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Similarities between visual processing of shear and uniform motion

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Abstract

A number of papers have claimed that at moderate to high contrasts, sensitivity is higher for shear motion than for uniform motion. We show in a 2×2AFC task, designed to minimize any potential artefacts due to criterion level or response bias, that sensitivities are essentially equal for shear and uniform motion under general conditions. It has also been claimed that position tracking enhances sensitivity for shear motion. We added moving sinusoidal gratings to stationary sinusoidal gratings of the same spatial frequency and orientation, to create stimuli in which position changes and motion energy have opposite directions, to show that shear and uniform motion are both subserved by motion-energy mechanisms at speeds above 2.0 deg/s and by position tracking at slower speeds.

1. Introduction

When two elements or two regions of a visual field move in opposite directions, the motion is termed "shear" motion (Fig. 1(c) and (d)). When the two elements or regions both move in the same direction at the same speed, the motion is uniform relative to the observer and so is termed "uniform" motion (Fig. 1(a) and (b)). Shear motion is a common occurrence in natural scenes (Sachtler & Zaidi, 1995; Scott & Longuet-Higgins, 1991), for example at the boundaries of objects moving in front of stationary scenes. Shear information extracted from optic flow can be used to estimate the surface gradient (Longuet-Higgins & Prazdny, 1980), especially when shears are combined into deformations of the optic flow (Atchley, Andersen, & Wuestefeld, 1998; Koenderink & van Doorn, 1975, 1976, 1992; Meese, Harris, & Freeman, 1995). This has led to the idea that the brain may have specialized mechanisms for shear detection (Longuet-Higgins & Prazdny, 1980). Computational proposals for such detectors have involved center-surround motion units (Murakami & Shimojo, 1996; Nakayama & Loomis, 1974; Sachtler & Zaidi, 1995). There is also growing evidence of center-surround motion antagonism in cells of area MST (Eifuku & Wurtz, 1999; Orban et al., 1992).

Comparisons between sensitivity to uniform and shear motion have been made using a variety of methods (Krauskopf & Li, 1999; Lu & Sperling, 1995; Moller & Hurlbert, 1996; Nakayama & Tyler, 1981; Sachtler & Zaidi, 1995; Seiffert & Cavanagh, 1998; Snowden, 1992). At least two studies in the literature claim that, at moderate to high contrasts (>0.1), observers are more sensitive to shear than to uniform motion (Krauskopf & Li, 1999; Snowden, 1992). Snowden reported that uniform motion thresholds are twice as high as those of shear motion using random dots. Krauskopf and Li reported that the sensitivity for shear motion is 1.5 times higher than uniform motion, for Gaussian-windowed vertical gratings that were initially aligned in phase. Krauskopf and Li measured displacement thresholds using a motion/no-motion task for interleaved shear and uniform motion trials, whereas Snowden separated shear and uniform motion trials and used different 2AFC tasks, clockwise/counter-clockwise for shear and left/right for uniform motion.

The increased sensitivity for shear versus uniform motion has been explained by postulating either specialized center-surround neural mechanisms for shear motion (Kim & Wilson, 1997, see also Sachtler & Zaidi, 1995) or by claiming that in conditions where uniform motion is sensed by motion-energy mechanisms, the sensitivity to shear motion can be enhanced by comparisons of relative positions (Krauskopf & Li, 1999; Snowden, 1992). The difference between motions perceived by extracting motion energy versus comparisons

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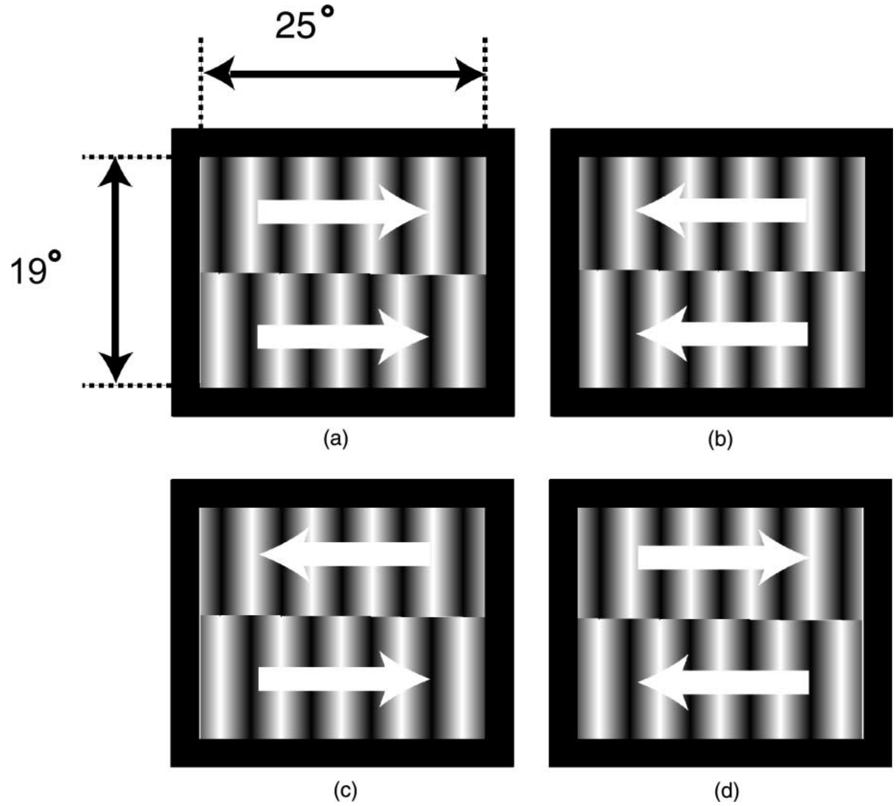

Fig. 1. The four possible pairs of directions of the top and bottom gratings in the displacement threshold experiment.

of positions over time is a fundamental question (Julesz, 1971; Lu & Sperling, 1995; Zaidi & DeBonet, 2000). In the present case, this issue is germane to whether specialized shear-motion detectors exist in the cortex.

The purpose of this paper is to examine both the claims relating to sensitivity and the claims relating to mechanism. We used a 2×2AFC (two times two-alternative-forced-choice) method that forces observers to independently choose a direction of each moving grating, thus minimizing any potential artefacts due to criterion level or response bias. In contrast, in previous studies using a 2AFC procedure, observers chose right or left directions of uniform motion and clockwise or counter-clockwise directions of shear motion. In these procedures, observers could respond to motion direction of one grating and infer the direction of the other grating without actually perceiving it. We find that when shear and uniform motions are interleaved using the 2×2AFC task, sensitivity is essentially equal for shear and uniform motion. Control experiments showed that the previous results claiming an advantage for shear motion are due to specific edge alignment conditions and motion detection tasks. We also used a stationary pedestal plus moving test paradigm to identify position-tracking and motion-energy regimes (Lu & Sperling, 1995; Zaidi & DeBonet, 2000), and found that both shear and uniform motion are subserved by position tracking at slow speeds and by motion energy at higher speeds.

2. Methods

2.1. Experiment 1: displacement thresholds for shear and uniform motion

2.1.1. Stimuli

Two adjacent vertical sinusoidal gratings were presented in the upper and lower halves of an image that subtended $25° \times 19°$ on the monitor. Each grating could independently move right or left in a trial. Fig. 1 shows the four possible pairs of directions of the top and bottom gratings. Spatial and temporal frequencies of both top and bottom gratings were the same, and initial spatial phases of both gratings were assigned separately and randomly for each trial. Stimuli had one of six temporal frequencies (0.25, 0.5, 1, 2, 4 and 8 Hz), three spatial frequencies (0.5, 1 and 2 c/deg) and two contrasts (0.05 and 0.20) for a total of 36 stimuli. The CIE (x, y) coordinates for a grey background were $(0.33, 0.33)$ and mean luminance was 35.0 cd/m^2. A fixation cross at 50% contrast, subtending 0.8°, was presented in the center of the screen between trials.

2.1.2. Apparatus

The stimulus was generated by a video controller (Cambridge Research Systems VSG2/5) in a 1 GHz Pentium computer and displayed on a color monitor (SONY GDM-F500R). The size of the display was $25^\circ \times 19^\circ$ surrounded by a dark frame. The resolution of the monitor was 800×600 pixels and the frame rate was 150 Hz. Each phosphor was driven by a 15-bit digital-to-analog converter. The monitor was gamma corrected and tested for linearity by using the OPTICAL device provided by Cambridge Research Systems.

2.1.3. Observers

Two observers participated in the experiment (including the first author). The observers were seated 89.7 cm in front of the display monitor and binocularly viewed the stimuli.

2.1.4. Procedure

The fixation cross was presented in the center of the screen during the initial adaptation period of 2 min. After the initial adaptation, a session of experimental trials began. The fixation cross was presented on a mid-grey screen for 3 s, then two adjacent vertical sinusoidal gratings were presented moving for the period of the trials, then the cross appeared again on a mid-grey screen until the observer responded.

We measured minimum displacement thresholds for shear and uniform motion. A staircase procedure was used to measure the displacement threshold at which directions of motion of both gratings were identified correctly 79% of the time. Displacement was decreased by 0.1 log unit after three successive correct pairs of response and increased by the same factor after each error. Each threshold was estimated from the average of the last nine reversals in one session. Data were obtained from two sessions (i.e. 18 reversals). The thresholds for shear and uniform motion were measured in the same session by interleaved staircases. We used a 2×2AFC method: observers had to choose left or right as directions of motion for each of the top and the bottom gratings simultaneously, and to indicate this by using two toggle switches on a switch box.

2.1.5. Results

Fig. 2 shows displacement thresholds for two observers at contrasts of 0.05 (Fig. 2a) and 0.20 (Fig. 2b). Each panel represents displacement thresholds for shear and uniform motion measured in one spatio-temporal condition. The panels are arranged so that each column represents one spatial frequency (c/deg) and each row

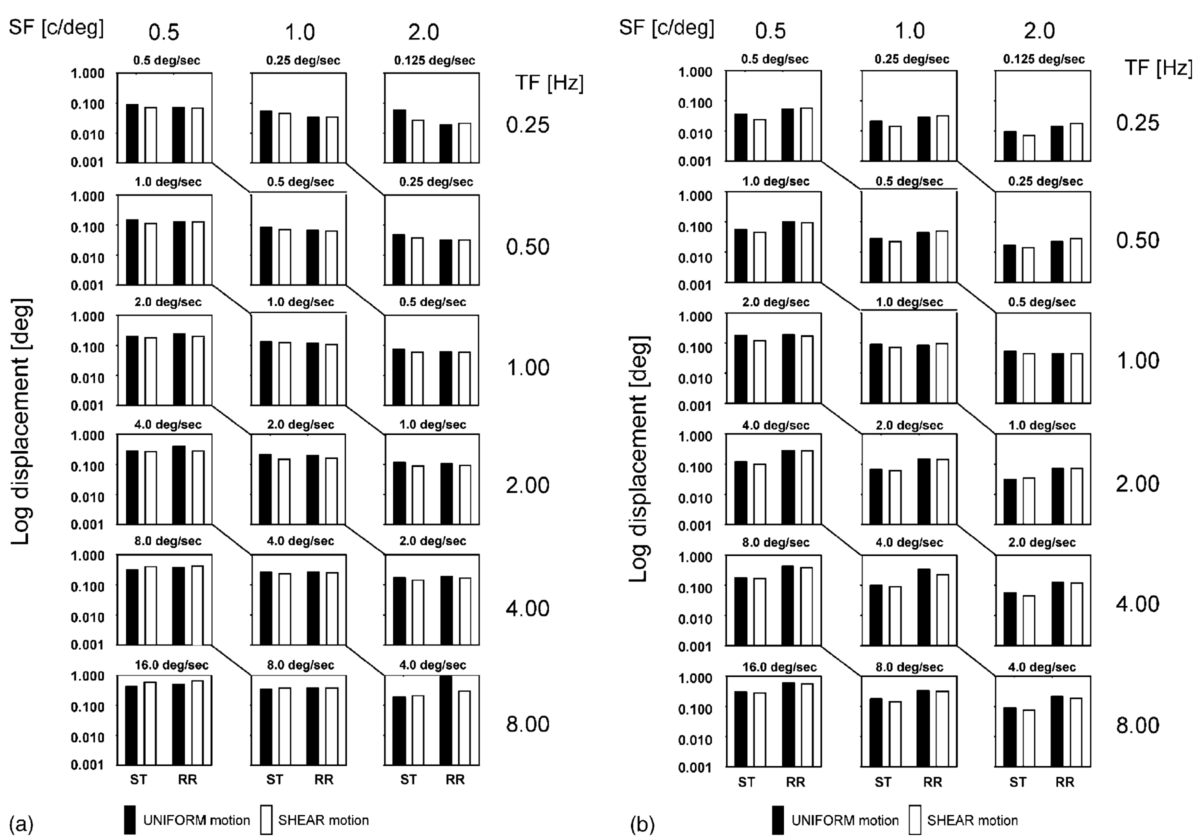

Fig. 2. Displacement thresholds for observers ST and RR. (a) Test contrast is 0.05, (b) test contrast is 0.20. The black bars represent log displacement thresholds (base 10) for uniform motion and white bars represent those for shear motion.

represents one temporal frequency (Hz). Speed in deg/s is indicated on the top of each panel. Panels with the same speed are linked with solid lines. The top right panel represents the slowest speed and the bottom left panel represents the fastest speed. The black bars represent log displacement thresholds (base 10) for uniform motion and white bars represent those for shear motion. In each panel, the two bars on the left represent results for observer ST and on the right for observer RR.

The results show that displacement thresholds were essentially similar for shear and uniform motion for all speeds at contrasts of 0.05 and 0.20. This is different from previous reports by Krauskopf and Li (1999) and Snowden (1992). Snowden reported that uniform motion thresholds are twice (0.30 log unit) as high as those of shear motion. Krauskopf and Li reported that at contrasts above 0.1 the sensitivity for shear motion is 1.5 times (0.18 log unit) higher than uniform motion.

There were a few important differences between our procedures and the studies mentioned above. First, in our experiment, the top and bottom gratings were initially assigned random phases, whereas Krauskopf and Li (1999) used Gaussian-windowed vertical gratings that were initially aligned in phase, and Snowden (1992) used random dots of which a few would have been aligned across the motion boundaries by chance. In a second experiment, therefore, we repeated the first experiment, but test stimuli were initially aligned in phase. Second, our 2×2AFC method was designed to minimizes any potential artefacts due to criterion level or response bias. It forced observers to independently choose a direction of each grating. In the second experiment, in an additional condition, we used Snowden's (1992) tasks to compare results.

2.2. Experiment 2: displacement thresholds for spatially aligned gratings

In Experiment 2, we measured displacement thresholds when top and bottom gratings were initially presented spatially aligned in phase. All other parameters were the same as those used in Experiment 1. Fig. 3 shows displacement thresholds for spatially aligned gratings at a contrast of 0.2 for the two observers. The arrangement of the panels is the same as that for Fig. 2. The black bars represent log displacement thresholds for uniform motion and white bars represent those for shear motion.

The results show that the displacement thresholds for shear and uniform motions were still similar, but the displacement thresholds for uniform motion were slightly higher than those for shear motion for almost all spatio-temporal conditions. Fig. 4 shows log threshold differences between shear and uniform motion for both observers. Positive values indicate that thresholds for

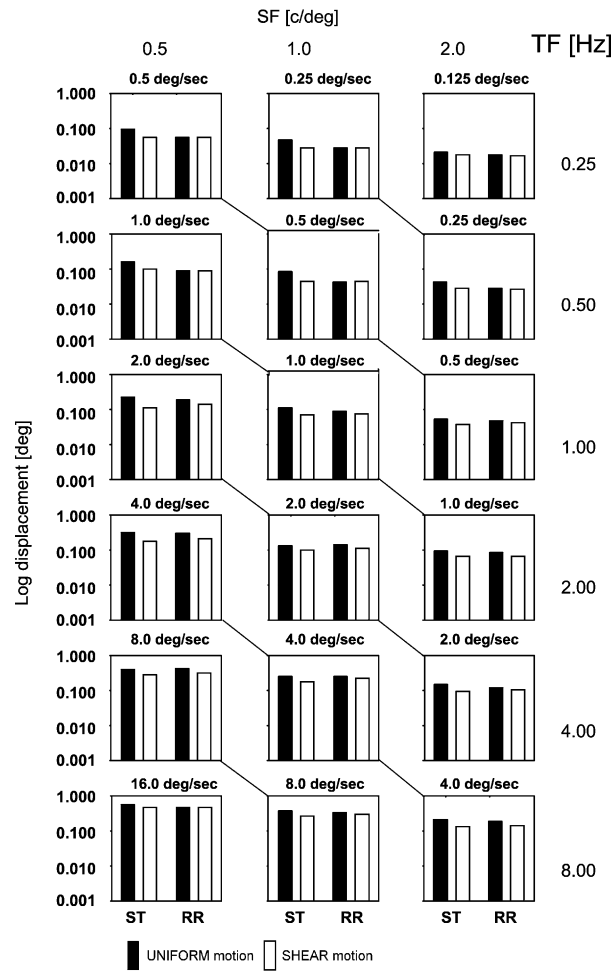

Fig. 3. Displacement thresholds for spatially aligned gratings at the contrast of 0.2 for observers ST and RR. The arrangement of the panels is the same as that of Fig. 2. The black bars represent log displacement thresholds for uniform motion and white bars represent those for shear motion.

uniform motion were higher than those for shear motion. The three columns on the left represent the spatially aligned conditions in Experiment 2 and the three columns on the right represent the data obtained in Experiment 1, i.e. the randomly aligned conditions.

The log threshold differences between shear and uniform motions in the spatially aligned condition range from −0.02 to 0.14 for observer ST and from 0.08 to 0.29 for observer RR. The mean log threshold differences were 0.06 for ST and 0.18 for RR. In the randomly aligned condition the log threshold differences between shear and uniform motions range from −0.09 to 0.18 for observer ST and from −0.04 to 0.18 for observer RR. The mean log threshold differences were 0.00 for ST and 0.09 for RR. Snowden (1992) reported a log threshold difference between uniform and shear motion of about 0.3 using random-dot patterns and Krauskopf and Li (1999) reported a value of about 0.10 at a contrast of 0.2 with spatially aligned gratings inside a Gaussian

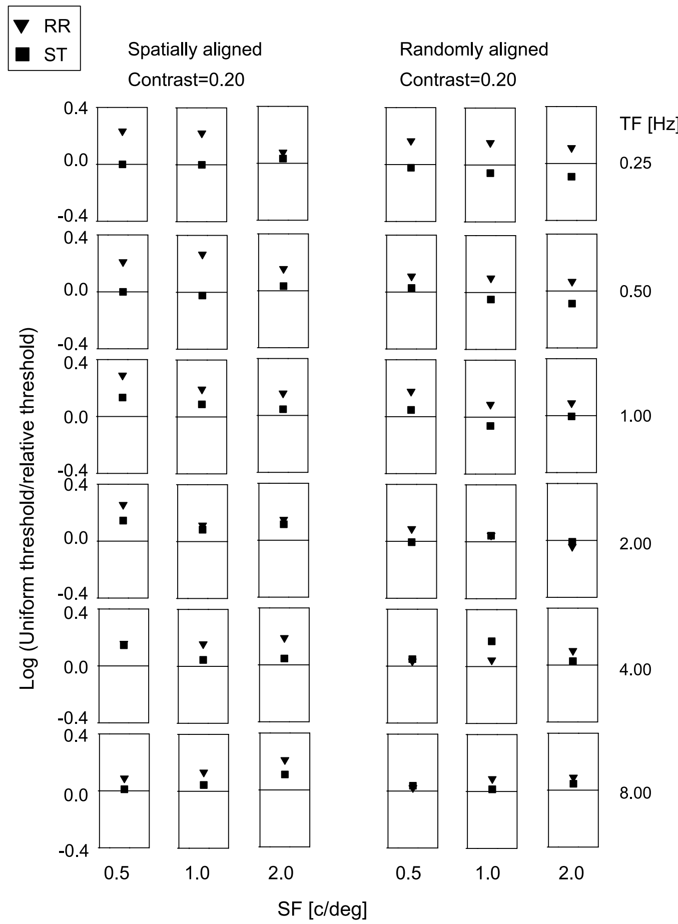

Fig. 4. Log threshold differences between shear and uniform motion at the contrast of 0.2 for observer ST and RR. Positive values indicate that thresholds for uniform motion were higher than those for shear motion. The three columns on the left represent the spatially aligned conditions in Experiment 2 and the three columns on the right represent the data obtained in Experiment 1, i.e. the randomly aligned conditions.

window. For the spatially aligned condition our results are close to those of Krauskopf and Li (1999).

In a second condition, we used Snowden's (1992) 2AFC procedure to measure the displacement thresholds for shear and uniform motions. Observers had to choose right or left directions of uniform motion, and clockwise or counter-clockwise directions of shear motion. Shear and uniform motion conditions were presented in separate sessions. The stimulus parameters were the same as those of the previous experiment, but we measured thresholds only in the four extreme conditions: 0.125 deg/s (SF $=$ 2 c/deg, TF $=$ 0.25 Hz), 0.50 deg/s (SF $=$ 0.5 c/deg, TF $=$ 0.25 Hz), 4.0 deg/s (SF $=$ 2.0 c/deg, TF $=$ 8 Hz) and 16.0 deg/s (SF $=$ 0.5 c/deg, TF $=$ 8 Hz).

In Fig. 5 the top four panels show the displacement thresholds in linear units for shear and uniform motion when we used the 2AFC method in the spatial alignment condition. For comparison the results for the randomly aligned 2×2AFC condition are replotted in linear units in the four panels at the bottom. Sensitivity for shear motion was higher than that for uniform motion in the 2AFC condition, and the amount of the difference was much greater than that with the 2×2AFC method. The log threshold difference for shear compared to uniform motion ranges from 0.09 to 0.18 for ST and from 0.09 to 0.36 for RR with mean differences of 0.15 for ST and 0.22 for RR, respectively. Compared to the results in Fig. 4, the 2AFC procedure increases the log threshold difference between uniform and shear motions by 0.11 for ST and by 0.07 for RR. However, even in the 2AFC spatially aligned condition, the sensitivity difference between shear and uniform motion is appreciably lower than that reported by Snowden (1992). He reported that uniform motion thresholds were 0.30 log units lower than shear motion thresholds.

2.3. Experiment 3: motion energy and position-tracking regimes for shear and uniform motion

In Experiments 1 and 2, we found small differences in thresholds between shear and uniform motions. We also found that the differences were strongly dependent on the stimulus parameters and procedure. For instance,

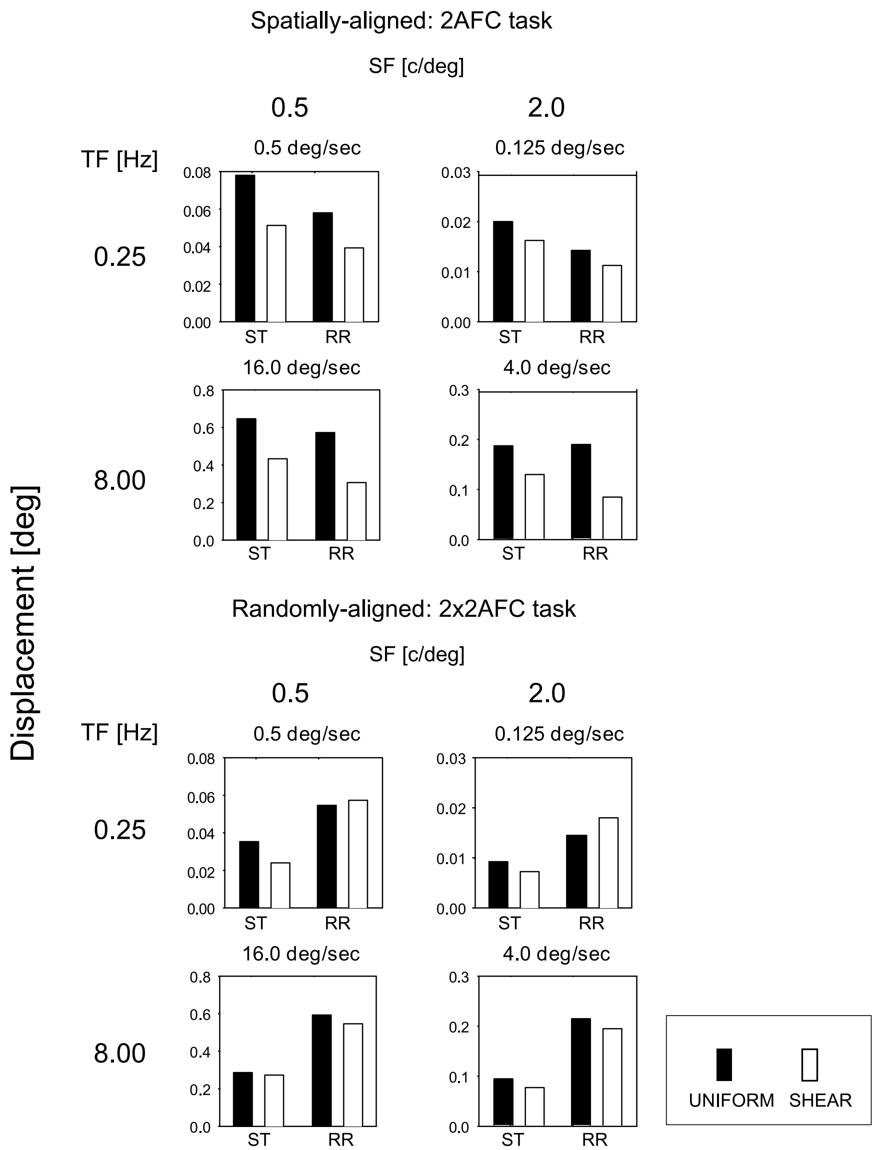

Fig. 5. Displacement thresholds in linear units for shear and uniform motion when we used the 2AFC method in the spatial alignment condition (top) and in the randomly aligned 2 × 2AFC condition (bottom).

initial spatial alignment raised sensitivity to shear motion as compared to uniform motion. Motion judgments for initially spatially aligned stimuli seem similar to position displacement judgments in vernier-type static stimuli. Possibly because of this reason, position-tracking mechanisms have been hypothesized as underlying the enhanced sensitivity to shear motion (Krauskopf & Li, 1999; Snowden, 1992). Since motion involves a change in physical position over time, perceived motion can be the result of a position-based system that identifies a change in location over time, or the output of motion detectors that respond to the orientation of spatio-temporal energy (Lu & Sperling, 1995; Zaidi & DeBonet, 2000). A number of methods have been devised to distinguish position tracking from motion-energy computations, e.g. Lu and Sperling (1995) and Zaidi and DeBonet (2000) showed that by superimposing moving sinusoidal gratings on stationary gratings of the same spatial frequency and orientation, stimuli can be constructed where the position of the stimulus changes in one direction while the motion energy is in the same or opposite direction depending on the relative phases of the moving and stationary gratings.

Fig. 6 explains the logic of this procedure. The horizontal axis represents space and the vertical axis represents samples of time for a half-cycle of motion. The left panels represent steady stationary gratings which act as pedestals. The middle panels represent the rightward-moving test gratings of lower amplitude than the pedestal. Adding the test and pedestal gratings results in compound gratings (right panels) of the same spatial frequency and orientation whose motion directions and

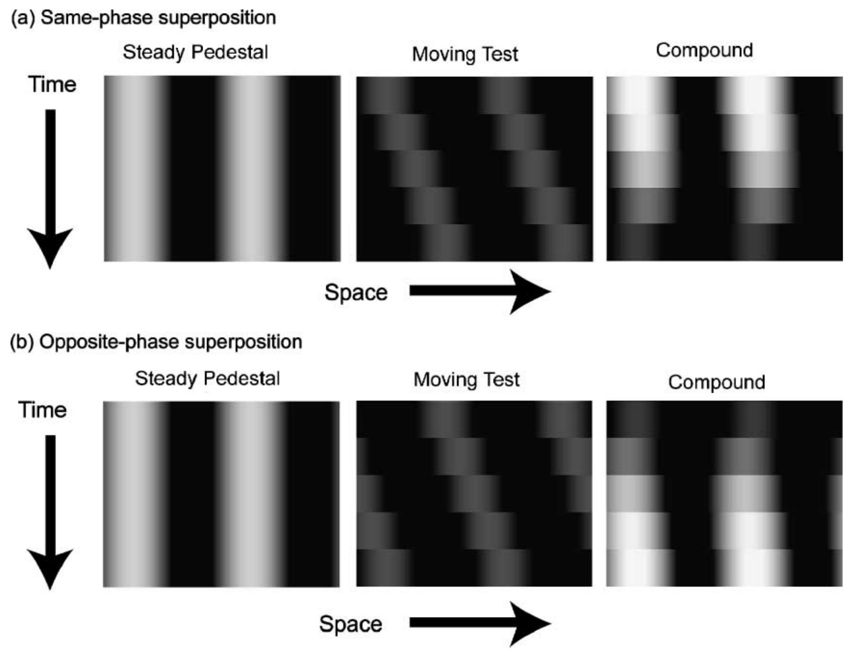

Fig. 6. A schematic diagram which explains the logic of Experiment 3. The left panel represents a steady stationary grating pedestal. The middle panel represents the rightward-moving test grating. Adding the test and pedestal grating results in the compound grating in the right panel. The initial direction of the compound grating is the same as the test grating when the initial superposition of test and pedestal gratings is in phase (a), and in the opposite direction when the initial superposition is in opposite phase (b).

amplitudes oscillate with time. The initial direction of the compound grating is the same as the test grating when the initial superposition of test and pedestal gratings is in phase (Fig. 6a), and in the opposite direction when the initial superposition is in the opposite phase (Fig. 6b). When an observer is presented with one of the compound stimuli, the observer can reliably detect the direction of the moving grating only if the visual system can parse the compound stimulus into moving and stationary components. This task could be accomplished by direction selective cortical neurons whose responses can be modeled as extracting oriented spatio-temporal energy (Adelson & Bergen, 1985; van Santen & Sperling, 1984; Watson & Ahumada, 1985). If the spatio-temporal parameters of the compound stimulus do not activate motion-energy neurons, the observer has to rely solely on position tracking, and can at best perceive the oscillatory motion of the compound.

In Experiment 3 we used a variant of the moving test + static-pedestal paradigm to identify stimulus domains where motion is detected by motion-energy mechanisms and domains where motion is detected by position-tracking mechanisms. In this paradigm, moving sinusoidal test gratings were presented in the top and bottom regions of the monitor as in Experiment 1, and were superimposed on stationary gratings of the same spatial frequency and orientation but of four times the contrast. In each trial, the stationary pedestals alone were initially presented for 2 s, then the moving gratings were added for half a cycle of motion, and then the pedestals remained on for an additional second. Observers had to indicate initial directions of motion of both top and bottom gratings in the same 2×2AFC task as Experiment 1.

In this experiment, we used the same four possible moving grating combinations as in Experiment 1 (Fig. 1). Stationary pedestals were assigned random phases on each trial. Each moving grating was initially superimposed on its pedestal either in the same or in the opposite phase. Therefore, for each condition in Fig. 1, there were four possible compound stimuli, leading to a total of 16 conditions in this experiment. Fig. 7 shows eight out of the sixteen experimental conditions. In the other eight conditions, the directions of both moving gratings were reversed. Each category shows the directions of the moving gratings and the initial direction of motion of the compound gratings. The categories were grouped by phase of superposition of the moving test and the steady pedestal gratings. In Category 1, since the top and bottom gratings were superimposed in the same phase as the pedestals, the directions of the moving gratings and the initial directions of the compound gratings are the same. In contrast, in Category 4 since both gratings were superimposed in the opposite phase, the initial directions of the compound gratings are opposite to the directions of moving gratings. Category 4 will be used to isolate motion-energy mechanisms from position-tracking mechanisms. If motion is detected by motion-energy mechanisms, the observer should be able to extract the direction of the moving grating, whereas if

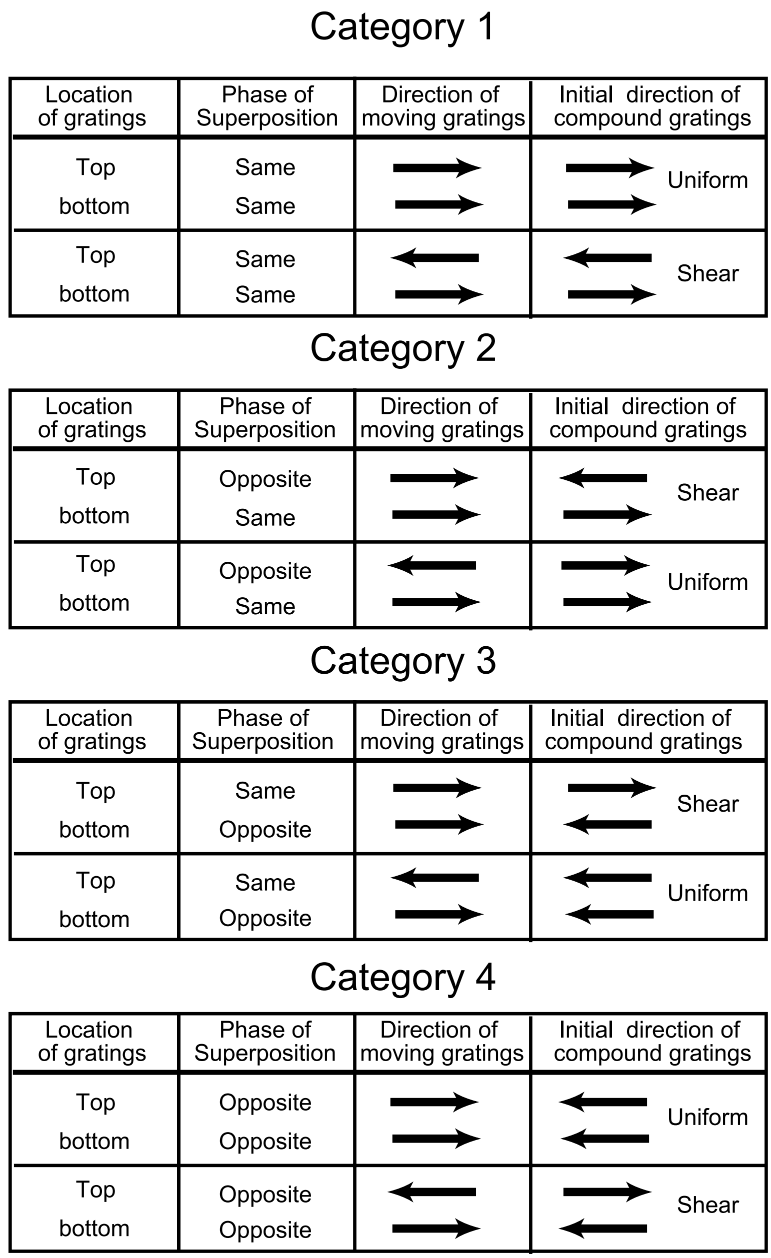

Fig. 7. Eight out of sixteen experimental conditions. In the other eight conditions, the directions of both moving gratings were reversed. Each category shows the directions of the moving gratings and the initial direction of motion of the compound gratings. The categories were grouped by phase of superposition of the moving test and the steady pedestal gratings.

motion is detected solely by position-tracking mechanisms, the observer should perceive an initial motion in the opposite direction. In Categories 2 and 3, only one of the upper or bottom gratings was superimposed in the opposite phase. Under these conditions if motion energy indicates shear motion, position tracking will indicate uniform motion and vice versa.

2.3.1. Results

When both the top and bottom superimpositions are in opposite phase (Category 4), detection of the correct directions of the test gratings indicates the extraction of motion energy, since each compound grating initially moves in the direction opposite to the test grating. For instance, in the case of the top row of Category 4 in Fig. 7, the response was defined as correct when the observer's response was rightward motion for both top and bottom gratings. For the conditions of Category 4, Fig. 8(a) shows the proportion of trials in which both top and bottom gratings were reported to move in the same directions as the moving test gratings. The horizontal axis represents spatial frequency and the vertical axis represents temporal frequency. Therefore, a diagonal of negative slope represents the same speed (temporal fre-

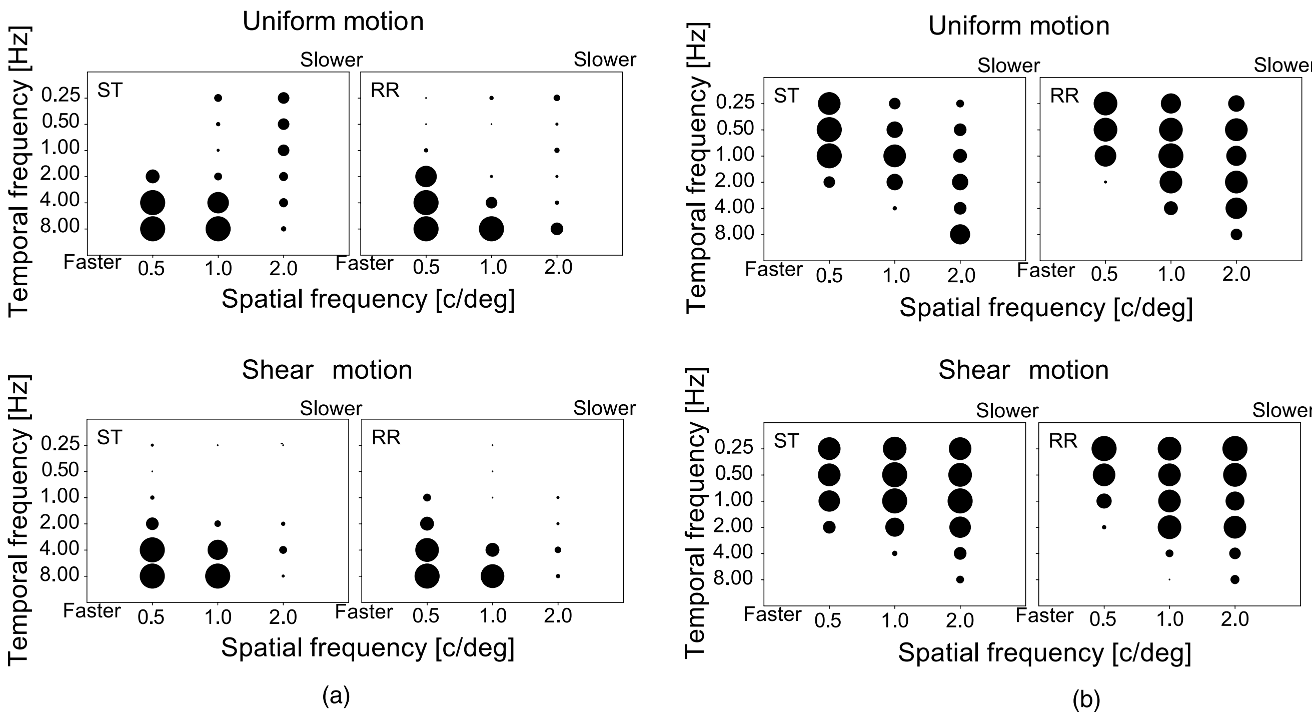

Fig. 8. (a) The proportion of trials in which both top and bottom gratings were reported to move in the same directions as the moving test gratings for uniform motion (top) and for shear motion (bottom). The horizontal axis represents spatial frequency and the vertical axis represents temporal frequency. Therefore, a diagonal of negative slope represents the same speed at several spatio-temporal frequencies. The diameter of each data point is proportional to the percentage of correct response at each spatio-temporal frequency. The largest diameters in this figure represent one hundred percent correct responses. (b) The proportion of trials in which both top and bottom gratings were reported to move in the same directions as the initial direction of the compound gratings for uniform (top) and shear (bottom) motion.

quency/spatial frequency) at several spatio-temporal frequencies. The diameter of each data point is proportional to the percentage of correct response at each spatio-temporal frequency. The largest diameters in this figure represent one hundred percent correct responses. The top panels show the results for uniform motion of the moving gratings, and the bottom panels for shear motion of the moving gratings. The results for both shear and uniform motions show that observers identified the directions of both top and bottom stimuli as those of the test gratings only at speeds above 2 deg/s, suggesting that motion energy was extracted only for these spatio-temporal parameters.

For the same experimental conditions, Fig. 8(b) shows the proportion of trials in which both top and bottom gratings were reported to move in the same directions as the initial direction of the compound gratings. In this figure, in the case of the top row of Category 4 in Fig. 7, the response was defined as correct when the observer's response was leftward uniform motion. For both shear and uniform motion, at the slower speeds (<2 deg/s), both observers reported initial motions in the directions of the compound gratings. The results for Category 4 show that both shear and uniform motion were detected by motion-energy mechanisms for speeds above 2 deg/s, and were detected by tracking the positions of the compound stimuli at speeds slower than 2 deg/s. For both observers, at the slowest speeds, shear motion of the compound gratings is detected more reliably than uniform motion of the compound gratings. Note that we did not count trials in which either only the top or only the bottom grating was reported to move in the same direction as the moving test grating. These were 5.6% of trials for observer ST and 5.8% for observer RR.

In the conditions in Categories 2 and 3 in Fig. 7, either the bottom superposition is in the opposite phase and the top in the same phase or vice versa. Thus, uniform test motion leads to shearing compound motion, and shearing tests lead to uniform compound motion. Hence, if position tracking indicates shear motion, motion energy will indicate uniform motion and vice versa. This will be used to separate the position-tracking mechanism from motion-energy mechanism. In analyzing the results of these categories, we were only concerned with whether observers reported shear or uniform motion. Since Categories 2 and 3 are the same in terms of shear or uniform response we added responses from conditions in both categories.

Fig. 9 shows the proportion of trials in which top and bottom gratings were reported to move (a) in the opposite directions (i.e. shear motion) or (b) in the same

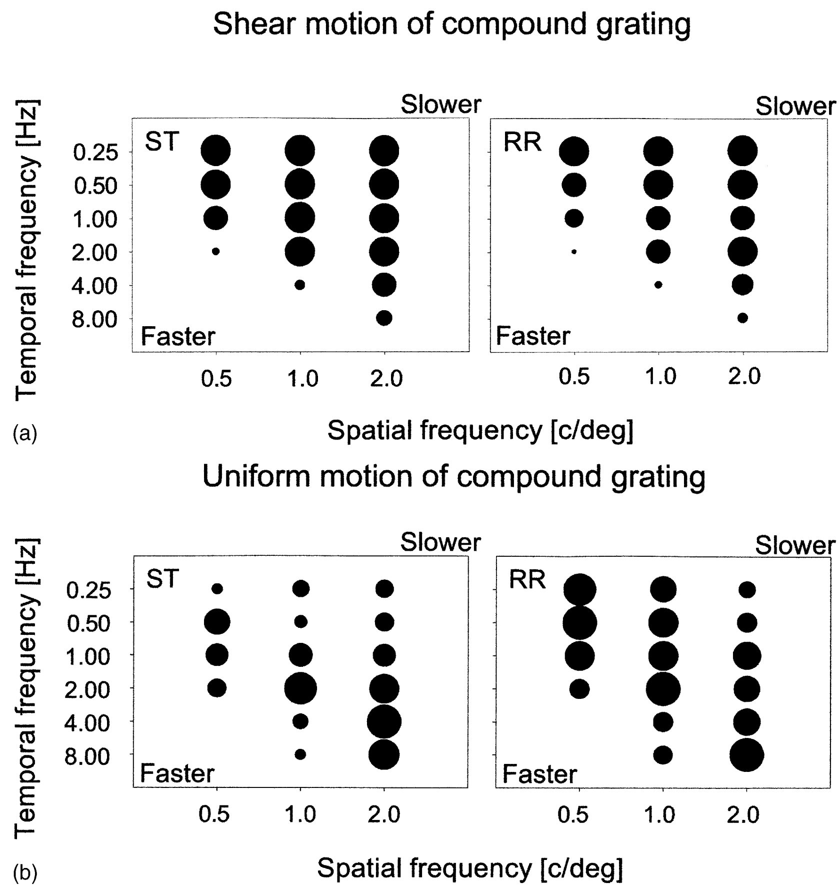

Fig. 9. The proportion of trials in which both top and bottom gratings were reported to move (a) in the opposite directions (i.e. shear motion) and (b) in the same directions (i.e. uniform motion) as the initial direction of the compound gratings. Similar to Fig. 8, the horizontal axis represents spatial frequency, and the vertical axis represents temporal frequency.

directions (i.e. uniform motion) as the initial direction of the compound gratings. In Fig. 8 we had used "rightward" or "leftward" motion response to separate position-tracking mechanisms from motion-energy mechanisms, whereas here we use shear or uniform motion response. The horizontal axis represents spatial frequency, and the vertical axis represents temporal frequency. Observers could extract the initial direction of motion for both the top and bottom compound stimuli only at speeds slower than 2 deg/s for both shear and uniform conditions, suggesting that both motions were detected by position tracking only at speeds below 2 deg/s. At the slowest speeds both observers detect shear motion of the compound gratings more reliably than they detect uniform motion of the compound gratings. This suggests that the relative changes of position caused by shear motion are easier to track than the correlated changes of position caused by uniform motion.

3. Discussion

The results of this study are straightforward. When the same 2×2AFC design is used for measuring displacement thresholds for shear and uniform motion, it minimizes any potential artefacts due to criterion level or response bias. Under these conditions, displacement thresholds were similar for shear and uniform motion. This result contradicts previously published results claiming superior sensitivity for shear motion (Krauskopf & Li, 1999; Snowden, 1992). Can a concern be raised that the 2×2AFC procedure measures sensitivity to the components of shear and uniform motion, but not to the compound motions per se? This objection would be valid if we had measured sensitivity to each component in different trials, but we did not do so. The 2×2AFC method is designed to equate the correctness of reports of shear and uniform motion. In addition, lateral interaction models of shear detection (e.g., Nakayama & Loomis, 1974; Sachtler & Zaidi, 1995) would predict higher sensitivity to the simultaneously presented components in the shear condition than in the uniform motion condition. These models are thus refuted by our data even if the 2×2AFC method were measuring sensitivity to the individual component that were simultaneously presented in brief trials.

In control experiments we showed that when abutting stimuli were spatially aligned, there was an advantage for shear motion similar to that reported by Krauskopf and Li (1999). Further, if trials for shear and uniform motion are separated and different 2AFC tasks are used for measuring thresholds, then the advantage for shear motion approaches but is still significantly lower than the values reported by Snowden (1992). The 2×2AFC procedure is as reliable as previously used 2AFC procedures. When displacement thresholds measured with the 2×2AFC procedure in the randomly aligned case are compared on average with the 2AFC spatially aligned condition thresholds, observer RR shows little change in thresholds for uniform motion and higher thresholds for shear motion in the 2×2AFC condition, whereas observer ST shows smaller thresholds for both types of motion in the 2×2AFC condition.

It is worth comparing these results to the predictions of models designed to detect shear motion. In the Sachtler and Zaidi (1995) model, motion discontinuities are detected by spatial differencing of the outputs of Adelson and Bergen (1985) type motion-energy units. These units are similar to V1 complex cells (Emerson, Bergen, & Adelson, 1992) in being insensitive to the phase of the sinusoidal grating. Therefore, any shear model based only on such motion-energy units should predict no difference between the randomly aligned and spatially aligned conditions. In the domain where position tracking underlies the detection of physical motion, one could expect an advantage for shear motion in the spatially aligned task, as it is easier to tell relative position changes. This may underlie the increasing sensitivity to shear motion at slower speeds, which is based on comparisons between shear and uniform motion data collected within the same sessions. If sensitivity to just shear motion is compared between spatially and randomly aligned conditions, observer ST's data show a slight advantage for spatially aligned stimuli, but observer RR's data do not show this difference. This comparison is less reliable because the spatially and randomly aligned data were collected in different sessions separated by many days.

A fundamental question in motion perception is the role of position tracking versus the role of direction-sensitive motion-energy mechanisms. In shear motion, positions of stimuli change with respect to one another, whereas in uniform motion, stimuli retain their relative positions. It is thus worth asking whether for the same spatio-temporal conditions shear motion is subserved by position tracking and uniform motion by motion-energy extraction. We used a variant of the procedure used by Zaidi and DeBonet (2000, Experiment 1) to answer this question. Moving gratings of low or moderate contrast were added to steady stationary gratings of the same spatial frequency at four times the contrast, for half-cycles of motion. In the Zaidi and DeBonet (2000) procedure, the initial superimposition was either in $+90°$ or in $-90°$ phase, whereas in the present procedure the initial superposition was in either $+0°$ or $+180°$ phase. The new procedure had the property that there were contrast transients at the beginning and end of the superposition, but no spatial transients. We used this method to show that in the opposite-phase superpositions, where the compound and moving gratings initially move in opposite directions, observers reported motion in the direction of the moving grating only for speeds greater than 2 c/deg, irrespective of whether the motion was shear or uniform. Since only neurons that can extract the motion of the moving grating from the compound, can subserve a correct response in opposite-phase superimpositions, these results indicate that both shear and uniform motion are subserved by motion selective neurons at speeds above 2 deg/s. For conditions where the two moving gratings move in the same direction, but one of them is added in phase and one in opposite phase, the compound stimulus indicates shear motion. The results show that in these conditions, observers report shear motion for speeds slower than 2 deg/s. Similarly when the moving gratings indicate shear motion whereas the compound stimulus indicates uniform motion, observers report uniform motion for speeds less than 2 deg/s. These results indicate that shear and uniform motions are both subserved by position tracking at slower speeds. At the slowest speeds, both observers were able to track relative changes of position better than uniform changes.

Our results showed that, at higher speeds observers could extract the direction of a test grating on a pedestal, whereas at slow speeds they could not. These results suggested that at high speeds the sensitivity of the motion-energy mechanism is higher than that of the position-tracking mechanism, whereas at slow speeds the sensitivity of the position-tracking mechanism is higher than that of the motion-energy mechanism. However, given that in Experiment 3 the relative duration of the moving grating compared to the steady pedestal decreases as temporal frequency increases, one would expect more overlap between the Fourier spectra of the two components at lower temporal frequencies. We wanted to make sure that this was not an artefact that was separating the position-tracking and motion-energy mechanisms. For this reason we calculated motion energies of the compound gratings in spatio-temporal frequency space. We divided the space into four quadrants and calculated the energy in each quadrant. In the two-dimensional energy distributions, the first and third quadrants are symmetric around the origin, as are the distributions in the second and fourth quadrants. The asymmetry of the energy distribution between the positive diagonal quadrants and the negative diagonal quadrants indicates the prevalence of motion energy in one direction or the other (Adelson & Bergen, 1985; Watson & Ahumada, 1985). When the energy in the first and the third quadrants is higher than that in the second

Table 1
Simulation results at several temporal frequencies

TF	Ratio
0.25	1.102
0.5	1.066
1.0	1.051
2.0	1.045
4.0	1.045
8.0	1.043

The values are ratios of the maximum energy of the first and second quadrants of spatio-temporal frequency space to maximum energy in the second and fourth quadrants. Values of more than 1.0 mean that the energy of the first and third quadrants is higher than that of second and fourth quadrants, indicating rightward motion.

and fourth quadrants, motion energy is greater in the rightward direction. In contrast, when the energy in the second and the fourth quadrants is higher than that in the first and third quadrants, motion energy is greater in the leftward direction. Therefore, we compared the magnitude in the first and third quadrants with that in the second and fourth quadrants.

Table 1 shows the results of calculations at several temporal frequencies. The contrast of the rightward-moving grating was 0.1 and that of the pedestal grating was 0.4. The values are ratios of the maximum energy of the first and third quadrants to that of the second and fourth quadrants. Values of more than 1.0 mean that the energy of the first and third quadrants is higher than that of second quadrant, indicating rightward motion. The ratios in Table 1 are all greater than 1.0 and have similar values, however, the ratios decrease as temporal frequency increases. These simulations suggest that there is actually slightly less asymmetric motion energy in higher temporal frequency conditions. In contrast, our results showed that the observer could extract the direction of test grating motion correctly only at higher temporal frequencies. Therefore, the empirical results of thus study are not caused by a stimulus artefact, but are a property of motion-energy mechanisms.

In conclusion, the results of this paper show that for general conditions observers are essentially equally sensitive to shear and uniform motion at all speeds. Both motions are subserved by position tracking at speeds below 2 deg/s. At speeds above 2 deg/s both motions are processed by motion-energy mechanisms. These results suggest that if motion-energy based "shear-detectors" exist in the cortex, their effect is not evident at displacement threshold. Such mechanisms have also been postulated for the phenomenon of "induced motion" (Levi & Schor, 1984; Reinhardt-Rutland, 1988). Given that motion is induced only at speeds below 2.5 deg/s (Levi & Schor, 1984), we intend to use the methods of the present study to examine the nature of the mechanisms underlying induced motion (Tsujimura & Zaidi, 2002).

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