

Motion distorts visual space: shifting the perceived position of remote stationary objects

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To perceive the relative positions of objects in the visual field, the visual system must assign locations to each stimulus. This assignment is determined by the object's retinal position, the direction of gaze, eye movements, and the motion of the object itself. Here we show that perceived location is also influenced by motion signals that originate in distant regions of the visual field. When a pair of stationary lines are flashed, straddling but not overlapping a rotating radial grating, the lines appear displaced in a direction consistent with that of the grating's motion, even when the lines are a substantial distance from the grating. The results indicate that motion's influence on position is not restricted to the moving object itself, and that even the positions of stationary objects are coded by mechanisms that receive input from motion-sensitive neurons.

The visual system integrates information from multiple sources to judge the relative positions of objects in the visual field. These sources include the position and movement of the eye¹⁻⁴, the retinal location and motion of the object⁵⁻¹³, and vestibular or proprioceptive signals¹⁴. For example, flashing a stimulus just before the initiation of a saccade leads to presaccadic mislocalization¹, bidirectional spatial compression², and relative position shifts³ of stationary stimuli.

In addition to eye movements, the movement of the object itself strongly influences its perceived position. For example, the initial⁵ or final¹⁵ position of a moving object can appear shifted in the direction of motion, the position of a moving stimulus can appear to lead a stationary flashed target⁷⁻⁹, and a stationary patch filled with moving texture appears not only to move, but also to be positionally shifted in the direction of the apparent motion^{10,11}. In all these motion-based phenomena, the perceived position of an object is shifted in the direction of its apparent motion, which suggests that the locations assigned to stimuli interact with their motion signals. Many explanations argue that the locations of moving and stationary stimuli are processed differently^{5-11,16-20}. However, if the motion of one object shifts the position of another, stationary object, then the position shifts found for moving stimuli may actually reflect a more fundamental and generalized position-coding mechanism that analyzes moving and stationary stimuli alike.

Here we show that when a moving stimulus is presented in one region of visual space, stationary flashes that are briefly presented concurrently in remote areas of the visual field appear to be displaced in the direction of motion. Unlike previously reported phenomena¹⁰⁻¹³, the displacement occurs even when the flashes do not appear to move and are physically separated from the motion. This provides direct evidence that the localization of a physically and perceptually stationary stimulus depends on motion-processing mechanisms that are active even at some distance from the stimulus.

RESULTS

The first experiment examined the distance over which the motion of a grating influenced the perceived positions of stationary flashed lines. Two physically aligned flashes that straddled a rotating radial grating (Fig. 1a) appeared to be misaligned in a direction consistent with that of the nearest motion. To avoid adaptation, the grating reversed direction every 2.25 ± 0.5 seconds (Fig. 1b). The flashes were presented within ± 1 second of the reversal.

A vertical misalignment was perceived between the two flashed lines (Fig. 2a) when the configuration in Fig. 1b was presented. The misalignment is plotted as a function of the difference in time (interstimulus asynchrony or ISA) between the reversal of the moving grating and the presentation of the flashes. The separation between the inner edge of the flashes and the nearest outer edge of the radial grating was three degrees. When a sigmoid was fit to these data ($y = a((\exp(b(x+c)) - 1) / (\exp(b(x+c)) + 1)) + d$, where the parameter a estimates the height of the function along the ordinate), the overall misalignment ($2a$) was found to be about 20 minutes of arc for both subjects.

Note that although the flashes appeared misaligned in a direction consistent with that of the nearest motion, a misalignment was present at 0 ISA, when the grating was physically stationary (Fig. 2a). This would arise if there were a longer delay for assigning positions to the flashes than for registering the grating's motion^{16,17}.

There was a noticeable effect of grating size on the misalignment, but almost no effect of flash eccentricity on the magnitude of the illusion (Fig. 2b). The misalignment remained roughly constant with increasing flash-to-grating separation. This clearly demonstrates that motion in one region of the visual field can directly influence the perceived positions of stationary objects at distant locations.

Consistent with previous studies²¹, the threshold flash misalignment (vernier) rose with increasing eccentricity of the

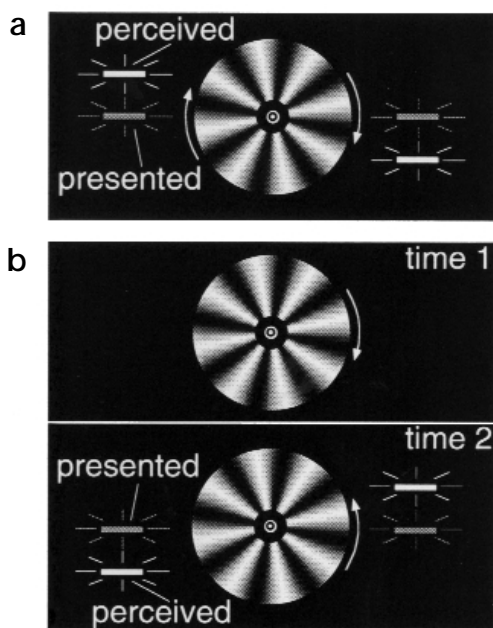
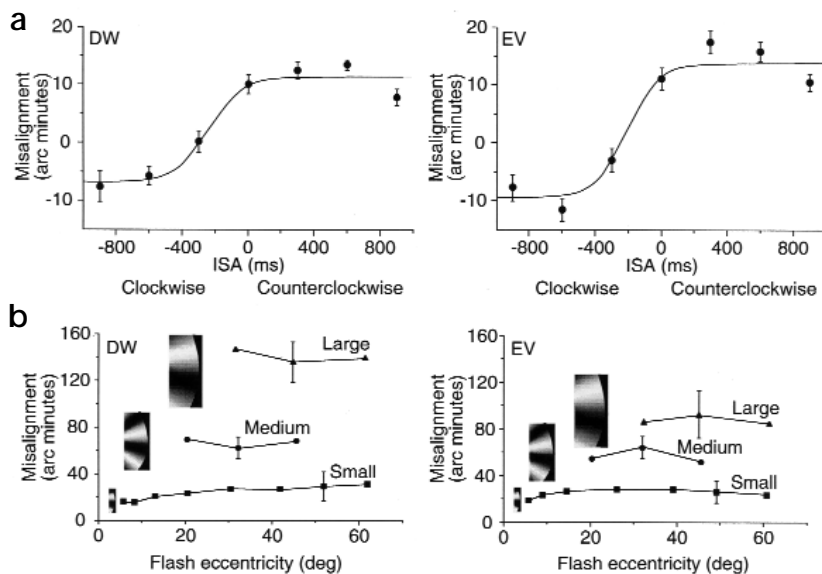


Fig. 1. A schematic view of the stimulus configuration and perception. (a) An illusory misalignment between two physically aligned flashes occurred when they were presented on either side of a rotating radial grating. The apparent misalignment was consistent with the direction of motion and occurred even when the flashed lines were distantly separated from the rotating grating. (b) The stimulus configuration used in the first experiment. The two flashed lines were presented at various interstimulus asynchronies (ISA) before or after the radial grating reversed direction. See <http://visionlab.harvard.edu/> for demonstrations.

flashes (Fig. 3). This trend contrasts with the largely constant misalignment we measured across eccentricities. One consequence of the difference in these functions is that the visibility of the misalignment caused by the motion of the grating was below threshold when the flashed lines were at large eccentricities.

Fig. 2. Experiment 1 results for subjects DW and EV. (a) The ordinate shows the perceived misalignment between the two flashes, as measured by the number of arc minutes that the flashes had to be displaced to make them appear aligned (Methods). The abscissa shows the time (ISA) between the presentation of the test flashes and the grating's reversal. (Negative ISA indicates that the flashes were presented before the reversal of motion.) Data have been merged so that the motion of the grating is clockwise, then counterclockwise, as indicated along the abscissa. Each of the seven data points represents a single psychometric function (not shown). The separation between the inner edge of each flash and the nearest outer edge of the grating was three degrees. A sigmoid (see text) was fit to the data to measure the overall misalignment observed (the height of the sigmoid). Error bars, s.e.m. (b) Overall misalignment for three gratings of different sizes and various flash eccentricities. Insets, outer edges of the radial gratings. The distance between each of the data points and the horizontally adjacent inset indicates the flash-to-grating separation. Each of the data points on these graphs represents the height of a sigmoid like that in (a). The error bars show representative s.e.m for each flash-to-grating separation. Data for a third subject were similar.



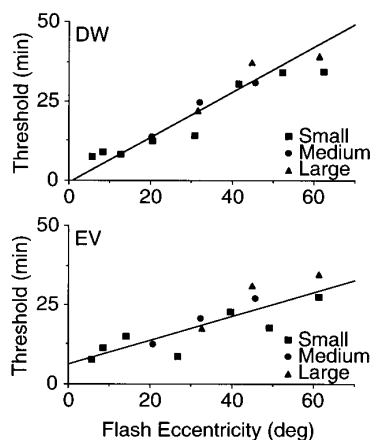
This misalignment, produced at such a distance from the motion of the grating, might suggest that rotational eye movements (for example, torsion) are responsible for the effect²². Small torsional eye movements can be induced by rotary motion^{23,24}, such as the grating in the first experiment, so it is possible that the misalignment observed between the two flashed lines is simply a product of small compensatory torsional adjustments²⁵. In a second experiment, we rejected this explanation by presenting two pairs of linear gratings that moved in opposite directions (Fig. 4a). Three flashed lines were then presented: two straddled the outer gratings, and one was superimposed on the fixation point (Methods). If eye movements of any kind were responsible for the misalignment illusion, we would then expect to find no perceived misalignment between the two outer flashes and the central flash in Fig. 4a, because the eye cannot move in two directions simultaneously; we verified the results both monocularly and binocularly. A misalignment was still observed between the central and two outer flashed lines, in contrast to the eye-movement hypothesis (Fig. 4b). Similar results were also obtained when the experiment was replicated using two radial gratings that rotated in opposite directions.

The results of the second experiment also addressed an alternative explanation for the misalignment based on a frame of reference effect^{26,27}. For example, if the radial grating in the first experiment created an apparent tilt in some frame of reference, such as the monitor, then the flashes could have appeared displaced relative to this tilted frame. However, because the gratings moved in opposite directions in the second experiment and still produced the apparent misalignment, the frame-of-reference explanation was effectively ruled out.

Given the remote nature of motion's effect on position judgments, as found in experiments 1 and 2, we were interested in examining the possibility that higher-level motion processes might be contributing to precise perceptual localization. In a third experiment, we tested this by using a dichoptic display: the radial grating from the first experiment was presented to one eye while the flashed lines were presented to the other eye. If the motion of the grating in one eye affects the perception of

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Fig. 3. Thresholds from experiment 1 for subjects DW and EV. Threshold misalignments (minutes of arc) are plotted for each of the points on Fig. 2b as a function of the flash eccentricity. Thresholds were calculated as half the distance between the 25th and 75th percentiles on each psychometric function, then averaged across ISA. The threshold misalignments were similar whether or not the radial grating was presented.



flash alignment from the other eye, it is because motion information is reaching cortical areas with binocularly driven neurons before influencing the processing of the flashes. The results with dichoptic presentation (Fig. 5) were very similar to those of the first experiment (Fig. 2a), indicating that the binocularly driven cortical neurons that responded to the moving grating also influenced the assignment of the flashes' relative positions.

We next investigated the relationship of this flash misalignment to previously reported phenomena, such as the position shifts of perceptibly moving stimuli. When a moving pattern is viewed through a stationary aperture, the aperture not only seems to move, but also appears displaced in the direction of motion (when the mean luminance inside and outside the aperture are equated)^{10,11}. This phenomenon has been interpreted as possible evidence of an extrapolation^{10,11} or motion-capture mechanism^{10,28}. In both these cases, motion signals are assigned to the aperture. This illusory motion of the aperture may then cause it to appear shifted in the direction of motion in the same way that the above motion-based position displacements occur.

To investigate whether the underlying mechanism for our misalignment effect is also mediated by an illusory motion, we measured the perceived speed of the stationary flashes in a fourth experiment. If the misalignment is produced even though the flashes appear stationary, this would argue against explanations that have been proposed for previously reported phenomena, as these explanations require the stimulus to move to appear displaced. The flashes appeared stationary when they were presented for longer than 120 ms (Fig. 6), and yet these perceptually and physically stationary flashes still appeared substantially misaligned. The perceived flash speed increased at shorter durations, where judgments are very noisy²⁹. At longer durations, the perceived speed of the flashes was judged more accurately, and converged convincingly to a stationary percept

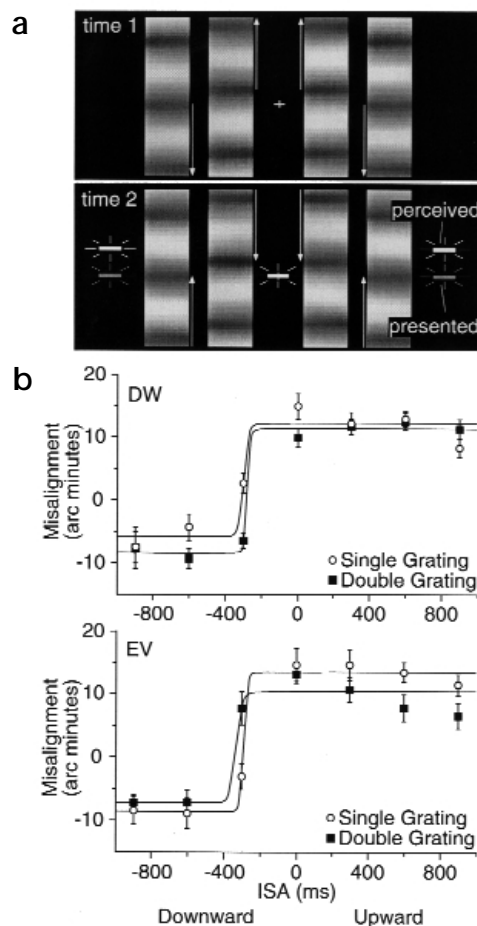
Fig. 4. Experiment 2. (a) Schematic view of experiment 2 stimulus and perception. When three flashed lines were presented in physical alignment, the flashes appeared misaligned consistent with the direction of the nearest motion (white flashes). (b) Results for subjects DW and EV (squares). (For comparison, the circles indicate the results for a comparable stimulus in the first experiment.) The ordinate shows the perceived misalignment between the inner and outer flashes as measured by a nulling procedure (Methods). The abscissa shows the time between the flashes and the motion reversal (ISA). Error bars, s.e.m.

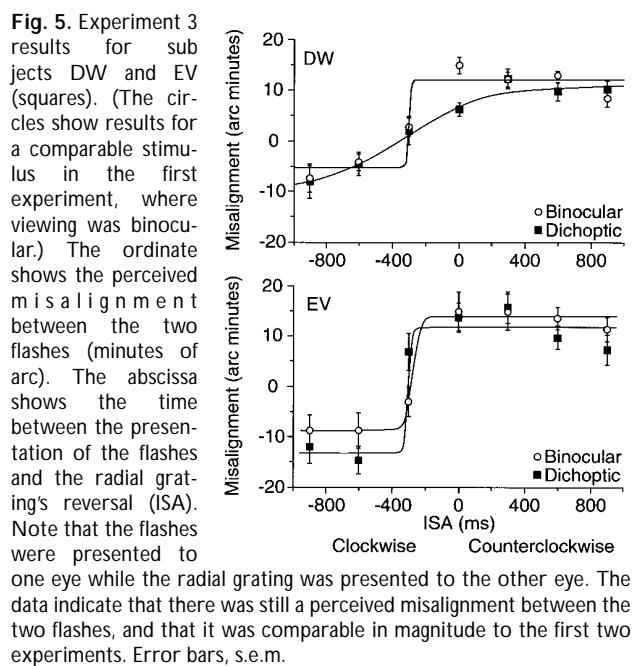
at flash durations where there was still a misalignment present. This pattern of results was consistent across all grating sizes and flash-to-grating separations.

Reported displacements in position are always accompanied by perceived motion of the target whose position is shifting¹³. The present misalignment effect, however, was seen for stimuli that are neither physically nor perceptually moving. Furthermore, the magnitude of the misalignment observed in this experiment was much larger than that for many previous phenomena¹⁰⁻¹³. The misalignment also remained constant with increasing eccentricity, which contrasts with the only previous comparable measurement showing a position shift of an apparently moving stimulus that increases substantially with eccentricity¹¹.

The finding that the misalignment was observed between flashes that were stationary rules out anticipatory retinal responses²⁰ and latency variations¹⁶⁻¹⁸ as explanations for the mislocalization. In addition, because the flashes in our experiments were not moving physically or perceptually, they could not trigger an extrapolation mechanism that would shift the apparent locations of moving stimuli in the direction of motion to compensate for the lag in their perceived positions caused by unavoidable neural delays^{7,9-11,20}.

We next asked whether the misalignment was due to a local mechanism that acts on each of the two flashes independently or on a configural process that requires a comparison between positions that span across a moving stimulus. In this fifth experiment, we tested whether the flashes were mislocalized in a local manner by presenting one of the flashes from Fig. 1b





twice at the same location (that is, on only one side of the radial grating), once before and once after the reversal of the motion; the interval between flashes was varied. If the misalignment illusion were due to a local mechanism that acts on a single flash independently, then the two successive flashes should appear displaced from each other as they are shifted first one way and then the other. For example, following the data for the medium grating from experiment 1, if a single flash is presented 900 ms before and 300 ms after the reversal, the two flashes should appear displaced from each other by about 30 to 35 minutes of arc (derived from the overall misalignment divided by 2 in Fig. 2b). This did not occur, however. The local shift in this single location test was 4 and 6 minutes for subjects DW and EV, respectively, about one-sixth of the comparable values in experiment 1, which suggests that much of the misalignment was produced only when two locations that straddled a moving stimulus were compared.

To explore this further, we conducted a sixth experiment, in which a pair of flashes were always presented on the same horizontal plane as the fixation point, while a pair of linear gratings were vertically offset above or below this plane. The misalignment dropped off rapidly as the vertical distance between the

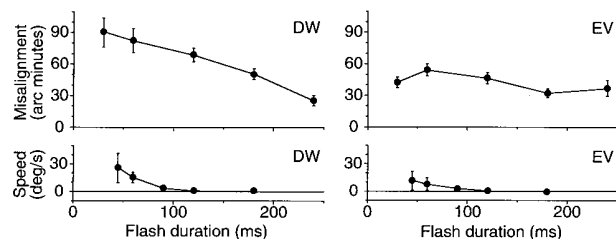


Fig. 6. Experiment 4 results. (a) The overall flash misalignment (as in Fig. 2b) is plotted as a function of flash duration for DW and EV. (b) The perceived speed of the flashes is plotted as a function of flash duration. To measure the perceived speed of the flashes, they were physically moved at velocities that nullled any apparent motion. Error bars, s.e.m., shown only when they are larger than the symbols.

flashes and gratings increased (Fig. 7). These results were consistent with the previous experiment in that a misalignment depended largely on the presence of motion in the space spanned by the comparison flashes.

We manipulated the grating's temporal frequency in a seventh experiment to measure the velocity dependence of the flash misalignment and to test whether it is due to attentional tracking³⁰ of the moving gratings. The misalignment was roughly band-pass, which resembles the temporal contrast sensitivity function³¹ (Fig. 8). Interestingly, the misalignment does not appear similar to the low-pass characteristics of the motion sensitivity function³². Because the misalignment occurred even at temporal frequencies above 12 Hz, the mislocalization was not due to attentional tracking of the grating, as the ability to track positions on a rotating grating falls off dramatically at around 7 Hz³³.

DISCUSSION

We showed that motion information in one region of the visual field influenced the perceived positions of apparently stationary objects, even when those objects were located in distant areas of the visual scene. The perceived misalignment was not due to eye movements, a frame-of-reference effect or attentional tracking. The magnitude of the misalignment depended on the size of the moving stimulus and the duration of the flashes, but it was always in the direction of the nearest motion. These experiments suggest the involvement of higher cortical areas that are binocularly driven and specialized in the processing of motion. In contrast to previous results^{7-13,20}, the misalignment occurred even when the flashes appeared stationary, showing that position displacement does not depend upon physical or even apparent motion of the test stimulus, although, of course, motion must be present in the display.

The remote effect of motion on localization, as reported here, indicated that assigning positions to brief stimuli depends on the configuration of motion signals throughout the visual field. These long-distance interactions were similar in range to that for motion capture²⁸ and induced motion³⁴ (motion assimilation and contrast), where motion at one location can influence perceived motion at some distance³⁴⁻⁴⁰. Yet, motion capture and induced motion differ from the position shifts observed in this study on at least two factors. First, the induced motion phenomena generally fall off with increasing separation between the moving inducer and the induced target⁴⁰, a pattern that did not hold for the misalignment reported here. Second, and, more importantly, the misalignment we report occurred even when the flashes appeared stationary—when no motion assimilation or contrast had occurred.

Position shifts of apparently moving stimuli are well documented and have garnered a number of explanations including extrapolation^{7,9}, attention shifts⁸, differential latencies¹⁶⁻¹⁸, integration or interpolation of the moving object's trajectory¹⁹, and anticipatory retinal responses²⁰. Yet, none of these diverse models can explain how an apparently stationary stimulus could be displaced in position by motion in a remote area of the visual field. This is primarily because these models are intended to address the question, "How is a moving stimulus coded differently from a stationary one?" Because apparently stationary stimuli can be shifted in position, however, this may not be the right question to ask. The misalignment reported here could reflect a more basic mechanism that underlies or contributes to many of the motion-based position displacement phenomena mentioned earlier. The issue, then, is not the dissociation

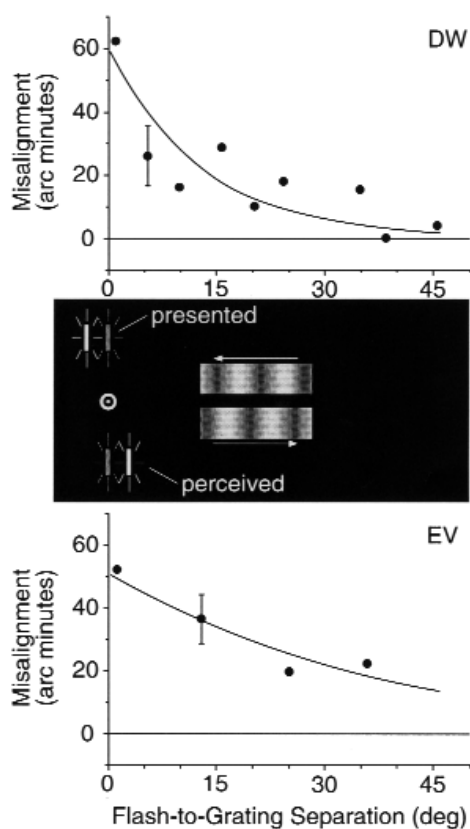


Fig. 7. Experiment 6 results. The ordinate shows the overall perceived misalignment between the two flashes (as in Fig. 2b). The abscissa shows the vertical separation between the flashes and the linear grating, as measured from the center of the grating to the horizontal plane on which the flashes were presented. A schematic view of the linear gratings is shown along the abscissa (though the linear gratings were vertically, not horizontally, offset in the experiment). The linear gratings were centered between the flashes in the 0.0 deg separation condition. A single error bar is shown for one data point in each plot to indicate a representative s.e.m.

between the coding of stationary and moving stimuli, but how the configuration of motion in the visual field influences the localization of both moving and stationary stimuli.

A potential criticism of this interpretation is that the magnitude of the misalignment reported here is different from that reported for other phenomena. For example, the flash-lag misalignment (in which a moving object appears to lead a flash presented at an adjacent location), is often much greater than the flash-to-flash misalignment we measured for the same flash-to-motion separation. Indeed, given that the mislocalization of the flash that occurred in our stimulus should also occur in the flash-lag studies, it should reduce the flash-lag phenomenon by shifting the flash in the direction of the moving stimulus. The actual mislocalization of the moving bar in flash-lag experiments may therefore be greater than those experiments revealed. Further, if the mislocalization mechanism that we report applies to moving objects as well as to stationary ones, then it must shift the perceived position of moving stimuli by an even greater amount than the flashed stimuli.

The experiments reported here suggest the involvement of cortical areas, such as MT or MST, whose neurons have large^{41–43} binocularly driven receptive fields^{41,44} that are selective

for the size⁴³ and motion of a stimulus^{41–46}. Given the strong feedback connections from these areas to V1 (ref. 47), where retinotopic localization is very precise^{11,48}, it is possible that the misalignment reflects a re-entrant mechanism^{13,47,49} by which motion information influences position judgments of moving and stationary stimuli. This mechanism subserves both stationary and moving stimuli and may therefore underlie a number of visual phenomena that involve localizing a stimulus in the presence of motion.

METHODS

Stimuli were presented on a high-resolution CRT monitor (832 × 624 pixels, 75 Hz refresh) controlled by a computer (Apple Power Macintosh, Cupertino, California). Subjects were immobilized with a chin rest 12 cm from the visual display, unless otherwise noted. A fixation bull's-eye was provided at the center of the screen. DW and two well practiced, naive subjects participated in the experiments. Subjects had normal or corrected-to-normal visual acuity.

Experiment 1. The radial grating subtended 8.9°, 23.6° or 47.2° in diameter, with a 2.05° hole in the center for the fixation bull's-eye. The grating had a sinusoidal luminance modulation of 8 cycles per rotation at 98.5% contrast on a dark (0.01 cd/m²) background. Each experimental trial consisted of clockwise or counterclockwise rotation of the grating (1.4 Hz) for 2.25 ± 0.5 seconds, followed by an equivalent rotation in the opposite direction. At varying periods of time before or after the grating's reversal (ISA), two flashed lines were presented simultaneously for 60 ms on either side of the grating. Each flash (34.5 cd/m²) was 6° × 0.85°. The flashes were vertically offset from one another, and subjects judged whether the flash on the right appeared above or below the flash on the left (method of constant stimuli, two-alternative, forced-choice task). A psychometric function was fit to the data for each of the various ISAs, and the physical misalignment between the flashes that created an apparent alignment was measured. The initial direction of motion was randomized across trials in either a clockwise or counterclockwise direction. The data from the two directions were then merged. The separation between the inner edge of each flash and the nearest outer edge of the radial grating was varied across experimental sessions between 1.3° and 58°.

Experiment 2. Four linear gratings were presented behind rectangular apertures, two on either side of a fixation point. The gratings had sinusoidal luminance modulations of 0.2 cycles per degree visual angle at 99.5% contrast on a dark (0.01 cd/m²) background. Each linear grating was 20.5° high and 3.6° wide. The outer two gratings were centered 8.98° left and right of the fixation point, which was at the center of the visual display. The inner two gratings were centered 3.85° left and right of the fixation point. The inner two gratings always translated in a vertical direction opposite the

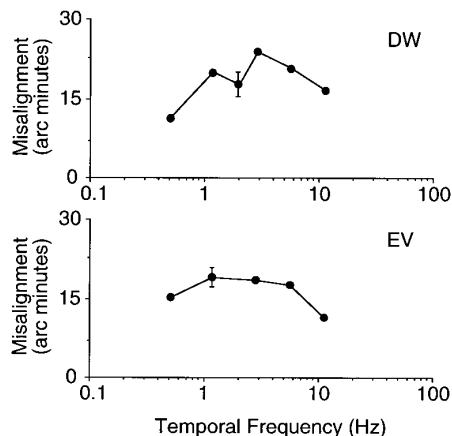


Fig. 8. Experiment 7 results. The overall perceived misalignment between the two flashes is plotted as a function of the grating's temporal frequency (Hz). Error bars, s.e.m.

outer two gratings, and the initial direction of the inner gratings was randomized across trials (upward or downward). As in the first experiment, the gratings translated (2.67 Hz) for 2.25 ± 0.5 seconds before reversing direction and translating for an equal period of time. Two flashed lines ($2.05^\circ \times 0.25^\circ$) were presented straddling the outer gratings at various ISAs before or after the reversal of direction. A third flash ($1.025^\circ \times 0.125^\circ$) was presented superimposed on the fixation point. All flashes were presented simultaneously for 60 ms. For the two outer flashes, the separation between the inner edge of each flash and the outer edge of the nearest grating was 1.54° . The two outer flashes were vertically misaligned relative to the fixed position of the center flash, and subjects were asked to judge the direction of misalignment. As in the first experiment, the physical flash misalignment that created an apparent alignment was measured. The viewing distance was 40 cm.

Experiment 3. A single radial grating, identical to the 8.9° grating from the first experiment, was presented on the left side of the monitor with a fixation bull's-eye at its center. On the right side of the monitor another fixation bull's-eye was presented. A haploscope was provided to assist subjects in fusing the two fixation points. The procedure was identical to the first experiment except that the flashes (each $2.7^\circ \times 0.27^\circ$) were presented on the right side of the monitor, centered on the right fixation bull's-eye. The flashes were separated by 12.83° . When the two fixation points were fused, the inner edge of each flash was 1.3° from the nearest outer edge of the radial grating. The procedure was identical to that in the first experiment, except that only one flash-to-grating separation was tested. The viewing distance was 40 cm.

Experiment 4. A pair of linear gratings (each $17.4^\circ \times 5.8^\circ$) translated in opposite directions at the center of the display. A pair of flashes (each $6^\circ \times 0.85^\circ$) were presented straddling the gratings for various durations between 30 and 300 ms. The inner edge of each flash was 9.9° from the nearest linear grating's outer edge. The procedure for measuring the apparent flash misalignment was identical to that in the first experiment. To measure the perceived speed of the flashes, we physically moved the flashes in opposite vertical directions. Subjects judged whether the flashes moved clockwise or counterclockwise (although they only moved vertically and did not rotate). As in the first experiment, a psychometric function was fit to the data, and the point of subjective equality (where the flashes appeared stationary) was measured.

Experiment 6. The stimulus was identical to that in experiment 4 (flash duration, 60 ms). The flashes were always presented on a horizontal plane with the fixation. The pair of linear gratings were vertically displaced either above or below this plane randomly across trials. The vertical separation between the center of the linear gratings and the flashes varied from 0.0° to 35° . The procedure for measuring the apparent flash misalignment was identical to that in the first experiment.

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