) and (C) and for low-contrast tests matched to higher contrast standards (D), (E) and (F) for three subjects. The number next to each symbol in the legend indicates the contrast of the test. For clarity, standard deviations are only plotted for the 2.5, 10, and 20% contrast test conditions. The dashed line represents veridical matching. The 70 and 10% test data are replotted from the lefthand side of Fig. 2. The 40% test data were generated by matching to 5, 10, 20 and 30% contrast standards. The 20 and 2.5% test data were generated by matching to 2.5, 5, 10, and 20% contrast standards.

not perform the task above 8.25 Hz. In addition, these two subjects were tested at 8.25 Hz with two different test contrasts (35 and 70%). Just as in the previous figure at the lower temporal frequency, the effect was nearly identical at the two absolute contrast levels. Finally, very similar results were obtained for these same two subjects tested with 5 and 10% contrast tests sped up to match higher contrast 8.25 Hz standards (data not shown). Therefore, at least over the range tested, spatial and temporal frequency as well as absolute speed has little effect on the contrast-induced misperception of relative speed.

Experiment 2: Effect of Relative Orientation

Methods

In this second set of experiments, we made a preliminary assessment of the effect of relative orientation/direction on contrast-induced speed-matching errors (Fig. 6). The stimuli consisted of two gratings viewed through circularly symmetric Gaussian windows (SD 0.36°) located 1.3° above and below the fixation point. In one experiment [Fig. 6 and data used to generate the predictions in Fig. 7(A, B)], one grating was oriented horizontally and the other vertically (90° relative angle). In another experiment [data used to generate the predictions in Fig. 7(C, D)], one grating normal was oriented 60° to the right of vertical while the other was oriented 60° to the left (120° relative angle). In both of these experiments, which of the two orientations appeared in the upper and lower window was randomized (two possible spatial arrangements). Subjects were presented with a single interval during which both gratings drifted perpendicular to their orientation in a random direction:

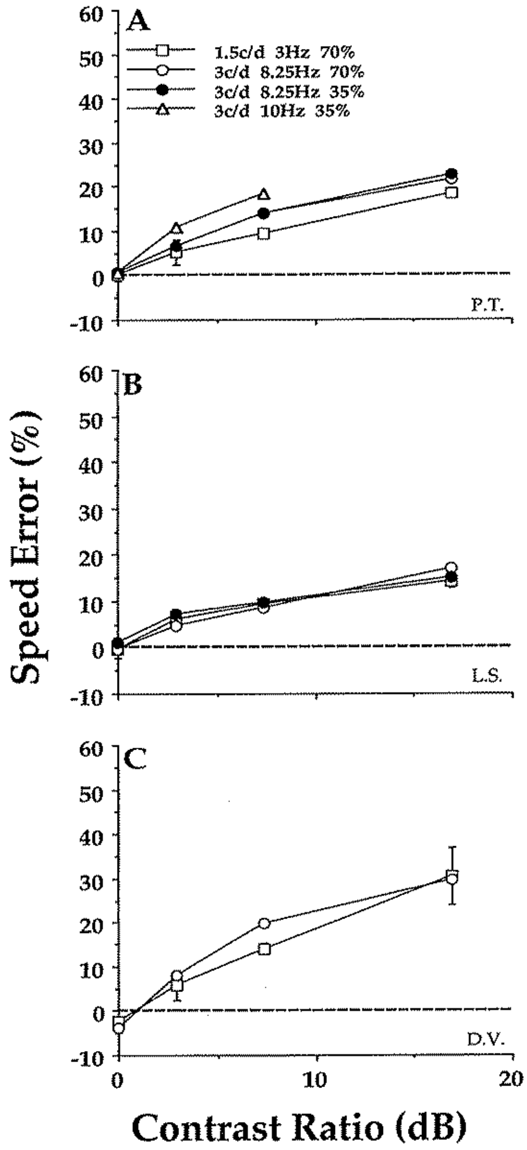

FIGURE 5. Contrast-induced speed errors are insensitive to small changes in temporal and spatial frequency. Mean speed error over three sessions is plotted as a function of the contrast ratio for different spatial/temporal frequencies and test contrasts for three subjects. The numbers next to each symbol indicate respectively the spatial frequency of the standard (and test), the temporal frequency of the standard, and the contrast of the test. The 70% contrast test was slowed to match 50, 30, and 10% contrast standards. The 35% was slowed to match 25, 15, and 5% contrast standards. For clarity, standard deviations are only plotted for the 1.5 c/deg condition. The dashed line represents veridical matching.

for the orthogonal gratings either left/right or up/down (four possible combinations per spatial arrangement) while for the gratings oriented 120° apart either both upward or both downward (two possible combinations per spatial arrangement). The standard patch (randomly either orientation and either location) moved at 2°/sec while the test-patch speed was determined by two interleaved up–down staircases. Subjects were asked to ignore all other factors (contrast, orientation, and direction), to fixate the center cross, and to determine in a two-alternative forced-choice which patch (top or bottom) moved faster. Only the 90° data are presented in Fig. 6. However, both the 90 and 120° data were used to generate the predictions in Fig. 7.

Results

The effect of contrast on perceived speed is sensitive to the relative orientation of the gratings. Figure 6 plots the results of the three subjects (including one naive) who were tested in conditions where the upper and lower gratings were orthogonal. The effect of contrast on perceived relative speed appears different from the case in which the gratings were parallel (see Figs 2 and 4). The effect showed greater inter-subject variability, evidence of saturation, and dependence on absolute contrast. For one subject (PT), the lower contrast gratings still appear slower although the effect was greater at lower absolute contrast. For a second subject (LS), the effect is nearly gone [compare open squares in Figs 4(B) and 6(B)] and speed matches are essentially veridical except at high contrast ratios and low absolute contrast. For the third subject (JC), the results are less clear. Saturation is

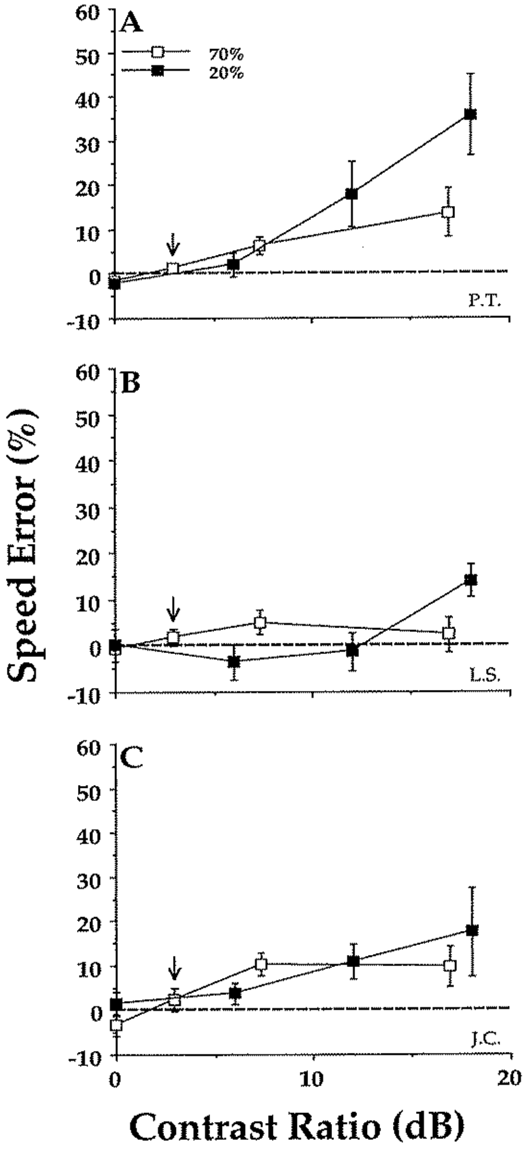

FIGURE 6. Contrast-induced speed errors for orthogonal gratings. Mean speed error is plotted as a function of the contrast ratio for two different contrasts using orthogonal gratings for three subjects. The number next to each symbol indicates the contrast of the test. Error bars are standard deviations over three sessions. The dashed line represents veridical matching.

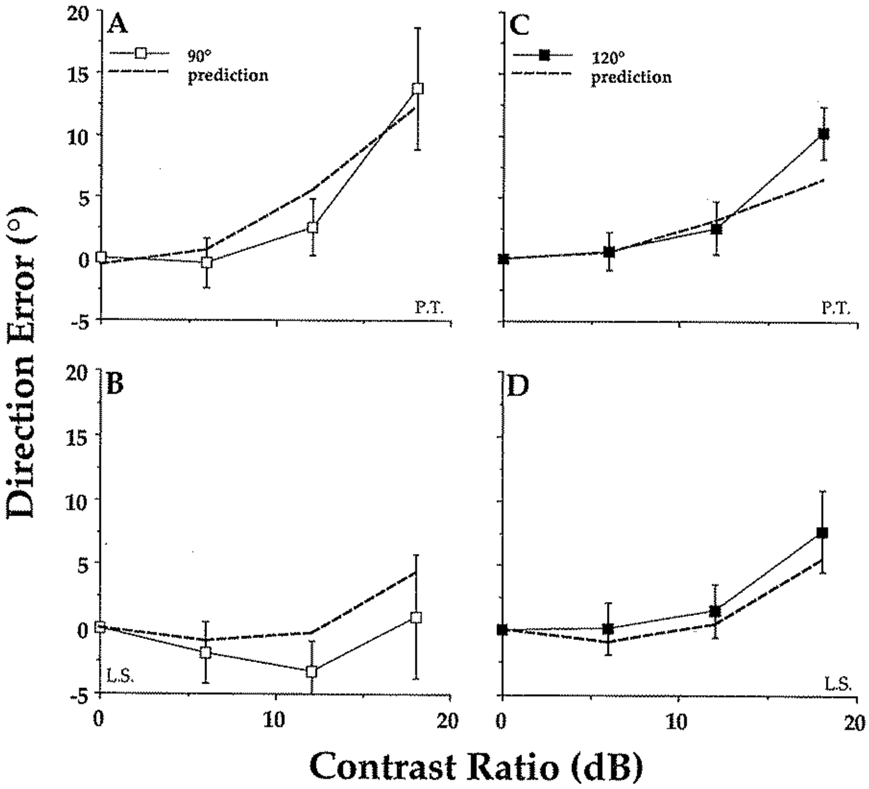

FIGURE 7. Contrast-induced grating-speed errors can explain contrast-induced plaid-direction errors. Mean plaid-direction errors (squares) over three sessions are plotted as a function of contrast ratio at two different relative orientations (90 and 120°) for two subjects. Errors bars are the mean uncertainty (standard deviation of the fitted Gaussian). The dashed lines represent simulated plaid-direction errors using equation (1) and measured mean grating-speed errors over three sessions in the same subjects.

suggested by the fact that none of the three subjects showed a significant difference in the perceived speed of a 70% test and a 50% standard when tested with orthogonal gratings (see downward arrows), while four of six subjects (including PT and LS) showed a significant difference when tested with parallel gratings (Fig. 2). Furthermore, for the two subjects tested with a 20% contrast test and a 10% contrast standard under both the parallel and orthogonal conditions (PT and LS), both made significant speed-matching errors in the parallel condition [$P < 0.05$ in a one-tailed t-test; Fig. 4(A, B)] but not in the orthogonal condition [Fig. 6(A, B)]. We conclude that the relative orientaton of the gratings affects the contrast-induced misperception of relative speed.

Experiment 3: Contrast-Induced Misperception of Plaid Direction

Methods

In this third set of experiments, we measured the effect of contrast on the perceived direction of moving plaids consisting of components with different contrasts (Fig. 7) using a previously established protocol (Stone *et al.*, 1990b). The plaid consisted of the sum of two superimposed gratings of different orientations viewed through a single stationary circularly symmetric Gaussian window (SD 0.95°) and centered on the fixation point (which was extinguished during the actual stimulus presentation). The components were either orthogonal (normal vectors 45° off vertical) or 120° apart (normal vectors 60° off vertical). Therefore, the differences between the plaids in this set of experiments and the grating-pair stimuli in the previous set were the location of the grating patches, the absolute orientation of the gratings, whether or not they were superimposed, and the size of the stimulus patches. Subjects were presented with an upward-moving plaid and asked to determine in a two-alternative forced-choice whether the plaid appeared to move to the right or left of straight up. The actual direction of the plaid was determined by two interleaved up–down staircases and achieved by changing the speed ratio of the two components while keeping component orientation and plaid-speed constant.

Results

In a previous study, Stone *et al.* (1990b) showed that the relative contrast of the grating components within a plaid affected its perceived direction of motion. They postulated that a contrast-induced misperception of component speed was responsible. If the error in perceived component speed is fed into a mechanism that reconstructs plaid velocity from component information, plaid motion would be misperceived in a quantitatively predictable manner. If the reconstruction is achieved using the intersection of perpendicular constraints rule (Fennema & Thompson, 1979; Adelson & Movshon, 1982), the error in perceived plaid direction (Δ) is related

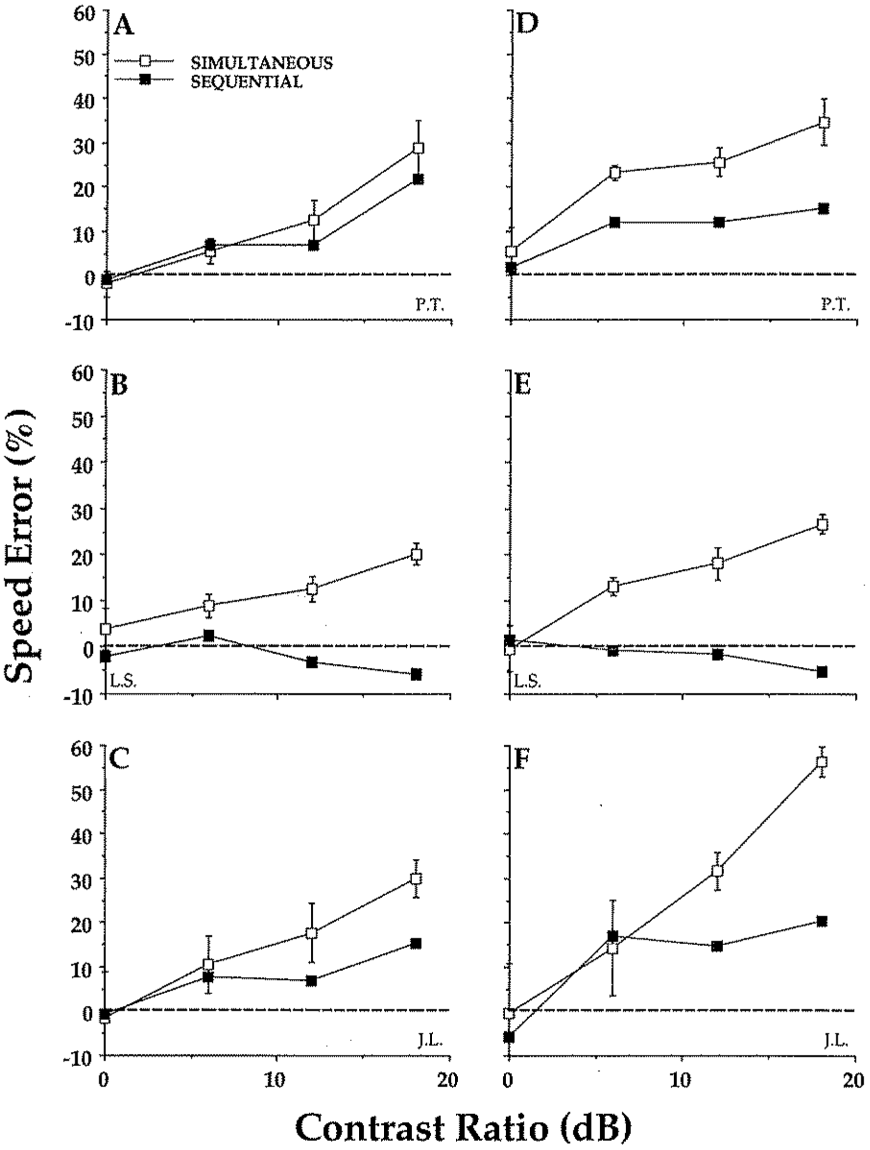

FIGURE 8. Contrast-induced speed errors are weaker with sequential presentation. Mean speed errors are plotted as a function of contrast ratio using both simultaneous (open squares) and sequential (solid squares) presentations. Error bars are standard deviations over three or four sessions and, for clarity, are only presented for the simultaneous condition. The dashed line represents veridical matching. The lefthand panels show the data generated by slowing a 20% test grating to match 20, 10, 5 and 2.5% contrast standards. The righthand panels show the data generated by speeding up a 2.5% test grating to match the same standards.

to the perceived ratio of the component speeds (R) by the following equation:

$$\Delta = \arctan\left(\frac{R-1}{R+1}\operatorname{cotan}\frac{\theta}{2}\right) \qquad (1)$$

with θ, the angle between the directions of motion of the two components.

We predicted the effect of contrast on the perceived direction of a moving plaid from contrast-induced biases in grating speed in two subjects. The predicted direction error was generated using equation (1), the known θ and the measured R in the same subjects. Figure 7 shows the actual and predicted responses. Although the subjects performed differently, the actual performance for both of them in the plaid-direction task (squares) is well predicted by equation (1) using their own grating speed-matching data (dashed line).

As shown above, individual subjects could show distinct differences in their performance when tested with non-parallel gratings. Specifically, the two subjects tested with plaids showed significant differences in their speed matching when presented with orthogonal gratings. Subject PT still showed a consistent contrast-induced misperception of relative speed [Fig. 6(A)] while subject LS did not [Fig. 6(B)]. The same dichotomy was found in their perception of moving plaids. Subject PT showed a large error in his perception of plaid direction [Fig. 7(A)] while subject LS did not [Fig. 7(B)]. The variability in grating-speed and plaid-direction perception between subjects was therefore self-consistent for the two subjects and the limited conditions tested. This consistency supports the idea that contrast-induced misperception in plaid direction is merely a manifestation of a contrast-induced misperception of component speed.

Experiment 4: Effect of Temporal Presentation

Methods

In this last experiment, we measured the effect of contrast on the perceived relative speed of *sequentially* presented horizontally oriented drifting grating patches (Fig. 8). Subjects were presented with two stimulus intervals. Each interval consisted of two horizontally elongated grating patches of identical contrast centered either 1.3° above or below the fixation cross at the center of the image. In one interval (standard), both gratings moved upward at exactly 2°/sec. In the other interval (test), both gratings moved upward at the same speed determined by two interleaved up–down staircases. The test and standard intervals were presented in random order. Subjects were asked to ignore contrast, to fixate the center cross, and to determine in a two-alternative forced-choice whether, in the first or second interval, the gratings appeared faster.

Results

The perception of relative speed is affected by the temporal presentation of the stimuli to be matched. A number of recent studies has suggested that speed-matching performance may be different when stimuli are presented simultaneously or sequentially (e.g. Kooi, 1990; Smith & Edgar, 1990; Ferrera & Wilson, 1991). This fact led us to examine the effect of contrast on speed matching in both simultaneous and sequential paradigms. Figure 8 shows the speed-matching data for three subjects (including one naive) when the stimuli were presented either simultaneously (open squares) or sequentially 500 msec apart (solid squares) and with the matching done either by slowing down a 20% contrast test (lefthand panels) or by speeding up a 2.5% contrast test (righthand panels). All stimulus intervals in both conditions contain pairs of grating patches with the same perifoveal spatial arrangement (above and below fixation). In the simultaneous condition, the speed match was made between the two patches in the same single stimulus interval (as done in all speed-matching experiments described above). In the sequential condition, both grating patches within a single interval moved at the same speed and the speed match was made between the two intervals. For all three subjects, the contrast-induced misperception of relative speed was less severe in the sequential condition. Subject LS actually made veridical matches in the sequential condition [Fig. 8(B, E)]. Furthermore, subjects PT and JL showed large reductions in their contrast-induced errors when the stimuli were presented sequentially. Therefore, the temporal presentation of two grating patches affects the perception of relative speed with gratings presented separately in time being more veridically matched.

DISCUSSION

Contrast-induced misperception of grating speed

In this study, we have shown that when two horizontal gratings moving upward at the same speed within nearby stationary windows are presented simultaneously, the lower-contrast grating appears up to 50% slower. This effect is evident over a wide range of contrasts (2.5–50%) and is not accompanied by systematic changes in uncertainty. The effect is a function of contrast ratio alone and is independent of the absolute contrast level except possibly at very low contrasts, with incomplete saturation even at 50%.

Contrast effects on perceived speed have been documented previously by Thompson (1982), but his study was different in two ways: he only examined contrasts at and below 17.8% and he used the method of adjustment and magnitude estimation. Thompson found that lower contrast gratings appear to move more slowly only at temporal frequencies below 8 Hz. He reported that the effect becomes smaller with increasing temporal frequency and even reverses at temporal frequencies above 8 Hz. However, we found no evidence for this reversal. In fact, for all three subjects examined at multiple temporal frequencies, the effect was still robust with lower-contrast gratings appearing slower at 8.25 Hz. However, we did find that the task became very difficult for one subject and impossible for another at temporal frequencies at and above 10 Hz. This suggests that, in our 10 Hz condition, subjects did not have a clear percept of speed.* The apparent reversal found previously is therefore probably an artifact of the experimental method with subjects making "speed" matches based on some other criterion. With our two-alternative force-choice staircasing procedure, we report the point of subjective equality only if it is located on a clear psychometric curve with measured precision. The methods of adjustment and magnitude estimation generate apparent matches regardless of whether the underlying matching performance is well-behaved (i.e. is a sigmoidal function of test speed).

The fact that speed perception is dependent on contrast suggests that speed discrimination should be degraded by random large fluctuations in contrast. Any changes in contrast should be perceived as perturbations in speed and should therefore add to the observed uncertainty. However, McKee *et al.* (1986) showed that randomization of contrast did not adversely affect speed discrimination. This apparent discrepancy with our present results can, however, be resolved by our finding that the temporal presentation of the stimuli to be compared is important. At an interstimulus-interval (ISI) of 500 msec, subjects showed either a reduced or nonexistent effect of contrast on perceived relative speed. McKee *et al.* used the method of single stimuli that, like our sequential condition, presented stimuli one at a time. Their experiments were self-paced so it seems

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*McKee *et al.* (1986) obtained good speed discrimination at temporal frequencies of 10 Hz and higher. However, at those temporal frequencies, performance could be degraded at spatial frequencies above around 2 c/deg (see their Fig. 4). This degraded performance at higher temporal frequency is particularly evident at lower contrast and shows considerable intersubject variability (McKee, personal communication). Furthermore, the smaller number of visible cycles and perifoveal viewing used here may have exacerbated the problem.

reasonable to assume that the ISI under such conditions exceeded 500 msec. Therefore, the fact that they found no contrast effect is not inconsistent with our results.

The magnitude of the difference between our simultaneous and sequential conditions was different for the different subjects. In fact, one subject actually made veridical matches when stimuli were presented sequentially. Given the results of McKee *et al.*, it would be interesting to know whether, at sufficiently long ISIs, all subjects would have made veridical matches. Further studies will be needed to elucidate the time–course of this putative washing out of the contrast-induced speed-matching errors.

There are, however, a few confounding issues. The spatial arrangement of our sequential stimulus (two patches moving at same speed) was a bit unusual in order to match the exact spatial arrangement of the simultaneous stimulus. Unfortunately, subjects could have paid attention to or even looked at (although told to fixate the center cross) one of the patches in a given interval since its motion contained all the necessary information to make the match with the second interval. However, the sequential-simultaneous difference is unlikely to be due to foveal vs perifoveal viewing because in this (Fig. 7) and a previous study (Stone *et al.*, 1990b) errors in perceived plaid direction were observed when the components had different contrasts even with foveal viewing. Furthermore, because the motion was upward in both intervals and the ISI was only 500 msec, it could be argued that the mismatches in the sequential paradigm were contaminated by a motion aftereffect. This is unlikely to be the case because any such effect would always tend to make the second stimulus appear slower and we randomized the order in which the test and standard were presented. But it could be argued further that, if the aftereffect were stronger when the first stimulus had the higher contrast, then the resulting asymmetry could produce mismatches qualitatively similar to those observed. However, this process would be expected to produce parallel increases in uncertainty such that the uncertainty and the mismatch would have had similar amplitudes (Stone *et al.*, 1990b). In fact, uncertainty was nearly independent of the contrast ratio and, at high contrast ratios, small compared to the mismatches. In addition, it is unlikely that a motion aftereffect across trials significantly contaminated our results, because we tested one subject (PT) in the simultaneous condition with the motion of both patches randomized upward or downward and found no change in our basic finding. Finally, it is unlikely that eye movements significantly affected our results because the foveal fixation point is likely to have allowed subjects to suppress eye movements during the relatively brief perifoveal stimulus presentations and because any tracking movements would have lowered the retinal speed of both the test and the standard patches equally.

Plaid motion

In a previous study, Stone *et al.* (1990b) showed that when a moving plaid consists of components with different contrasts, its direction is misperceived with a bias in the direction of motion of the higher contrast grating. They suggested that this bias was due to a reduction in the perceived speed of the lower-contrast component. In this study, we explicitly tested this hypothesis by measuring perceived relative component speed and plaid direction in the same subjects under similar conditions. These results and similar recent findings by others (Kooi, 1990) suggest that both the contrast-induced plaid-direction and grating-speed misperception are manifestations of the same underlying mechanism. Adelson and Movshon (1982) hypothesized that plaid motion is determined using a two-stage mechanism. First, the plaid is decomposed into the motion of the individual components. Second, plaid velocity is reconstructed using the intersections of constraints rule (Fennema & Thompson, 1979). The data presented in Fig. 7 provide direct evidence for the hypothesis proposed by Stone *et al.* (1990b) that the contrast-induced misperception of component motion is fed through the intersection of constraints rule to yield the misperception in plaid direction.

A striking difference between the previous plaid results (Stone *et al.*, 1990b) and our present grating results is that Stone *et al.* documented contrast-induced misperceptions in plaid direction only at low contrast but the contrast-induced mismatches in grating speed shown here occur over potentially the entire range of contrasts. Thompson (1982) explored perceived grating speed only at the low end of the contrast scale so Stone *et al.* (1990b) did not identify this conflict. However, this puzzling discrepancy can be resolved by noting that the saturation apparent in plaid-direction judgments occurs with non-parallel grating components while the non-saturation apparent for grating speed-matching occurs with parallel gratings. In fact, when subjects were asked to match non-parallel gratings, their performance did show signs of contrast saturation sufficient to explain the plaid-direction results for both subjects tested despite the considerable differences between the two subjects.

The inter-subject variability provides further evidence for the two-stage hypothesis (Adelson & Movshon, 1982) because the plaid and grating paradigms yield consistent results within subjects. The subject who speed-matched orthogonal gratings veridically showed little or no plaid-direction error for plaids consisting of orthogonal gratings. The subject who showed a significant misperception of relative speed of orthogonal gratings also misperceived plaid direction. Why there should be such inter-subject variability is unclear. However, the variability in the orientation effect on the contrast-induced grating-speed misperception may underlie the considerable inter-subject variability in the orientation effect on the contrast-induced plaid-direction misperception shown previously (Stone *et al.*, 1990b).

Because the effect of relative orientation on both plaid and grating perception is so variable, further studies will be required for quantitative analysis. One possible explanation for the variability in speed-matching of orthogonal gratings is that, because we used circularly symmetric apertures in the orthogonal condition, the stimuli were smaller and therefore less salient than in the parallel conditions. Furthermore, the smaller size could have contributed to the change in the contrast effect for orthogonal gratings. We believe size is unlikely to have been entirely responsible because orientation dependence of contrast effects on plaid-direction perception was seen here and in a previous study (Stone *et al.*, 1990b) despite using stimuli that were larger than those used to document the strong contrast effect on the speed-matching of parallel gratings.

Despite the smaller size of the grating stimuli and the different spatial arrangement for the plaids and gratings, our predictions of plaid-direction errors are nonetheless surprisingly accurate. For grating-speed perception, the gratings must be non-overlapping and therefore perifoveal to be symmetric. For plaid-direction perception, the gratings must be overlapping (and were presented foveally for convenience). Because it is not possible to design an experiment in which the spatial arrangements are identical and because this comparative approach merely provides a quantitative correlation between two phenomena and can never provide a causal link, a more thorough examination is unwarranted.

Other studies have recently found that variables that affect grating-speed perception also affect plaid-direction perception in a manner consistent with the two-stage hypothesis (Adelson & Movshon, 1982). Using an adapting grating to reduce the apparent speed of a single component (Derrington & Suero, 1991) or using a plaid consisting of gratings of different spatial frequencies (Kooi, 1990; Smith & Edgar, 1991) also yields directional errors consistent with a component-driven analysis. Although no actual causal link has been established, these results, together with speed and direction discrimination studies (Welch, 1989; Stone, 1988, 1989, 1990) and the results presented here, show that, in a wide number of circumstances, plaid-motion perception is consistent with a component-driven mechanism that uses the intersections of constraints rule to reconstruct pattern (plaid) motion from component motion. However, some studies have recently found that, for some plaid-angle configurations, plaid motion is not consistent with a two-stage component-driven model, leading to the suggestion that other mechanisms may also be at work (e.g. Ferrera & Wilson, 1987, 1990; Stone, 1988; Derrington & Badcock, 1990).

Speed perception

The question of whether humans perceive speed directly or whether speed is derived from other sources has been addressed in a number of studies (e.g. Lappin, Bell, Harm & Kottas, 1975; McKee, 1981; Orban, de Wolf & Maes, 1984). They proposed that perceived speed is unlikely to be derived from distance or duration perception because speed discrimination is better than distance or duration discrimination. However, there is evidence to suggest that size and distance traveled does affect perceived speed (e.g. Brown, 1961; Katz, Gizzi, Cohen & Malach, 1990). McKee *et al.* (1986) used the same discrimination argument to suggest that speed perception is not derived from temporal frequency. This latter result is, however, unconvincing because one of the two subjects showed an equal ability to discriminate small differences in either speed or temporal frequency. Furthermore, the lack of physiological evidence for a clear representation of speed anywhere within visual cortex (see Maunsell & Newsome, 1987) suggests that speed may be inferred from other measures. The issue of the primary nature of speed perception remains unresolved.

A second related issue is whether or not humans perceive speed veridically. The concept that speed is veridically perceived was supported by the results of McKee *et al.* (1986) and McKee (1981) who showed that random perturbations of duration, distance traveled, spatial and temporal frequencies do not have a significant effect on speed discrimination. They did, however, show a small effect of spatial frequency on perceived speed with higher spatial frequencies perceived as faster. Ferrera and Wilson (1991) have also found this although their effect was much larger. Smith and Edgar (1990), however, found the converse. This apparent discrepancy can be resolved by noting that, when two gratings were presented simultaneously, the lower spatial frequency grating appears slower (Smith & Edgar, 1990) and, when stimuli are presented sequentially, the higher spatial frequency gratings appear faster (Diener, Wist, Dichgans & Brandt, 1976; Campbell & Maffei, 1981; McKee *et al.*, 1986; Ferrera & Wilson, 1991). The grating-speed results are consistent with the finding that the perceived direction of moving plaids composed of components of different spatial frequency is biased in the direction of the lower spatial frequency component (Kooi, 1990; Smith & Edgar, 1991). These results complement those presented here and provide a convincing ensemble of data that demonstrates that speed is not veridically perceived in a wide set of situations. Furthermore, they provide additional evidence that simultaneously and sequentially presented moving stimuli are processed differently.

Speed coding within visual cortex

From the physiology and anatomy of monkey visual cortex, it appears that direction and speed information are represented in fundamentally different ways. Direction information appears to be coded within a place map in which there is a systematic representation of each possible direction of motion in an orderly array of cortical columns within MT (Albright *et al.*, 1984). Presumably, perceived direction of motion is extracted by determining which direction column is the most active. A recent study has in fact shown that localized electrical stimulation, presumably within a single direction column, biases direction judgments in the direction of the column (Salzman *et al.*, 1990). Although contrast affects the absolute level of neuronal activity in both striate cortex and MT neurons (e.g. Sclar *et al.*, 1990; Albrecht & Hamilton, 1982), the spatial distribution of activity is most likely robust to the contrast level.* Nakayama and Silverman (1985) found that indeed direction discrimination, as measured by the minimum motion necessary to discriminate direction, was unaffected by increases in contrast above about 3%. The ability to determine the direction of motion is therefore thought to saturate at very low contrast.

The coding of speed information is poorly understood and is likely to be different. Directionally selective cortical neurons are tuned for speed but, unlike direction (Albright *et al.*, 1984), orientation (Hubel & Wiesel, 1968; Hubel, Wiesel & Stryker, 1978), ocular dominance (Hubel & Wiesel, 1968, 1974; Wiesel, Hubel & Lam, 1974; Tootell, Hamilton, Silverman & Switkes, 1988a), or even spatial frequency (Tootell, Silverman, Hamilton, Switkes & De Valois, 1988b), there is no apparent spatial organization for speed tuning. Therefore, how speed is coded remains an open question, although speed cannot be coded in the firing rate of individual neurons (no such cells have been found in the visual cortex) nor by a place code (no organized spatial arrangement has been found). One possibility is that speed is coded in the firing rate of a set of neurons. The fact that firing rate is very sensitive to contrast in both striate cortex and MT (e.g. Albrecht & Hamilton, 1982; Sclar *et al.*, 1990) could be remedied by taking ratios of the firing rates of different neurons. If the contrast sensitivities were equal, any contrast effect could thus be canceled. A ratio scheme of this type has been proposed for speed coding by Harris (1980) and it gains some plausibility from psychophysical evidence suggesting just two populations of speed-tuned cells, one preferring slow rates of movement (below 4 Hz) and the other faster rates (Watson & Robson, 1981; Thompson, 1983).

The problem of contrast and speed coding has been of particular concern to theoreticians who have postulated that the visual system uses linear oriented spatio-temporal filters to extract motion information because such filters are sensitive to changes in contrast (Watson & Ahumada, 1983). One solution to this problem would be to use the temporal frequency of the output modulation of the filters, a measure which is independent of contrast (Watson & Ahumada, 1985). However, this assumes that temporal frequency is veridically encoded independently of contrast. Another approach would be to use motion energy (Adelson & Bergen, 1985; Heeger, 1987), a phase-independent measure derived from the output of the linear spatio-temporal filters, but motion energy is proportional to the square of contrast. Therefore, in order to yield a contrast-independent measure of speed, motion energy must first be divided (normalized) by another energy signal with the same contrast sensitivity. Specifically, one can take the difference between the outputs of rightward and leftward motion energy sensors and divide that by the "stationary" energy to yield a true speed signal (Adelson & Bergen, 1986). However, the critical issue remains what signal is actually used as the "stationary" energy.

A potential neuronal implementation would be to normalize the output of striate cortical complex cells, postulated to encode motion energy (Emerson, Bergen & Adelson, 1992), with an "average-contrast" signal constructed by pooling the output of all complex cells over a range of orientation and spatial frequencies and over a wide spatial area (Heeger, 1992). If the area over which the pooling is done is large enough to encompass both patches of our stimuli while the motion energy associated with the patch is detected over a smaller spatial extent, then the signal detected by the higher contrast grating would be normalized by an inappropriately low average contrast. Conversely, the motion energy generated by the lower contrast grating would be normalized by an inappropriately high average contrast. Thus, a contrast-normalized motion-energy scheme can qualitatively explain the observed contrast-induced misperception of relative speed.

This scheme can be extended to explain our additional findings. If the contrast is normalized by a signal pooled only over similar orientations/directions then two orthogonal gratings would be normalized largely independently. This could explain why the contrast effect is dependent on the relative orientations/directions of the gratings with a tendency to be weaker for orthogonal gratings. The normalization in the orthogonal case might be more correct since the two different energy signals from the two patches would only partially interfere with each others' normalization. Further experiments examining the entire range of relative orientations are needed to determine the role of orientation in this putative normalization process.

The normalization scheme can also explain the fact that the perceived relative speed of simultaneously presented gratings is more contrast dependent than that of two sequentially presented gratings: the normalization takes place over a finite time. Two gratings presented sequentially would be normalized separately. The normalization in the sequential case would be more correct since the two different energy signals from the two intervals would only partially interfere with each others normalization. Further experiments examining a wider range of ISIs are needed to determine the temporal extent of the putative normalization process.

A third experiment that could be used to examine the normalization hypothesis would be to determine whether the distance between the grating patches is important. The normalization hypothesis predicts that speed-matching should become more veridical with increased distance. Experiments examining a range of inter-patch distances are needed to determine the spatial extent of the putative normalization process.

A more specific model of contrast normalization must be developed to predict quantitatively our results, particularly the finding that perceived relative speed is a quasilinear function of log contrast ratio. However, there is other empirical evidence for this quantitative

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*This is only true above some minimal contrast level necessary to recruit most neurons. In MT, most neurons are firing at half-maximum by about 10% (Sclar *et al.*, 1990).

relationship between speed and contrast. Using an induced-motion paradigm, Raymond and Darcangelo (1990) recently found a similar interaction between perceived speed and contrast. They moved a surround grating of variable contrast to impart apparent motion in the opposite direction to a stationary center grating. The induced speed was a quasilinear function of log contrast of the surround up to 60% contrast. However, they found that changing the center contrast had no effect. Despite this apparent contradiction, their second result is entirely consistent with our results and the contrast-normalization model. The motion energy of their center stimulus was always zero because the center was stationary so its contrast is irrelevant.* Furthermore, in a preliminary report, Rubin and Legge (1981) showed that the relative latency of adjacent drifting gratings was misperceived in a manner consistent with their relative speed being a linear function of log contrast ratio over the entire range of contrasts (tested up to 80%). Finally, Chubb, Sperling and Solomon (1989) have shown that the perceived contrast of a patch of texture is influenced by the contrast of the surrounding texture. Although this is not a motion phenomenon, it demonstrates the existence of another type of contrast normalization similar to the one proposed here, particularly since their phenomenon appears to be orientation specific (Solomon, Chubb & Sperling, 1990).

In conclusion, our results show that the human visual system is only partially successful in its endeavor to extract speed independently of contrast. These results together with a large body of recent studies show that speed is often not veridically perceived and is a function of a number of other factors most notably contrast and spatial frequency (Diener *et al.*, 1976; Campbell & Maffei, 1981; Stone *et al.*, 1990b; Kooi, 1990; Smith & Edgar, 1990, 1991; Ferrera & Wilson, 1991). Our results put new constraints on models of human motion perception and provide additional insight into how primate cortex processes visual motion.

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