

Human heading judgments in the presence of moving objects

CONSTANCE S. ROYDEN and ELLEN C. HILDRETH
Wellesley College, Wellesley, Massachusetts

When moving toward a stationary scene, people judge their heading quite well from visual information alone. Much experimental and modeling work has been presented to analyze how people judge their heading for stationary scenes. However, in everyday life, we often move through scenes that contain moving objects. Most models have difficulty computing heading when moving objects are in the scene, and few studies have examined how well humans perform in the presence of moving objects. In this study, we tested how well people judge their heading in the presence of moving objects. We found that people perform remarkably well under a variety of conditions. The only condition that affects an observer's ability to judge heading accurately consists of a large moving object crossing the observer's path. In this case, the presence of the object causes a small bias in the heading judgments. For objects moving horizontally with respect to the observer, this bias is in the object's direction of motion. These results present a challenge for computational models.

The task of navigating through a complex environment requires the visual system to solve a variety of problems related to three-dimensional (3-D) observer motion and object motion. To reach a desired destination, people must accurately judge their direction of motion. To avoid hitting objects in the scene, they must be able to judge the position of stationary objects and the position and 3-D motion of objects moving relative to themselves. Because we often move through scenes that contain moving objects, our heading judgments ideally should not be affected by the presence of these objects. For example, a driver on a busy street must make accurate heading judgments in the presence of other moving cars and pedestrians. It is clear from psychophysical experiments that, for translational motion, people can accurately judge their heading when approaching stationary scenes (Crowell & Banks, 1993; Crowell, Royden, Banks, Swenson, & Sekuler, 1990; Rieger & Toet, 1985; van den Berg, 1992; Warren & Hannon, 1988, 1990). However, little has been done to measure human ability to judge heading in the presence of moving objects. Furthermore, most computational models have been designed to make heading judgments given stationary scenes. The presence of moving objects in the scene adversely affects their performance. In this paper, we present experiments that test whether the presence of moving objects similarly affects human ability to judge heading.

To illustrate the difficulties involved in judging heading in the presence of moving objects, we first describe some of the computational models that have been put forth to compute heading from visual input. Most of these models have been developed to solve the problem of computing both the translation and the rotation components of motion for an observer moving through a stationary scene. We will focus our discussion on models that are the most biologically plausible. Following the discussion of computational modeling, we briefly summarize previous experimental work on human heading perception. The remainder of the paper presents our new experimental findings on heading perception in the presence of moving objects.

Models of Heading Recovery

Gibson (1950, 1966) proposed the first concrete model of human heading detection for an observer moving along a straight line. He pointed out that one could locate one's own heading by finding the location of the focus of expansion (FOE) in the image. The focus of expansion is the point away from which all image points move during forward translation. A point located at the FOE would have zero image velocity. Therefore, one could easily find one's heading by finding the intersection of lines through the velocity vectors corresponding to two or more points in the image. In a noisy image, one could use an approximation method, such as least squares, to find the best intersection. Although Gibson's approach worked only for pure translational motion, Bruss and Horn (1983) generalized the least squares approach to find both translation and rotation parameters of observer motion. Clearly, the presence of a moving object in the scene would adversely affect this type of approach to finding the parameters of observer motion. The image points associated with the moving object would be moving in a di-

This work was funded by a Science Scholar's Fellowship from the Bunting Institute of Radcliffe College to C.S.R. and by NSF Grant SBR-930126 to E.C.H. and C.S.R. The authors thank Martin Banks for helpful comments, and Edy Gerety, Lucia Vancura, and Elizabeth Ameen for help with the data collection and analysis. Correspondence should be addressed to C. S. Royden, Department of Computer Science, Wellesley College, Wellesley, MA 02181 (e-mail: croyden@wellesley.edu).

rection inconsistent with the observer's motion and therefore would cause errors in the estimate of heading if they could not first be identified and discounted.

Heeger and Jepson (1992) presented a model that also uses a minimization technique to find the translation and rotation parameters that best fit a given set of image velocity vectors; it minimizes a residual function that is computed on the basis of the velocities of image points. This model was put into neural-network form by Lappe and Rauschecker (1993). Although in theory this model requires only velocity measurements from five image points to compute observer motion, in practice the use of many more points is required to reduce errors that occur from noisy velocity measurements. This model suffers from the same problem as the least squares models when presented with moving objects. If one or more of the image velocities used in the computation of the residual function come from the moving object, the heading estimate will be biased. Thus, one would prefer to identify the points associated with the moving object first, so that these points can be excluded from the computation.

Hatsopoulos and Warren (1991) created a two-layer neural network that they trained using the Widrow-Hoff learning rule to recognize the correct translational heading for an observer moving in a straight line. The input layer consisted of units that were tuned to direction and speed of motion. After training, the weights connecting the input and output layers in this network adapted so that the output neurons detected radial patterns of motion. Thus, this model became essentially a template model after the training of the network.

Perrone (1992) and Perrone and Stone (1994) have put forth a more complete template model for solving the heading problem. This model uses components that behave similarly to neurons in the primate medial temporal visual area (MT) in their response to motion. These components are inputs to another layer of cells and are arranged in a spatial pattern that mimics the flow fields that would be seen for given sets of observer translation and rotation parameters. In the first version of the model (Perrone, 1992), the rotation parameters were first estimated and then used to build the appropriate templates for different translation directions. In a subsequent version (Perrone & Stone, 1994), the number of rotational possibilities is limited by assuming that rotations are generated only by the observer making eye movements to track an object in the scene. As with the other models described above, a moving object in the scene would cause errors in the heading estimates made by this model, because it integrates information over a wide region of the visual field. The image motions from the moving object would cause the velocity field of the image to differ substantially from the template corresponding to a given observer translation and thus cause errors.

Another set of models is based on an analysis done by Longuet-Higgins and Prazdny (1980) and later extended by Rieger and Lawton (1985) and Hildreth (1992). These models use the fact that the translational components of the image velocities depend on the depth of the points in

the scene, while the rotational components are independent of this depth. Because of this fact, subtracting the image velocities from two points located at a depth discontinuity will eliminate the rotational components. One can then locate the translational heading using the resulting "difference vectors." This model, by itself, suffers the same failing as the others when presented with moving objects. However, Hildreth (1992) extended this model to deal with moving objects. Hildreth's model computes the best observer heading for multiple small regions of the image. It then finds which location is consistent with the image information from the majority of these regions. Thus, if the moving object covers a minority of the image, this model can ignore the influence of the difference vectors associated with the moving object when computing heading. This model has the advantage that one can determine where the moving object is located by finding which regions of the image have image velocities that are inconsistent with the recovered heading.

In summary, the models proposed to account for human heading perception almost all suffer from the same problem when computing heading from a scene that contains moving objects. If they cannot first locate the image points associated with the moving object and eliminate these from their computations, their heading estimates will be flawed due to the inconsistent image velocities associated with the moving object. These models need to develop ways to locate, or segment, the moving object in order to compute heading accurately in this situation. Of the models discussed above, only the Hildreth model incorporates a method for this segmentation of the moving object.

While most models of human heading recovery have assumed a stationary scene, several strategies for judging heading in the presence of moving objects have been proposed in the context of machine vision systems. One approach computes an initial set of observer motion parameters by combining all available data or by performing separate computations within limited image regions. One can then identify moving objects by finding areas of the scene for which the image motion differs significantly from that expected from these initial motion parameters (Adiv, 1985; Heeger & Hager, 1988; Ragnone, Campani, & Verri, 1992; Zhang, Faugeras, & Ayache, 1988). The initial estimates of motion parameters may have considerable error in these models. If all motion information is used initially to compute these parameters, then the inconsistent motions of moving objects can degrade the recovery of motion parameters. If one tries to avoid this problem by using spatially local information to compute the motion parameters, the limited field of view can yield inaccuracy. However, once the regions associated with the moving object are identified, one can improve the initial estimate of motion parameters by combining information from regions that exclude these moving objects. Thompson, Lechleider, and Stuck (1993) apply methods from robust statistics that treat moving objects as outliers in the computation of motion para-

meters, which improves the performance of this type of model.

Some models first focus on the detection of moving objects, which may contribute to the recovery of observer motion relative to a scene containing such objects. One strategy first stabilizes a moving image by effectively removing camera motion, analogous to human eye tracking. Any remaining image motion is attributed to moving objects (Braithwaite & Beddoes, 1993; Burt et al., 1989; Murray & Basu, 1994). A second method assumes that the camera undergoes pure translation. Under this condition, moving objects violate the expected pure expansion of the image (Frazier & Nevatia, 1990; Jain, 1984). If 3-D depth data are available, then inconsistency among image velocities, estimated observer motion, and depth data can signal moving objects (Nelson, 1990; Thompson & Pong, 1990). Finally, Nelson (1990) suggests that one can detect moving objects by identifying motion that changes rapidly over time. Once a moving object is detected, heading can be computed from the remaining stationary components of the scene.

While these models were not specifically developed to explain human heading performance, many of the ideas could easily be adapted to a more physiologically relevant model of heading judgments. For example, Hildreth's (1992) model, described above, incorporates several of the ideas from the machine vision models into a more physiologically plausible model.

Psychophysical Studies of Heading

While it is clear that many models cannot compute heading accurately in the presence of moving objects, this fact alone does not exclude these models from explaining human heading perception. The possibility exists that moving objects in the scene will affect human heading judgments in a way that is consistent with one or more of the computational models. That is, errors induced in human heading judgments by moving objects may be similar to those made by the models when moving objects are in the scene. Therefore, to distinguish between these models regarding their applicability to human vision, one must test how the presence of moving objects affects human heading judgments.

Recently, much research has been reported concerning how well people judge their heading from visual information. Many researchers have shown that people judge their heading quite well when translating toward a stationary scene (Crowell & Banks, 1993; Crowell et al., 1990; Rieger & Toet, 1985; van den Berg, 1992; Warren & Hannon, 1988, 1990), with discrimination thresholds as low as 0.2° when the heading is near the line of sight and increasing as the heading becomes more peripheral (Crowell & Banks, 1993). The retinal eccentricity of the heading information does not appear to have much effect on the accuracy of heading discriminations (Crowell & Banks, 1993). People apparently can judge their translational heading accurately in the presence of eye movements with small rotation rates (Royden, Banks, &

Crowell, 1992; Royden, Crowell, & Banks, 1994; Warren & Hannon, 1988, 1990); at higher rotation rates, information about the rate of eye movement becomes important (Royden et al., 1992; Royden et al., 1994). At high rotation rates, people perceive their motion to be on a curved path if they are not moving their eyes, whereas people perceive their translational motion quite accurately if the rotation is generated by an eye movement (Royden, 1994; Royden et al., 1992, 1994). Van den Berg and Brenner (1994a, 1994b) have reported that the addition of depth cues, both static and stereoscopic, can enhance the accuracy of heading judgments in the presence of added noise or observer rotations. Several people have shown that the ability to judge heading accurately remains high in the presence of moderate amounts of noise added to the stimulus (van den Berg, 1992; Warren, Blackwell, Kurtz, Hatsopoulos, & Kalish, 1991). These results suggest that the human mechanism for judging heading from visual stimuli is remarkably robust and performs quite well under a variety of non-optimal conditions. However, none of the above studies have addressed the problem of how well people judge heading when moving objects are present.

Recently, Royden and Hildreth (1994) and Warren and Saunders (1994, 1995a, 1995b) have begun to examine human ability to judge heading in the presence of moving objects. Both groups reported that, for specific conditions, a moving object has no effect on observer heading judgments when it does not cross the observer's path. When the object crosses the observer's path, however, both groups reported small biases in observer heading judgments. For the conditions they tested, Warren and Saunders found biases directed toward the object's focus of expansion (i.e., toward the observer's direction of motion relative to the object). They presented a simple neural model to account for these observer biases. Under other conditions, Royden and Hildreth found biases in the direction of object motion (i.e., in the direction opposite the observer's motion relative to the object). The following experiments test human heading judgments in the presence of moving objects under a broader range of conditions and shed light on the differences between the findings of Warren and Saunders (1994, 1995a) and those of Royden and Hildreth (1994).

Experiment 1 established the basic ability of observers to judge their heading in the presence of moving objects and showed the conditions under which errors in heading judgments occur. In Experiments 2–4, we examined in greater depth the visual cues that contribute to these errors. For example, we examined the contribution of the relative motions of the dots in the object and those in the stationary scene, and the contribution of the motion at object borders. In Experiments 5–7, we investigated whether variations on our basic experimental paradigm yield different results from those obtained in Experiment 1. Finally, in Experiments 8–10, we explored the differences between our paradigm and that of Warren and Saunders (1995b).

GENERAL METHOD

Five observers with normal vision participated in these experiments. Two of these, E.C.H. and C.S.R., had considerable experience as psychophysical observers and were aware of the experimental hypotheses. The remaining 3 observers, who were paid to participate, had no previous experience as psychophysical observers and were unaware of the hypotheses. These naive observers participated in several practice sessions to accustom them to the task and the experimental apparatus before they participated in the experiments with moving objects. All 5 observers were used in each experiment, unless otherwise noted.

We used a computer-controlled display of random dots to simulate observer motion toward a scene containing a moving object. The stationary part of the scene consisted of two transparent planes at initial distances of 400 cm and 1,000 cm from the observer. The motion of the dots in this part of the scene simulated observer motion toward a point that was 4°, 5°, 6°, or 7° to the right of the central fixation point and 0°, 2° above, or 2° below the horizontal midline. Simulated observer speed was 200 cm/sec. The viewing window was 30° × 30°, and the dots were clipped when they moved beyond this window. Dot density for the stationary scene was 0.56 dots/deg² and for the object was 0.8 dots/deg² at the beginning of each trial. In the trials that contained a moving object, the object consisted of an opaque square that moved in front of the stationary planes. The motion of the object was independent of the observer's simulated motion. The observers viewed the display monocularly at a distance of 30 cm, with their heads positioned by a chin-and-forehead rest. They were instructed to fixate a central cross during each trial. The motion of the dots lasted 0.8 sec for each trial, unless noted otherwise. The room was completely dark except for the display. The dots were single pixels subtending 3.0 arc min presented on a dark background, and they did not change size during a motion sequence. The stimuli were generated by an Apple Quadra 950 and presented on an Apple 21-in. monitor. Stimulus frames were drawn at a rate of 25 Hz, one third of the refresh rate of the monitor.

For each trial, the first frame of the motion sequence appeared on the screen before the trial began. The observers controlled the start of the trial with the press of a button. At the end of the trial, the last frame of the motion sequence remained while a cursor appeared on the screen. The observers used the computer mouse to position this cursor at the location on the display toward which they appeared to be moving. No feedback was given. Each condition was repeated 10 times, with the conditions randomly interleaved, and the data are the averaged positions indicated for the 10 trials. The experiments were run in the following order 1, 8, 5, 4, 3, 6, 2, 7, 9, 10. The only exceptions to this were for Subjects E.C.H. and E.C.A. For Subject E.C.H., Experiment 6 preceded Experiment 4, and the vertical object motion from Experiment 1 was run after Experiment 3. For Subject E.C.A., Experiment 6 preceded Experiment 5, and the rightward motion of the blank object (Experiment 3) was run after Experiment 9. Subject E.C.A. did not participate in Experiments 2 and 7.

EXPERIMENT 1

Horizontal and Vertical Object Motion

Method

This experiment tested how human heading judgments are affected by the presence of a moving object. The object was a 10° × 10° square that moved either horizontally or vertically with respect to the observer with a speed of 8.1°/sec; the object did not move in depth with respect to the observer during the entire trial and, thus, did not expand or contract in size. Therefore, the simulated distance between the object and the stationary scene decreased over the course of the trial. For horizontal motion, the vertical position

of the object was set so that the object was centered on the horizontal midline of the viewing window. The horizontal position of the object at the start of the trial varied within the viewing window for different runs of the experiment. For left object motion, the object's center began at -1.4°, 0.6°, 4.7°, 8.7°, 10.7°, and 12.7° from the center of the screen. For right object motion, the starting positions of the object were -9.9°, -5.9°, -1.9°, 0.2°, 2.2°, and 6.3° from the center of the screen. Negative numbers refer to positions to the left of the fixation point at the center of the screen. For vertical motion, the object was positioned vertically so that it moved symmetrically across the horizontal midline during the trial, starting and finishing the same distance from the midline. The horizontal position of the object varied with different runs of the experiment, with the center of the object positioned at -6.7°, -2.7°, 1.4°, 5.5°, 9.5°, and 13.5° from the center of the screen. Examples of these object motions are shown in Figure 1.

The experiments were run in blocks of trials. In each block, the starting position and direction of motion of the moving object were kept constant while the observer's heading was varied between 12 different positions: 4°, 5°, 6°, and 7° to the right of center and 0°, 2° above, and 2° below the horizontal midline. The vertical heading variations were added so that the observers could not attend to a single dot associated with the transparent planes and extrapolate its trajectory to the horizontal midline in order to gauge the position of the focus of expansion. The heading directions were presented in random order, with each heading presented 10 times, for a total of 120 trials per block. One block of trials in which there was no moving object but only observer mo-

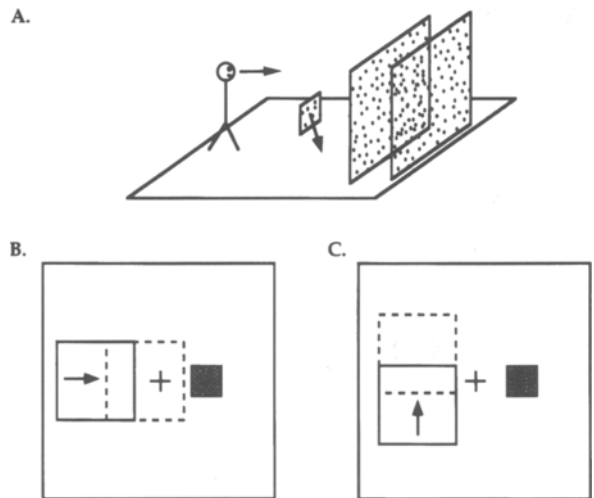


Figure 1. Simulated observer motion. (A) This diagram shows the simulated scene toward which the observer was moving. It consisted of two large transparent frontoparallel planes at distances of 400 and 1,000 cm from the observer. The object, shown as the small opaque square in front of the two transparent planes, moved at a speed of 8.1°/sec horizontally or vertically relative to the observer and thus approached the stationary planes during a trial. (B) This depicts the image of the scene toward which the observer moved during the simulated motion for horizontal object motion. The 10° × 10° object was centered on the horizontal midline of the 30° × 30° viewing window. The starting position of the object is indicated by the square enclosed in solid lines and the ending position by the dashed square. The hatched area to the right of the fixation cross indicates the region toward which headings were simulated. (C) This diagram is identical to B, except that it shows vertical object motion. The object moved symmetrically across the midline so that it was centered on the horizontal midline at the middle of the trial.

tion toward the stationary scene was presented in each experimental session for comparison with the blocks of trials in which there was a moving object present.

Results

The horizontal heading judgments were very similar for the three different vertical headings. Therefore, the data for the three different vertical headings have been averaged together to compute the results for the horizontal heading judgments. In the following discussion, all results given represent horizontal errors only. The results of this set of experiments are diagrammed in Figures 2–5. Figures 2 and 3 show typical results for 2 observers for two different starting positions of the leftward-moving object. Figure 2 shows typical results when the object was not crossing the observer’s path during most of the trial. In this case, there was essentially no difference in the observer’s responses between the case when the object was present and the case when it was not present. The average difference in response between these two cases, averaged over the 5 observers and four horizontal headings, was only 0.04°. In contrast, when the object crossed the observer’s path, there was a bias in the

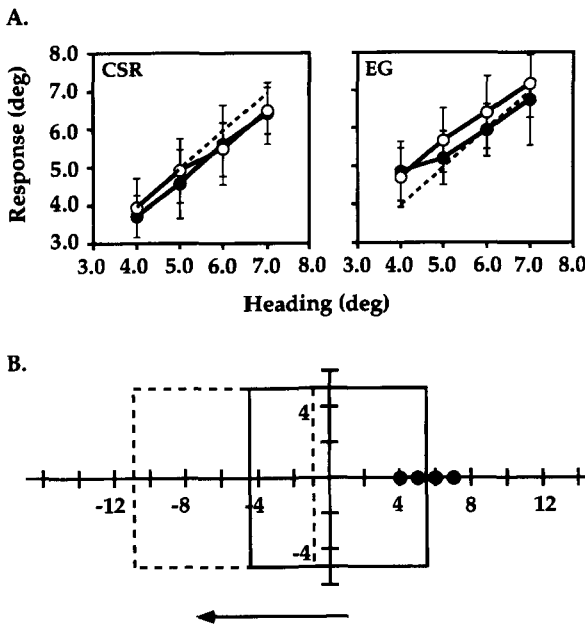


Figure 2. Typical results for an object not crossing the observer’s path. (A) The two graphs show typical data for 2 observers when the object did not cross the observers’ path for the majority of the trial. The object’s center started at 0.6° to the right of the central fixation point and then moved left during the trial. The data plotted are the averages of the 30 responses for each horizontal heading, averaged across the three vertical headings. Open symbols show the observer responses when the object was not present in the simulated scene. Filled symbols show the results for the case in which the object was present. (B) The diagram shows the starting and ending positions of the moving object with respect to the simulated headings for the condition shown in A. The solid line shows the starting position, and the dashed line shows the ending position of the object. The four filled circles show the horizontal positions of the simulated headings (the vertical positions are not shown).

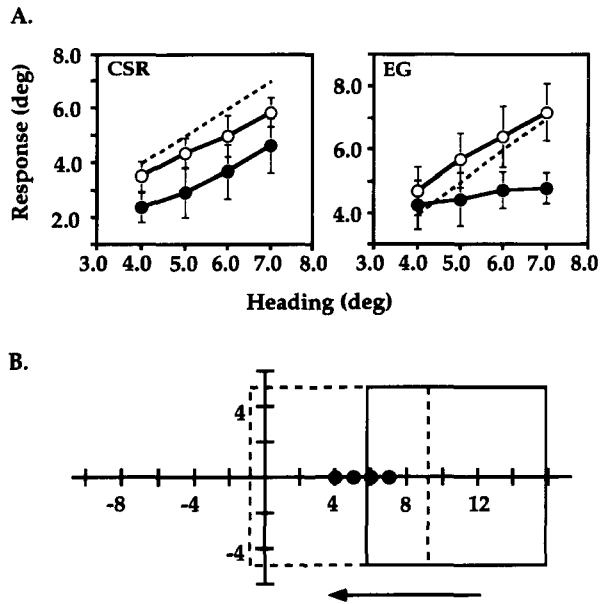


Figure 3. Typical results for an object crossing the observer’s path. (A) The two graphs show typical data for 2 observers for the condition when the object crossed the observers’ path, obscuring the focus of expansion for the majority of the trial. The object’s center started at 10.7° to the right of the central fixation point and then moved left during the trial. All symbols are the same as those in Figure 2. (B) The diagram shows the starting and ending positions of the object for the condition shown in A. All symbols are the same as those in Figure 2.

observer’s heading judgments induced by the presence of the moving object, as shown in Figure 3. The difference between the object-present and object-absent conditions for this case was 0.94° when averaged over the 5 observers and four headings. Thus, there is a small but consistent bias in observers’ heading judgments when an object moves in front of the focus of expansion.

Figure 4 shows the average bias with respect to starting position of the object. The bias is measured as the difference between the observers’ responses for the object-present and object-absent conditions. The shaded area on each graph shows the starting positions for which the object would cover all four headings for at least 50% of the trial and would cover at least one heading for at least 96% of the trial. Figure 4A shows these data for a leftward-moving object. In general, the leftward (or central) biases were always smallest for the 4° simulated heading, and the rightward biases were always smallest for the 7° simulated heading. Because the shapes of the curves were very similar for the four headings, with peak biases at the same object starting position, we have averaged the data from all the headings together. A two-way analysis of variance (ANOVA) for the factors of simulated heading and object position (with the no-object condition included as one condition in the object position factor) showed a significant main effect both for simulated heading [$F(3,112) = 39.019, p = .0001$], as would be expected, and for object position [$F(6,112) = 4.24, p = .0007$]. Post hoc analysis by Fish-

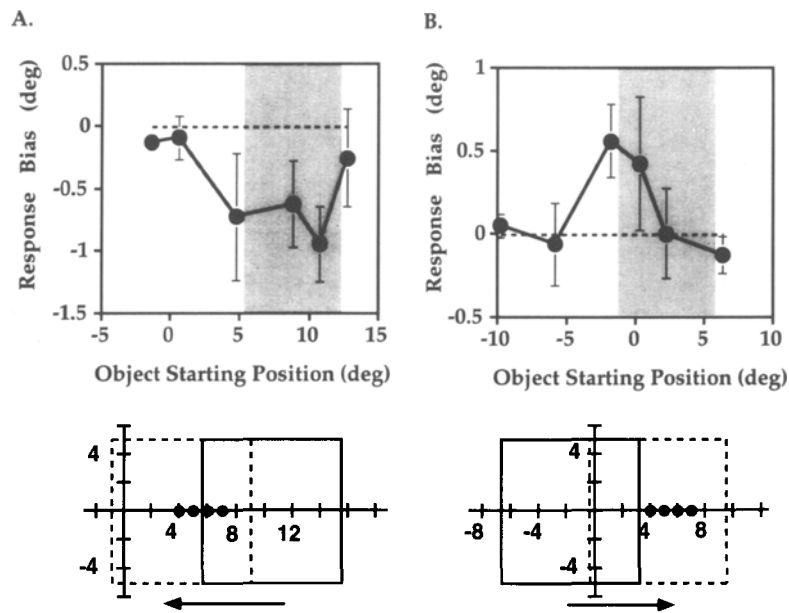


Figure 4. Average results for horizontal object motion. The graphs diagram the average response bias generated when an object was present in the simulated scene relative to the heading responses when the object was absent. A negative value indicates a bias toward the center of the screen or to the left. The starting position listed on the x-axis indicates the position of the object's center at the start of the trial. Each data point indicates the response bias averaged over all four headings and 5 observers. The error bars indicate ± 1 SE across observers. The dashed line at zero represents the case where the object was not present in the scene (which is zero by definition). The gray shaded area on each graph shows the starting positions for which all simulated headings would be covered by the object for at least 50% of the trial (and at least one heading would be covered for at least 96% of the trial). The diagram beneath each graph shows the starting and ending positions of the object in the condition that generated the most bias. The starting position is indicated by the square with the solid borders and the ending position by the square with the dashed borders. The filled circles indicate the horizontal heading positions. (A) This graph shows the bias generated for a leftward-moving object. (B) This shows the bias generated for a rightward-moving object.

er's protected least square difference (FPLSD) for starting positions to the left of the headings, such as at -1.4° ($p = .71$) and 0.6° ($p = .78$), showed that there was no significant difference in the observers' heading judgments between object-present and object-absent conditions. However, there was a region for which the observers showed significant bias in their responses, relative to the no-object condition. This occurred when the object center started at 5.5° ($p = .01$), 8.7° ($p = .03$), or 10.7° ($p = .0009$), corresponding to starting positions centered on or just to the right of the simulated headings. This bias was in the direction toward the center of the screen or to the left. Therefore, the observer bias in this situation was in the same direction as the object's motion.

Figure 4B shows the average response bias for object motion to the right. An ANOVA showed a nearly significant effect of object starting position [$F(6,112) = 2.145$, $p = .054$]. In this case, as with the leftward-motion, there was essentially no effect of the object when it did not cross the observer's path, as seen by the data points for starting positions of -9.9° and -5.9° . Post hoc analysis by FPLSD showed that observer responses for these

positions did not differ significantly from the no-object case ($p = .79$ and $.86$, respectively). However, when the object crossed the observer's path—for example, when it started at -1.9° , just to the left of the simulated headings—there was a small, consistent bias to the right or toward the edge of the screen (post hoc comparison with the no-object condition, $p = .025$). This bias was smaller than that seen with the leftward moving object.

Figures 5A and B show the average response biases for upward- and downward-moving objects. Again, the object starting position had a large effect on the amount of bias generated [for up motion, $F(6,112) = 4.337$, $p = .0006$; for down motion, $F(6,112) = 2.074$, $p = .06$]. In both cases, the largest bias, which was always toward the fixation point, was generated when the object was centered over the simulated headings at 5.5° . The response for this position was significantly different from the no-object condition for an upward-moving object ($p = .0007$) and approached significance for downward motion ($p = .06$). The bias generated by the downward-moving object appears to have been somewhat less than that generated by the upward-moving object.

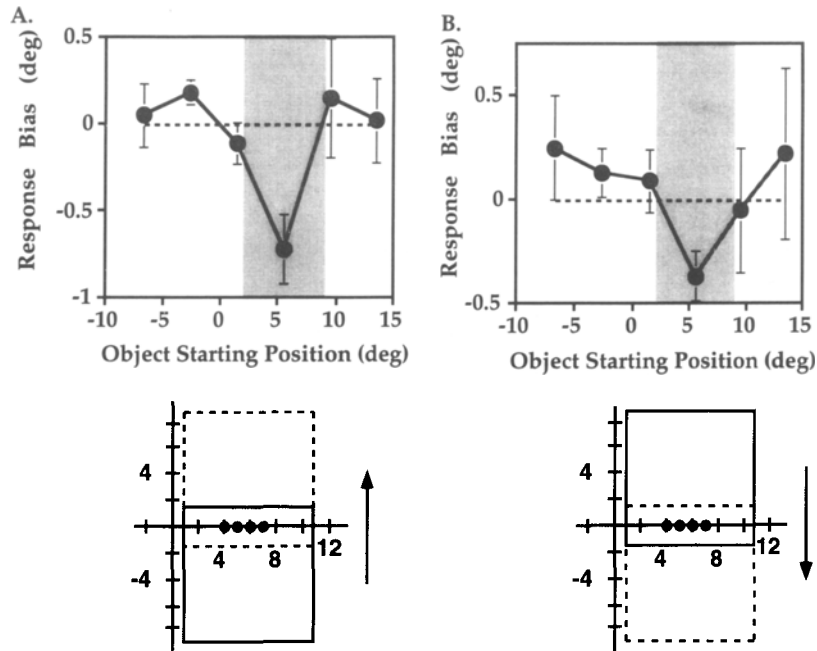


Figure 5. Average horizontal bias for vertical moving object. All symbols are as described for Figure 4. (A) Horizontal response bias for an upward-moving object. (B) Horizontal response bias for a downward-moving object.

Therefore, for laterally moving objects, the position of the moving object during the trial is extremely important in determining the amount of bias seen in the observer heading judgments. When the object did not cross the observer's path, there was little effect on the heading judgment. However, when the object did cross the observer's path, a small bias in heading judgment was generated. This bias was in the same direction as the object motion for the left and right object motions and was toward the center of the display for up and down motion. The fact that the bias is in the same direction as the motion of the object for left and right motion is surprising. For a leftward-moving object, the observer's motion relative to the object is to the right. Therefore, if the visual system averages between the two observer motion directions relative to the two surfaces—one for the stationary scene and one for the moving object—then one would expect a bias to the right from a leftward-moving object. This would be analogous to averaging between the two foci of expansion if the object had a component of motion toward the observer. Our data show a bias in the opposite direction.

EXPERIMENT 2 Stationary Object

The results of Experiment 1 indicate that visibility of the focus of expansion is important for accurate judgments of heading, but it is unclear whether the object must undergo motion to generate the biases seen when the object obscures the focus of expansion. To test whether or not motion of the object is essential to create a bias in observer

heading judgments, we repeated Experiment 1 using an object that was stationary with respect to the observer. The borders of the object and the dots within those borders did not move over the course of the trial. Only the dots surrounding the object moved, simulating the translation of the observer toward the stationary scene.

Method

Experiment 2 was run exactly as Experiment 1, with different object positions for different blocks of trials. The object and the points within it did not move on the screen during a trial. The object was $10^\circ \times 10^\circ$, as in Experiment 1. The center positions of the object were at -6.7° , -2.7° , 1.4° , 5.5° , 9.5° , and 13.5° from the center of the screen. These corresponded to the midpoints of the object motions from Experiment 1. Four of the observers used in Experiment 1 participated in Experiment 2.

Results

The average observer results for Experiment 2 are shown by the filled symbols in Figure 6. For comparison, Figure 6 also shows the results obtained from the moving-object conditions in Experiment 1. There was no significant difference in response between the object-present and object-absent conditions for any of the static object positions tested, including those that completely obscured the focus of expansion for the simulated headings [$F(6,84) = 0.653$, $p = .69$]. Thus, we can conclude that the biases seen in Experiment 1 could not have been due to a simple absence of heading information around the focus of expansion. Instead, they depend on the interaction of the object motion with the information in the flow field associated with the two frontoparallel planes.

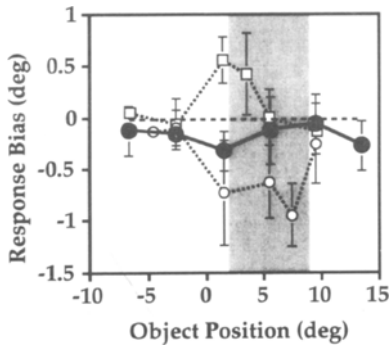


Figure 6. Average response bias for a static object. This graph shows the average response bias generated when a stationary object was present in the scene. The object did not move with respect to the observer. The filled symbols indicate the average bias for the static object. Open circles show the response bias for the leftward-moving object as in Figure 4. Open squares show the response bias for the rightward-moving object as in Figure 4. The object position on the x-axis refers to the position of the object's center in the middle of a trial.

EXPERIMENT 3 Blank Object

A question related to that posed in Experiment 2 is whether the biases seen in Experiment 1 were due to the relative motions of the dots in the moving object and the dots associated with the static scene. Relative motion between neighboring points in the image is used directly in the models of Rieger and Lawton (1985) and Hildreth (1992) for computing heading; therefore, relative dot motions could have a significant effect on observer heading judgments. The results of Experiment 2 showed that motion of the object is essential for the biases seen in Experiment 1. It is possible that, when the object crosses the focus of expansion, the motion of the dots in the object interacts with the dot motion associated with the stationary scene. It is known that the perceived direction of motion for a given dot can be affected by spatially nearby motions, as in the motion repulsion effect described by Marshak and Sekuler (1979). In this effect, the perceived difference in the motion directions for dots that are spatially close together is larger than the actual difference in direction. This motion repulsion could yield errors in the perceived motions of dots along the object border that result in a bias in the subsequent heading computation, as shown in Figure 7. If the dots immediately above the focus of expansion are affected by motion repulsion from the horizontally moving objects, then one might expect to see a bias in the position of the perceived focus of expansion in the direction of motion of the object. In Experiments 3 and 4, we tested whether relative motions of dots within the object and within the static surfaces are necessary and sufficient to explain the biases seen in Experiment 1. In Experiment 3, we removed the dots from the object, so that the object consisted of a blank space in the display that moved across the screen during the trial. This is similar to one of the experiments done

by Warren and Saunders (1995b). The removal of the dots means that there are no explicit moving features within the object that would contribute to the motion repulsion effect in this condition.

Method

The method used in Experiment 3 was identical to that in Experiment 1, except that the object contained zero dots. Thus, the object appeared as a blank space in the display, whose borders moved during the course of the trial. The borders were implicitly defined only by the accretion and deletion of the background texture. Only left and right object motions were tested. All 5 observers from Experiment 1 participated in Experiment 3.

Results

The results of Experiment 3 are diagrammed in Figure 8. Again, the results of Experiment 1 are superimposed on this graph for comparison, and the gray shaded area shows the object starting positions for which the object covered the four simulated headings for a majority of the trial. While there was a small bias in observer responses seen when the object crossed the focus of expansion, the bias was much smaller than that seen when the object was defined by dots. For the leftward-moving object, some of this decrease was due to the data from 1 observer, whose direction of bias reversed in this condition. This observer said she had great difficulty with the task, and this is reflected in the large standard deviation in her data. However, even if the data from this observer are discounted, the overall bias seen with the blank object was still smaller than that seen with the dots present. An ANOVA showed that the starting position of the object had a significant effect [$F(6,112) = 2.5, p = .026$], with an object starting at 10.7° generating responses that differed significantly from those in the no-object condition (FPLSD, $p = .04$). An ANOVA comparison between the data for left motion in Experiment 1 and Experiment 3 showed a significant difference between the two curves [$F(1,192) = 10.497, p = .001$]. Although there

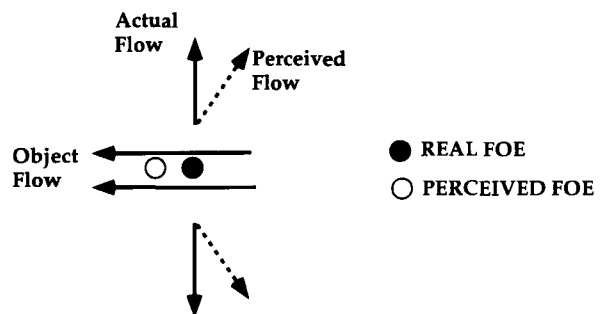


Figure 7. Motion repulsion effect. This diagram illustrates how the motion repulsion effect could affect the perceived position of the focus of expansion. The solid lines indicate the actual flow vectors in the simulated scene. The dashed lines indicate the direction of perceived motion due to the motion repulsion effect for vectors directly above and below the focus of expansion. The filled circle indicates the true focus of expansion. The open circle indicates the perceived focus of expansion calculated as the intersection of lines through the perceived velocity vectors.

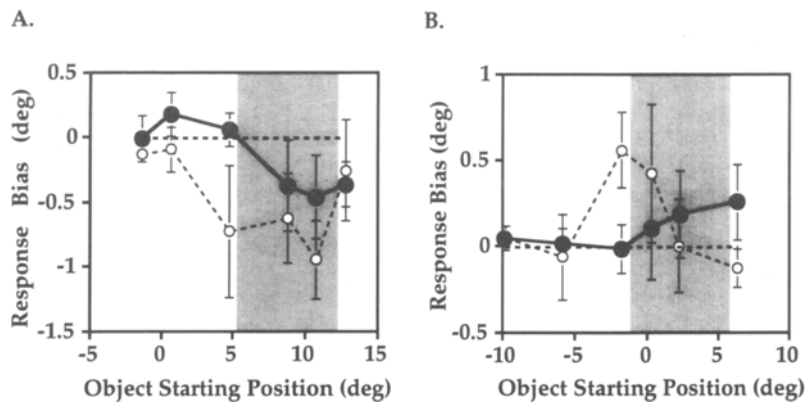


Figure 8. Response bias for a blank object. These graphs show the response bias averaged over 5 observers for an object moving horizontally that contained no dots. The bias is the difference between observer responses when the object was present and those when the object was absent. The filled symbols show the average response bias for a blank object. The open symbols show the results of Experiment 1 (the response for an object with dots within it). Error bars indicate ± 1 SE calculated across observers. The x-axis indicates the starting position of the center of the object. As in Figure 4, the gray shaded area on each graph shows the starting positions for which all simulated headings would be covered by the object for at least 50% of the trial. (A) Response bias for a leftward-moving object. (B) Response bias for a rightward-moving object.

was some bias in the observer responses when the object obscured the focus of expansion, this reduction in the size of the bias was consistent with the idea that the biases were caused by motion repulsion. The residual bias seen in the observer responses could have been due to a weak motion signal within the object generated by motion interpolation across the region between the moving object borders. It is also possible that the borders by themselves could have generated enough of a motion signal to affect the perceived direction of the dots associated with the stationary object.

For an object moving to the right, there was no significant bias generated at any object starting position [$F(6,112) = 0.627$, $p = .71$]. This result would also be consistent with the idea that the biases seen in Experiment 1 were a result of the motion repulsion effect.

EXPERIMENT 4 Moving Dots in a Stationary Window

If motion repulsion caused the biases seen in Experiment 1, then one would expect that an area of horizontally moving dots within the image would be sufficient to generate the observer biases seen. We tested this by generating a display in which the borders of the object were stationary, while the dots within the object moved horizontally either left or right. Thus, the dots appeared at one edge of the object, moved across, and disappeared on the other side.

Method

Experiment 4 was identical to Experiment 2, in which the borders of the object were stationary, except that the dots within the

object borders moved horizontally at a constant speed of 8.1°/sec. In separate runs of the experiment, the dots would move either left or right. For leftward dot motion, the object center was positioned at -1.4° , 0.6° , 4.7° , 8.7° , 10.7° , and 12.7° in different runs of the experiment. For rightward motion, the positions were -9.9° , -5.9° , -1.9° , 0.2° , 2.2° , and 6.3° from the center of the screen. These correspond to the starting positions of the object in Experiment 1.

Results

Figure 9 shows the results of Experiment 4, graphed as the average bias of observer responses when the object was present relative to their responses when the object was absent. As with Experiment 3, there appears to have been a small leftward heading bias for the leftward-moving dots when the object covered the focus of expansion. However, an ANOVA showed that none of the object starting positions generated observer responses that differed significantly from responses when the object was absent [$F(6,112) = 0.960$, $p = .46$]. The size of the bias was significantly smaller than that seen in Experiment 1 [$F(1,192) = 4.444$, $p = .036$]. For rightward motion, no rightward bias was seen when the object covered the focus of expansion, and, instead, a small left bias was seen for that object position. This bias was also not significant [$F(6,112) = 1.167$, $p = .33$]. These results are inconsistent with the idea that motion repulsion by itself accounts for the biases seen in Experiment 1. If these biases were all due to motion repulsion, one would expect to see biases that were of equal size as those seen in Experiment 1, and one would not expect to see a leftward bias for right dot motion in the object. Thus, while motion repulsion may play some role in the perception of heading when a moving object crosses the observer's path, it does not account for all of the bias that we see.

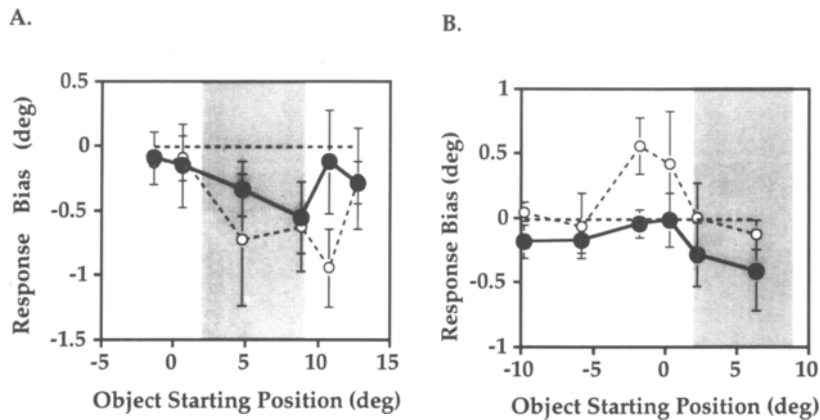


Figure 9. Response bias for static border experiment. This shows the results of Experiment 4, in which the borders of the object remained stationary while the dots within the border moved at a constant velocity either left or right. The filled symbols show the results of Experiment 4; the open symbols show the results of Experiment 1 for comparison. All other notation is the same as in Figure 8. (A) Response bias for leftward-moving dots. (B) Response bias for rightward-moving dots.

EXPERIMENT 5 Short Stimulus Duration

In Experiments 1–4, observers judged their heading quite well when the moving object was not crossing the focus of expansion. The duration of those experiments (0.8 sec) was much longer than the 300 msec needed to judge translational heading with good accuracy (Crowell et al., 1990). This extra time may allow the visual system to first segment the object so that it is not included in the heading computation and, subsequently, compute heading. To explore this issue, we ran the experiments with a shorter duration, to see whether a moving object has a greater effect on heading judgments in this case.

Method

Experiment 5 was identical to Experiment 1, with the exception that the duration of each trial was 0.4 sec. Only horizontal object motion, left or right, was tested.

Results

The average results for the 5 observers are shown in Figure 10. For left motion, the results did not differ significantly from those in Experiment 1 [$F(1,160) = 0.967, p = .33$]. While the effect of object position was not significant [$F(6,112) = 1.85, p = .095$], planned comparisons between the condition with no object and conditions with the object present showed that, as in Experiment 1, there was a small bias to the left when the object crossed the focus of expansion during the trial [Starting Position 8.7° , $F(1,112) = 6.5, p = .012$; Starting Position 10.7° , $F(1,112) = 5.13, p = .025$]. There was no bias when the object did not cross the focus of expansion [Starting Position -3.5° , $F(1,112) = 0.749, p = .39$; Starting Position 0.6° , $F(1,112) = 0.058, p = .81$]. For right motion, there was little effect on average for almost all conditions. While there was a significant effect of object position [$F(7,128) = 2.085, p = .0497$], planned comparisons showed that only one condition (Starting

Position 6.3°) differed significantly from the case with no object present [$F(1,128) = 6.34, p = .013$]. In this condition, for which the object covered the focus of expansion and moved right, most observers showed a small bias to the left. For the longer duration trials in Experiment 1, no bias was seen for this starting position. In general, when the object crossed the focus of expansion, there was much more variability in the direction of observer biases in this experiment than in Experiment 1. In some situations (e.g., Starting Position 10.7° for leftward object motion and Starting Position 0.6° for rightward object motion), some observers showed biases in one direction and others showed biases in the opposite direction.

We conclude that the observers' heading judgment accuracy does not deteriorate at the shorter duration when the object does not cross the focus of expansion. While the pattern of biases seen for the rightward-moving object differs somewhat between the 0.4- and 0.8-sec-duration experiments, the magnitude of the biases is similar in both cases. Thus, the visual mechanisms that compute heading with moving objects do not require an extended viewing time to achieve considerable accuracy.

EXPERIMENT 6 Mixed Object Positions

Another factor that could influence observers' abilities to judge their headings well in the presence of a moving object is the knowledge of the object's location before the beginning of the trial. In Experiments 1–5, we ran the experiments in blocks of trials in which the object always started in the same position and moved in the same direction. Perhaps prior knowledge of the object's location and direction of motion allowed observers to discount the object more readily. In Experiments 6 and 7, we ran conditions that intermixed different object locations and directions of motion within a single set of trials, so that the observers would not know in advance where the ob-

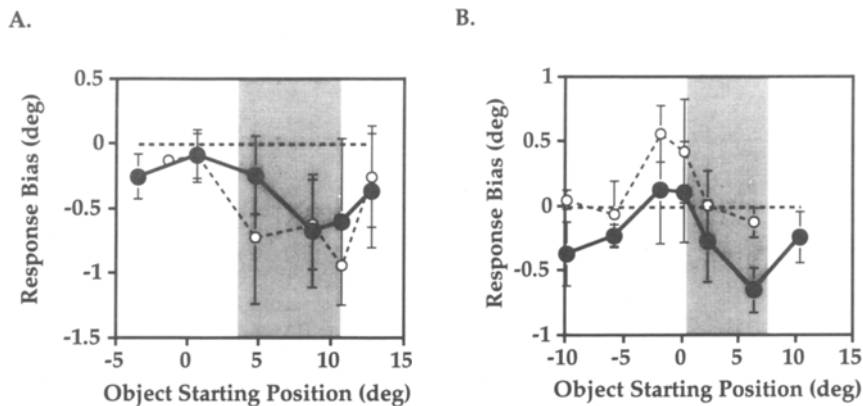


Figure 10. Response bias for short-duration experiment. This graph shows the results of Experiment 5, which measured heading judgments for trials with a duration of 0.4 sec. Filled symbols show the results of Experiment 5; open symbols show the results of Experiment 1 for comparison. All other notation is the same as in Figure 8. (A) Response bias for left object motion. (B) Response bias for right object motion.

ject would appear. The object was only apparent once the trial started and the observer could see the relative motion between the object and the stationary surface.

Method

In Experiment 6, the object's starting position could be in one of three locations, randomly intermixed within a set of trials. The initial center positions of the object for leftward motion were 0.6°, 8.7°, and 12.7°; those for rightward motion were -5.9°, -1.8°, and 2.2°. Negative starting positions indicate a position to the left of the fixation point. The other parameters were identical to those in Experiment 1. Within a single block of trials, the object always moved in a single horizontal direction.

Results

Figure 11 shows the results for Experiment 6. For both the left motion and the right motion, the response biases did not differ significantly from those in Experiment 1 [left, $F(1,96) = 0.782$, $p = .38$; right, $F(1,96) = 1.59$, $p = .21$]. As in Experiment 1, there was no observer bias when the object did not cross the observer's path for much time during the trial, as shown by the data points at 0.6° for leftward motion and -5.9° for rightward motion. When the object did cross the observer's path, the heading judgments showed a bias in the same direction as that seen in Experiment 1, and nearly the same magnitude. Thus, prior knowledge of the object's starting position is not necessary for the results we saw in Experiment 1.

EXPERIMENT 7 Mixed Heading Positions

Another possible piece of information that could aid subjects in making accurate heading judgments in Experiments 1–6 is the prior knowledge of the approximate heading location. In the preceding experiments, the headings were always located to the right of the fixation point, and, thus, observers could discount the possibility of any headings to the left. We therefore tested whether

mixing headings to the left and right of the central fixation point would cause observers to be less accurate in their heading judgments.

Method

All parameters were as in Experiment 1, except that 24 different headings and two different object motions were randomly intermixed in a single set of trials. The headings could be 4°, 5°, 6°, or 7° to the left or right of the central fixation point and -2°, 0°, or 2° above, or 2° below the horizontal midline. The object position was located at 10.7° to the right or left of the central fixation point and moved toward the center at a speed of 8.1°/sec. We also performed a control experiment in which all the headings were to the left of the fixation point, in order to show that there were no differences in observer judgments between left and right headings. These experiments were performed with 4 of our observers.

Results

In the control experiment with all the headings to the left of the fixation point, object motion caused observer biases consistent with those seen in Experiment 1, with object motion to the right (toward the center of the screen) causing a rightward bias when the object crossed the observer's path, as shown in Figure 12A. An ANOVA showed a significant effect of object position [$F(6,84) = 5.11$, $p = .0002$]. Post hoc analysis (FPLSD) showed that object starting positions of 8.7° ($p = .0002$), 10.7° ($p = .0003$), and 12.7° ($p = .0052$) differed significantly from the no-object case. Comparison of the response biases of this experiment and those of Experiment 1 showed no significant difference [$F(1,144) = 0.009$, $p = .92$]. The results of the experiments that had left- and right-heading trials intermixed are shown in Figure 12B. As with the results of Experiment 1, an ANOVA showed a significant effect of object position [$F(2,72) = 12.38$, $p = .0001$]. The observers showed a bias toward the center of the screen, which was the same direction of the object motion, when the object crossed the observers' path (post hoc analysis, $p = .0001$). When the object did not cross the observers' path, the ob-

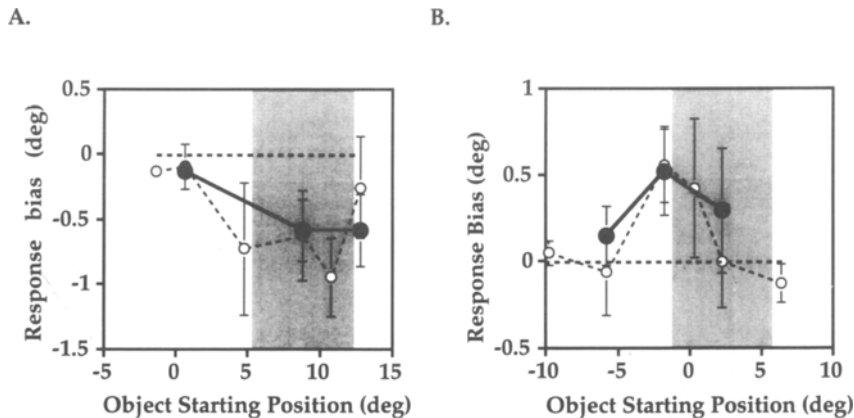


Figure 11. Results of mixed-object-position experiments. This diagram shows the results of Experiment 6, in which the starting position of the object was varied within individual runs. The filled symbols show the results of Experiment 6; the open symbols show the results of Experiment 1 for comparison. All notation is the same as described in Figure 8. (A) Response bias for left object motion. (B) Response bias for right object motion.

servers showed no significant difference in their heading response from the case when no object was present ($p = .40$). Thus, the consistent ability of the observers to judge their heading accurately in the presence of a moving object that does not cross their path is not due to prior knowledge of heading direction or object position.

EXPERIMENT 8 Object Motion in Depth

In their studies of human heading perception in the presence of moving objects, Warren and Saunders (1994, 1995b) used a two-alternative forced choice (2AFC) task to measure the effect that an object moving in depth had on observers' heading judgments. Their basic conclusion was similar to that reported here: Objects that did not cross the observer's path had no effect on heading judgments, whereas objects that did cross the path caused a bias in observer heading judgments. However, the direction of bias that they reported was in the direction of the moving object's focus of expansion, which is opposite to the direction of bias reported here. Warren and Saunders used an object whose focus of expansion was quite close to that of the stationary scene. It is possible that this is the critical difference causing the disparate results. Perhaps when the two foci of expansion, from the stationary scene and the moving object, are close together in space, the visual system averages the positions to generate a biased heading judgment. We tested this hypothesis in Experiment 8 with moving objects that moved in depth toward the observer and had foci of expansion that were close to those generated in the stationary scene by the simulated observer motion.

Method

Experiment 8 was identical to Experiment 1, except that the moving object now moved in depth toward the observer. The object had a focus of expansion (generated by its own motion com-

bined with the observer motion) at either 10° to the right of the central fixation point (and thus to the right of the simulated headings) or 1° to the right of the central fixation point (and thus to the left of the simulated headings). At the outset of the trial, the object appeared in the same plane as the closer stationary surface. It then moved out of this plane toward the observer at a speed that was 1.5 times the speed of the closer plane relative to the observer. The size of the object was $8^\circ \times 8^\circ$ at the beginning of the trial and expanded to about $20^\circ \times 20^\circ$ at the end of the trial. An example of this object motion is shown in Figure 13B. The horizontal starting position of the object was varied for different runs of the experiments. These positions were 0.6° , 2.25° , 3.9° , 5.5° , and 7.1° for both the focus of expansion conditions. In addition, a starting position of -1.0° was tested for the 1° focus of expansion and 8.7° for the 10° focus of expansion. The experiments were run in blocks of trials, with the moving object's starting position and focus of expansion staying constant within each block of trials. All 5 observers participated in this experiment.

Results

The results of Experiment 8 are diagrammed in Figures 13 and 14. As in Experiment 1, the effect of the moving object depended greatly on its horizontal starting position. Consistent with Warren and Saunders, and with our results from Experiment 1, we found that when the object did not cross the observer's path, its presence had essentially no effect on the heading judgment. However, when the object did cross the observer's path, the effects depended critically on the object's starting position and varied to a great extent between observers. Figure 13 shows some examples of differing effects for 2 different observers for an object with a 10° FOE, to the right of the simulated observer headings, with a starting position of 5.5° , centered within the horizontal headings. Observer C.S.R. had a large bias in response to the right for this condition, whereas Observer E.C.A. had a large bias to the left. For this particular condition, 3 observers showed rightward biases and 2 showed leftward biases. This kind of inconsistency between the observers makes it difficult to make general conclusions about the direc-

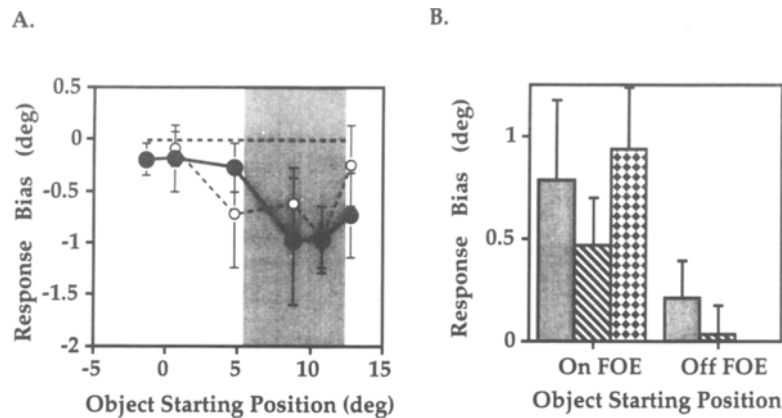


Figure 12. Results of mixed-left-and-right-heading experiment. These graphs depict the results of Experiment 7, in which the heading direction could be on either the right or the left of the fixation point. (A) Results of experiments with the heading direction to the left of the fixation point. Negative numbers on the y -axis indicate a response bias toward the center of the screen. Filled symbols show the results for headings to the left of fixation; open symbols show the results for headings to the right of fixation, from Experiment 1. For left headings, the object always moved to the right, and a positive object position indicates a starting position to the left of fixation. For right headings, the object moved to the left, and a positive object position indicates a starting position to the right. All other notation is as in Figure 8. (B) Results of experiments in which the headings to the left and right of fixation were randomly intermixed. Gray filled bars show the bias averaged over all headings and observers for headings to the left of fixation. Diagonal striped bars show the average bias for headings to the right of fixation. The checkered bar shows the results from Experiment 1 for comparison, for the right headings (only the case for the object crossing the FOE was tested in Experiment 1). The two sets show the results when the object crossed the focus of expansion (On FOE) or when it was in the opposite half of the visual field from the focus of expansion (Off FOE). Error bars show $+1$ SE across observers.

tion of bias generated by the object in these conditions. It is possible that different observers use different strategies to judge their headings in cases when they cannot see the focus of expansion for the stationary scene, and these different strategies yield different types of errors.

Figure 14 shows the average biases for the two different object motions with respect to the horizontal starting position. There was a significant effect of object position for the object with an FOE at 10° [$F(6,112) = 2.343$, $p = .036$] and a nearly significant effect for the object with an FOE at 1° [$F(6,112) = 1.97$, $p = .076$]. For the object with an FOE at 1° , only a starting position of 3.9° generated responses that differed significantly from those of the no-object condition (post hoc FPLSD, $p = .03$). The starting position of 5.5° approached significance ($p = .056$). Both of these biases were to the left, consistent with Warren and Saunders's (1995b) model for averaging the FOEs from the object and the stationary scene. For the object with a 10° FOE, post hoc analysis showed that only one object starting position (at 8.7° ; $p = .04$) yielded responses that were significantly different from the case with no object. This point yielded a leftward bias on average, and only 1 observer showed a slight rightward bias in this case. This leftward direction of bias for an object that has its FOE to the right of the simulated headings is inconsistent with the Warren and Saunders model that averages the positions of the FOEs.

Because of the inconsistency in observer biases seen for the 5.5° starting position for the object with an FOE at 10° , and because the leftward bias was generated for only one starting position (8.7°) for this object, we repeated these conditions for an additional 6 observers to give a total of 11 observers for these conditions. The new observers were all naive to the hypotheses of the experiment, and only 1 had participated previously in any kind of psychophysics experiment. In addition, we ran an experiment in which the object starting position was 10.7° for all 6 of these observers and 2 of the original subjects from Experiment 8. These results are plotted in the open symbols in Figure 14B. Clearly, the addition of new observers did not change the results much. Again, there was a strong effect of object position [$F(4,176) = 4.36$, $p = .002$]. For the 5.5° starting position, 4 observers showed rightward biases, 4 showed leftward biases, and 3 showed essentially no bias. The average response did not differ significantly from the no-object case for this condition ($p = .52$). Thus, the variability in observer responses was not due to 2 unusual observers in our original group. For the 8.7° starting position, only 2 observers showed rightward biases. The difference in the responses for this starting position and those for the no-object case approached significance ($p = .056$). For the 10.7° starting position, the responses differed significantly from those for the no-object case ($p = .016$). For this starting posi-

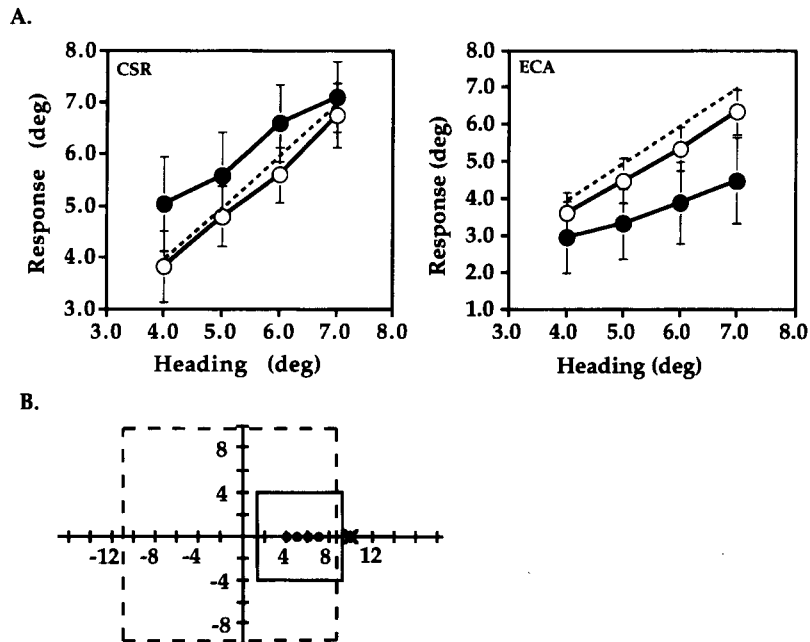


Figure 13. Example of observer variation for Experiment 8. (A) The two graphs show the average responses of 2 different observers for the same stimulus condition in Experiment 8. The center of the object started at 5.5° to the right of the fixation point. The focus of expansion for the object was at 10° to the right of center. Open symbols show observer responses when no object was present in the scene. Filled symbols show observer responses when the object was present in the scene. Error bars show $\pm 1 SE$. The dashed line shows the simulated heading. (B) Diagram of the object trajectory. The small square indicates the object's starting position; the large square indicates the object's ending position. The filled circles show the simulated headings. The cross shows the position of the object's focus of expansion.

tion, only 1 observer showed a rightward bias over the no-object condition. This observer had an extreme central bias for the no-object condition and did not appear to distinguish between headings in that condition. So, even though the responses for this observer with the object present were always to the right of the no-object condition, they were considerably to the left of the actual simulated headings. These results for an object with an FOE to the right of all the simulated headings (at 10°) clearly contradict the predictions made by Warren and Saunders's model.

EXPERIMENT 9 Single Plane With Free Eye Movements

In the experiments of Warren and Saunders (1994, 1995b), several other factors differed between their experimental paradigm and ours. Most notably, they used a single plane as their stationary surface, their subjects were allowed free eye movements, and they used a 2AFC task. Although the results of Experiment 8 suggest that the starting position of the object is the critical factor in the direction of bias seen when the focus of expansion for the object is close to the observer headings, it is possible that one of these other three factors could account

for the differences between the biases reported in their paper and those reported here. We therefore ran two control experiments to test the effect of these factors. In Experiment 9, we tested the effect of using a single plane as the stationary scene and allowing observers to make free eye movements. In Experiment 10, we tested the difference between a cursor placement task and a 2AFC task.

Method

Experiment 9 was identical to Experiment 8, except that the stationary surface was a single frontoparallel plane, and the fixation cross was absent from the display. The observers were told that they did not have to maintain fixation during the trial. We tested conditions for an object whose FOE was at 10° to the right of the center of the viewing window. The starting position of the object was either 5.5° or 8.7° to the right of center. The original 5 observers from Experiment 8 were tested in this experiment.

Results

Figure 15 compares the response biases generated in Experiment 9, using a single plane as the stationary scene and free eye movements of the observers, with those in Experiment 8, which used two transparent planes and a fixation point. While the magnitude of the bias generated with the single plane and free eye movements was generally larger than that seen in Experiment 8, in all but

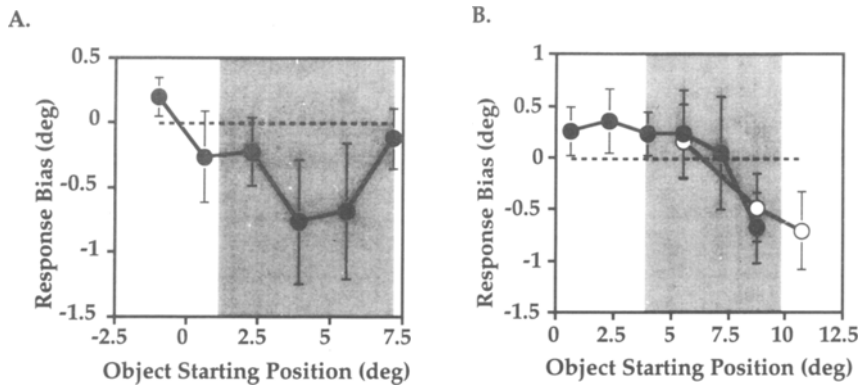


Figure 14. Response bias for objects moving toward the observer. This shows the results of Experiment 8, in which the object has a component of motion in depth. A negative response bias indicates a bias to the left or toward the center of the screen. The gray shaded region shows the starting positions for which the object obscured all four simulated headings for at least 50% of the trial. Error bars show ± 1 SE. (A) Average response bias for an object whose focus of expansion was at 1° to the right of the central fixation point. (B) Average response bias for an object whose focus of expansion was 10° to the right of the fixation point. Filled symbols show the average bias of the original 5 observers. Open symbols show the average bias after repeating the experiment with additional observers (11 observers' total for the points at 5.5° and 8.7° ; 8 observers' total for data point at 10.7°).

two cases the bias was in the same direction for both experiments. So, for this condition, as with Experiment 8, the size and direction of the bias seen depended on the observer and the object starting position.

EXPERIMENT 10 Two-Alternative Forced Choice

In this experiment, we tested the effect of using a 2AFC task similar to that of Warren and Saunders (1995b), as opposed to the cursor placement task used in the previous experiments.

Method

In Experiment 10, the motion of the dots during the trial was identical to that in Experiment 8. That is, the motion of the dots simulated observer motion toward two transparent frontoparallel planes. The moving object had a simulated FOE at 10° to the right of the fixation point and a starting position of either 5.5° or 8.7° to the right of the fixation point. At the end of the trial, a vertical line appeared on the screen, and the observers were asked to indicate by a buttonpress whether their heading had been to the right or to the left of the target line. The line appeared at 0.5° , 1.0° , 2.0° , or 4.0° to the left or right of the simulated heading, for a total of eight possible target offsets. The vertical heading component was either on the horizontal midline or 2° above or below the midline. Each target offset condition was repeated five times at each vertical heading, for a total of 120 trials. In each trial, the horizontal heading was chosen at random between the limits of 4° and 7° to the right of the central fixation point. In the analysis of the data, responses for each horizontal heading were averaged over all vertical headings, giving a total of 15 responses for each target offset. The percentage of trials in which the observer responded "right" was plotted against the target offset, and these data were fit with a cumulative Gaussian. The bias was calculated on the basis of the amount the cumulative Gaussian was shifted to the left or right of the zero position. All 5 original observers who participated in Experiment 8 were tested in this experiment.

Results

In Figure 16, the biases generated in Experiment 10, using the 2AFC task, are plotted alongside those from Experiment 8, using the cursor placement task. With the exception of 2 observers (E.C.A. and E.C.H. for the 5.5° starting position), all observer biases were in the same direction for the 2AFC and the cursor placement tasks. For 2 observers (C.S.R. and L.V.), the magnitude of the bias seen in the 2AFC task was similar to that seen in the cursor placement task. For 2 observers (E.G. and E.C.H.), the bias was considerably smaller in the 2AFC task for one object starting position but larger for the other starting position. For the other observer (E.C.A.), the bias from the 2AFC task was considerably smaller than that for the cursor task for both starting positions of the object. Despite these differences in results from the two tasks, the primary conclusion from Experiment 8 still holds. The direction and amount of the bias for an object moving in depth depends on the individual observer and the starting position of the moving object.

DISCUSSION

We have run a series of experiments to test how well people judge their heading when there are moving objects in the scene. The results of our experiments show that people judge heading in the presence of moving objects remarkably well for a variety of conditions. Even a fairly large ($10^\circ \times 10^\circ$) moving object has essentially no effect on an observer's heading judgments when it does not cross the observer's path. This is consistent with the results reported by Warren and Saunders (1995b), who also found no effect of a moving object when it did not cross the observer's path. Cutting, Vishton, and Braren (1995) have also reported that the addition of a moving

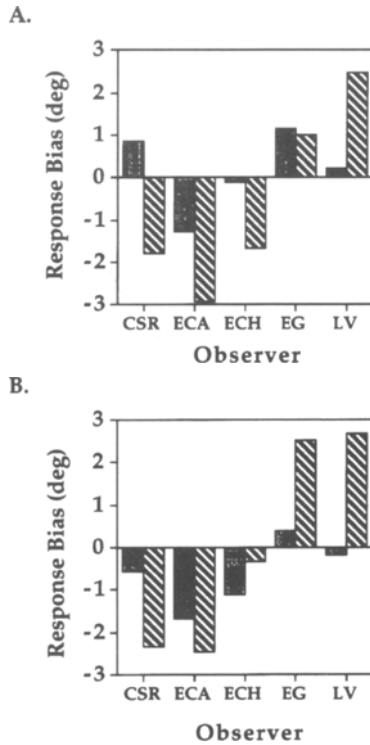


Figure 15. Response bias for motion toward a single plane with free eye movements. In this graph, the average response bias over all horizontal headings is shown for each observer for a moving object whose FOE is at 10° to the right of the center of the screen. The gray shaded bars show the average response bias from Experiment 8, in which the observers fixated a central cross during each trial and the simulated scene was two transparent frontoparallel planes. The diagonally hatched bars show the average response bias for the same observers when they moved toward a single frontoparallel plane and their eyes were free to move. (A) Average response bias for an object starting position of 5.5° to the right of center. (B) Average response bias for an object starting position of 8.7° to the right of center.

pedestrian into a tree-filled scene through which an observer is moving has little effect on the observer's ability to judge heading.

In our experiments, when the same large (10° × 10°) object crossed the observer's path, it caused a small bias in the observer's heading judgments. The amount of bias was as large as 2.9°, varying between observers and the starting position of the object, with the biggest average bias being 0.9°. Therefore, even in the worst case, the bias generated by a moving object was small. Under most conditions, the object would be crossing the observer's path only for a short period of time, unless the object were unusually large or moving straight toward the observer. Therefore, we can conclude that moving objects do not significantly affect an observer's heading judgments in real situations, when the observer has an extended period of time to view the scene while moving toward it. One possible exception to this is when the object is approaching the observer along the observer's path. In this case, perhaps it would be best for the ob-

server to change his or her direction of motion to avoid a collision with the object.

A second conclusion that can be drawn from our data is that the focus of expansion is important for an accurate heading judgment. In our experiments and those of Warren and Saunders (1995b), the only situation in which a moving object affected heading judgments was when it obscured the focus of expansion for the stationary part of the scene. This suggests that the visual system relies on the visible focus of expansion for the most accurate heading judgments. This is consistent with results from other studies. Crowell and Banks (1993) measured human ability to discriminate two different headings and found that there was an enhanced discrimination ability when the focus of expansion was visible and an even greater enhancement when the observers looked directly at the focus of expansion. Warren and Kurtz (1992) also showed that people performed better in judging heading relative to a target line when the focus of expansion was visible than they did when it was not. Neither of these studies measured possible perceived biases in observer responses when the focus of expansion was not visible. In our experiments with a static object, observers showed no biases when the object obscured the focus of expansion.

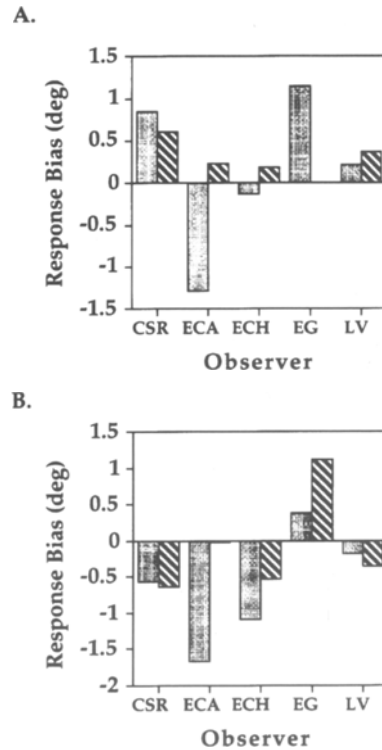


Figure 16. Response bias for 2AFC task. This graph plots the observer response bias for an object whose FOE was 10° to the right of the center of the screen. The gray shaded bars show the average response bias from Experiment 8, in which the observers performed a cursor placement task. The diagonally hatched bars show the response bias for the 2AFC task. (A) Response bias for an object starting position of 5.5° to the right of the center. (B) Response bias for an object starting position of 8.7° to the right of center.

This implies that motion of the object is essential for the generation of this bias. In experiments similar to ours, Warren and Saunders (1995b) found that when the object contained no dots, the bias disappeared. In our experiments, some bias remained, but it was decreased when no dots were present in the object. This suggests that, in addition to the presence or absence of the focus of expansion, the relative motions between the dots within the moving object and the dots in the stationary scene may enhance the bias.

Observer Bias

Direction of bias. In Experiment 1, we found that, for horizontally moving objects, the direction of the observer bias for an object crossing the observer's path was the same as the direction of motion of the object. This is the opposite direction from what one would expect if the visual system were computing a position between the observer's motion direction toward the static scene and the observer's motion direction relative to the object. One possible explanation for the bias seen in these cases would be that the bias is due to a motion repulsion effect (Marshak & Sekuler, 1979). The motion repulsion effect describes the bias in the perceived direction of motion of dots that are spatially nearby those that have slightly different directions of motion. The perceived directions of motions for these dots are farther apart than the actual directions of motion, as shown in Figure 7. If people rely more heavily on the motion of dots near the focus of expansion to compute heading, then the skewing of the perceived motion direction of the individual dots could lead to a bias in the computed position of the focus of expansion, as shown in Figure 7. For horizontal heading judgments, the most informative dots are those directly above or below the focus of expansion (Crowell & Banks, 1993, 1996). The perceived direction of motion of a dot directly above (or below) the true focus of expansion would have to be shifted by 10.2° to generate the average observed bias for the leftward-moving object in Experiment 1. This is somewhat larger than the amount of repulsion reported by Marshak and Sekuler for dots that moved in directions 90° apart from one another. However, for an object centered over the focus of expansion, a dot associated with the stationary scene just beside any corner of the object would be moving at an angle of 45° from the direction of motion of the object. The perceived direction of motion of this dot would only have to change by about 6° to generate the 0.9° bias seen in Experiment 1. Marshak and Sekuler reported motion repulsion effects of about 15° for dots moving at angles of 45° from each other. If one assumes that the skewing effect caused by motion repulsion is averaged across the upper and lower borders of the object, then it is probable that motion repulsion is strong enough to account for the bias we see. The results of Experiment 4, in which dots moved within a stationary window, suggest that motion repulsion does not account for the entire bias seen when the moving object is present. Otherwise, one would expect to see the same bias for this condition as with the

moving object. This was clearly not the case for the rightward-moving dots in Experiment 4. Furthermore, motion repulsion cannot account for all of the effects we see in different conditions. For example, the motion repulsion explanation does not account for the horizontal bias we see when the object is moving up or down.

Warren and Saunders (1995b) suggested that the bias we see for laterally moving objects in Experiment 1 could be similar to the illusion reported by Duffy and Wurtz (1993). In this illusion, Duffy and Wurtz reported that the perceived position of the focus of expansion was shifted when an expanding field of dots was superimposed on a field of laterally moving dots. The shift was in the direction of the laterally moving dots. The proposed explanation for this phenomenon is that the laterally moving dots provide a visual signal to the brain that the eyes are moving. This causes the brain to shift the computed center of expansion to account for the motion of the eyes (Duffy & Wurtz, 1993). Lappe and Rauschecker (1995) have shown how the performance of their computational model supports this explanation. While this may explain the results of Duffy and Wurtz, we do not believe it explains the biases we see here, for several reasons. First, our observers were fixating a stationary cross during each trial. The work of Royden et al. (1992; Royden et al., 1994) suggests that the visual system can distinguish between stationary and moving eye conditions, particularly for the rapid dot speeds used here ($8.1^\circ/\text{sec}$), and thus there was a strong nonvisual cue that the eyes were not moving. Furthermore, although the experiments were done in a dark room, the luminance of the display allowed the borders of the monitor to be visible after dark adaptation. This provided an additional visual cue that the eyes were stationary. Second, the size of our object was relatively small compared with the size that one might expect to generate an illusion of eye motion. Duffy and Wurtz used a large, $100^\circ \times 100^\circ$ field in their experiments. Our object was only $10^\circ \times 10^\circ$ and was surrounded by a larger field that had visual information consistent with stationary eyes. Finally, the bias we see is strongly dependent on the position of the object, and we would not expect an effect due to a misperceived eye motion to be so dependent on the object position. Thus, while we cannot rule out this explanation, it seems unlikely.

Recently, Saunders and Warren (1995) proposed an alternative explanation for the bias we see for the laterally moving objects. They suggested that the mechanism that computes the focus of expansion has a repulsion interaction between two foci of expansion if they are sufficiently far apart. This model can account for the bias we see with leftward- or rightward-moving objects, but not with objects moving up or down. It also does not account for the dependence of this bias on object position. The cells in visual area MST, which are thought to be involved in heading judgments (Duffy & Wurtz, 1991a, 1991b; Saito et al., 1986; Tanaka, Fukada, & Saito, 1989; Tanaka & Saito, 1989), have extremely large receptive fields that can cover a large part of the visual scene up to

100° × 100° (Duffy & Wurtz, 1991a). If, as proposed by Warren and Saunders, each of these cells is tuned to a specific focus of expansion or direction of observer motion, it should not matter where within the receptive field the information about that focus of expansion resides. Thus, a moving object with a focus of expansion at 10° to the right of center should stimulate a cell tuned to that focus of expansion, independent of the actual position of the object, as long as the object position is within the large receptive field of the cell. Warren and Saunders (1995b) propose that weighting the region around the focus of expansion more strongly would account for the position dependence of the heading bias, so that only an object crossing the observer's path would affect the perceived heading. However, in our Experiment 1, the objects moved laterally and thus had no visible focus of expansion in any of their positions. Thus, the contribution to the heading computation from the object should have been constant over the different positions tested. As for the contribution from the stationary scene, it can be seen in Figure 4B that the effect on the observer's heading judgments varied with position even within the region in which the object crossed the focus of expansion. A simple weighting scheme would not explain this fine positional distinction. Because of the dependence on the precise object position, we think that the model proposed by Warren and Saunders cannot fully describe the physiological mechanisms for computing optic flow in the presence of moving objects.

While we have not found a full explanation for the bias caused by laterally moving objects, the results of Experiments 2 and 3 shed some light on this phenomenon. Experiment 2 shows that the image motion of the object per se is important for the generation of the bias, because no bias is seen when the object is stationary. This suggests that interactions between the motion of the dots contained in the object and those contained in the scene cause some part of this bias. This idea is bolstered by the results of Experiment 3, in which removing the dots from the object decreased the bias seen for both leftward and rightward object motion. It is possible that the relative motion of the dots at the borders between the object and the stationary scene plays a role in creating the bias, although this idea remains to be thoroughly tested.

In their studies of heading in the presence of moving objects, Warren and Saunders (1994, 1995b) also found that objects affected heading judgments only when the object crossed the observer's path. However, the direction of the bias they saw was opposite that reported here. They found that, for an object with a focus of expansion to the right of the simulated headings, observers' heading judgments were biased to the right. When the object's focus of expansion was to the left, the heading bias was to the left. These experiments differ from our Experiment 1 primarily in the motion of the object. Their object moved in depth toward the observer and had a focus of expansion much closer to the simulated observer heading than did ours. We therefore ran Experiment 8 to see if an object with a focus of expansion that was close to

the observer headings would cause a bias toward the object's focus of expansion. As recently reported by Warren and Saunders (1995a), we found a different pattern of results depending on the angle of motion in depth of the object (path angle). However, in contrast to their reported results, we found that the bias in this experiment depended on the starting position of the object and the particular observer. The average data for all observers give results consistent with those of Warren and Saunders for a particular object starting position (5.5° in Figure 14), which was centered over the simulated observer headings. This is similar to the object position used in Warren and Saunders's experiments. However, a small shift in the starting position of the object (8.7° and 10.7° in Figure 14) gives an average bias for the object with a 10° focus of expansion that is in the opposite direction. Warren and Saunders tested a limited set of starting positions for their object that may not have revealed the effect that we observed. Therefore, the bias seen for an object moving in depth cannot completely be explained as an averaging between the observer's heading and the focus of expansion for the moving object, as suggested by Warren and Saunders (1995b). Furthermore, weighting the focus of expansion more strongly than other regions of the object, as proposed by Warren and Saunders (1995b), should actually increase the rightward bias for the object with a focus of expansion at 10° when it is centered at 10.7° because, in this case, the object's focus of expansion is visible during the entire trial. However, we see a leftward bias in this condition and see a more rightward bias when the object is centered at 5.5°, where its focus of expansion was not visible. Thus, these data cannot be explained by Warren and Saunders's model.

Asymmetry of bias. In all our experiments, including the condition when no object was present, there was a tendency for observers to choose a heading that was more central than the true heading when no object was present. This central bias has been reported previously for stationary scenes (Cutting, Springer, Braren, & Johnson, 1992; Johnston, White, & Cumming, 1973; Llewellyn, 1971) and was also seen by Warren and Saunders (1995b) for moving-object experiments. This central bias may be part of the reason for the asymmetry we see in the results for rightward- and leftward-moving objects. To generate a rightward, or more peripheral, bias in our experiments, the mechanisms leading to this bias from the moving objects must overcome whatever mechanisms cause observers to see their heading as more central than it actually is. Conversely, this tendency to see headings more centrally may enhance the leftward (central) biases we see from the leftward-moving objects.

Variability of Observer Responses

In Experiment 1, all our observers responded in the same way for all the conditions tested. The biases for the observers were in the same direction for all of the conditions when the object crossed the focus of expansion. In contrast, for Experiments 3–5 and 8–10, there was considerable variability in observer response when the

object crossed the focus of expansion. Often, some observers would show a large bias in one direction for a particular condition, whereas others would show a large bias in the other direction (e.g., as shown in Figure 13). This suggests that, in the absence of the focus of expansion, observers develop different strategies for estimating their headings. Some may be more adept at using information from elsewhere in the flow field and thus manage to maintain somewhat more accurate heading judgments, whereas others may be more influenced by the flow vectors within the object and thus make more erroneous judgments. For example, the conditions used in Experiments 8–10 made the heading task considerably more difficult than those in Experiment 1, and several subjects commented on this fact. The object in these experiments expanded to a size of $20^\circ \times 20^\circ$ and obscured the focus of expansion for the static scene. This condition could have caused some observers to guess a heading position near the object's focus of expansion, because most of the information in the viewing window at the end of the trial was associated with the object. Other observers may have been better able to ignore the object and use information from the static scene to make their judgments. This could account for the large observer variability we found in our experiments. The large difference in results suggests that there is no single mechanism in the brain that all people use to judge heading when an object moves in front of an observer's heading. Instead, it seems likely that people learn to deal with this situation through experience and develop their own strategies for coping with the absence of a focus of expansion.

Warren and Saunders (1995b) did not report a similar variability in observer responses for the conditions in which the moving object obscured the focus of expansion. Two factors may bear on this difference between their results and ours. First, they screened observers for their ability to perform the heading task with no moving object in the scene and excluded those who could not perform the task well. We did not screen out any observers, but we do not believe this would completely account for the difference in variability that we see, because some of our most reliable observers showed biases that differed in direction from one another. Second, their method of data analysis required that they exclude data that could not be fit to an ogive curve. Thus, they excluded about 10% of the data collected for the condition in which the object obscured the focus of expansion. Both of these factors might have led to greater consistency in the observer responses in their experiments. The possibility exists, however, that some difference in the experimental design led to the difference in observer variability. With Experiments 9 and 10, we ruled out the use of a single frontoparallel plane, free eye movements, and a 2AFC task as the crucial differences between our experiments. However, other differences in the display parameters, such as the image speed of the dots, dot density, or the duration of the stimulus, may have considerable effect on the observer heading judgments.

Implications for Computational Models

Several implications for computational models arise from the results of these experiments. The most important result is that an object that does not cross the observer's path has essentially no effect on the observer's heading judgments. This means that any model of human heading perception must be able to identify the location of the moving object so that the motion of the object does not affect the heading computation. There are several ways one might accomplish this. Hildreth's (1992) model divides the visual field into small regions and computes a heading estimate from the motion information within each region. The heading is assumed to be the location that most of the image regions indicate as their best heading. The object can then be detected by finding the image regions whose indicated headings are inconsistent with the computed observer heading.

Another approach would be to compute the heading using sequential estimates. In our simulations of several of the models (least squares, Perrone, and Rieger & Lawton), the presence of a moving object does not cause an extremely large error in the heading estimate. Therefore, one could make an initial estimate of heading direction using all the motion information available. Subsequently, one could fine-tune this estimate by using one of several alternative approaches. For example, one could locate the regions of flow that are inconsistent with the initial heading estimate and exclude those regions from subsequent heading computations as proposed by several researchers (Adiv, 1985; Heeger & Hager, 1988; Ragnone et al., 1992; Thompson et al., 1993; Zhang et al., 1988). Another possible solution would be to use only the information from the region that is close to the initial heading estimate in subsequent computations. This latter approach would fit well with our experimental results, because it would provide very accurate heading estimates when the object was away from the heading, but it would be unable to ignore the information from the object when it crosses the observer's path.

The second implication of our results for computational models arises from the direction of the biases when the moving object crosses the observer's path. In Experiment 1, we found that all our observers showed biases in the direction of the object's motion for the horizontally moving object. This direction is opposite to what one would expect if the brain mechanism were simply averaging the information from the stationary scene and the moving object to compute heading because, in that case, one would expect to generate a bias in the direction opposite to the object's motion direction. This implies that models that tend to average the foci of expansion, such as the models of Perrone and Stone (1994) and Hatsopoulos and Warren (1991), are insufficient to account for human heading judgments. A model that incorporates the effects of motion repulsion (Marshak & Sekuler, 1979) may account for some of the effects we see.

Finally, as discussed above, in Experiments 3–5 and 8–10, we often saw quite different results from different

observers. Each observer seemed to be self-consistent, but the direction of bias varied between individuals. This suggests that there is no single "hard-wired" solution that the brain uses to compute heading when the focus of expansion is blocked from view. The different results from different observers probably reflect different strategies for determining heading in this situation. These strategies could have been developed through each person's own experience in life and thus have no single explanation. Therefore, builders of computational models should remember not so much the direction or size of the bias but rather the importance of the region around the focus of expansion for accurate heading computations.

Summary

We have shown that observers can judge their heading very accurately in the presence of a fairly large moving object. When the object did not cross the observer's path, it had no effect on the observer's heading judgments. When the object did cross the observer's path, moving in front of the focus of expansion, there was a small bias in the observer's heading judgments. For horizontally moving objects, the bias was in the same direction as the direction of object motion. For objects moving in depth, the direction of the bias depended on the starting position of the object. These results are inconsistent with a model that finds an average location between the focus of expansion for the stationary scene and the focus of expansion for the object.

REFERENCES

- ADIV, G. (1985). Determining three-dimensional motion and structure from optical flow generated by several moving objects. *IEEE Transactions on Pattern Analysis & Machine Intelligence*, **PAMI-7**, 384-401.
- BRAITHWAITE, R. N., & BEDDOES, M. P. (1993). Estimating camera and object translation from a moving platform. In *Proceedings of the IEEE Intelligent Vehicles 1993 Symposium* (pp. 177-182). Piscataway, NJ: IEEE Industrial Electronics Society.
- BRUSS, A. R., & HORN, B. K. P. (1983). Passive navigation. *Computer Vision, Graphics, & Image Processing*, **21**, 3-20.
- BURT, P. J., BERGEN, J. R., HINGORANI, R., KOLCZINSKI, R., LEE, W. A., LEUNG, A., LUBIN, J., & SHVAYTSEV, H. (1989). Object tracking with a moving camera, an application of dynamic motion analysis. In *Proceedings of the IEEE Workshop on Visual Motion* (pp. 2-12). Washington, DC: IEEE Computer Society Press.
- CROWELL, J. A., & BANKS, M. S. (1993). Perceiving heading with different retinal regions and types of optic flow. *Perception & Psychophysics*, **53**, 325-337.
- CROWELL, J. A., & BANKS, M. S. (1996). Ideal observer for heading judgments. *Vision Research*, **36**, 471-490.
- CROWELL, J. A., ROYDEN, C. S., BANKS, M. S., SWENSON, K. H., & SEKULER, A. B. (1990). Optic flow and heading judgments. *Investigative Ophthalmology & Visual Science*, **31** (Suppl.), 522.
- CUTTING, J. E., SPRINGER, K., BRAREN, P. A., & JOHNSON, S. H. (1992). Wayfinding on foot from information in retinal, not optical, flow. *Journal of Experimental Psychology: General*, **121**, 41-72.
- CUTTING, J. E., VISHTON, P. M., & BRAREN, P. A. (1995). How we avoid collisions with stationary and moving objects. *Psychological Review*, **102**, 627-651.
- DUFFY, C. J., & WURTZ, R. H. (1991a). Sensitivity of MST Neurons to optic flow stimuli: I. A continuum of response selectivity to large-field stimuli. *Journal of Neurophysiology*, **65**, 1329-1345.
- DUFFY, C. J., & WURTZ, R. H. (1991b). Sensitivity of MST neurons to optic flow stimuli: II. Mechanisms of response selectivity revealed by small-field stimuli. *Journal of Neurophysiology*, **65**, 1346-1359.
- DUFFY, C. J., & WURTZ, R. H. (1993). An illusory transformation of optic flow fields. *Vision Research*, **33**, 1481-1490.
- FRAZIER, J., & NEVATIA, R. (1990). Detecting moving objects from a moving platform. In *Proceedings of the DARPA Image Understanding Workshop* (pp. 348-355). San Mateo, CA: Morgan Kaufman.
- GIBSON, J. J. (1950). *The perception of the visual world*. Boston: Houghton Mifflin.
- GIBSON, J. J. (1966). *The senses considered as perceptual systems*. Boston: Houghton Mifflin.
- HATSOPOULOS, N. G., & WARREN, W. H. (1991). Visual navigation with a neural network. *Neural Networks*, **4**, 303-317.
- HEEGER, D. J., & HAGER, G. (1988). Egomotion and the stabilized world. In *Second International Conference on Computer Vision* (pp. 435-440). Washington, DC: IEEE Computer Society Press.
- HEEGER, D. J., & JEPSON, A. D. (1992). Subspace methods for recovering rigid motion I: Algorithm & implementation. *International Journal of Computer Vision*, **7**, 95-117.
- HILDRETH, E. C. (1992). Recovering heading for visually-guided navigation. *Vision Research*, **32**, 1177-1192.
- JAIN, R. C. (1984). Segmentation of frame sequences obtained by a moving observer. *IEEE Transactions on Pattern Analysis & Machine Intelligence*, **PAMI-6**, 624-629.
- JOHNSTON, I. R., WHITE, G. R., & CUMMING, R. W. (1973). The role of optical expansion patterns in locomotor control. *American Journal of Psychology*, **86**, 311-324.
- LAPPE, M., & RAUSCHECKER, J. P. (1993). A neural network for the processing of optic flow from ego-motion in man and higher mammals. *Neural Computation*, **5**, 374-391.
- LAPPE, M., & RAUSCHECKER, J. P. (1995). An illusory transformation in a model of optic flow processing. *Vision Research*, **35**, 1619-1631.
- LLEWELLYN, K. R. (1971). Visual guidance of locomotion. *Journal of Experimental Psychology*, **91**, 245-261.
- LONGUET-HIGGINS, H. C., & PRAZDNY, K. (1980). The interpretation of a moving retinal image. *Proceedings of the Royal Society of London: Series B*, **208**, 385-397.
- MARSHAK, W., & SEKULER, R. (1979, September 28). Mutual repulsion between moving visual targets. *Science*, **205**, 1399-1401.
- MURRAY, D., & BASU, A. (1994). Motion tracking with an active camera. *IEEE Transactions on Pattern Analysis & Machine Intelligence*, **PAMI-16**, 449-459.
- NELSON, R. C. (1990, April). *Qualitative detection of motion by a moving observer* (Tech. Rep. No. 341). Rochester, NY: University of Rochester, Department of Computer Science.
- PERRONE, J. A. (1992). Model for the computation of self-motion in biological systems. *Journal of the Optical Society of America A*, **9**, 177-194.
- PERRONE, J. A., & STONE, L. S. (1994). A model of self-motion estimation within primate extrastriate visual cortex. *Vision Research*, **34**, 2917-2938.
- RAGNONE, A., CAMPANI, M., & VERRI, A. (1992). Identifying multiple motions from optical flow. In *Computervision—ECCV '92: Second European Conference on Computer Vision* (pp. 258-266). New York: Springer-Verlag.
- RIEGER, J. H., & LAWTON, D. T. (1985). Processing differential image motion. *Journal of the Optical Society of America A*, **2**, 354-360.
- RIEGER, J. H., & TOET, L. (1985). Human visual navigation in the presence of 3D rotations. *Biological Cybernetics*, **52**, 377-381.
- ROYDEN, C. S. (1994). Analysis of misperceived observer motion during simulated eye rotations. *Vision Research*, **34**, 3215-3222.
- ROYDEN, C. S., BANKS, M. S., & CROWELL, J. A. (1992). The perception of heading during eye movements. *Nature*, **360**, 583-585.
- ROYDEN, C. S., CROWELL, J. A., & BANKS, M. S. (1994). Estimating heading during eye movements. *Vision Research*, **34**, 3197-3214.
- ROYDEN, C. S., & HILDRETH, E. C. (1994). The effect of moving objects on heading perception. *Investigative Ophthalmology & Visual Science*, **35** (Suppl.), 1999.
- SAITO, H., YUKIE, M., TANAKA, K., HIKOSAKA, K., FUKADA, Y., & IWAI, E. (1986). Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey. *Journal of Neuroscience*, **6**, 145-157.

- SAUNDERS, J. A., & WARREN, W. H. (1995). An expansion template model accounts for biases in perceived heading. *Investigative Ophthalmology & Visual Science*, **36** (Suppl.), 359.
- TANAKA, K., FUKADA, Y., & SAITO, H. (1989). Underlying mechanisms of the response specificity of expansion/contraction and rotation cells in the dorsal part of the medial superior temporal area of the macaque monkey. *Journal of Neurophysiology*, **62**, 642-656.
- TANAKA, K., & SAITO, H. (1989). Analysis of motion in the visual field by direction, expansion/contraction, and rotation cells clustered in the dorsal part of the medial superior temporal area of the macaque monkey. *Journal of Neurophysiology*, **62**, 626-641.
- THOMPSON, W. T., LECHLEIDER, P., & STUCK, E. R. (1993). Detecting moving objects using the rigidity constraint. *IEEE Transactions on Pattern Analysis & Machine Intelligence*, **PAMI-15**, 162-166.
- THOMPSON, W. T., & PONG, T. C. (1990). Detecting moving objects. *International Journal of Computer Vision*, **4**, 39-57.
- VAN DEN BERG, A. V. (1992). Robustness of perception of heading from optic flow. *Vision Research*, **32**, 1285-1296.
- VAN DEN BERG, A. V., & BRENNER, E. (1994a). Humans combine the optic flow with static depth cues for robust perception of heading. *Vision Research*, **34**, 2153-2167.
- VAN DEN BERG, A. V., & BRENNER, E. (1994b). Why two eyes are better than one for judgments of heading. *Nature*, **371**, 700-702.
- WARREN, W. H., BLACKWELL, A. W., KURTZ, K. J., HATSOPOULOS, N. G., & KALISH, M. L. (1991). On the sufficiency of the velocity field for perception of heading. *Biological Cybernetics*, **65**, 311-320.
- WARREN, W. H., & HANNON, D. J. (1988). Direction of self-motion is perceived from optical flow. *Nature*, **336**, 162-163.
- WARREN, W. H., & HANNON, D. J. (1990). Eye movements and optical flow. *Journal of the Optical Society of America A*, **7**, 160-169.
- WARREN, W. H., & KURTZ, K. J. (1992). The role of central and peripheral vision in perceiving the direction of self-motion. *Perception & Psychophysics*, **51**, 443-454.
- WARREN, W. H., & SAUNDERS, J. A. (1994). Perceiving heading in the presence of moving objects. *Investigative Ophthalmology & Visual Science*, **35** (Suppl.), 1999.
- WARREN, W. H., & SAUNDERS, J. A. (1995a). Perceived heading depends on the direction of local object motion. *Investigative Ophthalmology & Visual Science*, **36** (Suppl.), 829.
- WARREN, W. H., & SAUNDERS, J. A. (1995b). Perceiving heading in the presence of moving objects. *Perception*, **24**, 315-331.
- ZHANG, Z., FAUGERAS, O. D., & AYACHE, N. (1988). Analysis of a sequence of stereo scenes containing multiple moving objects using rigidity constraints. In *Second International Conference on Computer Vision* (pp. 177-186). Washington, DC: IEEE Computer Society Press.

(Manuscript received June 20, 1995;
revision accepted for publication December 4, 1995.)