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Long range interactions between object-motion and self-motion in the perception of movement in depth

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Abstract

Self-motion through a three-dimensional array of objects creates a radial flow pattern on the retina. We superimposed a simulated object moving in depth on such a flow pattern to investigate the effect of the flow pattern on judgments of both the time to collision (TTC) with an approaching object and the trajectory of that object. Our procedure allowed us to decouple the direction and speed of simulated self motion-in-depth (MID) from the direction and speed of simulated object MID. In Experiment 1 we found that objects with the same closing speed were perceived to have a higher closing speed when self-motion and object-motion were in the same direction and a lower closing speed when they were in the opposite direction. This effect saturated rapidly as the ratio between the speeds of self-motion and object-motion was increased. In Experiment 2 we found that the perceived direction of object-MID was shifted towards the focus of expansion of the flow pattern. In Experiments 3 and 4 we found that the erroneous biases in perceived speed and direction produced by simulated self-motion were significantly reduced when binocular information about MID was added. These findings suggest that the large body of research that has studied motion perception using stationary observers has limited applicability to situations in which both the observer and the object are moving.

1. Introduction

It is well known that humans are exquisitely sensitive to visual information about an approaching object's direction of motion-in-depth (MID) and its time to collision (TTC). The just-noticeable difference in the direction of MID can be as low as 0.1°–0.2° for an object approaching an observer's nose (Beverley & Regan, 1975; Portfors-Yeomans & Regan, 1997; Regan & Kaushal, 1994). For judgments of TTC, discrimination thresholds as low as 6–12% (Regan & Hamstra, 1993) and estimation errors for absolute TTC as low as 1.3% (Gray & Regan, 1998) [1] have been reported. Our ability to estimate TTC and the direction of MID is important in everyday life where we are often required to avoid or intercept an approaching object (e.g., when driving, hitting or catching).

What sources of visual information support this remarkable sensitivity? Lee (1976) proposed that human observers estimate TTC for a rigid spherical object directly approaching the eye at a constant speed on the basis of the following equation derived by Hoyle (1957)

$$\mathrm{TTC} \approx \theta/(\mathrm{d}\theta/\mathrm{d}t) \qquad (1)$$

where θ is the approaching object's instantaneous angular subtense, and θ is small. Some of the early research based on Lee's proposal has been severely criticized by Wann (1996). For example, in many early studies the participants viewed the approaching object with both eyes, and it has recently been shown theoretically that binocular information about TTC is available. In particular

$$\mathrm{TTC} \approx I/D(\mathrm{d}\delta/\mathrm{d}t) \qquad (2)$$

for an object directly approaching an observer's head, where I is the interpupillary separation, D is the object's

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[1] For the TTC values of 0.4–0.6 s associated with professional baseball a 1.3% estimation error corresponds to a temporal error of 5.2–7.8 ms which is well within the ±9 ms margin for error (Watts & Bahill, 1991) and is close to the 2–2.5 ms accuracy that can be required in cricket (Regan, Beverley, & Cynader, 1979).

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distance, $\mathrm{d}\delta/\mathrm{d}t$ is the rate of change of relative disparity, and $D \gg I$ (Regan, 1995). In addition

$$\mathrm{TTC} \approx 2(\mathrm{d}\delta/\mathrm{d}t)/(\mathrm{d}^2\delta/\mathrm{d}t^2) \quad (3)$$

Regan (2002), an equation that does not involve distance. Furthermore, it has recently been shown empirically that normally-sighted observers are able to use binocular information about TTC either by itself or in combination with the information expressed in Eq. (1) (Gray & Regan, 1998). However, the question of how information about TTC are combined for different perceptual-motor tasks is still incompletely understood.

As to the direction of an approaching object, again both monocular and binocular visual correlates are available. One monocular correlate of the direction of motion of an approaching rigid sphere is expressed in Eq. (4) (Bootsma, 1991; Regan, 1986; Regan & Beverley, 1980; Regan & Kaushal, 1994)

$$ns \approx 2(\mathrm{d}\phi/\mathrm{d}t)/(\mathrm{d}\theta/\mathrm{d}t) \quad (4)$$

where ns is the distance by which the centre of the sphere will miss the centre of the eye, s is the radius of the sphere, $\mathrm{d}\phi/\mathrm{d}t$ is the angular velocity and $\mathrm{d}\theta/\mathrm{d}t$ the rate of expansion of the sphere's retinal image. [2] Turning to binocular information, the ratio between the angular velocities of the approaching object's images in the two eyes is a correlate of the direction of MID, though only for motion within the plane containing the object and the two eyes (Beverley & Regan, 1973). Eq. (5), however, expresses a binocular correlate for motion within any meridian

$$\beta \approx \tan^{-1}[I(\mathrm{d}\alpha/\mathrm{d}t)/D(\mathrm{d}\delta/\mathrm{d}t)] \quad (5)$$

where β is the direction of motion relative to a line from the approaching object to a point midway between the eyes, D is the viewing distance, I is the interpupillary separation, $\mathrm{d}\alpha/\mathrm{d}t$ is the angular velocity of the object's binocularly-fused image, $\mathrm{d}\delta/\mathrm{d}t$ is the rate of change of relative disparity, $D \gg I$, and the object is straight ahead (Regan, 1993). Eq. (5) can be rewritten in the form

$$L \approx I(\mathrm{d}\alpha/\mathrm{d}t)/(\mathrm{d}\delta/\mathrm{d}t) \quad (6)$$

where L is the distance between a point midway between the eyes, and the location of the approaching object at the instant it passes the head (Regan et al., 1995).

Previous research on the perception of MID has been mostly restricted to the case of stationary observer and moving object (reviewed in Regan & Gray, 2000). Because Eqs. (1)–(6) are equally valid for the case of stationary observer/moving object, moving observer/stationary object, or any combination of the two, on the face of it one would not expect self-motion to affect either judgments of TTC or judgments of the direction of an approaching object's MID. Therefore, it might seem safe to assume that the results of laboratory experiments performed with a stationary observer would be valid in the everyday situation that a moving observer must judge an approaching object's direction of MID and its TTC. This, however, seems not to be the case.

When an observer moves forward through a three-dimensional visual environment a radially-expanding flow pattern is created on the retina, In a recent experiment the observer was stationary but the presence of the radial flow pattern created an illusion of self-motion (Gray & Regan, 2000b). We found that this radial flow pattern substantially altered TTC estimates based on monocular information alone (i.e., Eq. (1)) for a foveated approaching object. In particular, simulated forward self-motion shortened the perceived TTC by 10–13% and simulated backward self-motion lengthened perceived TTC by 17–23%. The key feature of this study was that our procedure allowed us to decouple simulated object-motion from simulated self-motion, i.e., that the peripheral flow field did not affect the value of $\theta/(\mathrm{d}\theta/\mathrm{d}t)$ for the approaching object.

The purpose of the study reported here was to further examine the interaction between simulated self-motion and the perceived speed and direction of motion of simulated object moving in depth. This was achieved by superimposing a simulated approaching object on a large-angle radial flow field. As was the case in our earlier study, the flow field and simulated approaching object were controlled independently. In Experiment 1, we investigated the interaction between the speed of simulated self-motion and the perceived speed of object-MID. In Experiment 2, we examined the interaction between the direction of self-motion and the perceived direction of object-MID. In Experiments 3 and 4, we investigated whether the addition of binocular information about the motion of the approaching object altered these interactions.

2. Experiment 1

2.1. Purpose and rationale

In a preliminary experiment we asked which optic variable(s) are used to estimate the speed of MID for a receding object. In the main experiment, we examined the effect of a radial flow pattern (i.e., simulated self-motion) on speed discrimination. To expand on our previous TTC study, in the present experiment we simulated (i) approaching and receding objects combined with simulated forward and backwards self-motion and (ii) interleaved different ratios of object-motion speed to self-motion speed. In Experiment 1, only monocular information about motion in depth was available, as was the case in our previous study (Gray & Regan, 2000b).

[2] Regan and Kaushal (1994) erroneously omitted the factor 2.

2.2. Methods

2.2.1. Apparatus

We simulated constant velocity self-motion in a straight line through a cloud of randomly-positioned stationary objects (i.e., radial optic flow). A flow pattern consisting of 80 small white squares was back-projected (Mitsubishi model #LVP-X7OU) onto a large (65° horizontal × 88° vertical) screen. The viewing distance was 1 m. To simulate forward self-motion, the flow elements increased speed and grew larger as they moved radially outward from the focus. [3] The backward (contracting) flow pattern was the reverse. A constant object density was maintained by replacing each object as it disappeared from view. The speed of simulated self-motion was varied as described below. Results obtained with these two types of simulated self-motion were compared with those obtained using a "static" condition in which all flow elements remained stationary and constant size. Displays were updated at a frame rate of 60 Hz.

A target square was presented at the center of the flow pattern. The square was purple and was easily distinguishable from the flow elements. A sensation of approaching (or receding) object-MID was created by increasing (or decreasing) the size of this object square according to the equation that relates object subtense to time (Regan & Hamstra, 1993). As shown in Fig. 1, no flow elements were presented in a central square region of the display. The side length of this square hole was varied as described below.

In the preliminary experiment the reference target on all trials simulated an approaching object with a value of $(\mathrm{d}\theta/\mathrm{d}t)/\theta$ equal to 0.54 s^{-1}. The test was receding on all trials and had a speed of MID that was chosen randomly from one of eight values of $(\mathrm{d}\theta/\mathrm{d}t)/\theta$: −0.43, −0.47, −0.5, −0.52, −0.55, −0.59, −0.63, −0.73 s^{-1}. The starting size of the target was varied as described for Experiment 1. The flow field was static for both the test and reference targets.

2.2.2. Procedure

Psychometric functions for discriminating trial-to-trial variations in the speed of object-MID were measured using the method of constant stimuli combined with two-interval forced choice. We first describe the procedure for simulated approaching objects. Each trial consisted of two presentations of a simulated approaching object: a "reference presentation" and a "test presentation". It has been proposed that the perceived closing speed of MID for approaching objects is inversely proportional to the object's TTC (Regan & Hamstra, 1993). Therefore we expressed the speed of object-MID in terms of the value of $(\mathrm{d}\theta/\mathrm{d}t)/\theta$. [4] In the "reference presentation" the flow elements remained stationary and the perceived speed of object-MID [expressed as the value of $(\mathrm{d}\theta/\mathrm{d}t)/\theta$] was proportional to the mean of the stimulus set (0.54 s^{-1}). In the "test presentation", either forward or backward self-motion was simulated and the speed of object-MID was chosen randomly from one of eight values (0.43, 0.47, 0.5, 0.52, 0.55, 0.59, 0.63, 0.73 s^{-1}). During this presentation the perceived speed of simulated self-motion (i.e., the rate of radial flow) depended on the ratio between self-motion and object-motion. [5] Eight ratios (0.5, 1.0, 1.5, 2.0, −0.5,

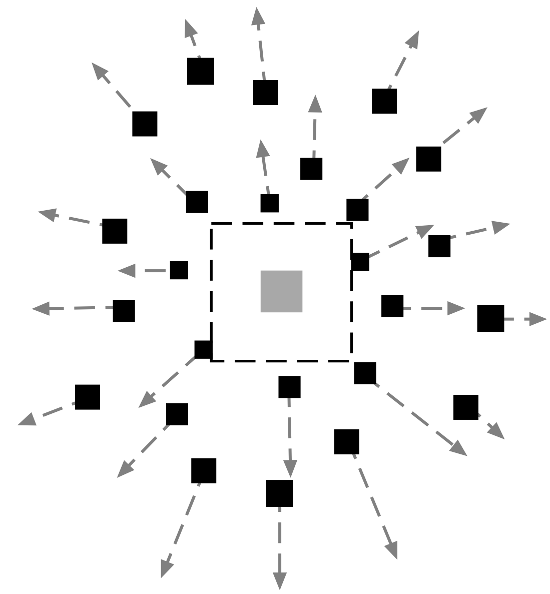


Fig. 1. Stimulus arrangement for Experiment 1. A simulated approaching square object was presented at the center of the radial flow pattern that was used to simulate either forwards of backwards self-motion. No flow elements were presented in a central square region of the display shown by the dashed box (this line was not visible in the actual display). The flow field and simulated approaching object were controlled independently so that different ratios of object-motion-in-depth to self-motion-in-depth could be presented. See text for details.

[3] We found previously that the effect of a flow field on estimates of TTC was considerably less when the flow elements remained constant in size as they moved outwards (Gray & Regan, 2000b).

[4] According to dimensional theory, the dimensions of both sides of an equation must match (Szirtes, 1998). Since speed has the dimensionality (length/time) and $(\mathrm{d}\theta/\mathrm{d}t)/\theta$ has the dimensionality (time^{-1}), the constant of proportionality must have the dimensionality (length).

[5] The ratio between the speed of object-MID and the speed of self-MID was equal to

$$K\frac{(\mathrm{d}\theta/\mathrm{d}t)_{t=0}}{\mathrm{d}\alpha/\mathrm{d}t}$$

where $(\mathrm{d}\theta/\mathrm{d}t)_{t=0}$ was the object's rate of expansion at time $t = 0$ and $\mathrm{d}\alpha/\mathrm{d}t$ was the angular velocity of the flow pattern (measured from the focus of expansion) and K was a constant. See Fig. 1. In the everyday world, constant K would depend on the distances of the various external objects represented by the individual squares in the flow pattern. However, since we studied the effect of different scaling factors, each of which was applied to the local velocity over the entire flow pattern, the value of K is irrelevant to our conclusions and for convenience we set it at unity.

−1.0, −1.5 and −2.0) were used and the value was varied randomly from trial-to-trial. Negative ratios indicate conditions where the direction of object-MID and self-MID were opposite. The observer's task was to indicate, by pressing one of two response keys, in which presentation the *object* was moving faster. The order of the two presentations was chosen randomly and the duration of each presentation was 450 ms.

In order to determine whether observers based their responses on the task-relevant variable $[(d\theta/dt)/\theta]$ as opposed to any of the task-irrelevant variables (e.g., the rate of expansion $d\theta/dt$), [6] the values of initial $(d\theta/dt)/\theta$ and $d\theta/dt$ were varied orthogonally in an 8×8 stimulus array by varying the starting size (i.e., at time $t = 0$) of the simulated approaching square. (See, Regan and Hamstra (1993) for a further description of this procedure.) The starting size ranged between 0.4° and 1.2° for the approaching target. The threefold range of starting sizes was used because we have found in previous research that an adequate variation to sufficiently decorrelate $(d\theta/dt)/\theta$ and $d\theta/dt$ (Gray & Regan, 1998; Regan & Hamstra, 1993). The starting size for the target and reference were both chosen randomly on each trial.

A similar procedure was used to measure speed discrimination performance for receding targets. Previous research has not clearly identified the optical variables used to estimate perceived speed for receding objects. Described below is a formal test of whether it is also determined by the value of $(d\theta/dt)/\theta$. For receding targets, "the reference presentation" consisted of a static flow pattern and an object-MID speed of −0.54 (the mean of the stimulus set). In the "test presentation", either forward or backward self-motion was again simulated and the speed of object-MID was chosen randomly from one of eight values (−0.43, −0.47, −0.5, −0.52, −0.55, −0.59, −0.63, −0.73). We randomly interleaved the same eight self-MID speed/object-MID speed ratios as described for the approaching object. The starting size ranged from 1.5° to 4.5° for the receding target.

Each run consisted of 512 trials comprised of 64 moving objects × 4 self-motion/object-motion ratios × 2 directions of self-motion (forward and backwards). Psychometric functions for receding and approaching object-MID were measured on separate runs. Across runs we also varied the side length of the square hole with no flow elements (see Fig. 1). Five side lengths were used (9°, 11°, 13°, 18° and 26°) and the order was counterbalanced.

[6] In a separate control experiment we varied the presentation duration between 450 and 900 ms to remove the total change in size $\Delta\theta$ as a reliable cue to the speed discrimination task. The results from this control experiment we similar to those in Experiment 1.

2.2.3. Participants

Five observers completed Experiment 1. Observers 1 and 2 were authors R.G. and K.M., respectively. Observers 3–5 were naive as to the aims of the study and completed the experiments for partial course credit.

2.3. Results

2.3.1. Which optic variables determine perceived speed for receding motion?

Variable $(d\theta/dt)/\theta$ explained the most response variance (R^2 ranged from 0.69 to 0.88). The rate of size change explained a small (but significant) amount of additional variance for two of the observers (additional R^2 ranged from 0.05 to 0.11). We conclude that perceived speed for receding MID is predominantly determined by the variable $(d\theta/dt)/\theta$.

2.3.2. Effect of the direction of self-motion on the perceived speed of object-motion-in-depth

Fig. 2A and B shows, respectively, the psychometric functions for approaching and receding objects for observer 1. These particular functions are for a hole-size of 9° and self-motion/object-motion speed ratios of either 1.0 or −1.0 (see figure legends). Figures show experimental data to which psychometrical functions were fitted by using probit analysis. (Finney, 1971). It is clear that the direction of simulated self-motion had a substantial effect on the perceived speed of object-MID. Even though the peripheral flow field did not alter the value of $(d\theta/dt)/\theta$ for the moving object, objects moving in depth were perceived to be moving faster (i.e., there was greater percentage of "test faster" responses) relative to the reference target when the direction of object-motion was the same as the direction of self-motion and were perceived to be moving more slowly (i.e., lower percentage of "test faster" responses) relative to the reference target when the direction of self-motion and object-motion were opposite.

To quantify these effects we calculated the point of subjective equality (i.e., the 50% point) for the psychometric functions. Fig. 3A and B shows the points of subjective equality (PSE) for approaching and receding objects for the five observers. For all observers, objects were perceived to be moving faster (lower PSE) when the direction of object-motion was the same as the direction of self-motion (a ratio of 1.0 in Fig. 3) and were perceived to be moving more slowly (higher PSE) when the direction of self-motion and object-motion were opposite (a ratio of −1.0 in Fig. 3). Paired *t*-tests revealed the PSE was significantly smaller for simulated forwards self-motion than backwards self-motion when the object was approaching [$t(4) = 8.2$, $p < 0.001$] and that the PSE was significantly larger for simulated forwards self-motion than backwards self-motion when the

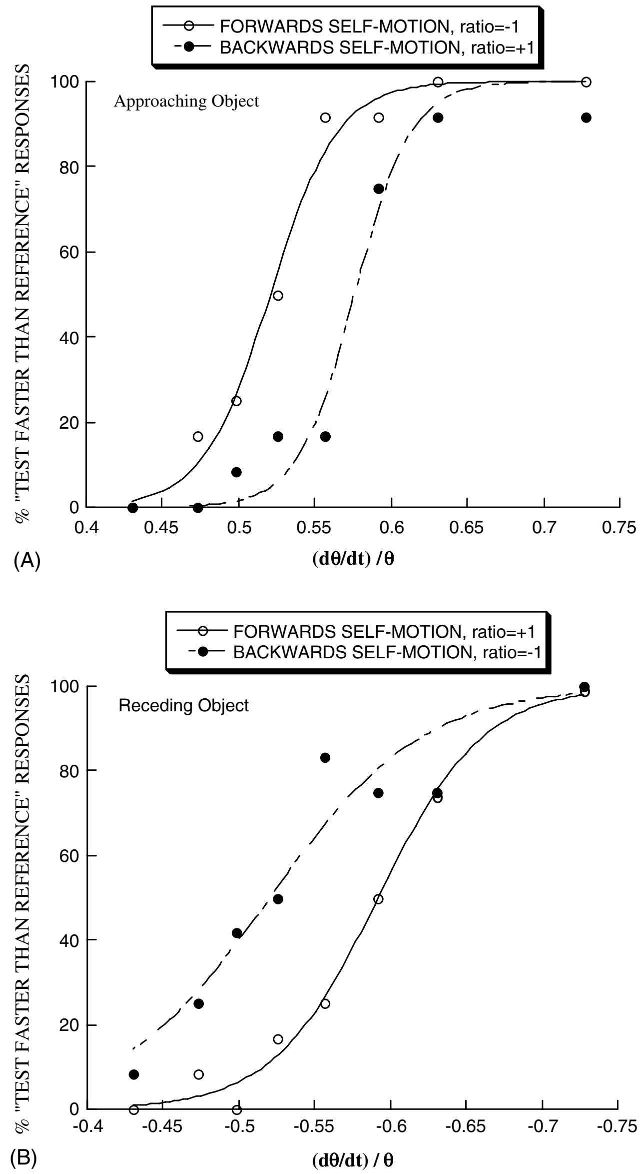


Fig. 2. Psychometric functions for discrimination of perceived object motion-in-depth speed for observer 1. These particular functions are for a hole-size of 9° and a self-motion/object-motion speed ratio of 1.0: (A) approaching object motion-in-depth and (B) receding object motion-in-depth. The lines are probit analysis curve fits.

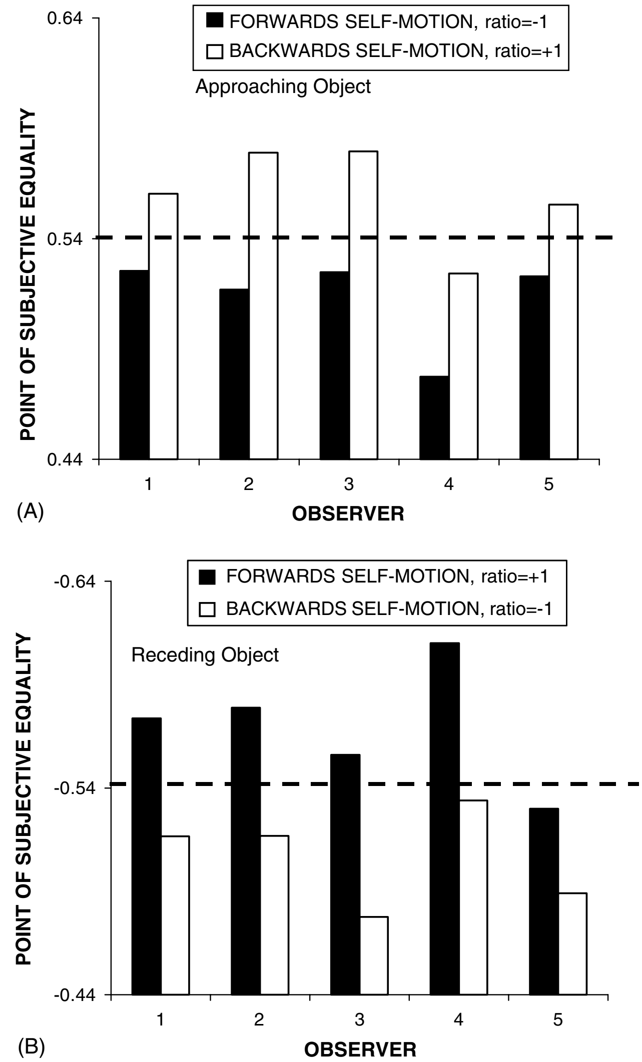


Fig. 3. The points of subjective equality (i.e., the 50% point on the psychometric functions) for discrimination of the perceived speed of object motion-in-depth H: (A) approaching object and (B) receding object. The speed of the reference target is indicated by the bold dashed lines.

object was receding [$t(4) = 9.2$, $p < 0.001$]. Further statistical analyses of these effects are described below.

From Fig. 3 it can be seen that for some conditions the shifts in perceived speed were roughly symmetrical about the speed of the reference target. However some observers did show large overall biases in speed perception. In particular, observer 4 in Fig. 3A and observer 5 in Fig. 3B showed a tendency to perceive all test targets as moving faster than the mean. Overall paired t-tests revealed no significant differences between the mean PSE (i.e., averaged over both directions of self-motion) and the speed of the reference target: Fig. 3A: $t(4) = -0.4$, $p > 0.5$; Fig. 3B: $t(4) = 0.2$, $p > 0.5$. Biases in speed perception are discussed in further detail below.

Speed discrimination thresholds were similar for all combinations of object-motion and self-motion. Discrimination thresholds were defined as $0.5 * (S_{75} - S_{25})$ where S_{75} and S_{25} were, respectively, the object-MID speeds for 75% and 25% "test target faster than the reference" responses. For the approaching target, thresholds ranged between 4% and 28% for forwards self-motion and the mean threshold was 12% (SE = 3%). For backwards self-motion, thresholds ranged between 9% and 25% and the mean threshold was 15% (SE = 3%). The difference between means was not statistically significant [$t(4) = 0.6$, $p > 0.5$]. For the receding targets, thresholds ranged between 6% and 21% for forwards self-motion and the mean threshold for forwards self-motion was 14% (SE = 3%). For backwards self-motion, thresholds ranged between and 6% and 27% and the mean threshold was 14% (SE = 4%). The difference between means was not statistically significant [$t(4) = 0.3$, $p > 0.5$].

2.3.3. *Effect of the self-motion/object-motion speed ratio on the perceived speed of object-motion-in-depth*

Fig. 4A shows the PSE for the eight different self-motion/object-motion speed ratios for observer 1. These data are for the approaching object. Increasing this ratio appeared to have two main qualitative effects on the perceived speed of object-MID: (i) there was an increase in perceived speed for both directions of self-motion, and (ii) the absolute difference between PSEs for the two directions of self-motion decreased until the effect reversed for the highest ratios. Similar patterns of data were obtained for the other four observers.

Quantitative analyses were consistent with these informal observations. We first performed a 2×4 repeated measures ANOVA with self-motion direction and ratio as conditions. This analysis revealed significant main effects of ratio [$F(3,12) = 23.8$, $p < 0.001$] and of self-motion direction [$F(1,4) = 50.6$, $p < 0.001$]. Post hoc trend analysis revealed a significant linear trend [$F(1,12) = 138$, $p < 0.001$] for ratio. Finally, a paired *t*-test revealed that the difference between the PSE for forwards self-motion and backwards self-motion was significantly greater for the ratio of 1.0 than it was for the ratio of 2.0 [$t(4) = 6.1$, $p < 0.001$].

The self-motion/object-motion speed ratio did not affect speed discrimination thresholds for the approaching target. A 2×4 repeated measures ANOVA performed on thresholds revealed non-significant main effects of ratio [$F(3,12) = 0.51$, $p > 0.5$] and self-motion direction [$F(1,4) = 5.1$, $p > 0.1$]. The ratio×direction interaction was also not statistically significant [$F(3,12) = 4.0$, $p > 0.05$].

Fig. 4B shows the PSE for the eight different self-motion/object-motion speed ratios for observer 1. These data are for the receding object. Varying the ratio produced the same effects as those described for the approaching target, i.e., an overall increase in perceived speed and a decrease in the effect of motion direction. The quantitative analyses were again consistent with the informal observations: significant main effects of ratio [$F(3,12) = 30.1$, $p < 0.001$] and of self-motion direction [$F(1,4) = 44.2$, $p < 0.001$].

As was the case for the approaching target, the self-motion/object-motion speed ratio did not affect the speed discrimination thresholds for the receding target. Significant results of the ANOVA were: ratio [$F(3,12) = 19.5, p > 0.001$] and direction [$F(1,4) = 33.2, p > 0.001$].

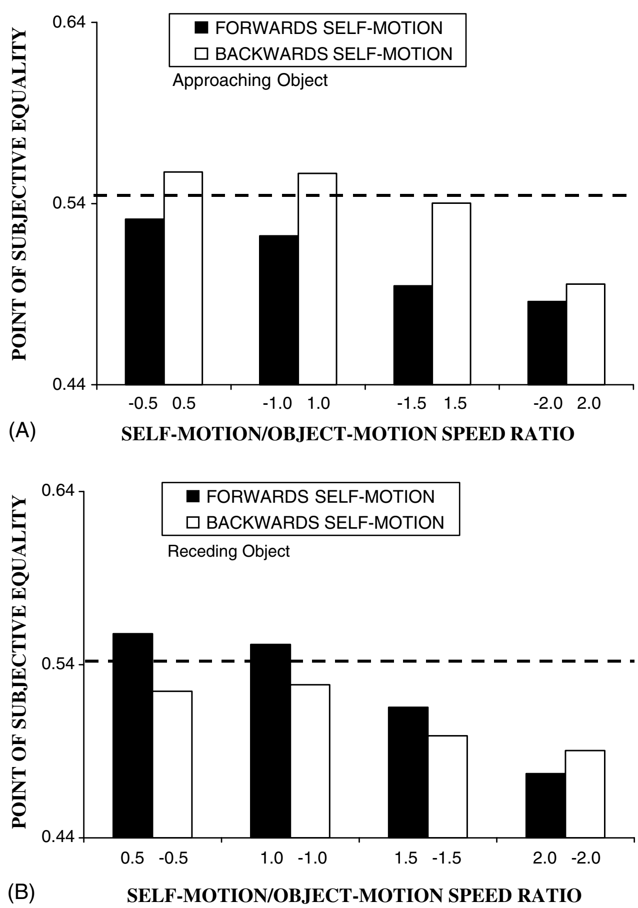


Fig. 4. The points of subjective equality for the four different self-motion/object-motion speed ratios for observer 1: (A) approaching object; (B) receding object. The speed of the reference target is indicated by the bold dashed lines.

2.3.4. *Effect of the central hole size on the perceived speed of object-motion-in-depth*

Fig. 5A shows the PSE for the five different central hole-sizes for observer 1. These data are for the approaching object. Increasing the size of the central hole appeared to reduce the effect of self-motion direction on the PSEs without causing any overall bias in perceived speed. Hole size data for the five observers were analyzed using a 5×2 repeated measures ANOVA with hole size and self-motion direction as factors. This analysis revealed a significant main effect of direction [$F(1,4) = 15.4$, $p < 0.05$] and a significant direction×hole size interaction [$F(4,16) = 6.2$, $p < 0.01$]. The main effect of hole-size was not significant. Post hoc interaction contrasts (Keppel, 1991) revealed that the effect of direction was significantly greater at hole size 9° than it was at a hole size 26° [$F(1,16) = 4.6$, $p < 0.05$]. There was no significant difference between the effect of direction for the 9° and 18° hole sizes [$F(1,16) = 2.3$, $p > 0.05$].

Similar results were obtained for receding objects. Fig. 5B shows the PSEs for the five different central hole-sizes for observer 1. Significant results of the

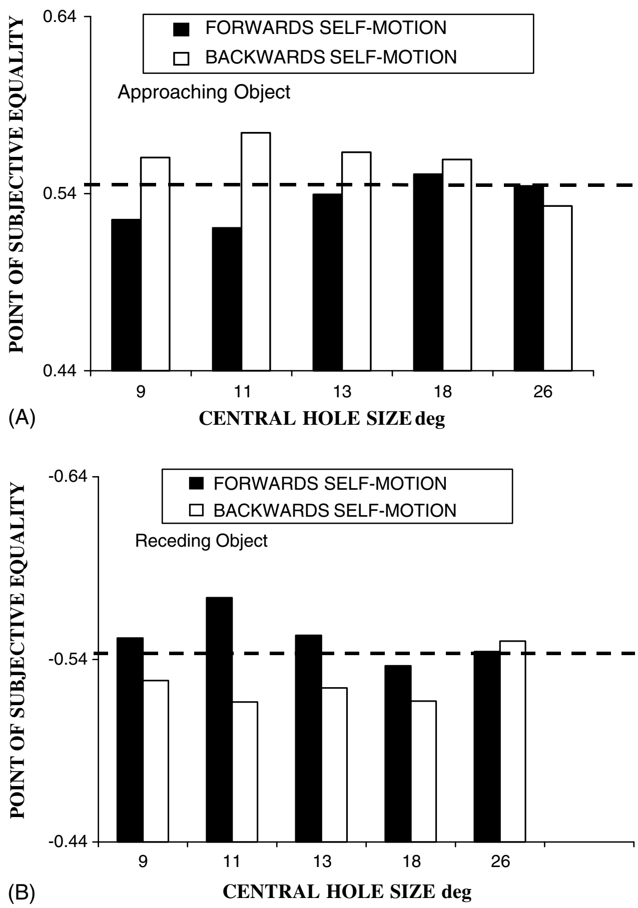


Fig. 5. The points of subjective equality (PSE) for the five different central hole-sizes for observer 1: (A) approaching object and (B) receding object. The speed of the reference target is indicated by the bold dashed lines.

ANOVA were as follow: significant main effect of direction [$F(1,4) = 10.3$, $p < 0.05$]; significant direction×hole-size interaction [$F(4,16) = 5.3$, $p < 0.05$]; significant interaction contrast between hole sizes of 9° and 26° [$F(1,16) = 5.2$, $p < 0.05$]. There was no significant difference between hole sizes of 9° and 18° [$F(1,16) = 0.2$, $p > 0.05$].

The central hole size did not affect the speed discrimination thresholds for either the approaching or receding target. A 5×2 repeated measures ANOVA with hole size and self-motion direction as factors revealed no significant effects.

2.3.5. Stepwise regression analyses

To determine whether observers based their responses on the task-relevant variable we submitted the data to a forward stepwise regression analysis. For all five observers the task-relevant variable $(d\theta/dt)/\theta$ accounted for a high proportion of total variance (R^2 ranged from 0.7 to 0.94) across conditions.

2.4. Discussion

The direction of simulated self-motion had a substantial effect on the perceived speed of object-MID. When the perceived speed of object-MID and self-motion was equal, simulated forward self-motion increased the perceived speed of object-MID by 5–12% and simulated backward self-motion decreased perceived speed by 3–10%. Qualitatively these effects are similar to results we reported for judgments of TTC (Gray & Regan, 2000b), however the effect of backwards self-motion on perceived speed (6% shift on average) in the present study was considerably smaller than the effect we reported previously (19% average shift). One likely explanation for this difference is that in our previous experiment we used a constant speed of self-motion and varied the TTC of the approaching object according to a staircase tracking procedure, so that the ratio between the speed of self-motion and the object's TTC varied randomly from trial-to-trial. As discussed next, this ratio appears to have a large influence on the interaction between self-motion and object-motion.

Increasing the ratio between the speed of simulated self-motion and the speed of object-motion resulted in a qualitatively different type of interaction between the two types of motion. The substantial effect of the direction of self-MID that was observed for small ratios saturated at larger ratios. The simulated self-motion created an increase in perceived speed for *all* combinations of the direction of self-MID and the direction of object-MID. This resulted in a complete reversal of the effect for backwards self-motion in Fig. 3A and for forwards self-motion in Fig. 3B. It should be emphasized that this dramatic change in overall speed perception occurred even though speed discrimination thresholds were unchanged and observers continued to base their responses on the task-relevant variable. Thus the effect of ratio we observed cannot be explained by a change in the strategy used to perform the task (e.g., basing the speed judgment on the rate of optic flow).

The effect of the direction of self-MID on the perceived speed of object MID (for a ratio of 1.0) extended over a large distance relative to the 1.5°–2.0° receptive field diameter of a changing-size detectors (Regan & Beverley, 1979). A significant effect was observed even when we introduced an 8° gap (i.e., 18° hole size) between the outer edge of the object and the inner edge of the peripheral flow pattern.

In the main experiment, our observers based their responses on the optical variable $(d\theta/dt)/\theta$ for all stimulus conditions. This finding is important for two reasons. First, it is strong support for the proposal that the perceived speed of object-MID is inversely proportional to the object's TTC (Regan & Hamstra, 1993). Second, it further supports our proposal that the interaction between simulated self-MID and object-MID

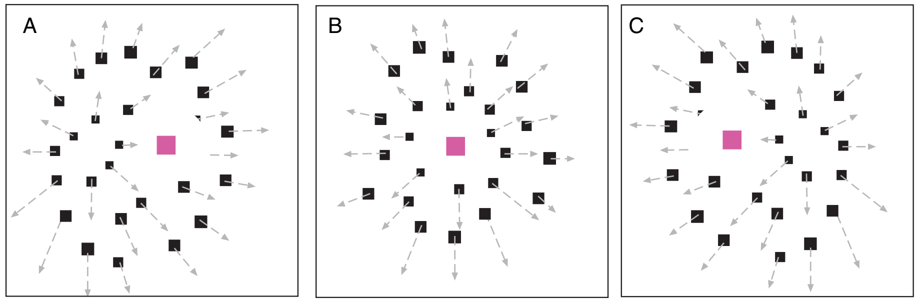


Fig. 6. Stimulus arrangement for Experiment 2. The location of the focus of expansion (FOE) was varied to simulate different directions of forwards self-motion. Three different FOE locations were used: (A) 7° left of the center of the display (−7°); (B) center of the display (0°) and (C) 7° right of the center of the display (+7°). Observers discriminated the direction of motion-in-depth for the square object superimposed at the center of the flow field.

occurs at the stage when the MID signal is generated rather than at the stage where changing image size is processed (Gray & Regan, 2000b). If this interaction occurred at the level of changing-size detectors we might expect the simulated self-motion to alter the effective value of $d\theta/dt$ for the approaching object, and that would have been evidenced by observers' placing more weight on this particular variable.

3. Experiment 2

3.1. Purpose and rationale

In Experiment 1, we found substantial interactions between the speed of simulated self-motion (i.e., the radial flow pattern) and the perceived speed of object-motion. In Experiment 2, we asked whether there are interactions for perceived judgments of direction? Previous research has focused on the influence of object motion on judgments of the direction of self-motion i.e., heading (Royden & Hildreth, 1996; Warren & Saunders, 1995), but the converse relationship has not previously been explored. In Experiment 2, we measured the discrimination of the direction of object-MID as a function of the direction of simulated self-motion.

3.2. Methods

3.2.1. Apparatus

The apparatus was as described in Experiment 1, except for the following. The location of the focus of expansion (FOE) of the flow pattern was varied from trial to trial to simulate different directions of self-motion. As shown in Fig. 6, there were three different FOE locations: (a) 7° left of the center of the display (−7°), (b) center of the display (0°) and (c) 7° right of the center of the display (+7°). Only the forward self-motion and static conditions were used in Experiment 2. The radial velocity of the flow pattern for the forward condition was varied randomly between 5°/s and 10°/s. As was the case in Experiment 1, no flow elements were presented in a central square region of the display so that the simulated object never overlapped the flow elements. *Therefore, the flow field did not alter the ratio between the rate of expansion of the approaching object and its angular speed within a frontoparallel plane, i.e., its direction of MID, see Eq. (4).*

3.2.2. Procedure

Psychometric functions for discrimination of the direction of the object's motion were measured using the method of constant stimuli combined with two interval forced choice. Each trial consisted of two intervals, in each of which an approaching object was simulated. In the reference interval, the flow elements remained stationary [7] and the direction of object-MID was the mean of the stimulus set (12.1° leftward of the midline). In the test interval, forward self-motion was simulated and the location of the FOE was chosen randomly from the three locations shown above. For this interval the object-MID direction was chosen randomly from one of eight values (0.6°, 4°, 8.5°, 11.3°, 14°, 16.7°, 17.7° and 23.7° leftward of the midline). The order of the two intervals was chosen randomly and the duration of each interval was 500 ms. The observer's task was to signal in which interval the simulated approaching object appeared to be moving more leftward by pressing one of two response keys.

In order to check that observers based their responses on the direction of the approaching object rather than task-irrelevant variables such as frontal-plane speed or the rate of expansion, we used the triple dissociation technique developed by Portfors-Yeomans and Regan (1997). In this technique, stimuli are divided into an

[7] In all reference intervals the layout of the flow elements was identical to the initial position of the elements for the corresponding test interval for that trial. So, for example, when the test interval had an FOE of −7° the reference flow pattern would be as shown in Fig. 6A and when the test interval had an FOE of +7° the reference flow pattern would be as shown in Fig. 6C.

array where the MID direction is varied along one axis of the array and frontal plane speed is varied along the other axis of the array. The rate of expansion is varied in the same way along both axes of the array (see Fig. 3 in (Portfors-Yeomans & Regan, 1997) for further details). In the present study each run consisted of 192 trials comprised of 64 approaching objects (8×8 array)×3 directions of self-motion (i.e., FOE locations). Across runs we also varied the side length of the square hole with no flow elements using the five values used in Experiment 1. We also collected data for a condition where the flow elements remained static for both the test and reference presentations.

3.2.3. Participants

Four observers completed Experiment 2. Observers 1 and 2 were authors R.G. and K.M., respectively. Observers 6 and 7, who were naïve to the aims of the study, completed the experiments for partial course credit.

3.3. Results

3.3.1. Effect of the direction of self-motion on the perceived direction of object-Motion-in-depth

Fig. 7 plots psychometric functions for the smallest central hole size (9°) for observer 1. The solid arrow indicates the direction of object-MID for the reference interval (i.e., the mean of the stimulus set). It is clear from Fig. 7 that the location of the FOE had a systematic effect on the perceived direction of object-MID. For simulated self-motion with a heading 7° to the left of the midline (i.e., Fig. 6A), this observer perceived the object's trajectory to be shifted roughly 3° leftward. Conversely, for simulated self-motion with a heading 7° to the right of the midline (i.e., Fig. 6B), this observer

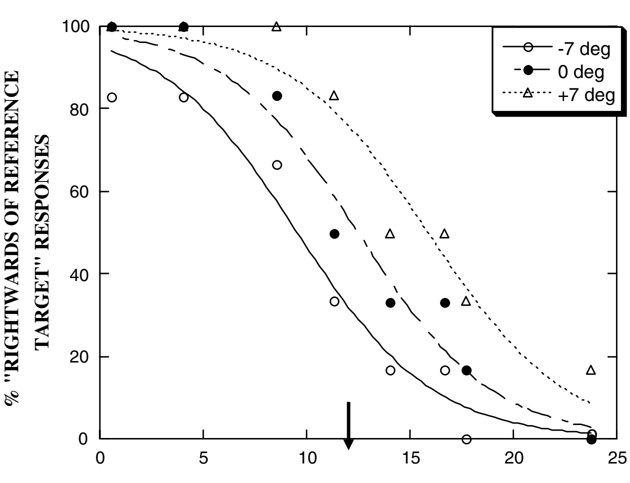


Fig. 7. Psychometric functions for discrimination of the direction of object-motion-in-depth during simulated forwards self-motion. The solid arrow indicates the direction of object-motion-in-depth for the reference interval. The lines are probit analysis curve fits (observer 1).

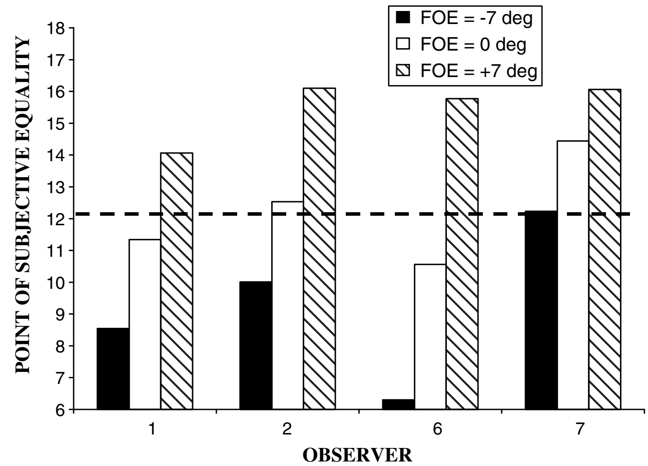


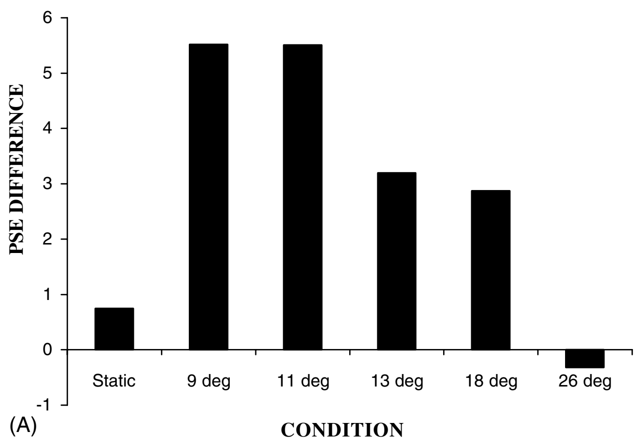
Fig. 8. The points of subjective equality for discrimination of the direction of object-motion-in-depth for the three different FOE locations. The direction of motion of the reference target is indicated by the bold dashed line.

perceived the object's trajectory to be shifted roughly 3° rightward. Similar results were obtained for the other three observers. Fig. 8 plots the PSEs for the three FOE locations for all four observers. Paired t-tests revealed significant differences between PSE (−7°) vs. PSE (0°) [$t(3) = 8.4$, $p < 0.001$] and between PSE (+7°) vs. PSE (0°) [$t(3) = 5.6$, $p < 0.001$]. The effect of self-motion direction on discrimination thresholds is described below.

3.3.2. Effect of the central hole-size on the perceived direction of object-motion-in-depth

Fig. 9A plots the difference between the PSE for the −7° FOE location and the PSE for the +7° FOE location for the five central hole sizes. Data are again for observer 1. The "Static" data show the PSE difference for the condition in which the flow elements were static for both the test and reference intervals. The effect of simulated self-motion on the perceived direction of object-MID decreased as the size of the central hole in the flow pattern was increased. Data were similar for the other three observers. To analyze the effect of hole size we performed a 3×5 repeated measures ANOVA with FOE location and hole size as factors. There was a significant main effect of FOE location [$F(2,6) = 6.5$, $p < 0.05$] and a significant FOE location×hole size interaction [$F(8,24) = 4.1$, $p < 0.01$]. Post hoc interaction contrasts (Keppel, 1991) revealed that the effect of direction was significantly greater at hole size 9° than it was at a hole size 26° [$F(1,24) = 5.8$, $p < 0.05$]. There was no significant difference between the effect of direction for the 9° and 18° hole sizes [$F(1,24) = 0.3$, $p > 0.5$].

A second effect can be seen in Fig. 9B. This figure plots the PSE values for the FOE of 0° (i.e., self-motion straight ahead) for the four observers. The "Static" data



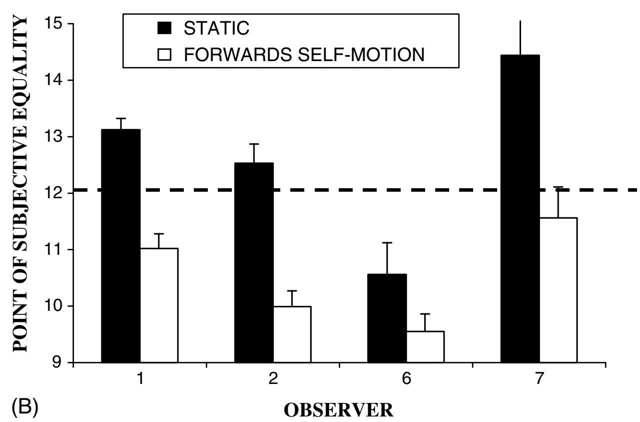


Fig. 9. (A) Difference between the point of subjective equality (PSE) for the −7° FOE location and the PSE for the +7° FOE location as function of the central hole size. The "Static" bar shows the PSE difference for the condition in which the flow elements were static for both the test and reference intervals. (B) The PSE values for the FOE of 0° (i.e., self-motion straight ahead) for the four observers. The "Static" bars are for the condition in which the flow elements remained stationary in both the test and reference intervals (observer 1).

are for the condition in which the flow elements remained stationary in both the test and reference intervals. It is clear from this figure that our observer had a "self-motion collision bias". That is, the perceived direction of object-MID during forward self-motion was shifted towards the nose (i.e., closer to an PSE equal to 0.0) relative to the static condition. Paired t-tests revealed that this difference was statistically significant [$t(3) = 6.8$, $p < 0.001$].

Finally, we found that simulated self-motion degraded an observer's ability to discriminate the direction of MID. Fig. 10 plots mean discrimination thresholds (collapsed across all FOE locations) for observer 1. When the hole size was less than roughly 17°, the mean discrimination threshold for the 'static' condition was lower than for simulated forward self-motion. Similar results were obtained for the other three observers. To analyze this effect we performed a 3×5 repeated measures ANOVA on the discrimination thresholds data

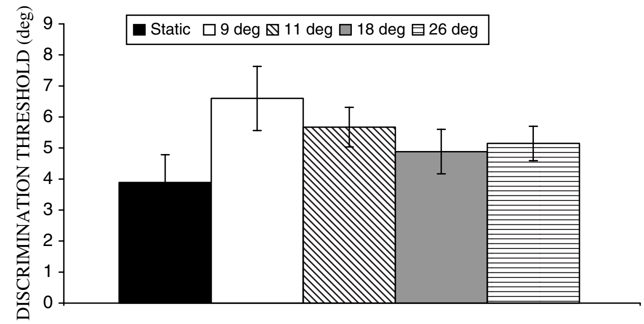


Fig. 10. Mean discrimination thresholds for object-motion-in-depth (collapsed across all FOE locations) as a function of the central hole size. The "Static" bar shows the mean threshold for the condition in which the flow elements were static for both the test and reference intervals. Error bars show ±1 standard error (observer 1).

with FOE location and hole size as factors. There was a significant main effect of hole size [$F(4, 12) = 6.6$, $p < 0.01$]. The main effect of FOE location and the location×hole size interaction were not significant.

3.3.3. Stepwise regression analyses

To determine whether observers based their responses on the task-relevant variable we submitted the data collected in Experiment 2 to a forward stepwise regression analysis. For all five observers the task-relevant variable (i.e., Eq. (3)) accounted for a high proportion of total variance (R^2 ranged from 0.75 to 0.89) across conditions.

3.4. Discussion

In the everyday world the ratio of an object's rate of expansion to its rate of lateral motion (i.e., Eq. (4)) provides reliable information about the direction of MID regardless of whether the approach is produced by self-motion, object-motion or a combination of both. Despite this fact, our observers appear to combine self-motion and object-motion information when judging the direction of object-MID. Simulated forward self-motion to a point 7° left of the midline shifted the perceived direction of object-MID leftwards (by 2.9° on average) and simulated forward self-motion to a point 7° right of the midline shifted the perceived direction of object-MID rightwards (by 3.2° on average). This significant interaction between self-motion object-motion was not abolished until the gap between the outer edge of the object and inner edge of the flow patter was greater than roughly 9°. This range is similar to that found for perceived speed judgments in Experiment 1.

It should be emphasized that, as was the case for the perceived speed and TTC findings, these shifts in perceived direction cannot be caused solely by a change in the relative motion between the object and the surrounding flow elements, because the shifts in perceived direction were in the same direction as the simulated self-motion. Instead we propose that it provides further evidence that MID signal generated by local changing size detectors that process object-motion is being combined (in a weighted sum) with the MID signal generated by the flow pattern.

Simulated self-MID degraded our observers' ability to discriminate the direction of object-MID. Direction discrimination thresholds during forwards self-motion were 37–62% higher (on average) than thresholds for a static flow-field. This is surprising given that self-motion did not affect discrimination thresholds for the speed of object-MID and also because there are many situations in the everyday world where we need to judge accurately the direction of object-MID while we are moving, for example when overtaking a vehicle on the highway. Our finding may be related to the report of (Probst, Brandt, & Degner, 1986) who found that thresholds for lateral motion increased by a factor of 5.5 during concomitant forwards self-motion and increased by a factor of 18 during concomitant lateral self-motion.

Relative to the static condition the perceived trajectory of object-MID (as indexed by the PSE) was biased towards the observer's midline during simulated self-motion, even though visual cues to object-MID were the same in both conditions. Furthermore, all observers reported that, "the object would have collided with my head when more frequently when I was moving forward then when I was stationary". This bias may provide a "safety first" ecological advantage.

4. Experiment 3

4.1. Purpose and rationale

Experiments 1 and 2 we considered only monocular cues to speed and direction. In Experiment 3, we ask whether the addition of binocular information about TTC and direction of MID reduces the judgment errors caused by self-motion. Our rationale is based on the finding that, for large objects, absolute estimates of TTC are more accurate when binocular information is available (Gray & Regan, 1998). Furthermore, the addition of binocular information permits accurate estimates of TTC in situations where TTC cannot be estimated accurately on the basis of monocular information alone [e.g., for small objects (Gray & Regan, 1998) and for rotating non-spherical object (Gray & Regan, 2000a)].

4.2. Methods

4.2.1. Apparatus

A flow pattern consisting of small white squares was displayed on an SVGA computer monitor that subtended 38° horizontal × 27° vertical. The viewing distance was 57 cm. A smaller display and closer viewing distance were used in Experiment 3 because they permitted a better quality stereo image than the LCD projector used in Experiments 1 and 2. The impact of these changes is discussed further below. The peripheral flow pattern was the same as described for Experiments 1 and 2. In all conditions of Experiment 3 the elements of the flow pattern all had zero retinal disparity.

As was the case in Experiments 1 and 2, a simulated approaching square was presented at the center of the flow pattern. In Experiment 3, the central hole size was held constant at 9°. The simulated approaching MID was created by increasing the angular size of the object and/or by increasing its relative retinal disparity. The disparity of the object was varied according to the equation

$$\delta_t = \delta_0 + \frac{It}{D_0 \mathrm{TTC}(1 - t/\mathrm{TTC})} \tag{7}$$

where δ is the retinal disparity relative to a fixed reference point and D_0 is the viewing distance (see Gray & Regan, 1998 for further details). Only approaching objects were simulated in Experiment 3.

4.2.2. Procedure

Psychometric functions for speed discrimination were measured as described for Experiment 1. The MID cues available to the observer were varied across runs. Each observer completed the following three conditions: (1) monocular information alone; (2) binocular information alone; (3) both monocular and binocular information signaled the same TTC.

In order to check that observers based their responses on task–relevant variables we used an 8×8 stimulus array. Within the array the values of initial $[I/D(\mathrm{d}\delta/\mathrm{d}t)]$ and $\Delta\delta$ (i.e., the total change in disparity within a trial) were varied orthogonally by varying the presentation duration (Δt) by ±40% about a mean value of 500 ms (see Gray and Regan (1998) for further details). Each run consisted of 128 trials comprised of 64 approaching objects × 2 directions of self-motion (forward vs. backwards). Psychometric functions for different object-MID cues were measured on separate runs and the order was counterbalanced.

4.2.3. Participants

Observers 1, 3, 4 and 5 completed Experiment 3.

4.3. Results

4.3.1. Monocular information alone

We replicated Experiment 1 using the Experiment 3 apparatus described above. The percentage difference in PSE values between forwards and backwards self-motion were as follows: observer 1, 7.2%; observer 3, 9.9%; observer 4, 5.3% and observer 5, 12%. A paired t-test revealed that these differences were not significantly different for the two experimental setups [$t(4) = 1.2$, $p > 0.5$].

4.3.2. Binocular information alone

Fig. 11A shows the psychometric functions for the condition in which object-MID was produced by binocular information alone (i.e., Eqs. (2) and (3)). Data are for observer 1. The most striking aspect of Fig. 11A is the complete inability of this observer to discriminate

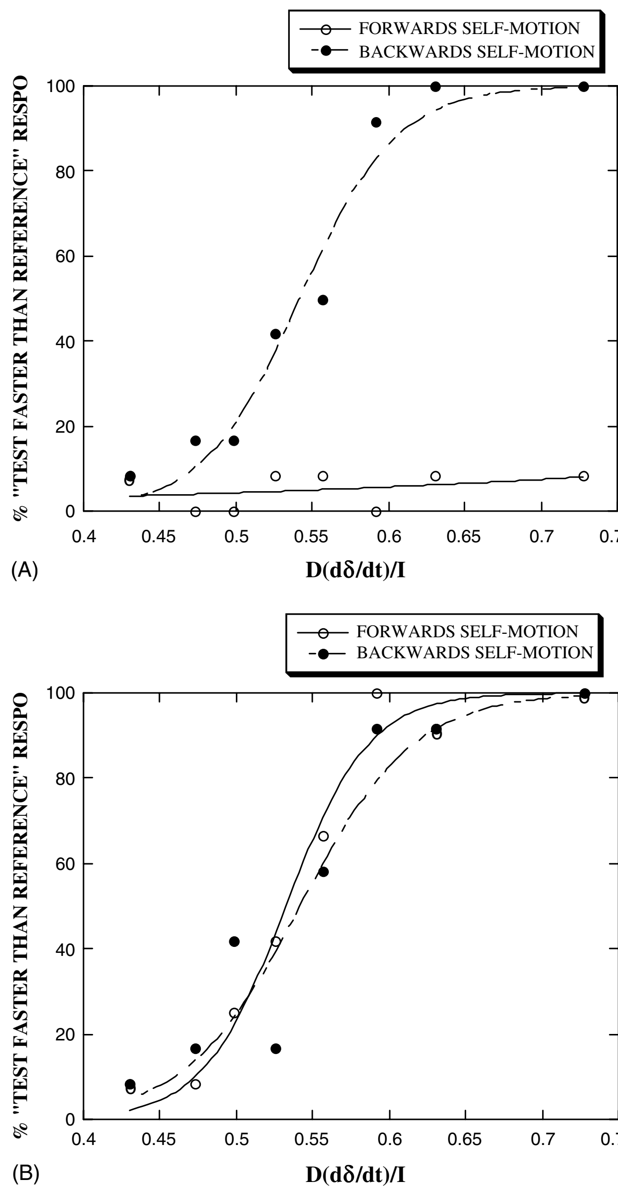


Fig. 11. (A) The psychometric functions for the discrimination of the speed of object-motion-in-depth (MID) when the perception of object-MID was produced by binocular information alone (i.e., Eq. (5)) and (B) the psychometric functions for conditions in which object-MID was produced by a combination of monocular and binocular information (observer 1).

perceived speed during simulated forwards self-motion (open symbols)—for all values of test target speed this observer perceived the reference target to be moving faster than the test target. Similar results were obtained for the other three observers. For all observers thresholds could not reliably be measured for the forward self-motion condition. Subjectively all observers reported only a very weak sensation of object-MID during simulated forwards self-motion. Possible explanations for this effect are discussed below.

Results were substantially different for backwards self-motion (solid symbols). All four observers could reliably discriminate the speed of object-MID and discrimination thresholds ranged from 6% to 15%. For backwards self-motion the PSE values were 0.54, 0.47, 0.51 and 0.44 for the four observers, respectively. These values are all less than the speed of the reference target (0.56), thus the effect of backwards self-motion on speed judgments based on binocular information alone was to increase the perceived speed of MID. This effect is opposite to that found for judgments based on monocular information alone (Fig. 3A). This result parallels our previous finding for TTC estimates for a stationary observer. TTC is underestimated when judgments are based on monocular information alone and overestimated when judgments are based on binocular information alone (Gray & Regan, 1998).

4.3.3. Monocular and binocular information combined

Fig. 11B shows the psychometric functions for conditions in which object MID was produced by a combination of monocular and binocular information. Data are again for observer 1. Relative to the judgments based on binocular information alone (Fig. 11A), speed discrimination performance for the forwards self-motion was dramatically improved when both MID cues were available. Discrimination thresholds in Fig. 11B were 5.3% for forwards self-motion and 7.3% for backwards self-motion. Similar results were obtained for the other observers (thresholds ranged from 5% to 19% for forwards self-motion and 7–18% for backwards self-motion). Relative to the judgments based on monocular information alone (Fig. 2A), the effect of self-motion direction on the perceived speed of object-MID was considerably reduced. Fig. 12 shows the PSE values for forwards and backwards self-motion for the four observers. For all observers, the pattern of results was the same as for monocular information alone (Fig. 3A) although the effect size was reduced. A paired t-test revealed that the difference between the PSE values in the forwards vs. backwards conditions (i.e., the effect size) was significantly smaller for judgments based on a combination of binocular and monocular information than for judgment based on monocular information alone [$t(4) = 7.5$, $p < 0.001$].

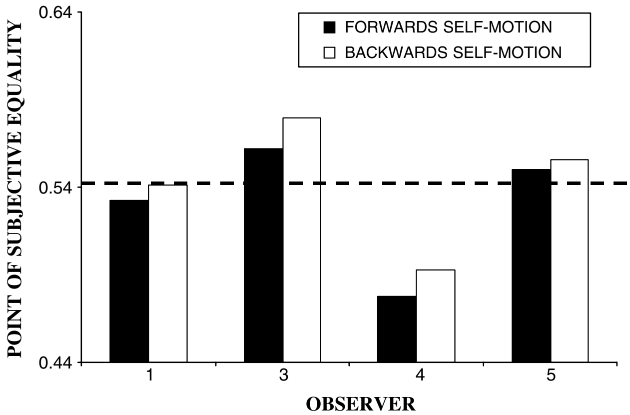


Fig. 12. The Points of subjective equality (PSE) values for the discrimination of the speed of object-motion-in-depth when judgments were based on a combination of monocular and binocular information.

4.4. Discussion

The addition of binocular information significantly reduced the effect of self-MID on the perceived speed of object-MID. The improvement in performance produced by the addition of binocular information parallels our previous findings for judgments of TTC made by stationary observers (Gray & Regan, 1998). When only monocular TTC information was available observers consistently underestimated the TTC of a simulated approaching object (by 2–12%). However, when both monocular and binocular cues to TTC were available there was no consistent tendency to underestimate TTC and errors were small (ranging from 1.3% to 2.7%). As discussed below, our proposed explanation for the finding that performance is improved for combined cues is that binocular and monocular information about MID is combined in a weighted averaging process that takes into account the reliability of each source of information (Gray & Regan, 1998).

An unexpected finding of Experiment 3 was that observers could not reliably discriminate object speed during simulated forwards self-motion when judgments were based on binocular information alone. It is has been well documented that the objects surrounding a target whose disparity is changing have a substantial effect on the sensation of motion of depth produced by the target. For example, in the complete absence of surrounding objects (i.e., so that the disparity change is absolute not relative), changing disparity produces (for small objects) only a weak sensation of MID or (for large objects) no sensation at all (Regan, Erkelens, & Collewijn, 1986). Furthermore, when surrounding objects are present the sensation of MID is strongest when the surrounding objects are at exactly the same distance as the target (Regan & Beverley, 1973). In Experiment 3 all the flow elements surrounding the changing disparity target were moving, therefore it is possible that the absence of stationary reference marks degraded the sensation of MID in the present study. This explanation seems unlikely, however, since the sensation of MID was not affected in the backwards self-motion condition that also had moving reference marks. We are unaware of any studies that have examined the effect of the motion of reference marks on the sensation of MID produced by changing disparity.

5. Experiment 4

5.1. Purpose

In Experiment 3, we found that the addition of binocular information about MID significantly reduced the interaction between object-motion and self-motion. The purpose of Experiment 4 was to determine whether a similar effect would occur for judgments of the perceived direction of object-MID.

5.2. Methods

5.2.1. Apparatus

The apparatus was as described in Experiment 3 except that we varied the location of the FOE as described in Experiment 2. We again used three different FOE locations: (a) 7° left of the center of the display (−7°), (b) center of the display (0°) and (c) 7 ° right of the center of the display (+7°). In Experiment 3, the direction of object-MID was varied according to Eq. (4) (i.e., monocular information) and/or Eq. (5) (i.e., binocular information).

5.2.2. Procedure

Psychometric functions for direction discrimination were measured as described for Experiment 2. The direction cues available to the observer were varied across runs. Each observer completed the following three conditions: (1) monocular information alone; (2) binocular information alone; (3) both monocular and binocular information signaling the same direction.

In order to check whether observers based their responses on the direction of the approaching object rather than on task–irrelevant variables such as frontal-plane speed or the rate of change of disparity, we used the triple dissociation technique described in Experiment 2. We also again collected data for a condition in which the flow elements remained static in both the reference and test intervals.

5.2.3. Participants

Four observers completed Experiment 1. Observer 1 was author R.G. The other three observers (observers 8–10) were naïve to the aims of the study and completed the experiments for partial course credit.

5.3. Results and discussion

5.3.1. Binocular information alone

Fig. 13A shows the psychometric functions for the condition in which the direction of object-MID was signaled by binocular information alone (Eq. (5)). Data are for observer 1. It is clear that direction discrimination performance was poor during simulated forwards self-motion. Direction discrimination thresholds for the three FOE locations were 11°, 19° and 13°, respectively. These thresholds are considerably higher than those found for monocular information alone in Experiment 2 (6.6°, 6.5°, and 6.7°, see Fig. 7) and are higher than that found for the 'static' condition of Experiment 4 (mean threshold 3.8°). Similar results were obtained for the other three observers. A paired t-tests revealed that the mean direction discrimination threshold for estimates based on binocular information alone was significantly higher than for estimates based on monocular information alone [$t(4) = 5.5$, $p < 0.01$]. It is also clear from Fig. 13A that there was no systematic effect of FOE location on the PSE (i.e., 50% point) when estimates were based on binocular information alone.

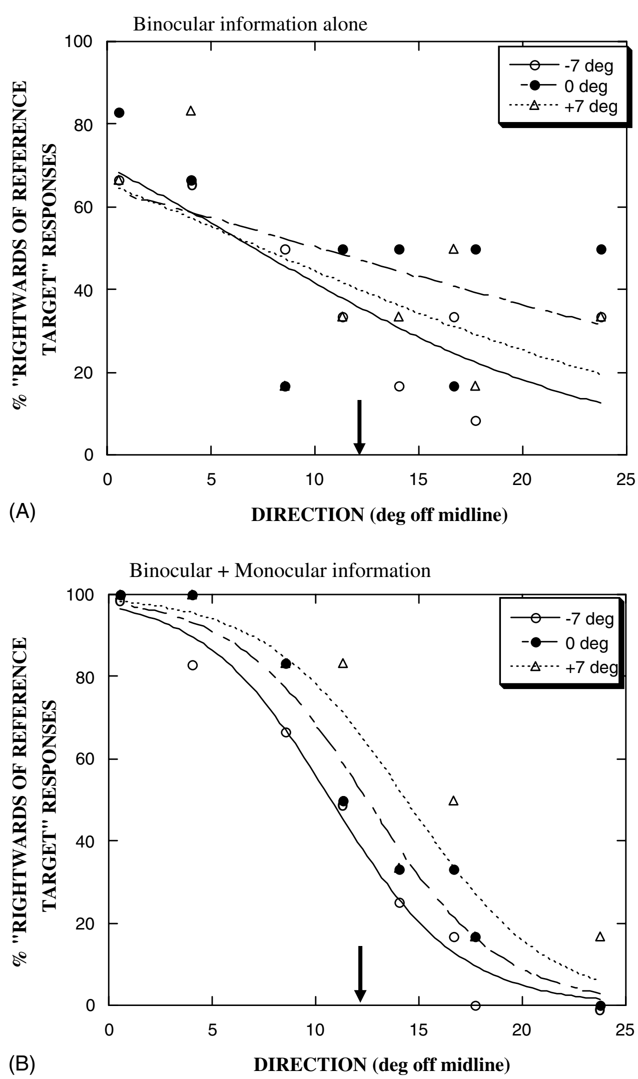


Fig. 13. (A) Psychometric functions for the discrimination of the direction of object-motion-in-depth (MID) when object-MID was produced by binocular information alone (i.e., Eq. (5)) and (B) psychometric functions for the discrimination of the direction of object-MID for conditions in which object-MID was produced by a combination of monocular and binocular information (observer 1).

5.3.2. Monocular and binocular information combined

Fig. 13B shows psychometric functions for conditions in which the direction of object-MID was signaled by a combination of monocular and binocular information. Data are again for observer 1. Relative to the judgments based on binocular information alone (Fig. 13A), direction discrimination performance during forwards self-motion was dramatically improved when both MID cues were available. Direction discrimination thresholds in Fig. 13B were 3.4°, 2.9° and 3.7° for the FOE locations of −7°, 0° and +7°, respectively. Similar results were obtained for the other three observers. Relative to the judgments based on monocular information alone (Fig. 7), the effect of self-motion direction on the perceived direction of object-MID was considerably reduced [$t(4) = 11.4$, $p < 0.001$].

6. General discussion

6.1. Crosstalk between the processing of object-motion and the processing of self-motion

It has been proposed that humans and animals process the motion of objects in their environment independently of their own self-motion (Frost, Wylie, & Wang, 1990) and there are several lines of evidence supporting this idea. For example, neurons in the tectofugal pathway of the pigeon are sensitive to various aspects of object-motion while effectively ignoring self-induced visual motion (Frost, Scilley, & Wong, 1981). Conversely, neurons in the pigeon's accessory optic system are sensitive to elements of self-motion. A similar functional segregation of motion processing has been also found between areas MT and MST in monkeys (Duffy, 1998; Tanaka et al., 1986; Tanaka & Saito, 1989) and the temporooccipital and temporoparietal cortex in humans (Wiest et al., 2001). At the behavioral level, the stimulus conditions which tend to produce the illusion of self-motion (i.e., movement of elements in peripheral vision that are perceived to be the background of the visual scene) are quite different from conditions which typically generate perceived object-motion (i.e., movement of elements in central vision that are perceived to be the foreground of the visual scene) (Brandt, Koenig, & Dichgans, 1973; Brandt, Wist, & Dichgans, 1975). It has been proposed that this independence between processing of the two types of motion may be an effective strategy for solving the classical problem of distinguishing the motion of external objects from retinal image motion produced by a body, head or eye movement (Frost et al., 1990).

However, we report here evidence that information about self-motion and object-motion are integrated in the perception of object movement in depth. In Experiment 1, the *perceived speed* of approaching are receding objects was altered by self-motion information (in particular, the angular speed and direction of the peripheral flow elements). In Experiment 2, the *perceived direction* of object-MID was altered by self-motion information (in particular, the location of the focus of expansion of the flow field). Two points about these findings should be emphasized. First, these changes in perceived speed and direction occurred even though the peripheral flow field did not affect the local information about MID generated by the object itself (i.e., Eqs. (1)–(5)). Second, the observed changes in perceived speed and direction would seem to be maladaptive since they would create inaccuracies in judging the future location of an approaching object under the everyday condition that the object's closing speed and trajectory is affected by self-motion.

In a series of papers Regan, Beverley, Hamstra, and Gray have developed a model of the processing of MID and generation of estimates of TTC and speed (reviewed in Regan & Gray, 2000). In this model, the final MID signal for an approaching or receding object is generated from a weighted average of (i) signals from local relative motion (RM) filters that encode changes in the angular size of the entire object, (ii) signals from local RM filters that encode changes in the angular size of texture elements on the surface of the object, (iii) signals from local RM filters that encode changes in the separation between adjacent texture elements on the surface of the object, and (iv) filters that encode the object's rate of change of disparity relative to a fixed reference point. The findings of Experiment 1 indicate that self-motion signals from filters that encode the velocity of radial flow are also part of this weighted average. The data shown in Fig. 5 suggest that this self-motion signal is based on all elements within roughly ±9° of the focus of expansion of the flow pattern. An expanding flow pattern would cause the object's closing speed to seem faster (and hence an underestimate of TTC); a contracting flow field would cause the object's closing speed to seem lower (and hence an overestimate of TTC). This model can also explain some of other findings we observed in the present study. For example, in Experiment 3 the addition of binocular information significantly reduced the effect of self-motion on perceived speed. This effect can be explained in the model because binocular information accurately encodes the speed of MID so that the changing–disparity signal would partially offset the self-motion signal in the averaging process. The model can also explain the saturation effect shown in Fig. 4A: as the speed of self-motion increases relative to the speed of object-MID it will have a larger impact on the final weighted average until at some point the final MID speed will be effectively determined only by the self-motion signal. Finally, a prediction that comes from our model is that the effect of self-motion on the perceived speed of object-MID should be larger for small objects because the signals from the RM filter that encode object expansion and the RM filters that encode texture element expansion are both smaller for small objects (Gray & Regan, 1998, 1999).

The interaction between self-motion and object-motion, and in particular the increase in MID detection thresholds caused by concomitant self-motion, has previously been explained in terms of a misdirected constancy mechanism (Probst et al., 1986), that is the internal signal (or 'efferent copy') used to cancel the retinal image motion of stationary objects during self-motion (von Holst & Mittelstadt, 1950) is somehow being misapplied to moving objects. However, this proposal cannot be used to generate quantitative predictions about the effect of different stimulus conditions on the interaction between self-motion and object-motion.

6.2. An adaptive interaction?

Why then does this interaction occur when it is seems to be maladaptive? We have previously suggested that the inaccuracies in object TTC perception produced by self-motion may in fact be ecologically advantageous (Gray & Regan, 2000b). Consider two cases of object interception: (i) a stationary observer reaching out to catch a ball and (ii) an observer running to catch a ball. It has previously been shown that binocular information acquired when the ball is within a few meters of the eyes is used to correctly time the finger flexions in catching (Alderson, Sully, & Sully, 1974). Therefore, in case (i) it would be advantageous if the initial estimate of TTC based on monocular information were an underestimate because the unavoidable variability in the estimate will never create the situation where there is no time left to acquire the essential binocular information. [8] When the observer is in motion [case (ii)], the mass that must be controlled on the basis of close-range binocular information is much greater than in case (i). Thus, it would seem advantageous for the initial estimate of TTC to be

[8] Several studies have shown that TTC is consistently underestimated when judgments are based on monocular information alone (Eq. (1)) (reviewed in Gray & Thornton, 2001).

an even larger underestimation during self-motion to allow the effects of body inertia to be overcome before binocular information becomes within the final few meters of the object's approach.

6.3. Implications for research on perception and action

Almost all work on human object-motion perception and all the animal experiments on object motion perception have involved a stationary observer and a real or simulated moving object (see Nakayama, 1985; Regan, 1986; Regan & Gray, 2000 for reviews). On the face of it, this choice of methodology would seem to have general validity because the local optical information provided by the object itself (e.g., Eqs. (1)–(5)) provides accurate information about the trajectory and speed of the object-motion regardless of whether the observer is stationary or moving. However, the results of the present study suggest that this large body of previous work has limited applicability to the more common situation where both the observer and the object are in motion: we find that the processing of object-motion during self-motion cannot in general be directly predicted from data obtained with a stationary observer.

6.4. Suggestions for future research

In the present study we demonstrated interactions between the processing of object-motion and self-motion for simulated constant velocity motion in a straight line (i.e., radial optic flow). Given that the processing of rotary optic flow (produced either by a curved path of motion or when an observer fixates an object that is eccentric to their direction of locomotion) appears to be very different from the processing of radial optic flow (Regan & Beverley, 1982; Warren & Hannon, 1988), it will be interesting for future research to investigate whether similar self-motion/object-motion interactions occur in these conditions. It has also recently been demonstrated that the addition of vertically-extended objects (e.g., posts or trees) to an optic flow display substantially improves heading judgments due to the added motion parallax information (Cutting, Wang, Fluckiger, & Baumberger, 1999; Li & Warren, 2000). Therefore, it may also be interesting for future research to investigate how motion parallax information influences the self-motion/object-motion interaction.

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