

# An effect of relative motion on trajectory discrimination

Scott A. Beardsley<sup>a,b,\*</sup>, Lucia M. Vaina<sup>b,c</sup>

<sup>a</sup> Department of Biomedical Engineering, Marquette University, P.O. Box 1881, Milwaukee, WI 53201, USA

<sup>b</sup> Brain and Vision Research Laboratory, Department of Biomedical Engineering, Boston University, Boston, MA, USA

<sup>c</sup> Department of Neurology, Harvard Medical School, Boston, MA, USA

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## Abstract

Psychophysical studies point to the existence of specialized mechanisms sensitive to the *relative* motion between an object and its background. Such mechanisms would seem ideal for the motion-based segmentation of objects; however, their properties and role in processing the visual scene remain unclear. Here we examine the contribution of relative motion mechanisms to the processing of object trajectory. In a series of four psychophysical experiments we examine systematically the effects of relative direction and speed differences on the perceived trajectory of an object against a moving background. We show that background motion systematically influences the discrimination of object direction. Subjects' ability to discriminate direction was consistently better for objects moving *opposite* a translating background than for objects moving in the *same* direction as the background. This effect was limited to the case of a translating background and did not affect perceived trajectory for more complex background motions associated with self-motion. We interpret these differences as providing support for the role of relative motion mechanisms in the segmentation and representation of object motions that do not occlude the path of an observer's self-motion.

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## 1. Introduction

A major goal of visual processing is to segment the scene into different objects. To achieve this segmentation the visual system uses differences in luminance, color, texture, disparity, or motion. Thus, the main characteristic of segmentation is the perception of contrasts among the visual attributes that define object and background. In the case of motion, objects can be reliably segregated from the surrounding environment based on motion discontinuities alone (Anstis, 1970; Baker & Braddick, 1982; Hildreth, 1983; Regan & Beverley, 1984). Studies involving 2-D structure from motion have shown that differences in the speed and/or direction between an object and its background can both be used to recover the shape of an object (Regan & Beverley, 1984; Vaina, Grzywacz, & Kikinis,

1994; Vaina, LeMay, Bienfang, Choi, & Nakayama, 1990), suggesting the existence of mechanisms sensitive to the relative motion between object and background.

Psychophysical studies of motion contrast support this view (Ido, Ohtani, & Ejima, 2000; Murakami & Shimojo, 1995, 1996; Tadin, Lappin, Gilroy, & Blake, 2003; Van Doorn & Koenderink, 1983). In a motion coherence task, Murakami and Shimojo (1996) showed that motion sensitivity within the central region of a stimulus was systematically enhanced when the motion of the surround was in the opposite direction. They also found that the optimal size of the central region increased linearly with eccentricity, suggesting perceptual correlates to center-surround neurons reported in middle temporal cortex (MT) (Allman, Miezin, & McGuinness, 1985; Born, 2000; Eifuku & Wurtz, 1998; Tanaka et al., 1986; Tanaka, Sugita, Moriya, & Saito, 1993; Xiao, Raiguel, Marcar, Koenderink, & Orban, 1995; Xiao, Raiguel, Marcar, & Orban, 1997). Tadin et al. (2003) showed a similar effect of stimulus size

\* Corresponding author. Fax: +1 414 288 7938.

E-mail address: [scott.beardsley@marquette.edu](mailto:scott.beardsley@marquette.edu) (S.A. Beardsley).

on stimulus duration thresholds for subjects discriminating motion direction in drifting Gabor or random dot patches. Based on the ‘critical size’ at which strong surround suppression began to occur they proposed that processing of center-surround neurons in MT might underlie observer’s performance.

The existence of perceptual correlates to the center-surround motion mechanisms in MT is intriguing and would seem ideal for motion-based segmentation of an object relative to its background. If such mechanisms exist, one might expect to observe center-surround motion effects associated with an object’s intrinsic properties of movement, such as speed, position and trajectory through space. Psychophysical studies have reported that the perceived 2-D speed of a moving target is a U-shaped function of the speed of the background (Norman, Norman, Todd, & Lindsey, 1996). Similarly, the instantaneous position of a moving bar has been shown to be systematically affected by nearby motion (Whitney & Cavanagh, 2002). Here we investigate the effects of surround motion on object trajectory.

We hypothesize that if center-surround motion mechanisms are utilized by the visual system to aid motion-based segmentation of objects from the background, then discrimination thresholds should be lower for objects that move *opposite* to the background than for those that move in the *same* direction as the background. Moreover, if motion-based segmentation is mediated by neural mechanisms similar to those reported in non-human primates (Allman et al., 1985; Eifuku & Wurtz, 1998; Tanaka et al., 1986, 1993), we would expect sensitivity to trajectory differences to be reduced as the relative difference between the motions of the object and background decreases.

In a series of four psychophysical experiments we examine systematically the effects of relative direction and speed differences on trajectory discrimination. Exp. 1 examines the effect of a moving background on sensitivity to object trajectory when the object’s motion is in the same and opposite direction as the background. Exp. 2 performs a more detailed sampling of background directions to quantify the effect of graded differences between the object trajectory and background. Exp. 3 quantifies the interaction between background and object speed and Exp. 4 examines the effect of radial background motions on trajectory discrimination. We discuss our results in the context of a relative motion mechanism that is distinct from local motion direction and discontinuity mechanisms in the brain.

## 2. General methods

### 2.1. Stimuli

Random dot kinematogram (RDK) stimuli were generated on a 400 MHz PowerMac G4 computer and presented on a 17" Apple Studio Display monitor. RDK motion sequences were presented at 75 Hz in a calibrated gray-scale mode, with 8-bit precision, and a screen resolution of  $832 \times 624$  pixels.

Each RDK contained a motion-defined circular object that traversed a background of coherently moving dots (Fig. 1). The background dot field consisted of 418 uniformly distributed dots ( $0.95 \text{ dots/deg}^2$ ;  $9.3 \text{ Cd/m}^2$ ), presented in a  $24^\circ$  diameter aperture. Dots were displayed on a low luminance ( $5.2 \text{ Cd/m}^2$ ), gray background to minimize dot persistence cues across frames. At the subject viewing distance of 54 cm, each dot subtended 9.8 min of visual angle.

During stimulus presentation, individual dot motions were calculated continuously over time and their corresponding positions were discretely sampled for each frame. Unless otherwise specified, all background dots moved coherently in a single direction across the screen at a speed of  $22.5 \text{ deg/s}$ . Uniform dot density was maintained by wrapping dot trajectories along the direction of background motion as they moved beyond the stimulus aperture.

The object consisted of an occluding  $4^\circ$  diameter circular aperture set to the background luminance of the display. Within the object aperture, 12 dots ( $0.95 \text{ dots/deg}^2$ ) moved in random directions along fixed trajectories to prevent discrimination of object trajectory based on individual dot motions. As dots moved beyond the object aperture, they were replaced consistent with the maintenance of a constant density display for relative dot motion (see Appendix). The luminance and speed of the “object” dots were matched to the background dot field such that the object was defined solely by the difference in internal dot motion relative to the background.

All stimuli were presented for 440 ms with a dot lifetime of 146 ms (11 frames). Dots were replaced asynchronously by uniformly distributing the initial dot lifetimes among the first 11 frames. When dots exceeded their lifetime they were randomly repositioned and given trajectories according to their pre-assigned designation as object or background. Position-based discrimination cues were controlled through the addition of a stimulus duration uncertainty centered around the nominal stimulus duration ( $440 \pm 40 \text{ ms}$ ).

### 2.2. Experimental procedure

Prior to the start of an experimental session, observers adapted to the background luminance of the monitor display in a quiet darkened room. During the task, observers were required to fixate a small central square ( $11 \times 11$  pixels;  $9.3 \text{ Cd/m}^2$ ) while pairs of motion stimuli were presented binocularly in a temporal two-alternative-forced-choice (2AFC) paradigm (500 ms interstimulus interval). An auditory trigger preceded each

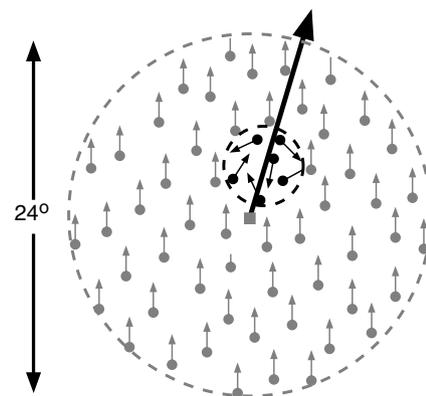


Fig. 1. Schematic of the trajectory discrimination stimulus. A  $4^\circ$  diameter circular object defined solely by random internal dot motion (shown here in black) moved across a  $24^\circ$  diameter background of coherently moving dots. Stimulus boundaries were illusory, as defined by an absence of dots at the stimulus aperture and a difference in dot motion at the object aperture. At the beginning of each stimulus presentation the object aperture was centered in the stimulus and moved along a fixed trajectory (solid arrow) to the left or right of vertical.

stimulus. The presentation of opposing motions, e.g., up/down, was randomly interleaved across trials to minimize adaptation to specific directions of motion.

Observer thresholds (79% correct), were estimated as the average over the last six reversals of the 3-down/1-up phase (constant step size) of an adaptive staircase procedure (Vaina et al., 2003). In all experimental conditions, observers' performance is reported as the mean threshold  $\pm 1$  standard error averaged across a minimum of five staircases.

### 2.3. Observers

In total, eleven observers participated across a series of three trajectory discrimination tasks. Their vision was normal or corrected to normal. Three of the 11 subjects (SB, MK, and FC) were experienced psychophysical observers. Two of the experienced observers (SB and FC), also participated in separate static background and position discrimination control tasks outlined in Experiments 1 and 3, respectively, and one naïve inexperienced observer (TB), participated in the static background task. With the exception of SB, all observers were naïve to the purpose of the study. Prior to participation in the study, written informed consent was obtained from all subjects in accordance with Boston University's Institutional Review Board Committee on research involving human subjects.

## 3. Experiment 1: Direction discrimination of object trajectories

Psychophysical studies of perceived object speed and position (Norman et al., 1996; Whitney & Cavanagh, 2002), suggest that center-surround motion mechanisms play an active role, not only in motion-based segmentation of an object from the scene, but also in processing the object's intrinsic motion properties. This suggests that background motion may directly impact other object

motion properties, such as direction. If MT-like center-surround mechanisms play a role in the processing of object direction, then we predict that direction discrimination thresholds for an object's trajectory should decrease when the background and object move in opposite directions.

### 3.1. Methods

Trajectory discrimination thresholds for a motion-defined circular object were measured as a function of the relative direction difference between the object's trajectory and a background of translating dots (Fig. 2A). Beyond the object aperture, background dots moved coherently in one of four directions (right, up, left, or down;  $\theta = 0^\circ, 90^\circ, 180^\circ,$  and  $270^\circ$ , respectively). In each trial, the nominal direction of object motion was randomly oriented to be in the *same* or *opposite* direction as the background. The object was positioned in the center of the stimulus aperture at the start of each motion sequence to minimize position-based discrimination cues associated with the object's initial location.

In a 2T AFC task, discrimination pairs of stimuli were constructed by rotating the object trajectory  $\pm\theta_p$  from its nominal direction. For vertical object motion ( $\theta = 90^\circ, 270^\circ$ ), observers were required to select the stimulus interval in which the object moved to the *right* of the vertical mid-line through the stimulus center. For horizontal object motion ( $\theta = 0^\circ, 180^\circ$ ), observers were required to select the stimulus interval in which the object moved *below* the horizontal mid-line through the stimulus center. To minimize

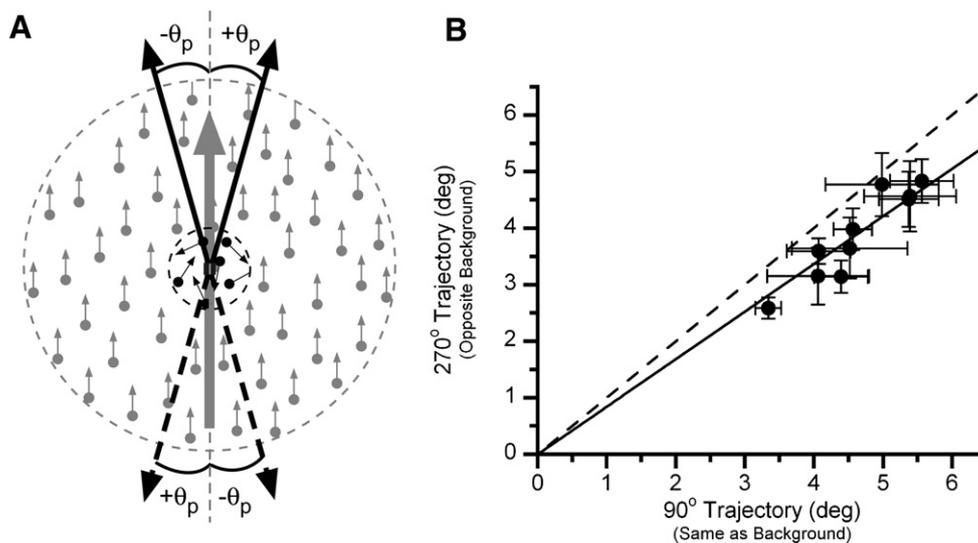


Fig. 2. (A) Schematic of the trajectory discrimination task for vertical motions. For each direction of background motion (shown here for upward motion – gray arrows), the object trajectory was oriented in either the *same* (solid arrows) or *opposite* (dashed arrows) direction. During the task pairs of stimuli were constructed by rotating the object trajectory  $\pm\theta_p$  relative to the axis of the background motion. (B) Trajectory discrimination thresholds for *same* (abscissa) vs. *opposite* (ordinate) object motion in ten observers presented with an upward background motion ( $\theta = 90^\circ$ ). Performance is reported as the mean threshold ( $\pm$ SE) across a minimum of six staircases for each observer and object direction. In half of subjects, thresholds were averaged across an extended set of 15–18 staircases per condition. The condition in which *same* and *opposite* object trajectories are equivalent is denoted by a dashed line along the diagonal. Points below the dashed line correspond to observers whose thresholds for object motion opposite the background were better than for object motion in the same direction as the background. Across observers, the ratio of *opposite/same* thresholds was approximately constant ( $=0.84$ ) as indicated by a least-squares linear fit ( $r^2 = 0.84$ ) through the origin.

perceptual bias associated with the type of judgment, i.e., rightward vs. leftward rotation, a subset of observers was tested using the reverse set of judgments, e.g., select the object moving to the left of vertical.

In a separate control condition, discrimination thresholds were obtained from a subset of observers when the background dots were static. The trajectory discrimination stimulus and task were the same as in Exp. 1 with the exception that the locations of the background dots were fixed. When a dot reached the end of its 11 frame lifetime a new fixed location was randomly assigned within the background aperture. This “static background” condition was used to quantify the contribution of background motion, i.e., facilitatory vs. inhibitory, to the relative motion percept.

### 3.2. Results

Trajectory discrimination thresholds were obtained from ten observers for an object moving vertically ( $\theta = 90^\circ, 270^\circ$ ), against an upward moving background dot field ( $\theta = 90^\circ$ ). Fig. 2B shows a scatter plot of subjects’ average thresholds plotted as a function of the object direction (*same* vs. *opposite*) relative to the background. All thresholds fell below a line of unit slope (dashed line), indicating that discrimination thresholds for objects moving *opposite* the background were consistently lower than for those moving in the *same* direction as the background. The difference in *same* vs. *opposite* thresholds, which was significant for observers SB and MK ( $p < 0.05$ ,  $t(24) \geq 2.59$ ), and nearly significant for observers TB, TS, and AP ( $p \leq 0.11$ ,  $t(26) \geq 1.26$ ), was well approximated as a constant proportion ( $=0.84$ ) across the population (Fig. 2B: solid line,  $r^2 = 0.84$ ).

In three of the 10 observers (SB, TB, and FC), direction discrimination thresholds were also obtained for the static background control condition. Across observers, thresholds were comparable to those obtained with the moving background ( $3^\circ$ – $4^\circ$ ). Fig. 3 shows the change in direction discrimination thresholds obtained for the moving background in Exp. 1, relative to those obtained in the static background task. Thresholds for objects moving in the *same* direction as the background and those when the background was static were not significantly different for the three observers ( $p \geq 0.225$ ;  $t(14) = 0.78$ ). Thresholds for objects moving *opposite* the background were consistently lower, indicating facilitation, although the effect was significant only for FC [FC,  $p < 0.05$ ;  $t(13) = 4.66$ ; TB,  $p = 0.13$ ;  $t(22) = 1.13$ ; SB,  $p = 0.18$ ;  $t(30) = 0.92$ ]. The decrease in *opposite* motion thresholds was inversely related to observers’ static background thresholds (Fig. 3), suggesting a potential floor effect on the level of facilitation such that subjects with lower static thresholds experienced less facilitation. Extrapolation of the minimum resolvable change in trajectory across subjects placed the “floor” at approximately  $3^\circ$ .

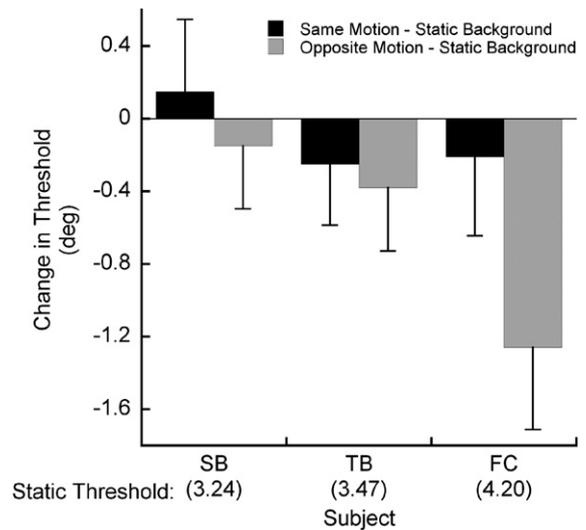


Fig. 3. Differences in trajectory discrimination thresholds between relative background motion (Exp. 1) and the static background control condition for three subjects (SB, TB, and FC). Static background thresholds are shown below each subject for reference and the corresponding difference in *same* and *opposite* object motion thresholds is shown along the abscissa.

In three observers (MK, SB, and TB), *same* vs. *opposite* motion thresholds were also obtained for the four cardinal directions of background/object motion (up, down, left, and right). Fig. 4 shows the difference in thresholds expressed as a relative motion ratio (RMR), in which thresholds for motion *opposite* the background are normalized with respect to motion in the *same* direction as the background. Across observers, thresholds for downward, leftward, and rightward motion were generally consistent with those for upward motion (Fig. 2), spanning a range of  $2.6^\circ$ – $5.3^\circ$ . However, the RMR was dependent on the overall direction of motion (horizontal vs. vertical), (Fig. 4A). In observers SB and MK, vertical motions showed a clear effect of object direction with thresholds for objects moving *opposite* the background being significantly smaller than for objects moving in the *same* direction as the background ( $RMR < 1$ ,  $p < 0.05$ ;  $t(14) \geq 1.94$ ). The difference was less pronounced in TB, particularly for downward background motion ( $\theta = 270^\circ$ ). By comparison, *same* vs. *opposite* thresholds for horizontal motion were not significantly different ( $p \geq 0.2$ ;  $t(19) = 0.83$  – except for MK with rightward background motion,  $p < 0.05$ ;  $t(28) = 1.93$ ).

The disparity between horizontal and vertical motions can be seen more clearly in Fig. 4B. As a class, vertical background motion showed a much stronger effect on trajectory discrimination. Fig. 5 shows thresholds averaged across observers as a function of object direction relative to background. At  $4.3^\circ$ , thresholds for vertical motion in the *same* direction as the background were significantly higher than those for horizontal motions or vertical motions *opposite* the background, which were themselves well matched ( $3^\circ$ – $3.5^\circ$ ). The pattern of *same* vs. *opposite* motion thresholds is similar to that found in the static background condition (Fig. 3 – static vs. vertical), and is

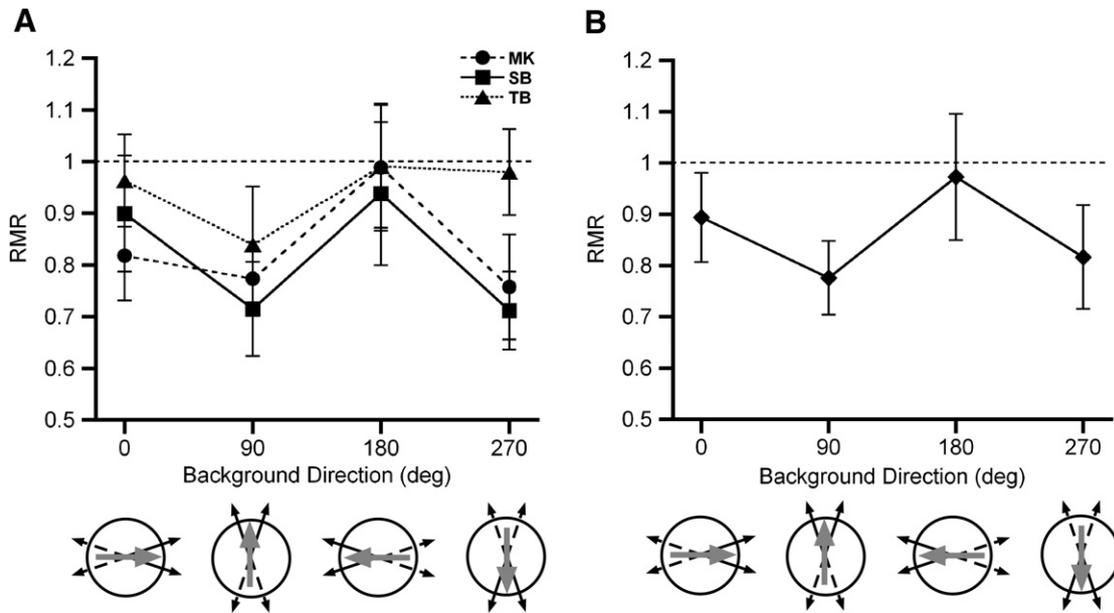


Fig. 4. Relative motion ratio (RMR) as a function of the common object and background direction. RMR is expressed as the ratio of *oppositesame* direction thresholds with respect to the background motion. (A) RMRs for three observers, MK (circles – dashed line), SB (squares – solid line), and TB (triangles – dotted line). Diagrams along the bottom of the figure denote the object motions tested (opposing paired arrows) for each direction of background motion (central arrow). In observers SB and MK, thresholds for objects moving opposite a vertical background were significantly less than for objects moving with the background. The difference was less pronounced in TB, particularly for downward background motion ( $\theta = 270^\circ$ ). For horizontal trajectories there was little if any effect of object direction across observers. (B) RMR averaged across observers. The motion of the background relative to the object had a consistently stronger impact on trajectory discrimination for vertical motion than for horizontal motion. Error bars are  $\pm 1$  SE.

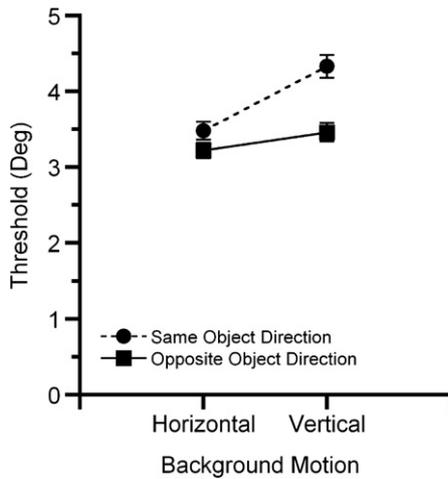


Fig. 5. Averaged trajectory discrimination thresholds across observers (SB, MK, and TB) for horizontal ( $\theta = 0^\circ, 180^\circ$ ) and vertical ( $\theta = 90^\circ, 270^\circ$ ) background motion. Thresholds for objects moving opposite the background (square – solid line) and for objects moving in the same direction as the background (circle – dashed line) are shown separately.

consistent with a minimum thresholds constraint (i.e., floor effect) on the extent to which opposing motions facilitate trajectory discrimination.

**4. Experiment 2: Relative changes in background direction**

In an extension of Exp. 1, we examined the interaction between background and object direction by systematically

changing the direction of background motion relative to the object trajectory. In this and subsequent experiments, subjects were tested with vertical object motion to maximize sensitivity to changes in the background motion.

*4.1. Methods*

Object trajectories were randomly oriented vertically up ( $\theta = 90^\circ$ ) or down ( $\theta = 270^\circ$ ) and rotated  $\pm\theta_p$  using an interleaved dual-staircase paradigm (Fig. 6). During the task, observers were required to select the stimulus interval containing an object moving to the right of an imaginary vertical line through the stimulus center. Trajectory discrimination thresholds were averaged across 14–20 staircases for each observer and each of four background directions ( $\theta = 0^\circ, 30^\circ, 60^\circ, \text{ and } 90^\circ$ ). Dot and object aperture speeds were held constant at 22.5 and 9.18 deg/s, respectively. Together with the interleaved presentation of opposing up/down object trajectories, the tested background directions resulted in a  $180^\circ$  range of direction differences between object and background.

*4.2. Results*

Fig. 7A shows trajectory discrimination for three observers (SB, MK, and AP) as a function of the direction difference between the object and background. The thresholds averaged across observers are shown in Fig. 7B. For comparison, thresholds were normalized to the zero

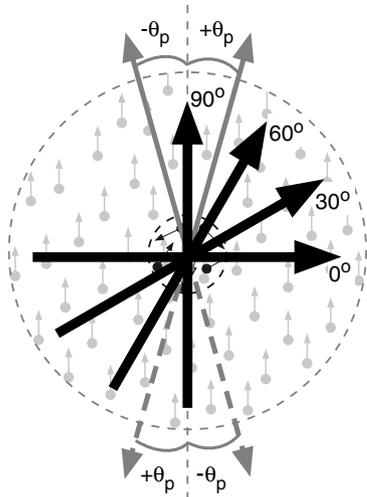


Fig. 6. Schematic of the trajectory discrimination task used to quantify the interaction between object and background trajectories. Discrimination thresholds for vertical object motion were examined as a function of four background directions ( $\theta = 0^\circ, 30^\circ, 60^\circ,$  and  $90^\circ$ ) for two directions of vertical object motion as described in Fig. 2. Together, the range of direction differences tested spanned  $180^\circ$ .

direction difference corresponding to  $90^\circ$  object and background motion. Thresholds systematically decreased across observers as the direction difference increased through  $90^\circ$ . With the exception of objects moving opposite the background, thresholds for direction differences greater than  $90^\circ$  were similar. While thresholds for opposing motion were consistently lower, the decrease was only significant for MK ( $p < 0.005$ ;  $t(39) = 3.18$ ).

### 5. Experiment 3: Interaction between object and dot speed

Experiments 1 and 2 indicate that discrimination of object trajectory is systematically influenced by the direction of background motion, however, they do not preclude the use of position-based cues associated with the localiza-

tion of motion discontinuities. In the trajectory discrimination task, the salience of the motion discontinuity at the object's leading edge is a function of the object's trajectory relative to the background. Motion opposite the background increases the salience of the discontinuity allowing better spatial localization of the object's position at the end of its trajectory. Under these conditions, the direction specific effect of the background motion is potentially confounded by differences in position-based estimates of object location associated with the salience of the motion discontinuity.

#### 5.1. Methods

To dissociate direction and position-based effects, we measured trajectory discrimination as a function of the object and dot speed and in a separate control task we measured position discrimination based on the endpoint of object motion for each speed condition. If the difference in *same* vs. *opposite* thresholds is dependent on the salience of the object and its final position, then we would predict that the RMR be correlated with the strength of motion contrast, which is proportional to the relative speed of the object.

Eight observers performed the vertical trajectory discrimination task in Exp. 1 across four combinations of dot (9.18 and 22.5 deg/s), and object aperture speeds (9.18 and 18 deg/s). For each combination of background and object speeds, the average threshold was calculated across six interleaved staircase runs. Observers SB and MK were tested more extensively with 10 and 14 staircases per condition, respectively. A three-way analysis of variance (ANOVA) was performed within observers and for the average thresholds across observers to test for speed dependent changes in RMR and across motion directions.

Two observers (SB and FC), also participated in a separate position discrimination task designed to control for

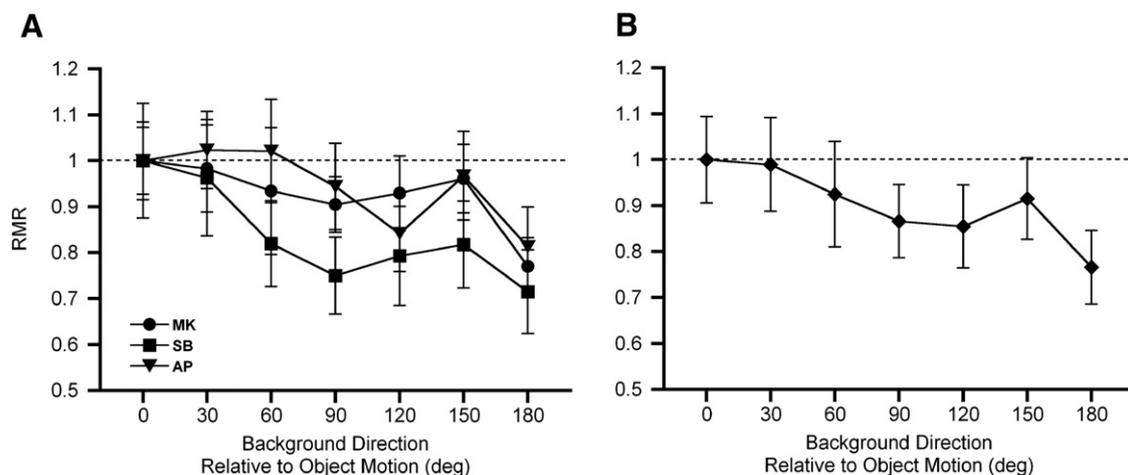


Fig. 7. (A) Trajectory discrimination as a function of the direction difference between the object and background for three observers (SB – squares, MK – circles, and AP – triangles). Performance for each observer is plotted as a relative motion ratio (RMR), obtained by normalizing thresholds relative to the  $0^\circ$  direction difference between object and background. Error bars are  $\pm 1$  SE.

the increase in horizontal offset of the object's final position with speed. Position discrimination was measured directly by presenting the static object aperture positioned at the end of the trajectory from Exp. 1. To approximate the position information available during Exp. 1, the object was presented for an average of 133 ms during the last third of the stimulus interval. Object onset was pseudo-randomized ( $307 \pm 27$  ms) to reduce temporal priming. In a 2T AFC task, observers were required to select the stimulus interval containing the object to the right of the vertical mid-line through the stimulus center.

## 5.2. Results

Average thresholds for the four combinations of object/background speed are shown in Fig. 8A for objects moving in the *same* (black bars) and *opposite* direction (gray bars) relative to the background. Thresholds for objects moving in the *same* direction as the background ( $\theta = 90^\circ$ ) were consistently higher than for objects moving *opposite* the background ( $\theta = 270^\circ$ ). A three-way ANOVA with object direction, object speed, and background speed as factors revealed main effects of both direction ( $p < 0.05$ ,  $F(1, 55) = 4.16$ ) and object speed ( $p < 0.0001$ ,  $F(1, 55) = 38.49$ ). Within subject comparisons revealed that both effects were consistent and significant ( $p < 0.05$ ) across all observers with the exception of object speed for SB ( $\theta = 270^\circ$ ;  $p = 0.24$ ,  $F(1, 57) = 1.38$ ). There were no significant interactions between factors ( $p > 0.2$ ,  $F(1, 55) = 1.58$ ).

By comparison, the ratio of *opposite/same* thresholds was not strongly affected by the speed of either the object or background. Fig. 8B shows the RMR averaged across

observers for each of the four speed combinations. A two-way ANOVA showed no effect of either object or background speed on RMR ( $p > 0.55$ ,  $F(1, 27) = 0.36$ ). There was a small but consistent decrease in RMR for speeds with greater local motion contrast, however, the interaction was not significant ( $p > 0.17$ ,  $F(1, 27) = 1.95$ ).

The lack of systematic changes in the RMR with speed and position indicate that the difference in *same vs. opposite* motion thresholds was not due to variations in the salience and localization of the object discontinuity. If the difference in discrimination thresholds for *same vs. opposite* object motion were due primarily to the salience of the object discontinuity, then the relative motion ratio (RMR) should have been inversely proportional to the speed difference between object and background. Instead, the data suggest that the decrease in thresholds for motion *opposite* the background arose from the interaction between the relative motion of the object and background.

At the same time, the decrease in thresholds with increasing object speed suggests that final object position may play a role in the task. Observers' performance on the position control task supports this interpretation (Fig. 9). In both observers, the decrease in direction thresholds with increasing object speed was mirrored by a decrease in angular position thresholds. Thresholds decreased by a factor of approximately two with a doubling of speed, consistent with discrimination based on absolute distance from the vertical mid-line.

One might conclude that this result supports discrimination based on the object's final position and not its trajectory *per se*. However, in the position control neither observer showed a consistent difference between objects

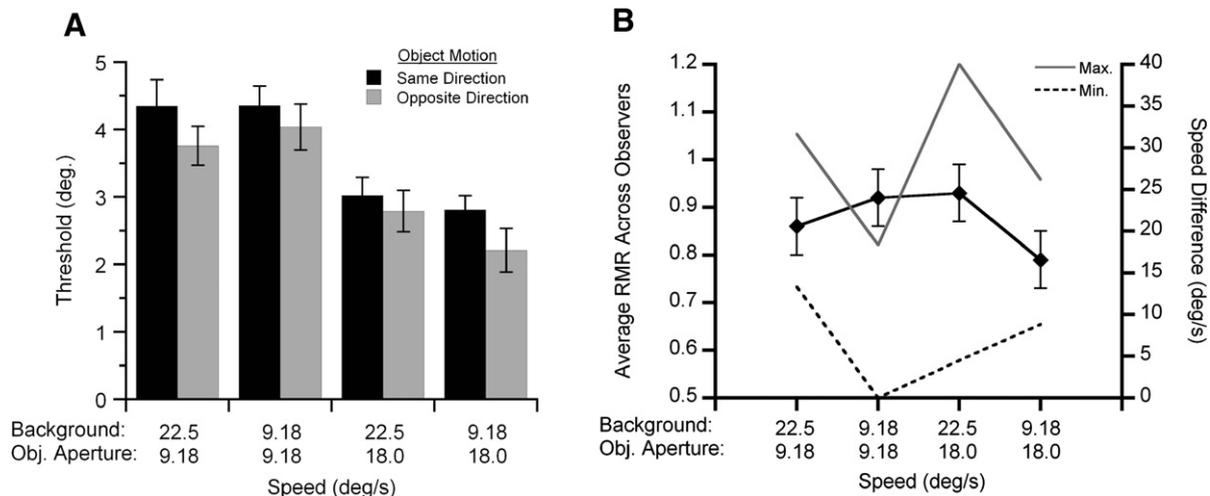


Fig. 8. Trajectory discrimination thresholds for vertical object motion as a function of background and object aperture speeds. In all conditions the background moved vertically upwards ( $\theta = 90^\circ$ ). (A) Thresholds averaged across seven observers for objects moving in the *same* ( $\theta = 90^\circ$ ; black bars) and *opposite* direction ( $\theta = 270^\circ$ ; gray bars) relative to the background. Thresholds for objects moving in the same direction as the background were consistently higher than for objects moving opposite the background. (B) RMR averaged across observers for each of the four speed combinations. The maximum and minimum speed differences in each condition, corresponding to object motions in the *opposite* and *same* direction as the background, respectively, are shown separately for comparison. In contrast to absolute thresholds the RMR showed no effect of either object or background speed. There was a small but consistent decrease in RMR for speeds with greater motion contrast, however, the interaction was not significant. Error bars are  $\pm 1$  SE.

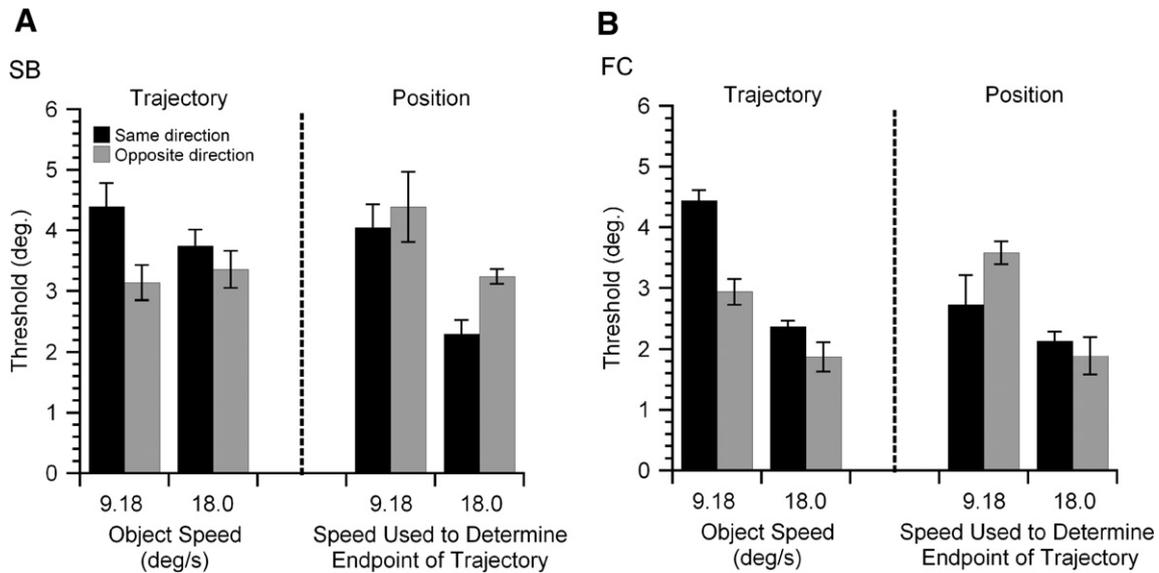


Fig. 9. Trajectory and position discrimination thresholds as a function of object speed for two observers (SB and FC). In the position discrimination task a static object aperture was presented at the object's final location obtained from the trajectory discrimination task (Exp. 1). Thresholds were obtained for objects positioned above ( $\theta = 90^\circ$ ; black bars) and below ( $\theta = 270^\circ$ ; gray bars) the horizontal mid-line through the stimulus center.

located at the endpoint of the *same* vs. *opposite* motion trajectories. With the exception of subject SB for the 18 deg/s control condition, thresholds for objects located along  $90^\circ$  and  $270^\circ$  trajectories were equivalent ( $p > 0.5$ ;  $t(8) = 1.65$ ). The lack of a consistent asymmetry in thresholds for endpoint position that mirrored the difference in *opposite* vs. *same* motion thresholds suggests that the effect of background motion was specifically associated with the object's motion, and did not depend on the salience of the discontinuity between object and background. We propose that the effect of object speed reflects increased spatio-temporal summation of object trajectory within a relative motion mechanism.

#### 6. Experiment 4: Discriminating object direction in radial motion

Experiments 1–3 demonstrated a relative motion effect on the perceived trajectory of an object across a moving background. This interaction suggests that, in the case of a simple translating background, the motion of the object was not fully segmented from the background. In Exp. 4 we examined the effect of radial background motion associated with self-motion through the environment. Psychophysical studies have shown that moving objects that do not occlude the path of self-motion have little effect on judgments of heading (Royden & Hildreth, 1996; Warren & Saunders, 1995). This has led to speculation that the visual system may segment unambiguous object motions from the visual scene prior to processing self-motion. For the trajectory discrimination task, such segmentation would predict that the perceived trajectory of the object be independent of its motion relative to the background.

#### 6.1. Methods

The task and basic experimental setup were the same as Exp. 1. Here the background consisted of either an expanding or contracting field of dots centered in the stimulus aperture (Fig. 10A). Background dots moved coherently through a radial speed gradient with a maximum dot speed of 22.5 deg/s at the outer edge of the stimulus aperture. Uniform dot density was maintained by randomly reassigning dots that moved beyond the stimulus aperture to new positions that were a non-linear function of the speed gradient and radial distance (see Clifford, Beardsley, & Vaina, 1999 for details).

The type of radial motion (expansion or contraction), was fixed at the beginning of each staircase and pseudo-randomized across staircases. As in Exp. 1, observers were required to discriminate changes in the direction of vertical object motion ( $\theta = 90^\circ, 270^\circ$ ). The type of radial motion presented, expansion or contraction, determined whether the object motion was in the same or opposite direction relative to the adjacent background (Fig. 10A). For each observer, average thresholds were estimated across ten staircases, five each for expansion and contraction (11 each for subject SB).

#### 6.2. Results

Five observers participated in the experiment. The object's nominal direction (up or down) had little effect on observer performance ( $p > 0.17$ ,  $t(5) = 1.06$ ; except expansion for subject BY,  $p < 0.05$ ,  $t(7) = 3.05$ ). Thus in the subsequent analysis, thresholds for both directions of object motion were combined to estimate trajectory discrimination for objects moving in the same (expansion)

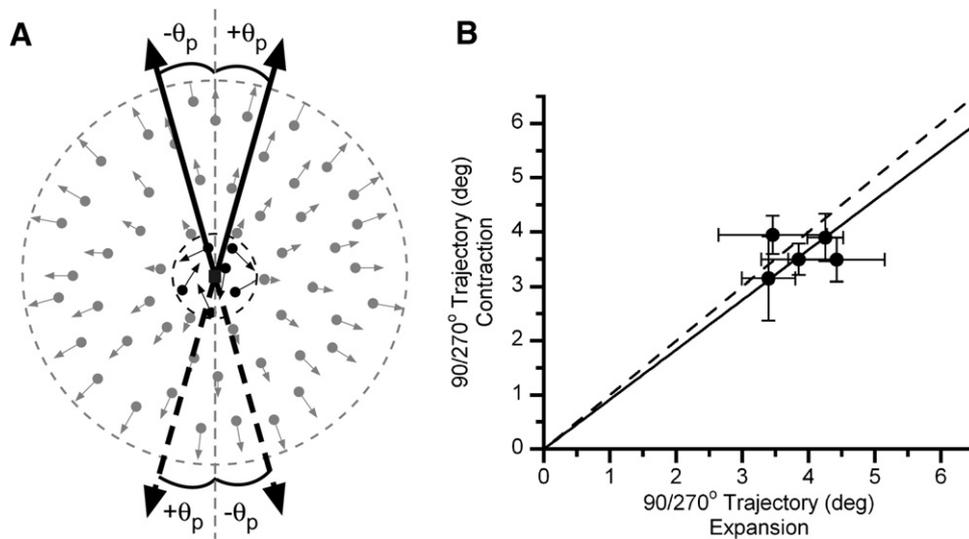


Fig. 10. (A) Trajectory discrimination task for radial background motions. For each type of background motion (expansion or contraction), the object trajectory was always oriented in the *same* (expansion) or *opposite* (contraction) direction relative to the local background motion. As in Exp. 1, stimuli were constructed by rotating the object trajectory  $\pm\theta_p$ . (B) Trajectory discrimination thresholds ( $\pm$ SE) for *same* (expansion) vs. *opposite* (contraction) object motion in five observers. With the exception of subject BY ( $p < 0.05$ ,  $t(7) = 3.05$ ), there was no significant difference between upwards and downwards object motion for expansion or contraction ( $p > 0.17$ ,  $t(5) = 1.06$ ). In the plot, performance for the two object trajectories has been combined into average thresholds for both expansion and contraction. The dashed line along the diagonal corresponds to the condition where discrimination thresholds for object motion in the *same* and *opposite* directions, relative to the background, are equal. Thresholds were tightly clustered along the diagonal indicating a decreased effect of the background direction on trajectory discrimination. Across subjects the ratio of *opposite* vs. *same* thresholds was well approximated as a constant ( $=0.92$ ; solid line).

and opposite (contraction) direction relative to the surrounding background motion (Fig. 10B).

Compared with Exp. 1, here thresholds for *same* vs. *opposite* object motion were more tightly clustered along the diagonal indicating a decreased effect of the background motion on trajectory discrimination. Across the five observers, the ratio of *opposite* to *same* motion thresholds was well approximated as a constant ( $=0.92$ ; solid line – Fig. 10B). Only subject GH showed a significant effect of the relative direction of the local background on trajectory discrimination ( $p < 0.05$ ,  $t(16) = 1.84$ ).

## 7. Discussion

In a series of trajectory discrimination tasks, we have shown that background motion systematically influences sensitivity to object direction. Discrimination thresholds were consistently lower for objects moving *opposite* a translating background than for objects moving in the *same* direction as the background. The effect, which was specific to translating backgrounds, was proportional to the direction difference between object and background and was robust to variations in the speed of the dots and the object itself. We interpret these differences as providing support for the role of center-surround motion mechanisms in the segmentation and representation of object motion in the visual scene.

Physiological studies support this type of specialization. In MT a subset of neurons respond to motion contrast between the center of the cell's receptive field and its sur-

round. In these center-surround neurons the magnitude of the preferred motion response in the center is maximal for surround motion in the opposite direction and systematically decreases as the center and surround motions become more similar (Allman et al., 1985; Born, 2000; Tanaka et al., 1986; Xiao et al., 1997). In addition to motion contrast, neurons in the lateral ventral region of the medial superior temporal cortex (MSTl/MSTv) respond to the relative motion of static objects that partially occlude a background moving in the neuron's anti-preferred direction (Eifuku & Wurtz, 1998; Tanaka et al., 1993). Single cell studies in the anterior superior temporal polysensory area (STPa), report comparable relative motion effects, extending previous observations that STPa is involved in processing the external motion of objects not defined by self-motion (Hietanen & Perrett, 1996).

### 7.1. Specialized mechanisms for processing relative object motion

As we noted in the general methods, the stimulus design was optimized to isolate the visual motion mechanisms associated with the segmentation and representation of object motion. The presentation of motion-defined object motion within a constant density random dot display removed potentially confounding position-based cues associated with differences in texture, luminance, and disparity. Similarly the use of random dot motion to define the object controlled for motion-specific cues by (a) preventing discrimination based on the absolute motion of object dots

held static relative to the object aperture, and (b) minimizing biases in perceived trajectory caused by coherent dot motion within the object aperture, e.g., theta motion (Zanker & Burns, 2001). Under these conditions the effect of background motion on trajectory discrimination cannot be based on non-motion cues or the perceived internal motion of the object.

It is possible that the effect of the background motion could result from differences in the salience of the motion discontinuity at the object border. Both the decrease in thresholds for object motion opposite the background and the overall decrease in thresholds with increased object speed are consistent with a spatial localization of the motion discontinuity. However, several aspects of the results and the stimulus itself argue against this type of strategy.

First, the stimulus duration uncertainty incorporated into the task randomly varies the length of the object trajectory making position-based estimates of final object position unreliable. Second, a position-based mechanism would not account for the difference in the background motion effect for horizontal and vertical motions (Exp. 2). Third, in Exp. 3 the relative difference in thresholds for *opposite* vs. *same* object motion was not significantly affected by changes in the speed of either the object or the background. Finally, observers' performance on the position control task (Exp. 3) showed no orientation-specific analogue to the relative motion effect observed between objects moving with and against the background.

While there is little doubt that discontinuity mechanisms are employed by the visual system to segregate the motion-defined object from the background (Anstis, 1970; Bradick, 1974; Vaina, Grzywacz, & LeMay, 1990; Vaina, Grzywacz, LeMay, Bienfang, & Wolpaw, 1998; Vaina et al., 1994), the lack of an equivalent effect in the position control task strongly argues against their primary role in the trajectory discrimination task. Together with the lack of other visual cues, these results suggest that the representation of object motion may be mediated by mechanisms that are preferentially sensitive to relative motion differences between an object and its background.

### 7.2. A direction specific effect of background motion

The systematic difference in the effect of horizontal and vertical background motions observed in Exp. 1 is intriguing. If, as we speculate, the effect of background motion on trajectory discrimination reflects perceptual correlates to center-surround type motion mechanisms then we would not have expected to observe a difference between horizontal and vertical motions. This was not the case. The effect of relative motion was consistently and significantly lower for horizontal background/object motions than for vertical motions.

The relative motion asymmetry in Exp. 1 could indicate a floor effect associated with a minimum resolvable change in object trajectory. The inverse relationship between

observers' static background thresholds and the decrease in opposing motion thresholds shown in Fig. 3 would seem to support this interpretation. Given the predominance of horizontal motions encountered as part of the natural environment (Bex, Dakin, & Mareschal, 2005), and the increased horizontal/vertical asymmetry in eye movements (Erickson & Barmack, 1980; Gronqvist, Gredeback, & Hofsten, 2006; Rottach et al., 1996; Wallman & Velez, 1985), the representation of object trajectories may be naturally biased more towards horizontal as opposed to vertical motion. In this context, the representation of horizontal motions may already be sufficient to maximize trajectory discrimination irrespective of the background, resulting in little if any improvement when both the object and background move.

Alternatively, the results could suggest a horizontal-vertical asymmetry in the representation of relative motion, analogous to that reported for direction discrimination (Raymond, 1994). Psychophysical studies of motion contrast have not explicitly compared effects for horizontal and vertical motions (Ido et al., 2000; Murakami & Shimojo, 1995; Murakami & Shimojo, 1996; Tadin et al., 2003). Although studies of object trajectory in static and dynamic random backgrounds suggest a homogeneous representation, Zanker and Burns (2001) did note a slight bias in perceived trajectories towards cardinal directions of motion.

Eye movements may also have contributed to the difference between horizontal and vertical motions. Asymmetries between horizontal and vertical eye movements have been reported during smooth pursuit (Gronqvist et al., 2006; Rottach et al., 1996), and as part of the optokinetic reflex (Erickson & Barmack, 1980; Wallman & Velez, 1985), suggesting that this possibility cannot be ruled out in the current experiments. During the task observers were explicitly told to maintain fixation, however, eye movements were not actively monitored. If subjects initiated saccades and/or smooth pursuit eye-movements to the object, the accompanying extra-retinal information could have provided an additional source of trajectory information that may have confounded the relative motion effect.

### 7.3. Perceptual correlates to a center-surround motion mechanism

The enhancement in trajectory discrimination for objects moving opposite a translating background is reminiscent of the opponent motion properties of center-surround neurons in MT and MSTv. In both areas, individual responses to motion in the center are maximal when the surround motion is in the opposite direction and strongly inhibited by surround motion in the same direction (Allman et al., 1985; Born, 2000; Eifuku & Wurtz, 1998; Tanaka et al., 1986, 1993; Xiao et al., 1997). The effect of surround direction in these neurons is both modulatory and graded such that center responses systematically decrease as the direction difference between center and surround decreases. In addition, neurons in MSTv respond to

the motion of small textured regions across their visual field and do not exhibit the wide field motion pattern preferences typically observed in the dorsal region of MST (Eifuku & Wurtz, 1998; Tanaka et al., 1993). Psychophysical performance on the trajectory discrimination task resulted in similar trends, with discrimination thresholds systematically decreasing as the motion difference between the object trajectory and the background increased.

In the context of the trajectory discrimination task, a simple interpretation of the visual motion properties reported in these regions might suggest that MT is involved in the motion-based segregation of the object from the background while MSTv is involved in encoding object trajectories relative to the background motion. Within a population coding framework, the response of center-surround neurons to opposing motion, whether via facilitation of opposing motions or inhibition of similar motions, would increase the pool of neurons active during the opposing motion trials thereby improving discrimination for changes in object trajectory.

In this scheme, a simple feed-forward increase in computational complexity from MT to MSTv would imply an early (MT) motion-based segregation of the object from the visual field that is later refined in higher visual motion areas such as MSTv to extract inconsistent ‘object’ motions from the observer’s self-motion. Anatomical studies indicating the presence of afferent connections between center-surround neurons in MT and MSTv support this type of computational structure (Berezovskii & Born, 2000), and together with the relative motion effects reported here suggest a more specific role for center-surround mechanisms in the segmentation and representation of object motion.

Dakin and Mareschal (2000), have proposed a similar segmentation role for relative motion computation to account for the ‘direction repulsion’ effect observed when the directions of motion in two fields of transparently moving dots differ by no more than 40° (Curran & Benton, 2003; Marshak & Sekuler, 1979). While the decrease in discrimination thresholds reported here for objects that move opposite the background, i.e., for direction differences greater than 90°, appears fundamentally different from the direction repulsion effect, this may be due partly to differences in the tasks, stimuli, and spatial scale over which the tasks were performed. Both phenomena could reflect a common underlying segmentation mechanism, wherein relative motions over small spatial scales are first used to infer the background motion and relative motions over larger spatial scales are used to segment object motion from the background.

#### 7.4. Trajectory discrimination during self-motion

The lack of a background motion effect for radial motion patterns agrees well both with psychophysical studies of heading and neurophysiology in MT/MST. Psychophysical studies of perceived heading have shown that object motions that do not occlude the path of self-motion

have little effect on heading (Royden & Hildreth, 1996; Warren & Saunders, 1995). This has led to speculation that the visual system segments unambiguous object motions from the visual scene to perceive heading. Our results support this view, demonstrating the reverse dissociation. Unlike simple planar motion, background motions simulating simple self-motion (i.e., expansion/contraction), have little effect on the perceived trajectories of moving objects. Such segmentation is consistent with the planar motion properties of center-surround neurons in MSTv (Eifuku & Wurtz, 1998; Tanaka et al., 1993), and may suggest that processing in these areas is optimized for segmenting object motion in regions located away from an observer’s heading.

## 8. Conclusion

The results on the tasks of trajectory discrimination suggest the existence of specialized detectors for relative motion in the human visual system. While the physiology in monkeys suggests that motion opponent cells in areas MT and MSTv may mediate such mechanisms, there is currently little psychophysical evidence available to elaborate the computational role of these mechanisms in the perceptual task. Additional psychophysical investigation is required to better isolate the perceptual mechanisms suggested here and to further refine their visual motion properties.

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## Appendix A. Internal object-dot motion

Displacement of the object aperture across successive frames results in an apparent object motion in the direction  $v_{\text{net}}$  from time  $(t)$  to  $(t + \Delta t)$ , where  $\Delta t = 1$  frame. During such motion, dots located in the black crescent ( $A$ ) fall outside of the object aperture at time  $(t + \Delta t)$  and must be randomly reassigned new positions within the gray crescent ( $B$ ), not previously occupied by dots (Fig. 11).

To facilitate real-time dot replacement, the bounds of region  $B$  must be calculated to optimize the random selection of spatial positions. From Fig. 11, the intersection angle ( $\phi_I$ ) between object apertures at time  $(t)$  and  $(t + \Delta t)$  can be calculated relative to the direction of object motion (i.e., relative to  $v_{\text{net}}$ ),

$$\phi_I = \cos^{-1} \left( \frac{|v_{\text{net}}|}{2R} \right)$$

where  $R$  is the radius of the object aperture. The distance of the leading edge for the  $(t + \Delta t)$  aperture relative object center  $(x(t), y(t))$  at time  $(t)$  can then be expressed as a function of  $\phi_I$  and  $v_{\text{net}}$  using the Law of Cosines (Fig. 12),

$$R_\phi^2 = R^2 + |v_{\text{net}}|^2 + 2R|v_{\text{net}}| \cos(\theta)$$

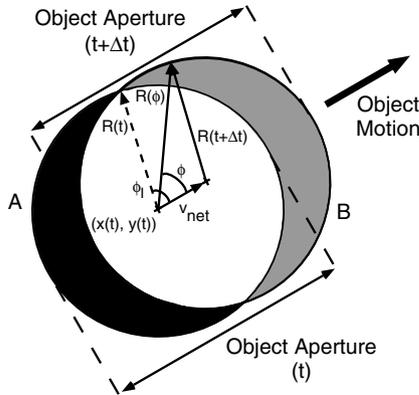


Fig. 11. Internal wrap-around procedure. In the general case of discordant internal dot and object aperture motions the vector difference yielded an ‘apparent’ object motion in the direction  $v_{net}$  from time  $(t)$  to  $(t + \Delta t)$ . During such motion, dots located in the black crescent (A) fell outside of the object aperture.

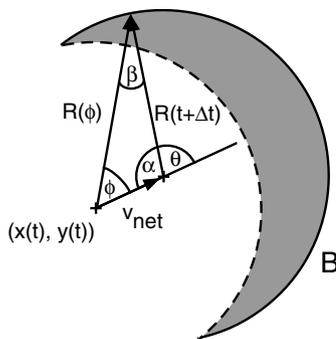


Fig. 12. Schematic diagram of  $R_\phi$  with respect to  $R(t + \Delta t)$ ,  $v_{net}$ , and  $\phi$ .

where

$$\theta = 180 - \alpha = \beta + \phi$$

Applying the Law of Sines,

$$\beta = \sin^{-1} \left( \frac{v_{net}}{R} \sin(\phi) \right)$$

the radius of the outer bound for region B relative to time  $(t)$ ,  $R_\phi$ , can be re-expressed in terms of the known parameters  $R$ ,  $v_{net}$ , and  $\phi$ ,

$$R_\phi^2 = v_{net}^2 + R^2 + 2v_{net}R \cos \left[ \phi + \sin^{-1} \left( \frac{v_{net}}{R} \sin(\phi) \right) \right]$$

Within the coordinate frame of the moving object at time  $(t)$ , dots positioned in region A at  $(t + \Delta t)$  are repositioned into region B by randomly selecting  $\phi$  over the range  $[-\phi_I, \phi_I]$ . Along  $\phi$  the maximum allowable displacement ( $R_\phi$ ) within the crescent can be calculated and a new radial position (referenced to the object center at time  $(t)$ ) randomly selected over the range  $[R, R_\phi]$ .

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