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Visual motion of missing-fundamental patterns: motion energy versus feature correspondence

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Abstract

Missing-fundamental gratings, generated by subtracting the fundamental Fourier components from square-wave gratings, appear to move backward when presented in quarter-cycle jumps, even though their edges and features all move forward. We used variants of these stimuli to test current models of motion perception. We found that missing-fundamental plaids, constructed from orthogonal missing-fundamental gratings, also appear to move backward. Forward motion was restored to missing-fundamental gratings and plaids by adding back small fractions of the original fundamental. In-phase and antiphase addition of the fundamental had similar effects on the perceived motion, despite having markedly different effects on the features, appearances and zero-crossings of the stimuli. The critical amplitude of fundamental needed to restore forward motion to plaids was the same as that needed to restore forward motion to their isolated component gratings, indicating that the plaids' emergent features, such as edge intersections and 'blobs', made little or no contribution to the perceived direction of motion in these stimuli. In two derivative experiments, missing-fundamental chromatic gratings and plaids, at approximate isoluminance, and missing-fundamental luminance barberpoles, also generated backward perceived motions, and these were also reversed by in-phase or antiphase addition of small amounts of fundamental. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Visual apparent motion is generally thought to involve two distinct processes (Braddick, 1974, 1980; Pantle & Picciano, 1976; Ullman, 1979; Anstis, 1980; Cavanagh, 1992; Lu & Sperling, 1995), although this standard dichotomy has been challenged (Cavanagh & Mather, 1989). The first process, called motion detection, responds to the motion energy in local, spatially filtered light signals, prior to form processing and without reference to perceptual features. Models of motion detection have involved a variety of different mechanisms (Reichardt, 1961; Barlow & Levick, 1965; Marr & Ullman, 1981; Adelson & Bergen, 1985; Watson & Ahmuda, 1985), but generally conform to the 'Motion From Fourier Components Principle' (Chubb & Sperling, 1988), which holds that the perceived direction of motion corresponds to the dominant motion in the Fourier components of the stimuli.

The second motion process, called 'feature-tracking', generates apparent motion from changes in the positions of salient features across space and time. While there is yet no consensus on a definition or metric for 'features', this generally refers to individuated, higher-level representations of the image, such as edges, blobs, shapes, depth and colors (Julesz & Payne, 1968; Ramachandran, Rao & Vidyasagar, 1973; Ullman, 1979; Anstis, 1980; Prazdny, 1986; Dawson, 1991; Cavanagh, 1992; Lu & Sperling, 1995; Georgeson & Freeman, 1996). The feature-tracking process, unlike motion energy, has been called 'interpretive' (Braddick, 1980) or 'cognitive' (Anstis, 1980), and may require conscious or attentional processes (Victor & Conte, 1990; Cavanagh, 1992; Smith, 1994; Lu & Sperling, 1995). The relative contributions of motion-detection and feature-tracking mechanisms to the perception of apparent motion has

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been a continuing source of controversy. For most ordinary motion stimuli, these two processes will generally agree on the direction of motion, so in order to functionally tease them apart it is often valuable to use exotic stimuli, such as the missing-fundamental gratings, plaids and barberpoles in our present study.

Adelson and Bergen (1985) showed that missing-fundamental gratings, when presented stroboscopically in quarter-cycle jumps, were predicted to move in opposite directions of motion from the two motion processes. A missing-fundamental (MF) grating is constructed by subtracting the fundamental Fourier component (F) from a square-wave (SW) grating, leaving only the third ($3F$), fifth ($5F$), and successive higher odd harmonics. MF gratings retain the spatial period, edges, and much of the appearance, of SW gratings (Campbell, Howell & Robson, 1971; Adelson & Bergen, 1985). Fig. 1 shows the luminance profiles (top row) and appearances (middle row) of SW and MF gratings. When a MF grating is displaced by a quarter-cycle, its edges and features, which still occur at the fundamental frequency, all move forward by a quarter cycle. But the dominant Fourier component remaining in a MF grating is $3F$, with 1/3 the spatial period of F. When the MF grating jumps forward by a quarter cycle, $3F$ jumps forward by 3/4 cycle, which is equivalent to a backward jump of 1/4 cycle. Thus, the dominant Fourier component ($3F$) will actually be moving backward when the MF grating jumps forward a quarter cycle. Therefore, the feature-tracking process would see forward motion in MF stimuli, but the motion-detection process, in accord with the 'Motion from Fourier Components Principle', would see backward motion in the same stimuli. Empirically, the motion actually perceived in MF stimuli is backward, providing strong support for motion-detection as mediating perception of MF stimuli (Adelson & Bergen, 1985; Baro & Levinson, 1988; Georgeson & Shackleton, 1989, 1992; Georgeson & Harris, 1990).

What happens to the direction of perceived motion as fractions of the missing fundamental F are incrementally restored to a MF grating? As an example of such stimuli, the third column of Fig. 1 shows the luminance profile (top row) and appearance (middle row) of a MF grating to which $0.24F$ has been added. From previous reports, we know the perceived motion in two limiting cases: forward motion for SW gratings ($1.00F$), and backward motion for MF gratings ($0.00F$). Presumably, there is some critical intermediate amount of restored F at which the perceived direction of motion reverses. A variety of motion-detection models can correctly predict the perceived motions in these two limiting cases, but diverge in their predictions for this motion-reversal point (see Section 4). Precise determination of this reversal-point would provide an important piece of information, and would facilitate quantitative testing of

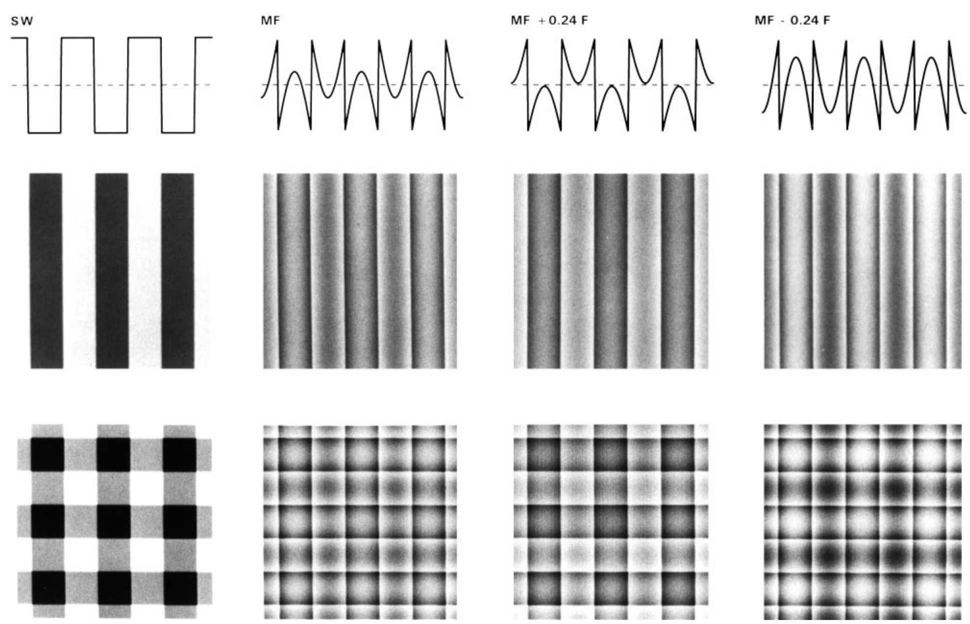

Fig. 1. Experimental stimuli. Top row: Luminance profiles of the waveforms used in the experiments. Solid line indicates the spatial variation of luminance; dotted line represents the mean luminance. Second row: 1-dimensional grating stimuli, corresponding to the luminance profiles in the top row. Third row: 2-dimensional plaid stimuli, generated by adding the gratings shown in the second row to orthogonal, but otherwise identical, gratings. Within each row, the first column shows a square-wave stimulus; the second column shows a missing-fundamental stimulus, constructed by subtracting the fundamental Fourier component from the square-wave; and the third and fourth columns show missing-fundamental stimuli to which 0.24 of the fundamental was restored, either in-phase (third column) or antiphase (fourth column). Stimuli shown in the second and third rows are meant as examples and the actual amplitude of the fundamental component may not be exactly as indicated due to changes in photo-reproduction process.

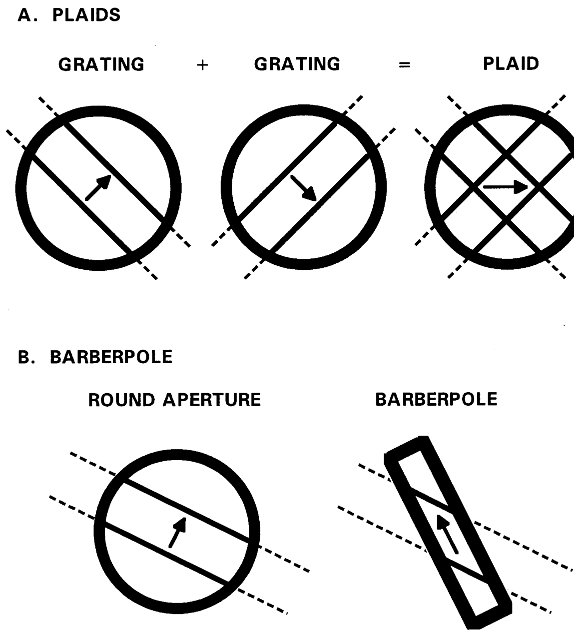

Fig. 2. Construction of stimuli used in the experiments. The heavy lines represent the apertures through which stimuli were visible. Thin solid lines represent the portions of the stimuli visible through the aperture, while dashed lines indicate the continuation of the occluded stimuli. (A) illustrates two orthogonal gratings, at $\pm 45°$, and their addition to generate a plaid pattern. Note that the directions of motion of the individual components were orthogonal, at $\pm 45°$, while the plaid pattern had a unique, horizontal direction of motion. (B) illustrates the stimuli used in the barberpole experiment. A grating oriented at 154° generates an orthogonal perceived direction of motion towards 64°, when viewed through a neutral, circular aperture. When the same grating is viewed through a barberpole aperture, oriented at 116°, the grating's perceived direction of motion is rotated toward the orientation of the barberpole. Note that the horizontal component of motion, to be reported by the subjects in this experiment, has been reversed by the barberpole. (Relative to the vertical, the direction of motion was $-26°$ in the round aperture, and $+26°$ in the barberpole.)

the various proposed explanations of this phenomenon. In our experiments, the direction of perceived motion was reported for MF stimuli to which variable fractions of F were restored, in order to determine the psychophysical motion-reversal points.

Another class of stimuli which has become very popular for testing and distinguishing between motion models is the plaid patterns formed from combinations of gratings at different orientations (Bonnet, 1981; Adelson & Movshon, 1982). Plaids constructed by linear superposition of two orthogonal gratings, as used in these experiments, are shown in the bottom row of Fig. 1, for SW, MF, and fractional F waveforms. The perceived direction of motion of a coherent plaid pattern is distinct from the perceived directions of motion of its isolated component gratings, as illustrated in Fig. 2A. Bonnet (1981) pointed out that additive plaid patterns have no Fourier components moving in the pattern direction, but it does contain features, such as contours and luminance extrema, moving in the pattern direction. Adelson and Movshon (1982) suggested that the perceived pattern motion of plaids is derived from their independently extracted Fourier components, with little or no contribution from the plaid features, and numerous subsequent studies have supported this model (Welch, 1989; Stone, Watson & Mulligan, 1990; Derrington & Suerro, 1991; Kooi, De Valois, Grosof & De Valois, 1992; Wilson, Ferrera & Yo, 1992). However, many other researchers have argued that plaids' emergent features, such as the 'blobs' at the intersections which are not present in the component gratings, are crucial for generating their perceived motions (Gorea & Lorenceau, 1991; Vallortigara & Bressan, 1991; Derrington & Badcock, 1992; Mingolla, Todd & Norman, 1992; Stoner & Albright, 1992; van den Berg & Noest, 1993; Wenderoth, Alais, Burke & van der Zwan, 1994). Because the emergent features in MF plaids still occur with the spatial period F, feature-tracking would be expected to signal forward motion. (In addition to their emergent features, plaids also contain nonlinear distortion products and second-order signals at F, which may also signal forward pattern motion.) If features do contribute importantly to the perceived motions of plaids, a MF plaid might not exhibit backward apparent motion at all, or may at least require less F to restore forward motion than does its component MF gratings. We hypothesized that any differential sensitivity to restored F between MF plaids and MF gratings could provide a sensitive measure for the contribution to apparent motion of signals arising from feature-tracking of the plaids' emergent features.

Motion models based on the independent analysis of the Fourier components of a stimulus are insensitive to the relative phases of the components (Reichardt, 1961). But the feature-tracking process should be phase-sensitive, as features depend very much on the relative phases of the Fourier components (Atkinson & Campbell, 1974; Piotrowski & Campbell, 1982; Morrone & Burr, 1988). Effects of the relative phases of the Fourier components of compound gratings can be interpreted as evidence for feature-based mechanisms (Akutsu & Legge, 1995). This led us to investigate whether the motion-reversal points for MF stimuli depended on the phase of restored F. The third and fourth columns in Fig. 1 show examples of MF gratings and plaids with partial restoration of F in-phase ($\mathrm{MF} + 0.24F$) and antiphase ($\mathrm{MF} - 0.24F$). These patterns have identical amplitudes in all their Fourier components, and differ only in the phase of F. But note that the appearance of the stimuli were quite asymmetric for inphase and antiphase restored F: restoring F in-phase smoothly restores the SW-like appearance of the stimuli, while restoring F in antiphase has the opposite effect of exaggerating the apparent differences from SW stimuli.

The observation that apparent motion in colored stimuli depends primarily on luminance but not chromatic signals (Ratleff, 1956; Anstis, 1970) led to the hypothesis that the motion-detection process, but not the feature-tracking process, is colorblind (Ramachandran & Gregory, 1978; Anstis, 1980; Braddick, 1980). Subsequent studies have indicated that the motion-detection process is at least weakly sensitive to purely chromatic signals (Cavanagh, Boeglin & Favreau, 1985; Mullen & Baker, 1985; Cavanagh & Anstis, 1991; Cropper & Derrington, 1996), but it is also thought that chromatic signals may be especially salient for the feature-tracking process (Cavanagh, 1992; Derrington & Henning, 1993; Dobkins & Albright, 1993; Edwards & Badcock, 1996). This suggests that the feature-tracking process may contribute relatively more to apparent motion for chromatic stimuli than luminance stimuli. So, in our second experiment, we presented chromatic MF gratings and plaids, at approximate isoluminance, to determine whether they also generate reversed apparent motion, and to measure their sensitivity to restored *F*.

Another well-known stimulus used in studies of visual motion mechanisms is the barberpole illusion (Wallach, 1976; Hildreth, 1984): a moving grating viewed through a stationary, elongated aperture has its apparent motion shifted toward a direction parallel to the long axis of the aperture (Fig. 2B). The barberpole may be considered a special case of a (non-additive) plaid, with one of its components stationary (Vallortigara & Bressan, 1991). Models of the barberpole effect have often invoked the tracking of features, specifically the edge terminators, along the contours of the barberpole aperture (Hildreth, 1984; Shimojo, Silverman & Nakayama, 1989; Vallortigara & Bressan, 1991). Because MF gratings retain the edges of SW gratings, feature-tracking models would not predict motion reversal for MF barberpoles. An alternative account of the barberpole effect relies on motion-detection along the contours of the barberpole aperture (Power & Moulden, 1992; Kooi, 1993), and these models would predict motion reversal for MF barberpoles. Our third experiment examined the perceived motions of MF barberpoles, and their sensitivity to partially-restored *F*.

2. Methods

2.1. Stimuli and apparatus

The basic waveform for all stimuli in our experiments was the MF grating, to which variable amounts of *F* were restored, either in-phase or antiphase, as illustrated in the top row of Fig. 1. (Note that the addition of antiphase fundamental is equivalent to the subtraction of in-phase *F*; we refer to antiphase *F* as $-F$.) Eighteen levels of fractional restored *F* were used to construct the stimuli: 1.00 (SW), 0.00 (MF), and $\pm$ 0.03, 0.06, 0.09, 0.12, 0.15, 0.18, 0.21 and 0.24.

In the luminance plaids experiment, the component gratings were 1-dimensional luminance distributions, modulated by the experimental waveform, as shown in the middle row of Fig. 1. Plaids were constructed by addition of orthogonal gratings, as illustrated in the bottom row of Fig. 1. The gratings and plaids were oriented at $\pm 45°$. The perceived motions of the isolated component gratings were normal to their orientations, and thus were along the $\pm 45°$ axes, while the plaid patterns had perceived motions along the horizontal axis, as shown in Fig. 2A. The spatial frequency of the SW gratings was 1.4 cpd. The fundamental components of the SW gratings had 50% contrast, resulting in a net SW grating contrast of $\pi/8$, or 39% (all contrasts expressed in Michelson contrast). The SW plaids, constructed by adding orthogonal SW gratings, had net contrasts of $\pi/4$, or roughly 79%. The mean luminance of the display was 70 cd/m^2 for all luminance stimuli. (SW gratings had luminances of 43 and 97 cd/m^2, and SW plaids had luminances of 15, 70 and 125 cd/m^2. MF stimuli, and fractional-*F* stimuli, all had roughly the same luminance extrema and contrasts as the SW stimuli, as can be seen in the luminance profiles in the top row of Fig. 1.

In the chromatic plaids experiment, stimuli had the identical spatial patterns as those in the luminance plaids experiment, but they had roughly isoluminant, chromatic modulation at the experimental waveform, in place of the achromatic, luminance modulation used for luminance stimuli. Chromatic modulation was along the axis defined by the red and blue phosphors of the monitor. (These endpoints were chosen to maximize the color saturation in the stimuli.) The CIE chromaticity coordinates of the endpoints, defining the maximum available chromatic modulation, were red: 0.630, 0.344 and blue: 0.155, 0.070. Chromatic gratings used 39% of this modulation, and chromatic plaids used 79% of this modulation. An isoluminant red-blue line was defined for each subject by the minimum motion method of Cavanagh, MacLeod and Anstis (1987), with subjects adjusting the intensity of the red phosphor to match the luminance of the full-intensity blue phosphor. The mean luminance of the chromatic stimuli was about 15 cd/m^2, depending on the individual equiluminance settings of each subject. Equiluminance was determined for each subject with 2.8 cpd sine-wave gratings, equivalent to 2*F*, as a compromise between the experimentally most crucial *F* and 3*F* spatial frequencies. The dependence of equiluminance settings on spatial parameters (Cavanagh et al., 1987) implies that no single equiluminance ratio can apply to all the components of the stimuli. Moreover we did not correct for chromatic aberration. Therefore the chromatic stimuli in this experiment must be considered only approximately isoluminant, with large chromatic contrasts and small, but nonzero, luminance contrasts.

In the barberpole experiment, the gratings were constructed just as described for the luminance plaids experiment, except that only a single grating, of spatial frequency 2.2 cpd and orientation $-26°$, was used. In the barberpole condition, this grating was only visible through a simulated barberpole aperture, in an otherwise homogeneous grey field of 70 cd/m^2. The barberpole was 0.4° of visual angle wide, and oriented at $-116°$. With this construction geometry, rightward movement of the grating behind the circular aperture generates a perceived direction of motion of 26° to the right of vertical, while the identical rightward movement of the grating behind the barberpole aperture generates a perceived direction of motion of 26° to the left of vertical, as shown in Fig. 2B. This reversal by the barberpole of the horizontal component of apparent motion could then be picked up in the subjects' binary responses of 'right' or 'left' perceived motion.

All stimuli were generated by a Number Nine Pepper SGT Plus graphics coprocessor board in a 386 PC, and displayed on a Tektronix 690SR color monitor at 60 Hz NI. The graphics output had 8 bits per channel, allowing up to 256 simultaneous discrete levels for either luminance or chromatic modulation. A linearizing look-up table was used to compensate for the gamma-nonlinearities in the monitor's output, with independent values for each of the three electron guns (Mulligan, 1986). All stimuli were viewed binocularly through a central circular aperture, with a diameter of 5° of visual angle, in a black cardboard frame covering the monitor. Each presentation consisted of nine frames, flashed for 100 ms per frame, with no inter-frame intervals. Stimuli jumped one quarter cycle between each frame, yielding a temporal frequency of 2.5 Hz for the fundamental component. A homogeneous gray field, of the same mean luminance and chromaticity as the stimuli, was displayed between trials. A small fixation cross was continuously present at the center of the display; it was red for the luminance stimuli, and white for the chromatic stimuli.

2.2. Procedure

Five experienced psychophysical observers with normal color vision, and normal or corrected-to-normal acuity, including both authors, were subjects in this experiment. There were three experimental sessions per subject (one for luminance gratings and plaids, one for chromatic gratings and plaids, and one for luminance grating and barberpole). Each session lasted approximately 1 h. Subjects sat in a dark room, and signaled the perceived direction of motion on each trial by pushing buttons on a trackball mouse. Subjects were instructed to make binary responses of 'right' or 'left' after every trial, based only on the horizontal components of perceived motion.

In each experimental session, there were five paired blocks of trials. The first paired block was just for practice and response stabilization, and data was only analyzed from the subsequent four paired blocks. Each paired block consisted of one block of 144 component grating trials, and one block of 144 pattern (plaid or barberpole) trials. Each block included eight trials of each of the 18 fractions of restored F, in random order. This yielded a total of 32 individual trials for each stimulus, per subject per experiment. Half the trials had rightward displacement of the stimulus, and half leftward, randomly intermixed. For the component gratings blocks of the luminance plaids and chromatic plaids experiments, the two grating orientations, $\pm 45°$, were each used on half the trials, randomly intermixed. In the barberpole experiment, the grating was always oriented at $-26°$. At the start of the chromatic plaids experiments, each subject established a personal equiluminance ratio for the red and blue phosphers, taken as the mean of ten minimum-motion settings, after five practice settings.

Responses were classified for analysis as forward or backward based on the perceived direction of motion of the SW grating in the circular aperture, as shown in Fig. 2. Rightward displacement of SW gratings in the circular aperture generated rightward apparent motion in all three experiments, so 'right' responses were interpreted as 'forward' for all rightward displacement trials. Rightward displacement of luminance SW plaids and chromatic SW plaids also generated rightward apparent motion. But note that with the barberpole aperture, rightward displacements of SW gratings generated leftward apparent motion, due to the barberpole illusion, so these were tallied as 'backward' responses. Motion-reversal points, defined as the fraction of F for which forward and backward responses were equally likely, were estimated by linear interpolation between the data points bracketing 50% forward response. Each experiment yielded four motion-reversal points per subject, with in-phase and antiphase reversals for both grating and pattern stimuli.

3. Results

3.1. Luminance gratings and plaids

In the first experiment, subjects reported the perceived directions of apparent motion for luminance gratings and luminance plaids, presented in quarter cycle steps. All five subjects always saw forward motion in SW gratings (160/160 total trials), and usually saw backward motion in MF gratings (147/160). This replicates several previous reports of reversed motion in MF gratings. In addition, all five subjects also always saw forward motion in SW plaids (160/160), and almost always saw backward motion in MF plaids (157/160). This establishes that MF plaids, like MF gratings, generate reversed apparent motion.

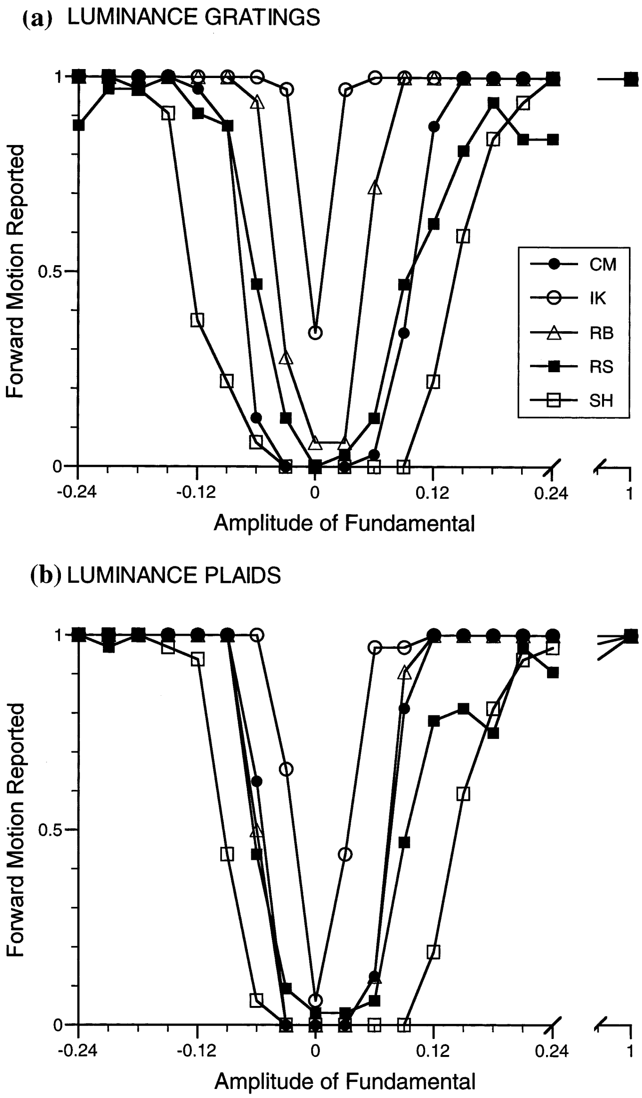

Fig. 3. Perceived direction of motion of luminance gratings and plaids. Each curve shows the proportion of forward responses reported by a subject for (A) 1-dimensional luminance gratings, and (B) 2-dimensional luminance plaids, as a function of the amount of partially restored fundamental. Each data point represents 32 trials. The origin of the abscissa represents pure missing-fundamental stimuli (0.00*F*). Positive values along the abscissa correspond to the amount of in-phase fundamental added back to missing-fundamental stimuli, as a proportion of the fundamental amplitude in the square-wave stimulus. Negative values along the abscissa correspond to further subtraction of in-phase fundamental from missing-fundamental stimuli, or equivalently, addition of antiphase fundamental. All subjects had a 1.00 frequency of reporting forward motion for both square wave gratings and square-wave plaids (points to right of the break), and near zero frequency of reporting forward motion for missing-fundamental gratings and missing-fundamental plaids. The subject legend is shown in (A), and applies to all data shown in Figs. 3, 5 and 7.

Fig. 3A plots the frequencies with which each of the five subjects reported forward motion in the isolated luminance gratings, as fractions of *F* were restored to MF gratings. The central data points, at 0.00 *F*, represent the responses to pure MF gratings. Points to the right of 0.00 represent addition of in-phase *F*, and points to the left of 0.00 represent addition of antiphase *F*. The far right data points, at 1.00, represent the pure SW grating. Each subject showed a sharp transition from backward to forward perceived motion, as *F* was incrementally restored either in-phase or antiphase. There was large inter-subject variability, however, in the locations of these transitions. In particular, note the large but consistent differences between subjects IK and SH, who reliably disagreed on the perceived directions of motion over a large range of stimuli.

Fig. 3B shows the corresponding data from the same experiment for luminance plaid stimuli. The pattern of responses was very similar to that for the luminance gratings shown in 3A. Each subject again exhibited sharp transitions from backward to forward motion as *F* was restored to the MF plaids, with large variability between subjects. Overall, forward motion was reported in 73% (2098/2880) of all the luminance grating trials and 73% (2093/2880) of all the luminance plaid trials, consistent with the hypothesis that the direction of motion of the plaids was entirely determined by the direction of motion of its Fourier components.

Motion-reversal points were estimated for each subject from the data shown in Fig. 3. Fig. 4A compares the motion-reversal points for each subject's responses to plaids versus gratings. The spread of data reflects the range of relative sensitivities among the individual subjects. These data lie very close to the hypothetical identity line of slope 1 (shown as the dotted line), indicating that for each subject the fraction of *F* needed to restore forward motion to MF plaids was approximately equal to that needed to restore forward motion to its component gratings. Thus for each subject, the plaid motion became ambiguous at the same critical amplitude of *F* which made the component grating motion ambiguous. This sensitive measure failed to find any evidence for feature-tracking motion signals in the plaid stimuli, beyond any which might be present in their component gratings.

The approximate symmetry of the data in Fig. 3A,B about the 0.00 point suggests that in-phase and antiphase *F* had roughly equivalent effects on the perceived direction of motion, although a slight skewing to the right suggests that antiphase *F* may have been somewhat more effective. For the grating stimuli (Fig. 3A), forward motion was reported in 71% (905/1280) of the trials with partial in-phase *F* (excluding the SW trials), and in 80% (1020/1280) of the trials with partial antiphase *F*. For the plaids, (Fig. 3B), forward motion

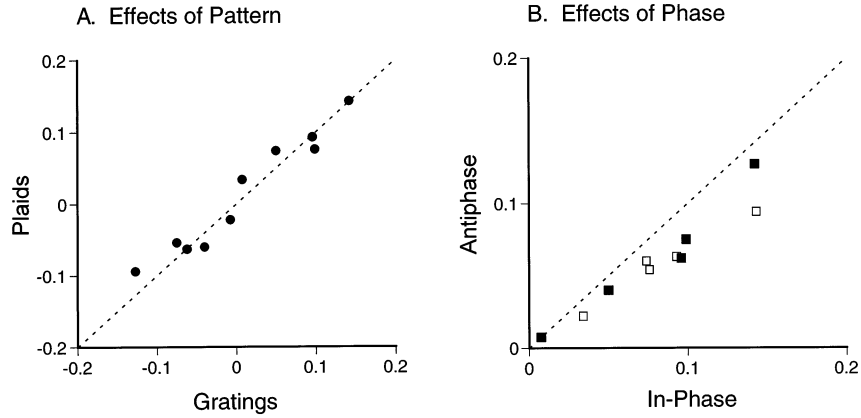

Fig. 4. Plots of the motion-reversal points for luminance gratings and plaids, derived from the data shown in Fig. 3, show the effects of (A) stimulus pattern and (B) phase of partially restored fundamental, on the perceived direction of motion. Motion-reversal points represent estimates of the values of restored fundamental which would give 50% forward responses for each subject. Each curve in Fig. 3 yielded two motion reversal points, one for in-phase fundamental, and one for antiphase. (A) To illustrate the effect of stimulus pattern, each motion reversal point for luminance gratings from Fig. 3A is plotted against the corresponding motion reversal point (i.e. same subject and phase of the fundamental) for luminance plaids from Fig. 3B. The broken line represents the hypothetical identity relationship between motion reversals for gratings and plaids. (B) For the effects of phase, the two motion reversal points from each curve, corresponding to in-phase and antiphase restored fundamental, are plotted against each other. Solid squares represent data from the luminance gratings in Fig. 3A, and open squares data from the luminance plaids in Fig. 3B. The broken line here represents hypothetical equivalence between in-phase and antiphase partial restoration of the fundamental.

was reported in 69% (884/1280) of the in-phase trials, and 82% (1046/1280) of the antiphase trials. Fig. 4B plots the relationship between each subject's motion-reversal points for antiphase F versus in-phase F, for both gratings (filled squares), and plaids (open squares). Both sets of points lie near, but below, the dotted identity line, consistent with a somewhat greater sensitivity to antiphase F for both types of stimuli.

3.2. Chromatic gratings and plaids

In the second experiment, stimuli were constructed just as in the first experiment, except that luminance modulation was replaced by chromatic modulation, along a roughly isoluminant, red-to-blue axis. The results for these chromatic stimuli were qualitatively the same as those for the luminance stimuli: All five subjects reported forward motion with 100% accuracy for both the chromatic SW gratings (160/160) and the chromatic SW plaids (160/160). All five subjects usually reported backward motion for both the chromatic MF gratings (150/160) and the chromatic MF plaids (158/160). We conclude that chromatic MF gratings and plaids, at approximate isoluminance, also generate reversed apparent motion when presented in quarter-cycle jumps.

The plots in Fig. 5A show the frequency with which each subject reported forward motion, as varying fractions of F were restored to chromatic gratings. Fig. 5B shows the corresponding data for chromatic plaids. As with the luminance stimuli, each subject had fairly sharp transitions from backward to forward motion as F was restored, but there was considerable variability between subjects in the reversal points. The apparent similarity of Fig. 5A (chromatic gratings) and B (chromatic plaids) suggests there was little differential sensitivity to partially restored F between chromatic gratings and plaids.

Overall, forward motion was reported in 64% (1851/2880) of all chromatic grating trials, and in 58% (1676/2880) of all chromatic plaid trials. In the comparison of motion reversal points for plaids versus gratings, shown in Fig. 6A, the data again fell near the hypothetical identity line of slope 1 (shown as the dotted line). This indicates that the apparent motion of chromatic plaids had roughly the same sensitivity to F as the apparent motion of their component chromatic gratings. The perceived motion of chromatic plaids, like that of luminance plaids, was apparently entirely accounted for by the direction of motion of their component gratings.

The symmetry about $0.00F$ of the plots in Fig. 5A,B suggests that in-phase and antiphase F had equivalent effects on chromatic MF stimuli. For chromatic gratings, forward motion was reported in 66% (840/1280) of the in-phase trials, and in 66% (841/1280) of the antiphase trials; for plaids, in 58% (741/1280) of the in-phase trials, and in 60% (773/1280) of the antiphase trials. Fig. 6B plots the relationship between subjects' motion-reversal points for antiphase versus in-phase F, for gratings (filled squares) and plaids (open squares), and reveals no effect of phase.

3.3. Barberpole experiment

In the third experiment, moving gratings were viewed through either the full, circular aperture as in previous experiments (grating condition), or through a simulated thin, oriented aperture (barberpole condition). Recall that rightward displacements of SW gratings generated rightward ('forward') apparent motion in the circular aperture, but leftward ('backward') apparent motion in the barberpole aperture, as diagrammed in Fig. 2B. (This is potentially confusing, as it means that if MF stimuli reverse the direction of apparent motion relative to SW stimuli, this reversal will be reported as 'forward' responses in the barberpole condition; that is, reversal of backward motion yields forward motion.) The component gratings in this experiment were similar to the component gratings in the luminance plaids experiment, and generated similar responses, with 100% forward motion reported for SW gratings in the circular aperture, and 96% backward motion reported for MF gratings in the circular aperture. As expected, the barberpole effect effectively shifted the perceived direction of motion, as all five subjects never reported forward motion for SW gratings in the barberpole aperture (0/160 total trials). But all five subjects always reported forward motion for MF gratings in the barberpole aperture (160/160). Thus SW gratings and MF gratings produced opposite perceived directions of motion in the barberpole aperture, as they did in all the other stimulus configurations we studied. This is most parsimoniously interpreted as the barberpole effect acting on the reversed apparent motion of the MF grating. (Although subjects only reported the horizintal component of motion, to our eyes these MF stimuli always appeared to move parallel to the long axis of the barberpole, in the opposite direction from SW gratings in the barberpole.)

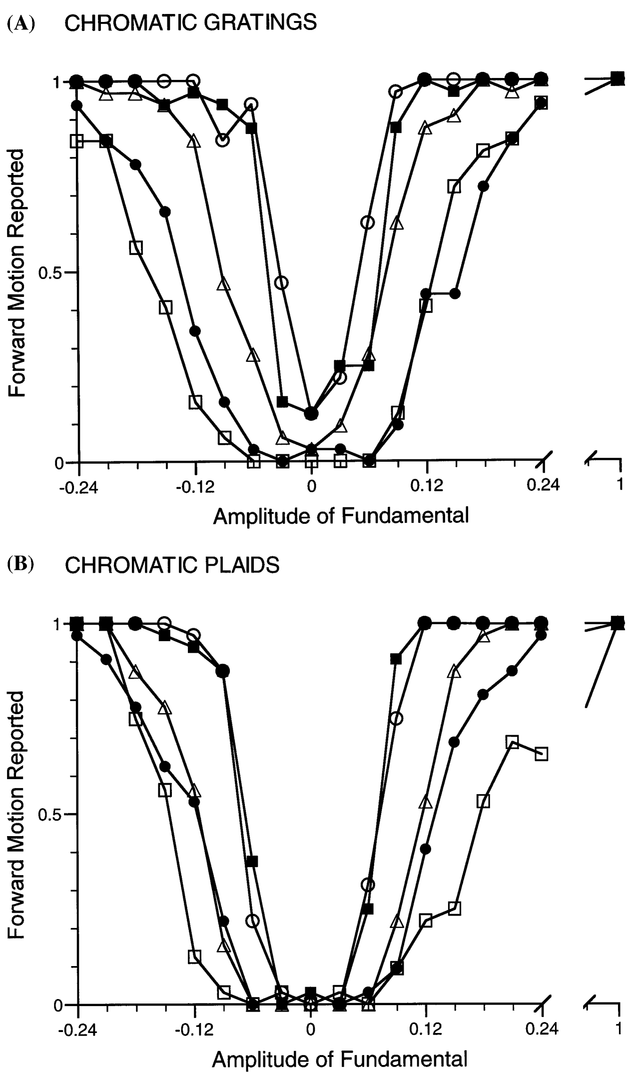

Fig. 5. Perceived direction of motion of chromatic gratings and plaids. Each curve shows the proportion of forward responses reported by a subject for (A) 1-dimensional chromatic gratings, and (B) 2-dimensional chromatic plaids, as a function of the amount of partially restored fundamental. Conventions and axes are the same as in Fig. 3.

Fig. 7A plots the frequency with which each subject reported forward motion, as varying fractions of F were restored to luminance gratings in the circular aperture. This essentially replicates the data plotted in Fig. 3A, with minor differences that may reflect the somewhat different spatial frequency, velocity and orientation in this experiment. Fig. 7B plots the corresponding data for luminance gratings in the barberpole aperture. Once again, subjects exhibited sharp reversals of apparent motion as F was restored, although small amounts of F added back to the MF stimuli appeared to be more effective in reversing the apparent motion of the isolated gratings (Fig. 7A) than the barberpole stimuli (Fig. 7B).

Forward motion was reported in 63% (1802/2880) of the trials in the circular aperture, and in 58% (1665/2880) of the barberpole trials. But because the barberpole effect itself reversed the reported motion of SW stimuli, this latter figure corresponds to SW-like motion being reported in only 42% (1215/2880) of barberpole trials. All five subjects saw SW-like motion more frequently in the circular apertures, with their individual ratios ranging from 1.16 to 2.94, indicating that the effectiveness of restored F to motion perception is reduced in barberpole apertures compared to that in the circular aperture.

The reduced sensitivity to F in the barberpole condition can be seen more clearly (and without double negatives!) in Fig. 8A, which compares the motion reversal points for gratings in the circular aperture versus barberpoles. All the motion reversal points in the barberpole required more F than the corresponding motion reversal points for gratings in the circular aperture. The dotted line of slope 1 shows the hypothetical identity relationship; the calculated best-fitting line through the data had a slope of 1.6. This reduced sensitivity to F in the barberpole display was contrary to the expectation that a contribution from feature-tracking along the barberpole contour would increase the sensitivity to F.

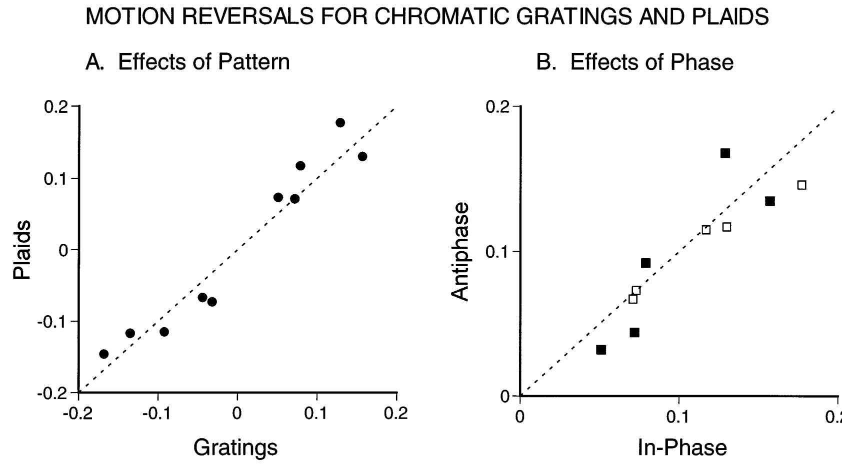

Fig. 6. Plots of the motion-reversal points for chromatic gratings and plaids, derived from the data shown in Fig. 5, show the effects of (A) stimulus pattern and (B) phase of partially restored fundamental, on the perceived direction of motion. Conventions and axes are the same as in Fig. 4.

The effects of in-phase and antiphase restoration of *F* in this experiment were again roughly symmetrical about 0.00 *F* (Fig. 7A,B). But as in the first experiment with luminance gratings and plaids, antiphase *F* appeared to be somewhat more effective. Overall, for gratings, forward motion was reported in 59% (749/1280) of the in-phase trials, and in 69% (886/1280) of the antiphase trials; for barberpoles, backward (i.e. SW-like) motion was reported in 40% (510/1280) of the in-phase trials, and in 43% (545/1280) of the antiphase trials. Fig. 8B plots the relationship between subjects' motion-reversal points for antiphase versus in-phase *F*, for gratings (filled squares) and plaids (open squares). Most of the data points lie below the dotted identity line, indicating a stronger effect of antiphase *F*.

4. Discussion

Adelson and Bergen (1985) discovered that MF luminance gratings appear to move backward when presented in quarter-cycle jumps. We report here that MF luminance plaids, constructed from orthogonal MF gratings, also appear to move backward when presented in quarter-cycle jumps. In our second and third experiments, we found that MF chromatic gratings and plaids, and MF luminance barberpoles, exhibit the same backward perceived motion.

In addition, we quantified the amplitude of *F* necessary to restore forward motion to these MF stimuli. Our subjects were all experienced psychophysical observers, and each exhibited reliable, sharp reversals of the perceived direction of apparent motion as small fractions of *F* were restored to MF stimuli. Nevertheless, there were remarkably large differences between the subjects in their sensitivity to *F*, with estimated motion reversal points ranging from 0.01 to 0.16 for luminance gratings and plaids, from 0.03 to 0.18 for chromatic gratings and plaids, and from 0.12 to 0.27 for luminance barberpoles. M.G. Harris (personal communication 1990, cited in Georgeson & Shackleton, 1992) noted that about 0.06*F* sufficed to restore forward motion to MF gratings. Baro and Levinson (1988) reported one observer consistently saw forward motion in MF gratings; perhaps that observer represents one end of a broad distribution of individual sensitivities to *F*, rather than a qualitatively different mechanism. In our study, one observer reported forward motion for MF luminance gratings on about 1/3 of the trials. The underlying cause of these large individual differences is unknown. Further work to identify the source of these individual differences may help identify the mechanism that is sensitive.

Because of these large individual differences in motion-reversal points, it would be specious to calculate a unique, critical fraction of *F* as the motion-reversal point for the human visual system. Still, it may be instructive to compare the range of empirically determined motion-reversal points (0.01–0.16*F* for MF luminance gratings) with the predictions based on a few standard models: (1) A pure feature-tracking process would not generate reversed apparent motion to begin with, as the features of MF gratings still move forward. (2) On the principle that the lowest spatial frequencies 'capture' higher spatial frequencies (Ramachandran, Ginsburg & Anstis, 1983), motion reversal would require only threshold levels of *F*, on the order of 0.01*F*. (3) If the direction of perceived motion was determined by the Fourier component with the largest amplitude, as originally suggested by Adelson and Bergen (1985), the motion-reversal points would be at 0.33*F*; that is, just equal to the amplitude of the third harmonic in a SW grating. (4) If it depended on the net energies of all forward and backward Fourier components (Van Santen & Sperling, 1984), reversal would occur at approximately 0.29*F*. (5) Gradient models, which have also been shown to account for reversed motion in MF stimuli (Mather, 1990; Johnston & Clifford, 1995), tend to predict motion reversal points comparable to those of the motion-energy models above. However, with careful adjustment of the spatial tuning and the relative weighting of filters, a considerable range of motion-reversal predictions could be accommodated (unpublished analysis).

Although motion-detection models successfully predict reversed apparent motion for MF stimuli, they

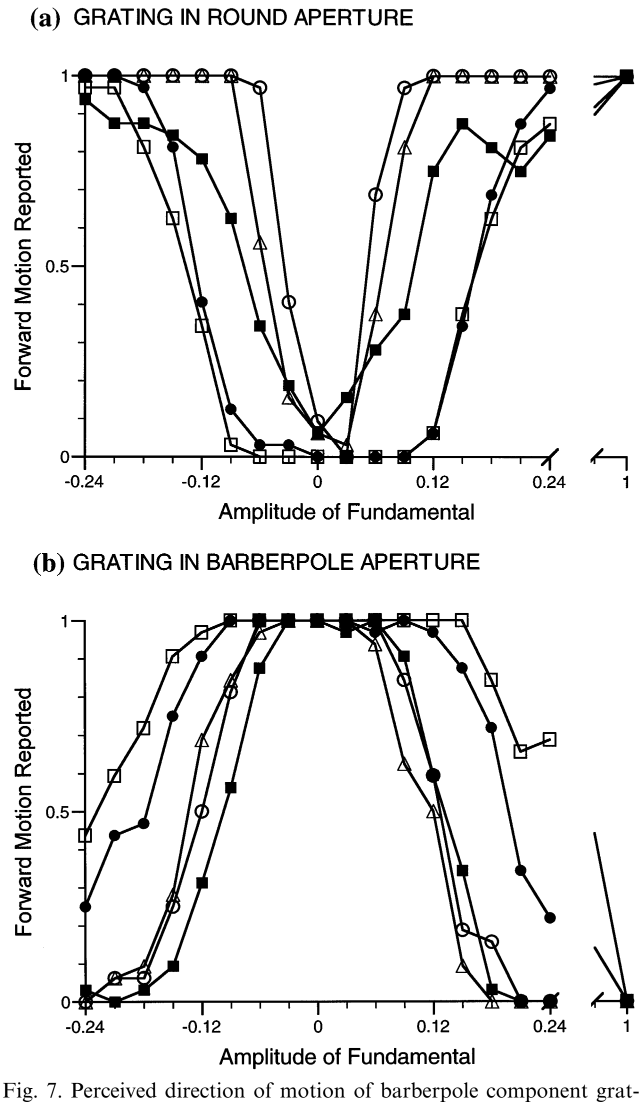

Fig. 7. Perceived direction of motion of barberpole component gratings and barberpoles. Each curve shows the proportion of forward responses reported by a subject for (A) 1-dimensional luminance gratings seen through the standard, round aperture, and (B) the identical gratings seen through a barberpole aperture, as a function of the amount of partially restored fundamental. Note that the barberpole reversed the reference 'forward' direction of motion, relative to the round aperture, due to its reversal of the horizontal components of perceived motion as illustrated in Fig. 2. Conventions and axes are otherwise the same as in Fig. 3.

generally fail to account for the empirically observed motion-reversal points. Mather, Cavanagh and Anstis (1985) hypothesized that perceived apparent motion depends on the net motion signals from both the motion detection and feature-tracking processes. If so, enhancing the feature signals should reduce the amount of *F* needed to restore forward motion. As discussed in the Introduction, plaids, chromatic stimuli, and barberpoles are all thought to be good candidates for the feature-tracking process, so we chose these manipulations to test this hypothesis. However, we found that none of these manipulations eliminated the reversed apparent motion, nor even reduced the amount of *F* necessary to restore forward motion. For both luminance plaids and chromatic plaids, the reversal of apparent motion was entirely accounted for by the independent motions of their component gratings, with no detectable contribution from feature-tracking of their terminators, intersections or blobs. The chromatic stimuli were somewhat less sensitive to the partially restored F than the corresponding luminance stimuli. And the barberpole aperture also reduced the effectiveness of the restored *F* for all five subjects, contrary to the hypothesis that feature-tracking may be of particular importance in the barberpole.

When fractions of *F* are restored to MF stimuli, the effects on features and overall appearance depend strongly on the phase of *F*. As the amplitude of *F* added to a MF stimulus is varied continuously from -0.24 (antiphase) to +0.24 (in-phase), the resulting stimuli appear to change monotonically, becoming more and more SW-like, with no apparent transitions associated with passing through 0.00*F* (see Fig. 1). Therefore one would expect restoring fractions of in-phase and antiphase *F* to have opposite effects on motion signals from the feature-tracking process. On the other hand, the Fourier energy in *F* is independent of phase, and so in-phase and antiphase *F* should be equivalent for motion processes that follow the 'Motion From Fourier Components Principle'. In our experiments, in-phase and antiphase *F* had roughly equivalent effects on the direction of perceived motion, as can be seen in the symmetry of responses about 0.00*F* (Figs. 3, 5 and 7), providing further evidence in support of the motion detection process. But with the luminance stimuli, antiphase F was somewhat more effective than in-phase *F* (Fig. 4B, Fig. 8B, Table 1). This skewing might be an indication of some involvement of a feature-tracking mechanism, although it was surprising that the more effective antiphase *F* made the stimuli look less SW-like than in-phase *F*. Alternatively, this skewing might be due to nonlinear distortion products, or a second-order motion detection process.

We did not vary the spatial and temporal parameters of our stimuli, and it is possible that a different configuration would have proven a more powerful stimulus for

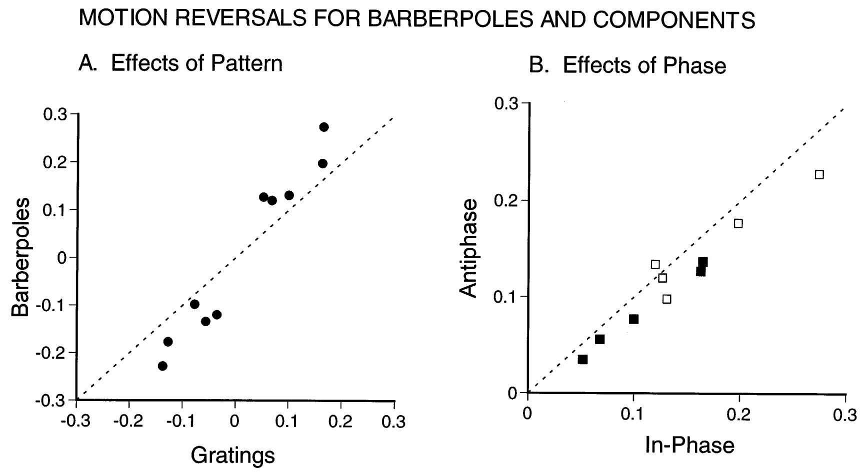

Fig. 8. Plots of the motion-reversal points for barberpole component gratings and barberpoles, derived from the data shown in Fig. 7, show the effects of (A) stimulus pattern, in this case round versus barberpole aperture, and (B) phase of partially restored fundamental, on the perceived direction of motion. Note, as in Fig. 7, that the reference 'forward' direction of motion is reversed by the barberpole relative to the standard, round aperture. Conventions and axes are otherwise the same as in Fig. 4.

the feature-tracking process. Feature-tracking has been reported to require low temporal frequencies and long presentation times, but our 2.5 Hz temporal frequencies and 900 ms presentations were well within the reported comfort zone for feature-tracking (Victor & Conte 1990; Lu & Sperling 1995). Moreover, Georgeson and Shackleton (1989) reported reliable forward motion from the feature-tracking process using dichoptically presented MF stimuli which were otherwise very similar to the ones we used. Georgeson and Harris (1990) also restored forward motion to MF gratings by intercalating short, blank interstimulus intervals (ISIs) between frames, which were interpreted as interrupting the motion detection process to isolate the feature-tracking process (Georgeson & Harris, 1990; Smith, 1994). Additional experiments have confirmed that ISIs also restore forward motion to our MF luminance gratings and plaids (R.O. Brown, unpublished observations). Therefore we believe that our MF stimuli were sufficient to drive the feature-tracking process.

We conclude that the apparent motion in our stimuli was dominated by motion-detection mechanisms. Our experiments turned up no evidence to support feature tracking, despite our best efforts to add strong feature-tracking signals to our stimuli. In particular, our analysis of motion-reversals provided a sensitive measure of the effects of small fractions of F on MF stimuli, and detected reliable inter-subject differences, yet failed to pick up any differences due to our manipulations of features.

Given the considerable evidence for a feature-tracking mechanism in visual motion perception, why was there no evidence for feature-tracking in our experiments? One possibility, originally suggested by Braddick (1980), is that the motion-detection process 'constrains' the feature-tracking process, and the forward feature-tracking signals in our MF stimuli were outside the constrained range consistent with the backward motion-detection signals. A second possibility is that feature-tracking only contributes to apparent motion in the absence of signals from motion-detection, being in effect the motion mechanism of last resort. Indeed, much of the experimental evidence for feature-tracking comes from studies in which motion-detection signals were made ambiguous to reveal feature-tracking. But arguing against both these possibilities, apparent motion can be determined by feature-tracking even in the presence of opposing signals from the motion detection process (Anstis & Cavanagh, 1981; Mather et al., 1985). A third possibility is that feature-tracking may provide an all-or-none signal, of fixed strength,

Table 1
Summary of results from all three experiments[a]

Experiment	Square-wave	Missing-fundamental	In-phase	Antiphase
Luminance				
Gratings	1.00	0.08	0.71	0.80
Plaids	1.00	0.02	0.69	0.82
Chromatic				
Gratings	1.00	0.06	0.66	0.66
Plaids	1.00	0.01	0.58	0.60
Barberpole				
Gratings	1.00	0.04	0.59	0.69
Barberpoles	1.00	0.00	0.40	0.43

[a] Table shows the proportion of forward responses in each experiment, on grating and pattern trials, for four types of stimulus waveforms: square-wave stimuli, $n = 160$ (per entry); missing-fundamental stimuli, $n = 160$; in-phase, partially restored fundamental stimuli, combining the eight values from $+0.03F$ to $+0.24F$, $n = 1280$; antiphase, partially restored fundamental stimuli, combining the eight values from $-0.03F$ to $-0.24F$, $n = 1280$.

and that the feature-tracking signals already available in the MF gratings sufficed to activate it, so that further strengthening the feature signals had no additional effect. Part of the difference may reflect the different amount of top-down modulation on motion perception. In our experiments, subjects were not specifically instructed to 'track' certain features. In the absence of *deliberate* tracking of visual features, the perceived direction of motion is largely determined by the direction of dominant motion energy.

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