

# Pursuit compensation during self-motion

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Received 9 December 2000, in revised form 5 August 2001

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**Abstract.** The pattern of motion in the retinal image during self-motion contains information about the person's movement. Pursuit eye movements perturb the pattern of retinal-image motion, complicating the problem of self-motion perception. A question of considerable current interest is the relative importance of retinal and extra-retinal signals in compensating for these effects of pursuit on the retinal image. We addressed this question by examining the effect of prior motion stimuli on self-motion judgments during pursuit. Observers viewed 300 ms random-dot displays simulating forward self-motion during pursuit to the right or to the left; at the end of each display a probe appeared and observers judged whether they would pass left or right of it. The display was preceded by a 300 ms dot pattern that was either stationary or moved in the same direction as, or opposite to, the eye movement. This prior motion stimulus had a large effect on self-motion judgments when the simulated scene was a frontoparallel wall (experiment 1), but not when it was a three-dimensional (3-D) scene (experiment 2). Corresponding simulated-pursuit conditions controlled for purely retinal motion aftereffects, implying that the effect in experiment 1 is mediated by an interaction between retinal and extra-retinal signals. In experiment 3, we examined self-motion judgments with respect to a 3-D scene with mixtures of real and simulated pursuit. When real and simulated pursuits were in opposite directions, performance was determined by the total amount of pursuit-related retinal motion, consistent with an extra-retinal 'trigger' signal that facilitates the action of a retinally based pursuit-compensation mechanism. However, results of experiment 1 without a prior motion stimulus imply that extra-retinal signals are more informative when retinal information is lacking. We conclude that the relative importance of retinal and extra-retinal signals for pursuit compensation varies with the informativeness of the retinal motion pattern, at least for short durations. Our results provide partial explanations for a number of findings in the literature on perception of self-motion and motion in the frontal plane.

## 1 Introduction

The motion of an object's image across the retina cannot directly specify the object's motion with respect to the head. Movements of the eye or head also affect the motion of the object's retinal image; for example, turning the eye to the right adds a component of leftward motion to the entire visual field. These effects of eye and head movements must be compensated for if we are to perceive accurately the motions of objects relative to the head or body. The same problem occurs in the context of perceiving self-motion from the pattern of motion in the retinal image; changes in this pattern of retinal-image motion caused by eye or head movements must be compensated for in order to support accurate perception of self-motion. We use the term *pursuit compensation* to refer to the perceptual canceling out or removal of any motion in the retinal image caused by a smooth eye or head movement, allowing us to perceive accurately relative motion between ourselves and the objects and scenes around us. In this paper, we address the specific problem of compensating for the effects of smooth-pursuit eye movements in visual self-motion perception. However, our results are also qualitatively

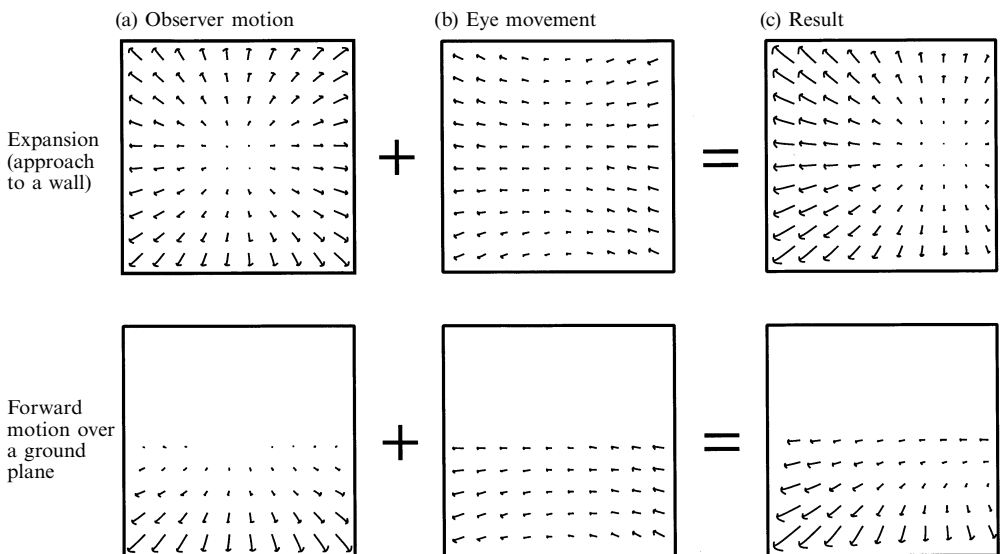
consistent with recent explanations for a number of phenomena in the perception of frontal-plane object motion during smooth eye movements.

### 1.1 Visual self-motion perception: The simple case of linear translation

Visual motion is an important source of information about self-motion. As we move about, the images on our retinas change in predictable ways. Moving forward in a straight line with the direction of gaze fixed causes a radial expansion in the retinal image. Figure 1a depicts the resulting pattern of retinal-image motion for two situations: approach to a frontoparallel wall (top) and forward motion across a ground plane (bottom). All of the retinal-image motions are directed away from a single point, termed the *focus of expansion* (FOE), that corresponds to the direction of self-motion, or *heading* (Gibson et al 1955). The visual system clearly can use this kind of motion pattern as a stimulus for perceiving self-motion; showing someone an animation containing such a radial motion pattern yields a clear sensation of self-motion in the direction specified by the FOE. This self-motion percept can be quite accurate: observers can judge simulated heading with respect to a marker in the scene with an accuracy of  $1^\circ$  (Royden et al 1994; Warren et al 1988) and under optimal conditions can detect changes in heading on the order of  $0.2^\circ$  (Crowell and Banks 1993).

### 1.2 Complications due to smooth pursuit

In everyday life, however, the problem of estimating self-motion is more complex. We typically rotate our eyes and head frequently while moving around; the added degrees of freedom complicate the task of interpreting the information contained in the retinal motion field. Figure 1b shows the pattern of retinal motion created by a rightward eye or head movement: the entire visual field shifts to the left. When the two movements (walking forward and making a rightward eye movement) are performed



**Figure 1.** Retinal motion patterns created by (a) forward observer translation towards a frontoparallel wall (top) or across a ground plane (bottom). In both cases the motion pattern is purely radial. (b) A rightward eye movement while viewing the same two scenes; the motion pattern is laminar (leftward) in both cases. The bowing of the arrows at the top and bottom of each figure are a consequence of the large simulated field of view (60 deg); to be geometrically correct, these figures would have to be viewed from a distance equal to  $\sim 87\%$  of their width. (c) The combination of (a) and (b), ie forward motion combined with a rightward eye movement. Note that the motion pattern for the frontoparallel wall is still radial, whereas that for the ground plane curves in from the right.

simultaneously, the resulting pattern of motion in the retinal image is the sum of the two component patterns (figure 1c)—a radial pattern plus a leftward laminar pattern.

A display that changes over time in the manner suggested by figure 1c (ie with a motion pattern that is the sum of radial and approximately parallel components) thus contains all of the motion information available in the retinal image of a person moving forwards and making an eye movement. A number of studies of self-motion perception have used displays simulating this situation, referred to as *simulated eye movement* or *simulated pursuit*. Interestingly, when shown an animation of this type, observers are often very bad at judging their simulated self-motion, making errors in the direction of the simulated eye movement (Banks et al 1996; Crowell et al 1998a; Royden et al 1992, 1994). The type of self-motion perceived in these studies depended on the scene geometry. If the scene consisted of a single frontoparallel wall, as in some experiments (Crowell et al 1998b; Royden et al 1994; Warren and Hannon 1990), the combination of simulated forward translation and pursuit led to a combined motion pattern that was still approximately radial with a displaced FOE (figure 1c, top); the resulting percept was of roughly linear motion in the approximate direction of the displaced FOE. In the case of a more three-dimensional (3-D) scene (figure 1c, bottom), observers generally reported that they appeared to be moving along a circular path, as though they were driving around a bend in the road while looking directly in front of the vehicle (Crowell et al 1998a; Ehrlich et al 1998). The combined motion pattern in the bottom panel of figure 1c is very similar to that which would be created by such a curvilinear self-motion.

### 1.3 *Extra-retinal and retinal signals for pursuit compensation*

Why are we not subject to such errors in everyday life? When we make an eye movement, we have additional information about the movement that is not contained in the retinal image, in the form of *extra-retinal signals*. The oculomotor centers send a signal (called an *efference copy*) to the visual system containing information about the eye movement. It has been proposed that the visual system uses this signal to compensate for the effects of the eye movement on the retinal motion field (von Holst 1954); the results described above are consistent with this proposal. This could explain why observers perceived self-motion accurately when making an eye movement while viewing animations like those depicted in figure 1a (referred to as a *real eye movement* or *real pursuit* condition), despite the fact that the pattern of motion in the retinal image resembled those depicted in figure 1c (Banks et al 1996; Crowell et al 1998a; Royden et al 1992, 1994; Warren and Hannon 1990). However, we will argue that pursuit compensation is more complicated than this explanation implies.

The studies just mentioned have established that the presence or absence of extra-retinal signals can have a large effect on our motion percepts. On the other hand, a number of computational papers have demonstrated that under many conditions there is, in principle, sufficient information in the pattern of retinal motion itself to allow the visual system to estimate the translational and rotational velocities of the eye without recourse to extra-retinal signals (Heeger and Jepson 1992; Lappe et al 1996; Longuet-Higgins and Prazdny 1980; Perrone and Stone 1994; Rieger and Lawton 1985). In other words, these models imply the possibility of purely *retinal* mechanisms for pursuit compensation during self-motion. However, Koenderink and van Doorn (1987) showed that retinal pursuit compensation during self-motion is only theoretically possible if the scene contains depth variation or if the field of view is large; a small field of view onto a scene consisting of a single, frontoparallel plane does not provide enough information to compute these motion parameters accurately.

The inaccuracy of self-motion judgments during simulated eye movements even when the scene is 3-D seems to imply that this information is not used, and that only

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extra-retinal signals are necessary to compensate for the effects of pursuit. However, two lines of evidence suggest that compensation for smooth pursuit is based on a complicated interaction between time-varying retinal and extra-retinal signals. First, variations in the retinal stimulus can also affect the accuracy of self-motion judgments during simulated eye movements; this should not happen if pursuit compensation were driven by purely extra-retinal signals.<sup>(1)</sup> Second, there are conflicting reports of the extent of pursuit compensation during real eye movements from experiments using apparently similar displays. We will describe findings related to the perception of self-motion during pursuit here; some analogous results from studies of perception of motion in the frontal plane will be mentioned in section 6.

#### *1.4 Improved self-motion perception during simulated pursuit*

Li and Warren (2000) have performed a number of experiments on perceived self-motion using more complex displays. These displays consisted of texture-mapped 3-D scenes that contained recognizable landmarks and spanned a larger portion of the field of view than those in prior experiments did. These innovations might be expected to improve the performance of purely retinal solutions to the problem of pursuit compensation. They provide independent information about scene geometry, eg gradients of texture and object size; this information formally simplifies the problem of estimating movement parameters. The presence of landmarks could allow subjects to use strategies based on changes in the perceived egocentric locations of objects as well as on perceived motion. Finally, larger fields of view would allow subjects to gather more information.

These investigators report much-improved self-motion judgments during simulated pursuit; this seems to imply that extra-retinal signals are unnecessary when the retinal information is sufficiently rich. However, there are a couple of things to keep in mind in interpreting these results. First, the earlier experiments were designed to isolate motion-sensitive mechanisms. The simulated scenes in these experiments contained recognizable landmarks; thus, performance could be based on a different and larger set of mechanisms, including those sensitive to the egocentric locations of objects. These results tell us more about how well people can make these judgments under more realistic conditions than about the properties of the underlying mechanisms.

Second, as mentioned above, the poor performance found in earlier studies using random-dot renditions of this type of scene consisted in misinterpreting simulated-pursuit displays with linear translation as depicting translation along a curved path. Interestingly, simulated self-motion on a curved path is perceived much more accurately (Ehrlich et al 1998; Warren et al 1991). In other words, the earlier results for random-dot displays suggest that, in the absence of appropriate extra-retinal signals, people perceive both linear self-motion with simulated pursuit and curvilinear self-motion as curvilinear self-motion. The visual system does not discriminate in its interpretation of the two types of displays. The results of Li and Warren (2000) indicate that linear self-motion with simulated pursuit is interpreted correctly in the presence of recognizable landmarks; it remains to be demonstrated that people's interpretations of these two types of motions are different under these conditions. The visual system may simply adopt a different bias, causing both types of displays to be interpreted as linear self-motion. There is evidence to support this hypothesis: Li and Warren (1998) showed subjects displays simulating linear self-motion with simulated pursuit, but gave different instructions in different blocks of the experiment. In some blocks, subjects were actually told that the displays simulated a linear self-motion path, whereas in others they were told that the displays simulated curvilinear self-motion. Subjects' responses varied greatly depending on the instructions, and the subjects actually thought that

<sup>(1)</sup>Unless the changes in the retinal stimulus affect the gain of speed-sensitive visual mechanisms proportionately, as eg a change in contrast might (Freeman and Banks 1998).

they were viewing different classes of displays. The ability to discriminate these two types of displays without prior knowledge of the type of self-motion being simulated would imply that purely retinal information is often of paramount importance in self-motion perception during pursuit.

Grigo and Lappe (1999) presented evidence that the relative effectiveness of retinal and extra-retinal signals depends specifically on the parameters of the retinal motion stimulus. As mentioned above, Koenderink and van Doorn (1987) showed that a large field of view is necessary for accurate estimation of translational and rotational velocities from the retinal motion pattern when the scene contains little or no depth variation. The reason for this is evident in the top row of figure 1. The upward and downward bowing of the motion vectors at the top and bottom of the motion field caused by an eye movement (figure 1b) decrease as the field of view decreases. As the motion vectors become more uniform, the combined motion pattern (figure 1c, top) becomes more similar to the purely radial pattern that would be created by observer translation to the side. On the other hand, as the field of view increases, the bowing increases and the retinal motion pattern becomes less purely radial. Initial studies of self-motion perception during approach to a frontoparallel wall with simulated pursuit confirmed that people's judgments of self-motion are inaccurate when the field of view is relatively small (Royden et al 1994; Warren and Hannon 1990); the displays used in these studies were 30–40 deg across. Grigo and Lappe (1999), on the other hand, reported that if the field of view was much larger (90 deg  $\times$  90 deg), accuracy depended on the duration of the display. Performance was poor if the duration was 500 ms or longer; if it was less than 500 ms, on the other hand, judgments were quite accurate on average, though not for all individual observers. Grigo and Lappe interpreted this to mean that both retinal and extra-retinal signals are used in pursuit compensation; however, extra-retinal pursuit-compensation signals have a slower time course. As a result, the relative weight applied to the extra-retinal pursuit signal increases in time over the course of the eye movement. Observers could use the information in the retinal motion pattern provided by the large field of view at short durations; at longer durations, this information was overridden by an extra-retinal signal informing the visual system that the eye had not moved and that no compensation was necessary. This result implies that retinal motion signals can effect pursuit compensation even in the absence of recognizable landmarks.

### 1.5 *Poor self-motion judgments during real pursuit*

Recent studies by Freeman and colleagues (Freeman 1999; Freeman et al 2000) suggest that self-motion perception is not always accurate even during real eye movements. In their experiments, observers pursued a horizontally oscillating target while viewing displays simulating forward linear self-motion across a ground plane. Observers reported that their simulated heading appeared to oscillate slightly under these conditions; Freeman et al termed this percept the *slalom illusion*. The existence of this illusion suggests that pursuit compensation is imperfect; either the compensatory signal is too small or too large (ie has a gain different from one), or its timing is off relative to that of the retinal motion signals (ie it has a phase lag or lead). Freeman et al quantified the illusion using a nulling procedure. They added a simulated pursuit (roughly speaking, a lateral oscillation of the entire display) of the same temporal frequency as the real eye movement to the self-motion display. Observers were instructed to adjust the amplitude and phase of the simulated pursuit such that the self-motion path seemed as straight as possible. Surprisingly, observers reported that their path appeared straightest when they added a simulated pursuit that was on average 30% as fast as the real pursuit and in roughly the opposite direction (with a very small phase lag,  $\sim 5^\circ$ ). The simplest interpretation of this result would be that the

compensatory signal had a gain of only 70%. This relatively low estimate of the compensatory gain appears to conflict with the earlier reports mentioned above of accurate self-motion judgments when using very similar displays but a different psychophysical task.

Recently, we (Crowell et al 1998b) reported poor self-motion judgments during both simulated and real pursuit eye movements using displays simulating approach to a frontoparallel wall. Observers were asked to judge where they would hit the wall. Recall that, with this type of simulated scene, there is little or no information in the retinal motion pattern created by the frontoparallel wall to support accurate self-motion perception unless the field of view is large. We confirmed that this held for our relatively small displays by finding large errors during simulated pursuit; observers responded that they appeared to be moving towards the displaced focus of expansion (figure 1c, top). During real pursuit, observers also made large errors; on average, these errors were 60% as large as those made during simulated pursuit. We concluded that the gain of the extra-retinal compensatory signal in our experiment was only 40%.

Interestingly, this result appears to directly contradict those of earlier studies with very similar displays. Warren and Hannon (1990, experiment 4) and Royden et al (1994, experiment 3) reported accurate self-motion judgments during approach to a frontoparallel wall. We cannot estimate a compensatory gain for the Warren and Hannon experiment because of the way the data were presented; in the case of the Royden et al experiment, however, the gains were on the order of 90% (based on their figure 7). What is the reason for this discrepancy?

One difference between the displays in the Royden et al (1994) and Crowell et al (1998b) experiments was what surrounded the experimental display in both time and space. In both experiments, the observer pursued a target for a fraction of a second before the simulated self-motion began. In the experiments of Royden et al (1994), a stationary wall was visible in the display during this pursuit target acquisition phase. In the Crowell et al (1998b) experiments, however, the screen was black except for the pursuit target itself until the simulated self-motion began. The spatial context was also reduced in our experiments: we flooded the screen with bright light between trials to keep observers light-adapted, so they could not see anything other than the display itself. Observers were allowed to dark-adapt over the course of a session in the Royden et al (1994) experiments, allowing them to faintly see the edges of the computer monitor and perhaps other objects in the room.

There is reason to believe that this difference in spatiotemporal context might be important. Haarmeier and Thier (1996) reported that a motion stimulus that the observer saw before the actual test display can have a large effect on a phenomenon of frontal-plane motion perception called the Filehne illusion.

### 1.6 *Effect of prior retinal motion on the Filehne illusion*

The Filehne illusion (Filehne 1922, cited by Mack and Herman 1978) refers to the fact that a stationary background object in an otherwise dark room appears to move in the direction opposite to a pursuit eye movement. When observers are asked to adjust an added motion of the target object until it appears to be stationary, they typically set it moving in the same direction as pursuit. This implies that pursuit compensation in the context of object motion perception is imperfect under these conditions. This result is generally interpreted to mean that an extra-retinal, pursuit-related signal underestimates the speed of eye movement.<sup>(2)</sup> Measurements of the strength of the Filehne illusion vary considerably, but there is some evidence that it

<sup>(2)</sup>Freeman and Banks (1998) pointed out that the retinal motion of the target may also be overestimated and that these experiments can only measure the ratio of extra-retinal and retinal motion signal gains.

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depends on the size of the background: larger backgrounds may suppress the illusion (Mack and Herman 1978).

In a recent study of this illusion, Haarmeier and Thier (1996) found that they could strengthen, weaken, or even reverse the Filehne illusion by presenting a display moving in either the same direction as, or opposite to, the eye movement a few seconds before the target object was presented. They called the prior motion stimulus a *conditioning stimulus*; motion of the prior conditioning stimulus in the same direction as pursuit increased the magnitude of the illusion, whereas prior motion in the opposite direction decreased or even reversed the effect. The same prior retinal motion had little or no effect on perceived motion when the eye was held stationary, implying that its action was not due to a classical motion aftereffect. Thus, Haarmeier and Thier (1996) argued that pursuit compensation for object motion perception could not be based on a purely extra-retinal signal. Can we make a similar argument in the case of self-motion perception?

The Haarmeier and Thier result suggests that what observers see immediately before the display is presented might be important. In the Royden et al studies, observers began making pursuit eye movements for 200 ms across an objectively stationary display immediately before they saw the self-motion display; this would have given rise to a retinal motion pattern consistent with the eye movement and potentially provided information about its speed. During the presentation of the self-motion display they were able to see the stationary contours around it, also giving rise to retinal motion consistent with the eye movement. Warren and Hannon (1990) did not have subjects begin pursuing before the self-motion display began, but a stationary display was visible for 1 s before both the self-motion display and the pursuit target started moving. Thus, it is conceivable that spontaneous eye movements made before the self-motion display created a retinal motion signal.

In the Crowell et al (1998b) study, on the other hand, observers did not have information from prior retinal motion about pursuit velocity; the screen was blank except for the pursuit target before the self-motion display was presented. If retinal motion signals—even *prior* motion signals—were important for pursuit compensation, then this difference in the experimental conditions could explain the difference in the results.

## 2 Experiments

These experiments were designed to discover interactions between retinal and extra-retinal pursuit-related motion signals that would have been missed by earlier studies.

In experiment 1, we examined the effect of prior retinal-image motion on self-motion judgments during real and simulated pursuit with simulated approach to a frontoparallel wall. If such effects were present and of similar magnitude during both real and simulated pursuit, that would be consistent with a purely retinally based motion aftereffect. In other words, the prior motion could simply fatigue retinal motion detectors tuned to its direction of motion, biasing the perception of the subsequent self-motion display in a manner independent of the pursuit condition. On the other hand, if the effects were of greater magnitude during real pursuit than during simulated pursuit, that would imply a more complex interaction between the two types of pursuit-compensation signals. We found evidence for such an interaction.

Experiment 2 was identical to experiment 1, except that a more 3-D scene consisting of floor and ceiling planes was used. This experiment tested the hypothesis that an interaction between retinal and extra-retinal signals was responsible for the high level of accuracy in self-motion judgments previously observed during simulated forward translation across a ground plane. Interestingly, we found no evidence of an interaction using this type of display.

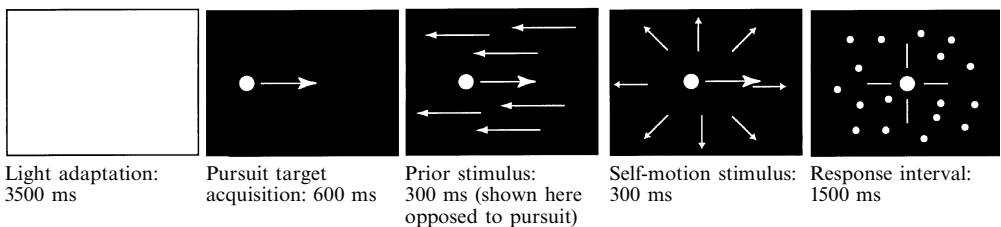
Experiment 3 tested a possible explanation for the difference in results between experiments 1 and 2. It is possible that the effect of prior motion is overridden by an enhanced retinal pursuit-related signal extracted from motion patterns created by more informative, 3-D scenes. To test this hypothesis, we examined self-motion judgments in the presence of mixtures of real and simulated pursuit.

## 2.1 General methods

**2.1.1 Observers.** Three observers, the first author and two naïve observers, participated in the experiments. All had corrected-to-normal vision and were experienced with similar psychophysical tasks and displays.

**2.1.2 Display hardware and software.** Displays consisted of patterns of anti-aliased moving dots. Experiments were run and dot coordinates were computed in MATLAB on a Power Macintosh G3/233 and displayed with the aid of a custom-written C code on an Apple 17-inch monitor (experiments 1 and 3) or an NEC 20-inch monitor (experiment 2), both driven at 75 frames  $s^{-1}$ . A chin/head rest supported the observer's head. Displays were viewed monocularly from a distance of 30 cm through a positive lens that placed accommodation near infinity. In all experiments the stimuli were clipped to a 40 deg  $\times$  40 deg software window; during simulated pursuit this window moved across the screen at an equal and opposite rate to that of the simulated pursuit. A viewing hood made of black poster-board was attached to the front of the monitor and observers were light-adapted between trials (see below), so the only things they could see during a trial were the dots comprising the display and a faint afterimage of the light-adaptation stimulus.

**2.1.3 Sequence of events in a trial.** Timing of all experiments was entirely under computer control. Each trial consisted of five intervals, except in experiment 3, in which interval (iii) was omitted. The sequence of events is indicated in figure 2: (i) The observer was light-adapted for 3.5 s (the entire screen was filled with the brightest possible yellow). (ii) A tone sounded, the screen went black, and the pursuit/fixation target (a small yellow cross) appeared; it immediately began moving to the left or right at 9 deg  $s^{-1}$  (real pursuit) or remained stationary (simulated pursuit) for 600 ms. (iii) The prior, 'conditioning' stimulus was displayed for 300 ms while the observer continued to pursue or to fixate; it consisted either of a pattern of dots that were stationary or moved to the left or right, or of an empty (black) screen. (iv) The self-motion stimulus was displayed for 300 ms. If the prior stimulus consisted of dots, then these same dots were used for the self-motion stimulus; their motions simply changed at the beginning of the fourth interval. (v) The entire display froze and a marker appeared on the screen. The observer had 1.5 s to respond by pressing a key.



**Figure 2.** The sequence of events within each experimental trial (see text for details).

**2.1.4 Eye-movement monitoring.** Eye position was monitored during the prior motion and self-motion periods [intervals (iii) and (iv)] with an ISCAN infrared video-based pupil-tracking system with a sampling frequency of 60 Hz. At the end of each trial, the mean speed across these intervals and the speed in each of three overlapping 300 ms bins that spanned the same 600 ms period were computed (ie bin 1 lasted from



0–300 ms, bin 2 from 150–450 ms, and bin 3 from 300–600 ms). The trial was rejected if the mean speed deviated from the target speed by more than  $-15\%$  or  $+25\%$ , or if the speed in any of the bins deviated by more than  $-30\%$  or  $+40\%$ . No attempt was made to remove saccades from the traces before the analysis; trials containing saccades generally exceeded the speed limit in one of the bins and were rejected. The observer was given auditory feedback about pursuit performance by a series of musical notes; if the trial was not rejected, this feedback occurred after the observer's response. Observers were allowed to abort a run and terminate the day's session if they were failing an abnormally high proportion of trials owing to fatigue. This happened in one session out of every four or five; data from aborted runs were not saved. Statistical hypotheses about pursuit speeds were tested using the distribution-free Gore test, which tests for the effect of one factor in the presence of a second with different numbers of trials in each cell (Deshpande et al 1995).

**2.1.5 Psychophysical procedure and data analysis.** In all experiments the observers were instructed to judge whether their self-motion path would carry them to the left or right of a visual marker. If the self-motion path appeared curved (experiments 2 and 3), they were instructed to attempt to extrapolate the curve (see figure 4); this task can be performed to a fair degree of accuracy when the display actually simulates motion on a curved path (Ehrlich et al 1998; Warren et al 1991). The path or the marker position was adjusted across trials by means of a 1-down, 1-up staircase; staircases for left and right pursuit were interleaved in alternation on each run. There were at least four runs for each experimental condition; additional runs were sometimes added in cases of high response variability. The resulting data were accumulated into psychometric functions across runs and the 50%-'right' point (corresponding to the perceived location of the self-motion path at the distance of the probe, see figure 4) was estimated by fitting a cumulative normal distribution function to the data. The fitting was done by iteratively maximizing the likelihood function with the assumption that the percentage of correct values at each point on the psychometric function were independent and binomially distributed (probit regression, Crown 1998). Approximate confidence intervals depicted in figures 3b, 5b, and 6b were estimated from a Monte Carlo simulation of this model (Manly 1997); however, these confidence intervals were for graphical purposes only and were not used in statistical testing. Statistical hypotheses were tested with the likelihood ratio test. If  $L_u$  is the likelihood of the data given an unrestricted model (ie when two or more psychometric functions are fit independently) and  $L_r$  is the likelihood given a restricted model (for example, one in which two or more normal distribution functions are required to have the same mean), then  $D = -2 \ln(L_r/L_u)$  (often referred to as the *deviance*) is approximately  $\chi^2$ -distributed with degrees of freedom equal to the difference in number of parameters between the two models (Crown 1998; Neter et al 1996). In other words, larger values of  $D$  correspond to more significant effects.

### 3 Experiment 1: Approach to a frontoparallel wall

As mentioned above, our finding of poor self-motion judgments during simulated approach to a frontoparallel wall (Crowell et al 1998b) conflicts with earlier reports (Royden et al 1994; Warren and Hannon 1990). Experiment 1 was designed to test the hypothesis that prior motion signals affect pursuit compensation and could explain the difference between these results.

#### 3.1 Displays

In the self-motion period of each trial [interval (iv)], displays simulated approach to a frontoparallel wall defined by random dots. Expansion rate (speed gradient) was held constant over the course of a single display at  $0.5 \text{ (deg s}^{-1}) \text{ deg}^{-1}$ . Observers either

fixated a stationary '+' or pursued leftward or rightward at  $9 \text{ deg s}^{-1}$ . On some of the fixation trials a simulated pursuit at  $\pm 9 \text{ deg s}^{-1}$  was added to the display.

During the prior motion period [interval (iii)], the display was either blank (condition 'N') or the same set of dots moved so as to simulate pursuit at a variety of speeds. The *retinal* velocities of the prior motion stimuli were approximately matched in real and simulated pursuit, as opposed to their velocities on the display. During real pursuit, the prior motion stimulus either moved with the pursuit target at the same speed (retinal velocity =  $0 \text{ deg s}^{-1}$ , condition '0'), remained stationary on the screen (retinal velocity =  $-9 \text{ deg s}^{-1}$ , condition '9'), or moved with the same speed in the opposite direction (retinal velocity =  $-18 \text{ deg s}^{-1}$ , condition '18'). During the corresponding simulated-pursuit conditions it was either stationary on the screen or moved opposite the direction of simulated pursuit at  $9$  or  $18 \text{ deg s}^{-1}$ .

### 3.2 Task

At the end of the self-motion period, a response probe (a cross) appeared centered on the pursuit target. Observers responded whether they would hit the looming wall to the left or right of the response probe. On subsequent trials, the heading was varied to find the direction that appeared to correspond to direct approach to the response target.

### 3.3 Pursuit speed data

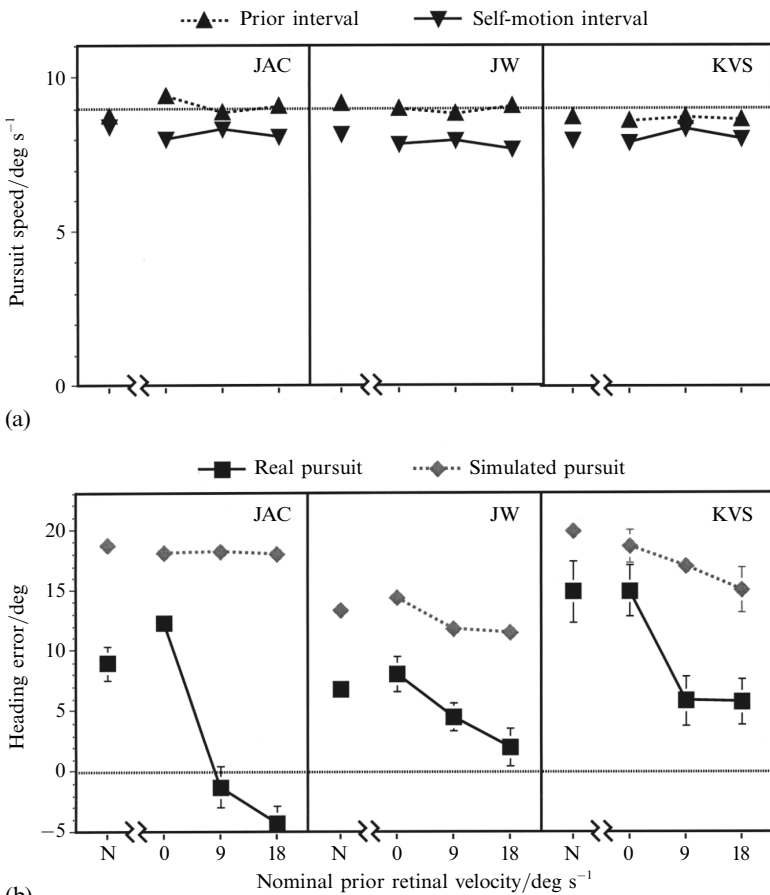
18% of trials were rejected because of inadequate pursuit performance in this experiment. The median pursuit speeds in the prior and self-motion intervals of successful trials are plotted separately for the three observers in figure 3a. Interquartile ranges varied from  $\sim 0.7$ – $1.6 \text{ deg s}^{-1}$ .

Each observer demonstrated similar performance across experimental conditions, but there were small differences between observers. Interestingly, all three observers' eye movements slowed down in the self-motion interval, doubtless because of the diversion of attention to the psychophysical task. This decrease averaged  $\sim 10\%$  and was highly significant for all three observers; the lowest value of  $\chi^2$  from the Gore test (for KVS) was 104,  $df = 1$ , which yields a  $p$ -value too small for MATLAB to compute.

### 3.4 Results

Observers perceived the displays to be simulating linear approach to a frontoparallel wall, but their judgments of the point of impact were generally inaccurate. Heading error (the visual angle between true and estimated points of impact) is plotted in figure 3b for three observers as a function of the nominal retinal velocity (ie assuming perfect pursuit performance) of the prior motion stimulus. During real pursuit, '0' indicates that the reference stimulus moved along with the pursuit target, '9' that it was stationary on the screen, and '18' that it moved in the opposite direction; during simulated pursuit, these correspond to the actual speeds on the screen. 'N' indicates that the prior stimulus period was blank, as in the Crowell et al (1998b) experiments.

The first thing to note is the improvement in the performance of all three observers caused by the mere addition of an objectively stationary prior stimulus during real pursuit (condition '9' in figure 3b). For two observers, this effect was large, but it was statistically significant even for the third (JW:  $D = 22$ ,  $df = 2$ ,  $p = 2 \times 10^{-5}$ ). This effect explains most of the discrepancy between the results of Crowell et al (1998b) and those of Royden et al (1994). Second, prior stimulus velocity had a significant effect on all observers' judgments: prior motion with (ie in the same direction as) pursuit degraded performance, but prior motion opposite to pursuit had little or no effect. These effects were much smaller or absent in the simulated-pursuit conditions; the data were not consistent with a model that required the data functions for real and simulated pursuit in the '0', '9', and '18' conditions of figure 3b to be parallel (smallest value of  $D$ , for JW, was 17.3,  $df = 5$ ,  $p = 0.004$ ). Because the retinal stimuli were very similar in the two



**Figure 3.** (a) Median pursuit speeds for three observers during the prior and self-motion intervals of the real-pursuit conditions of experiment 1. (b) Heading errors as a function of the nominal retinal velocity of the prior motion stimulus in experiment 1 for three observers during both real and simulated pursuit. 'N' represents a condition with no prior motion stimulus (ie a blank screen during that interval of the trial). Error bars represent approximate 90% confidence intervals and are in many cases smaller than the plot symbols.

sets of conditions, this means that the large effects during real pursuit were mediated by a nonlinear interaction between retinal and extra-retinal signals, as reported by Haarmeier and Thier (1996) for the Filehne illusion. Contrary to Haarmeier and Thier, we found a greater effect of prior motion with pursuit (the difference between conditions '0' and '9') than against pursuit (the difference between '9' and '18'); we have no explanation for this discrepancy. Finally, it is interesting to note that having no prior stimulus (ie a blank screen) was roughly equivalent to a prior stimulus that moved with pursuit, ie 'no prior stimulus' was similar to 'no retinal motion'.

#### 4 Experiment 2: Forward self-motion between floor and ceiling planes

The results of experiment 1 suggest that the presence of a static prior stimulus was necessary for accurate self-motion perception in previous experiments that simulated approach to a frontoparallel wall. Most studies of self-motion perception during simulated self-motion through a 3-D scene have found complete or near-complete pursuit compensation during real pursuit eye movements. In many of these studies a static display was presented during pursuit target acquisition. The results of experiment 1 suggest that the high degree of accuracy observed in these studies could have been

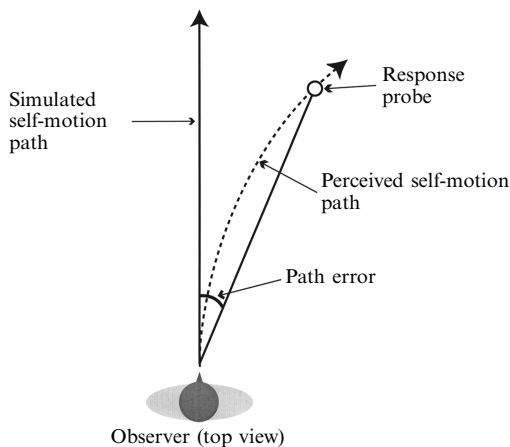
caused in part by the presence of this static prior stimulus. Experiment 2 was designed to test this hypothesis and to examine the effect of prior motion on self-motion judgments with more complex scenes.

#### 4.1 Displays

Earlier experiments have generally used scenes consisting mainly of a ground or floor plane. We added a ceiling plane to make the displays more similar in size and symmetry to those used in experiment 1. In the self-motion period of each trial, displays simulated linear, horizontal self-motion at  $3 \text{ m s}^{-1}$  between two planes positioned 160 cm above and below the eye. The two planes extended beyond the edges of the screen to either side and to a distance of 30 m in front of the observer. There was thus a vertical gap of 6 deg between the far ends of the two planes; pilot data indicated that the addition of such a gap would not have changed the results of experiment 1.

#### 4.2 Task

At the end of the self-motion period, a vertical line appeared that simulated a post standing on the ground 20 m in front of the observer. As illustrated in figure 4, the observer responded whether the perceived (possibly curved) self-motion path would continue to the left or to the right of the post.



**Figure 4.** The self-motion path task used in experiments 2 and 3. Observers were to respond whether their extrapolated self-motion path (which might or might not appear to be curved) would carry them to the left or right of the response probe.

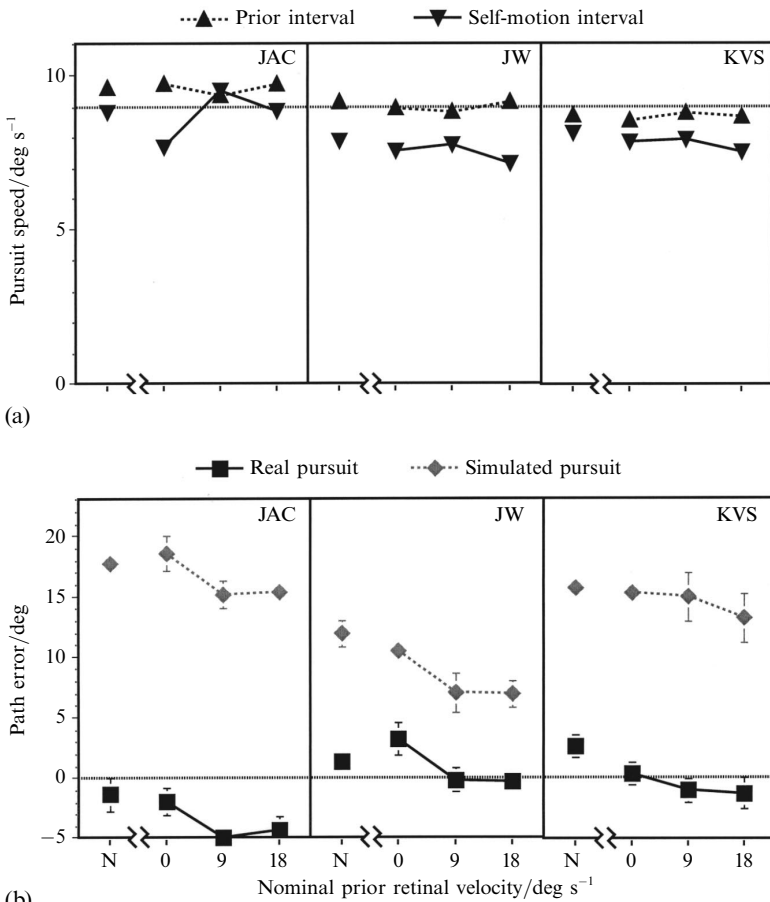
#### 4.3 Pursuit speed data

As in experiment 1, 18% of trials were rejected because of inadequate pursuit performance in this experiment. The median pursuit speeds in the prior and self-motion intervals of successful trials are plotted separately for the three observers in figure 5a. Interquartile ranges varied from  $\sim 0.9$ – $2 \text{ deg s}^{-1}$ . Again, there was a small ( $\sim 12\%$ ) but highly significant decrease in pursuit speed from the first to the second interval; the smallest  $\chi^2$  value from the Gore test (JAC) was 136, with a  $p$ -value too small to compute.

#### 4.4 Results

Judgments were quantified in terms of the path error, the visual angle between true and perceived self-motion paths at the post distance (figure 4). Figure 5b contains plots of path error during real and simulated pursuit against the nominal retinal velocity of the prior motion stimulus for three observers.

Interestingly, prior motion had a much smaller effect in this experiment than it did with the frontoparallel wall of experiment 1. The effect of prior motion in the real-pursuit conditions was not significantly different from that in the simulated-pursuit conditions: the largest value of  $D$  for a restricted model that required the data functions for real and simulated pursuit to be parallel (in the '0', '9', and '18' conditions



**Figure 5.** (a) Median pursuit speeds for three observers during the prior and self-motion intervals of the real-pursuit conditions of experiment 2. (b) Path errors as a function of the nominal retinal velocity of the prior motion stimulus in experiment 2 for three observers during both real and simulated pursuit. 'N' represents a condition with no prior motion stimulus (ie a blank screen during that interval of the trial). Error bars represent approximate 90% confidence intervals.

of figure 3b) was 1.81 for JAC,  $df = 5$ ,  $p = 0.87$ . This indicates that any effect of prior motion was probably a purely retinal effect; in other words, it could have been caused entirely by a classical retinal motion aftereffect, as described above. In particular, the absence of a static prior stimulus did not lead to much poorer performance in this experiment, as it did in experiment 1. We can conclude that the good pursuit compensation observed in many earlier studies of self-motion perception with respect to a 3-D scene was not caused by the presentation of a stationary prior stimulus.

### 5 Experiment 3: Floor and ceiling planes with mixtures of real and simulated pursuit

Why does a prior motion stimulus have a large effect on pursuit compensation with frontoparallel but not ground and ceiling planes?

One possible reason is the greater informational content of the scene consisting of floor and ceiling planes; it contains sufficient information to support a retinally based estimate of pursuit and self-motion parameters, whereas the frontoparallel wall does not. This point has been made in a number of theoretical papers on self-motion estimation on two different theoretical grounds. Some models of self-motion estimation

explicitly require depth variations in the scene in order to function (eg Longuet-Higgins and Prazdny 1980; Rieger and Lawton 1985). These models will fail in the presence of a single frontoparallel plane. Koenderink and van Doorn (1987) made the more general point that in the presence of noise, the performance of any self-motion model must degenerate as the amount of depth variation in the scene or the field of view decreases. Thus, we hypothesize that the visual system uses prior retinal motion in conjunction with extra-retinal signals to estimate pursuit velocity when the current retinal motion is uninformative (as in the case of a frontoparallel wall). When the current pattern of motion can provide such an estimate, however, the effect of prior retinal motion is overridden.

We can make this hypothesis more concrete by considering a particular feature of the retinal motion pattern that is specifically related to pursuit velocity. In experiments 1 and 2 the prior motion stimulus consisted of laminar motion along the pursuit axis, ie either with or against the eye movement. As one can see in figure 1c, the horizon of a ground or ceiling plane contains this kind of motion. Thus, in the case of our 3-D scenes, the self-motion display contains a region (near the horizon) in which the motion is similar to that in the prior motion interval; perhaps this laminar motion of the horizon overrides the effect of the prior motion stimulus. If so, then we should be able to affect pursuit compensation by manipulating the speed of laminar motion of the horizon during real pursuit.

A straightforward way to do this is to add a simulated pursuit to the self-motion display during real pursuit. As shown in figure 1b, the motion pattern created by simulated pursuit is laminar. In fact, if there are retinal mechanisms involved in pursuit compensation, then a simulated-pursuit motion pattern should be their preferred stimulus. Studies have already been reported in which observers were presented with such mixtures of real and simulated pursuit (Banks et al 1996; Beintema 2000), with apparently contradictory results. These studies will be discussed further below.

Can we affect the gain of pursuit compensation by mixing real and simulated pursuit?

### 5.1 Displays

The prior stimulus period [interval (iii)] was omitted. In the self-motion period of each trial, observers either fixated or pursued a target to the left or to the right at  $9 \text{ deg s}^{-1}$  while viewing displays simulating both forward translation and pursuit. Simulated pursuit was at  $2.25\text{--}9 \text{ deg s}^{-1}$  in steps of  $2.25 \text{ deg s}^{-1}$  in fixation trials and from  $9 \text{ deg s}^{-1}$  in the direction opposite to pursuit to  $4.5 \text{ deg s}^{-1}$  in the same direction as pursuit (with the same step size) in pursuit trials. It is important to note that we did not attempt to match the *retinal* motion patterns between fixation and pursuit conditions of this experiment; rather, we were interested in the effect of real pursuit versus fixation on the perception of the same displays.

### 5.2 Task

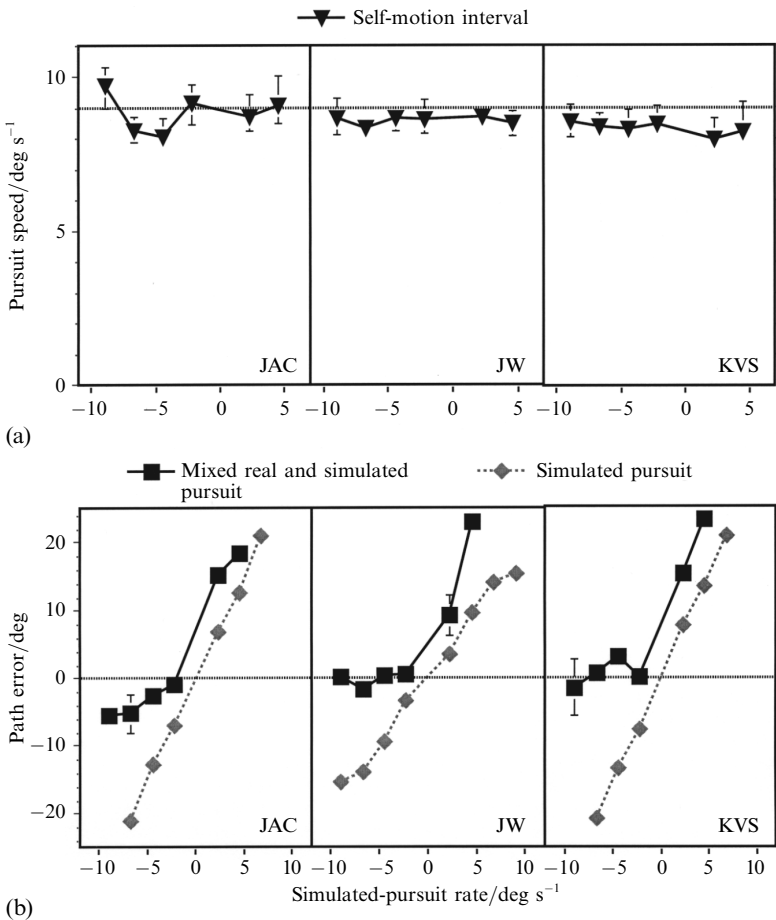
The task was the same as in experiment 2.

### 5.3 Pursuit speed data

23% of trials were rejected because of inadequate pursuit performance in this experiment. The median pursuit speeds in the self-motion intervals of successful trials are plotted separately for the three observers in figure 6a; error bars represent interquartile ranges.

### 5.4 Results

Path error (defined as in experiment 2) is plotted against simulated-pursuit velocity during fixation and real pursuit for three observers in figure 6b. For real pursuit, positive values on the horizontal axis indicate that real and simulated pursuit were in the same direction, negative values indicate that they were in opposite directions;



**Figure 6.** (a) Median pursuit speeds for three observers during the self-motion interval of the real-pursuit conditions of experiment 3. Error bars represent interquartile intervals. (b) Path errors as a function of simulated-pursuit speed in experiment 3 for three observers during purely simulated pursuit and mixtures of real and simulated pursuits. Real pursuit was always at  $9 \text{ deg s}^{-1}$  to the left or right. Positive abscissa values represent simulated pursuits in the direction of real pursuit, negative values indicate the direction opposite to the real pursuit. Error bars represent approximate 90% confidence intervals.

errors were averaged across leftward and rightward pursuit. Data for simulated pursuit during fixation were also averaged across leftward and rightward pursuit and reflected through the origin.

We found a large asymmetry in the pattern of errors with respect to the relative directions of real and simulated pursuit. When real and simulated pursuit were in the same direction, self-motion paths appeared extremely curved, and observers made large errors. In fact, under these conditions we were limited to a maximum simulated-pursuit speed of  $4.5 \text{ deg s}^{-1}$  by the width of the display; at higher speeds, observers' responses tended to place the probe off the edge of the screen. For the same reason, we were limited to a simulated-pursuit speed of  $6.75 \text{ deg s}^{-1}$  for JAC and KVS during fixation. On the other hand, when simulated pursuit was added in the opposite direction to the real pursuit, the two naïve observers did not always notice the addition and all three made much smaller errors. Lateral motion of the horizon caused by a simulated pursuit of  $-2.25 \text{ deg s}^{-1}$  was never noticed, whereas  $-4.5 \text{ deg s}^{-1}$  was usually detectable. When larger simulated pursuits were added in the opposite direction, a

paradoxical percept emerged. Observers reported that, although they were aware that the entire scene was moving with respect to the head, the motion pattern defined by the dots composing the floor and ceiling planes appeared radial. Hence, the simulated self-motion path appeared to be straight in the frame of reference of the simulated scene. They were instructed to respond solely on the basis of the path percept; thus, these data do not capture the entire percept in these conditions.

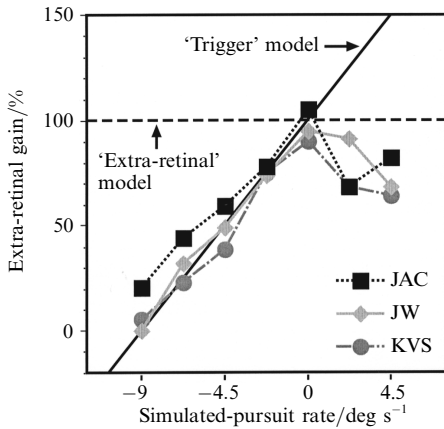
The symbols representing judgments with a simulated pursuit of  $-9 \text{ deg s}^{-1}$  during real pursuit are particularly interesting, as these represent the case of a radial motion pattern that was approximately stabilized on the retina during pursuit. The scene as a whole appeared to drift laterally relative to the head in this condition, but observers reported that the motion pattern nonetheless appeared to be roughly radial.

It is interesting to re-plot these data in terms of a purely extra-retinal compensatory gain—to calculate the effectiveness of pursuit compensation assuming that it is based entirely on extra-retinal signals. We can estimate this quantity from the two functions in each panel of figure 6b; the equation is derived in the Appendix. Briefly, it can be understood as follows: real pursuit at any given velocity adds a certain amount of laminar motion to the retinal motion pattern. If it were totally compensated for (ie if the compensatory gain were 100%), this added laminar motion should have no effect on the resulting percept; it should be perceptually cancelled out. However, the observer would not do well at the self-motion task when there was a component of simulated pursuit; there is additional laminar motion in the display caused by the simulated pursuit that should not be compensated for by a purely extra-retinal mechanism. Thus, if the compensatory gain were 100%, the subject should make the same judgment as in the corresponding simulated-pursuit condition; in other words, the squares in each graph of figure 6b should sit on top of the diamonds. If, on the other hand, the compensatory gain were 0%, then there should be little or no difference in performance between real and simulated pursuit; if pursuit were perfectly accurate, the retinal motion patterns would be identical, and the only difference between the two conditions would be a completely ineffective extra-retinal signal. Thus, the laminar motion added by the real eye movement should have the same effect as the same amount of laminar motion added by a simulated eye movement. The prediction for any given mixture of real and simulated pursuit is equal to the error in the simulated-pursuit condition at an abscissa value equal to the sum of the simulated and real pursuit velocities. Predictions for other gain values can be computed by linear interpolation between these two extremes.

The resulting gains are plotted in figure 7 as a function of the simulated-pursuit rate for each of the three observers. For the case of real and simulated pursuit in opposite directions, the gain is directly proportional to the total amount of pursuit-related flow in the retinal image (which falls to zero when real and simulated pursuits are equal and opposite, ie simulated-pursuit rate =  $-9 \text{ deg s}^{-1}$ ). When real and simulated pursuits are in the same direction, the gain once again decreases; we have too little data to examine the form of the decrease. Note also that calculating the extra-retinal gain for these conditions requires extrapolation of the simulated-pursuit data (as described in the Appendix) beyond any existing data.

Two predictions are also plotted in figure 7, based on the simple models described by Banks et al (1996). The *extra-retinal* model assumes that pursuit compensation is mediated by a purely extra-retinal signal with a gain of 100% regardless of the added simulated pursuit. Clearly, the data do not follow this prediction or that of any model assuming a purely extra-retinal compensatory signal (which would predict a horizontal line in figure 7). For the case of real and simulated pursuits in opposite directions, they are approximately consistent with the *trigger* model of Banks et al. In this model, the extra-retinal signal acts as a simple gate or trigger. The only information it





**Figure 7.** 'Extra-retinal' compensatory gain, calculated from the data of figure 6 as described in the Appendix.

carries is that an eye movement has occurred; the system then looks to the retinal image for information about the speed of pursuit. The data follow the prediction closely when real and simulated pursuits are in opposite directions. When real and simulated pursuits are in the same direction, on the other hand, the computed gains do not conform to any of the predictions of Banks et al (1996); as noted above, however, they are based on an extrapolation beyond any existing data.

## 6 Discussion

### 6.1 Summary of results

(i) During simulated approach to a frontoparallel wall, a static prior stimulus led to improved performance relative to a condition with no prior stimulus. Prior stimulus velocity had a much larger effect on observers' judgments during real than during simulated pursuit. Prior motion in the direction of the eye movement led to greater errors (ie decreased pursuit compensation); prior motion in the opposite direction had little or no effect. This implies that pursuit compensation is based on an interaction between retinal and extra-retinal pursuit-related motion signals.

(ii) Prior motion had a much smaller effect on performance during simulated translation through a more 3-D scene consisting of ground and sky planes. The effect during real pursuit was not significantly greater in magnitude than during simulated pursuit, a result that is consistent with a purely retinal motion aftereffect. Errors were small even in the absence of a prior stimulus.

(iii) We observed an asymmetrical pattern of errors during simulated translation through the 3-D scene with mixtures of real and simulated pursuits. Real pursuit in the same direction as simulated pursuit led to an increase in error over the corresponding condition of pure simulated pursuit. When real pursuit was opposite to simulated pursuit, observers made little or no error. The latter result is consistent with the 'trigger' model of Banks et al (1996), in which the only function of the extra-retinal signal is to inform the visual system that the eye is rotating, but not at what rate.

### 6.2 Other possible reasons for poor self-motion judgments during approach to a wall

We chose to concentrate on one difference between the experiments of Crowell et al (1998b) and those of Warren and Hannon (1990) and Royden et al (1994) to motivate our first experiment. There were other differences that could have contributed to the effect. First, eye movements were not monitored in either of the other studies. Pursuit gains less than one would have created less pursuit-related flow in the retinal image and could have led to slightly better apparent pursuit compensation. Also, in the case

of the Warren and Hannon experiment, a stationary display was visible for 1 s before the self-motion display and the pursuit target started moving. Because pursuit initiation is not instantaneous, observers must have been briefly fixating a stationary target immediately after the self-motion display began. It is conceivable that their judgments were influenced by the unperturbed radial pattern of retinal motion that they would have seen during this brief interval. Furthermore, the pursuit target in the Warren and Hannon experiment moved as though it were attached to the wall; in our experiments it moved across the wall at constant velocity.

It is also possible that the differences in performance were due in part to the differences in display duration between the three studies. The displays of Crowell et al (1998b) lasted only 500 ms in order to minimize the difficulty of the monitored pursuit task, whereas the displays of Royden et al and Warren and Hannon lasted 1250 ms and 3000 ms, respectively. It is quite possible that this difference in duration contributed to the difference in results; extra-retinal signals might become more effective at longer durations. As mentioned in section 1, Grigo and Lappe (1999) have argued that extra-retinal signals become more important at stimulus durations greater than 500 ms. It would be interesting to repeat our experiments with a longer display duration.

### 6.3 *Prior studies of mixtures of real and simulated pursuit*

Self-motion judgments with mixtures of real and simulated pursuit have been examined in two other studies, with results that appear at first glance to conflict with each other; one of them appears to conflict with the results of our experiment 3.

Banks et al (1996) reported data from four experiments in which observers were presented with such mixtures. The least variable data they presented were from their experiments 1 and 4; in both of these experiments, observers made errors that increased in proportion to the amount of simulated pursuit and showed little or no effect of real pursuit. Recall that in experiment 3 we found an asymmetrical pattern of errors: when real and simulated pursuits were in opposite directions, our data supported their 'trigger' model; when real and simulated pursuits were in the same direction, the data did not support any of the simple models that they described. By contrast, they concluded that their results were consistent with their 'extra-retinal' model, in which pursuit compensation is entirely driven by extra-retinal signals. However, there were several differences between the experimental conditions, subject instructions, and displays of the two studies that could explain the differences in conclusions.

(a) The simulated scenes were different: In the Banks et al experiments they consisted of a 3-D random-dot cloud or of a ground plane with the fixation point attached to the ground; we used floor and ceiling planes with a pursuit target that moved laterally at constant speed.

(b) Our pursuits (both real and simulated) were considerably faster. The fastest combined pursuit speed in their experiments was  $7.5 \text{ deg s}^{-1}$ , so the real and simulated components were both slower than that.

(c) They combined real and simulated pursuits in the same direction only, whereas most of our data were collected for opposite directions.

(d) They did not monitor pursuit speed; pursuit inaccuracy could have affected their results.

(e) The display durations were quite different: 300 ms in our experiment 3 versus 1000–1260 ms in the Banks et al experiments. As mentioned above, it is possible that the importance of extra-retinal pursuit signals increases with display duration.

(f) The instructions given to the observers were considerably less specific; they were to indicate the 'heading' (a direction) with a mouse cursor. As Royden (1994) and Ehrlich et al (1998) have pointed out, without more specific instructions it is difficult to know what strategy observers are using in this situation when confronted with the percept of a curved self-motion path. This problem becomes particularly acute when

the distance of the response probe is not clearly specified, as a curved path exists in different directions at different distances. The response-probe distance was not clearly specified in any of the Banks et al experiments.

Finally, it is not necessarily the case that the two sets of results are even inconsistent. We can calculate an extra-retinal compensatory gain like that plotted in our figure 7 for some of the Banks et al data. We obtain gains in the range  $\sim 70\%–130\%$  for the highest pursuit speeds used in their experiments 2 and 4 (data from their figures 6 and 10). Our results for real and simulated pursuits in the same direction fall entirely within this range ( $\sim 70\%–90\%$ ). Furthermore, our calculation of the extra-retinal gain is most assumption-laden when the two pursuit components are in the same direction, as it requires extrapolation of the simulated-pursuit data. Thus, there may not be a real discrepancy between the two sets of results.

More recently, Beintema (2000) also examined self-motion judgments during mixtures of real and simulated pursuit. He presented observers with displays simulating self-motion through a 3-D random cloud; they had to use a mouse cursor to indicate the heading direction. Thus, they might have been subject to the concerns regarding response strategy raised in (f) above. Beintema reported that performance with equal and opposite real and simulated-pursuits (comparable to the point plotted as a black square at a simulated-pursuit rate of  $9 \text{ deg s}^{-1}$  in our figure 6b) was considerably more accurate than would be predicted from a simple extra-retinal model of heading perception. Beintema also reported that observers often were unsure whether a given trial contained equal and opposite real and simulated pursuits or ordinary real pursuit with no added simulated pursuit. Our observers were always aware of the difference between these two conditions because of the apparent lateral head-centric motion of the scene, but the motion patterns did appear very similar. Unfortunately, Beintema did not include a pure simulated-pursuit condition, so we cannot directly compare the extent of pursuit compensation to that of Banks et al (1996) or of our experiment 3.

#### 6.4 *Explaining the slalom illusion*

Our results provide a partial explanation for one puzzling result: the low compensatory gain observed by Freeman et al (2000) in their study of the slalom illusion. They had observers pursue a sinusoidally oscillating target during simulated self-motion across a ground plane. Observers adjusted (between presentations) the speed of an added simulated pursuit to make the path appear to be as straight as possible. From the resulting settings they estimated the extra-retinal:retinal gain ratio (equivalent to our 'compensatory gain') to be around 70% on average, a figure that appears to conflict with the higher values reported in most studies of self-motion perception.

However, our results suggest that in adjusting the amount of simulated pursuit observers may have been simultaneously adjusting the compensatory gain. Suppose, for example, that a given observer had an initial compensatory gain of 90%. To this observer, a simulation of self-motion on a linear path viewed with no simulated pursuit would appear slightly curved. If the observer were to add a simulated pursuit equal to  $-10\%$  of the real pursuit, then the self-motion path should now appear straight—if the compensatory gain were in fact constant. However, by adding a simulated pursuit, the observer would have decreased his or her compensatory gain, and as a result the self-motion path would still appear slightly curved. Thus, the observer would add a bit more simulated pursuit on the next trial, further decreasing the compensatory gain, and so forth. The part missing from this account is an explanation of why observers stopped at an added simulated-pursuit velocity of  $-30\%$  of the real pursuit. Perhaps they stopped when the perceived head-centric motion of the entire scene reported by our observers became reliably detectable; the subjective reports

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from our experiment 3 suggest that this would occur with a simulated pursuit between  $-25\%$  and  $-50\%$  of the real pursuit.

### 6.5 Pursuit compensation in the perception of motion in the frontal plane

In our experiments we examined relative 3-D motion between observer and scene. However, these experiments were motivated by an earlier study of the effect of prior motion on the perception of motion in the frontal plane. As described in section 1, Haarmeier and Thier (1996) reported that prior motion changed the Filehne illusion; we found a qualitatively similar effect of prior motion on perceived self-motion towards a frontoparallel wall, but not on perceived self-motion through a 3-D scene. This suggests that pursuit compensation during self-motion is partially mediated by the same mechanisms as pursuit compensation for the perception of object motion in the frontal plane. We will draw further parallels between our results and results from the perception of frontal-plane motion below.

### 6.6 Asymmetries in perception of speed in the frontal plane during pursuit eye movements

Two recent studies on the perception of speed in the frontal plane during eye movements have found asymmetrical patterns of errors, qualitatively similar to those from our experiment 3. Brenner and van den Berg (1994) found that the function relating actual speed of an object to its perceived speed during smooth-pursuit eye movements depends dramatically on the relative directions of eye and background motion. They had observers pursue a target that initially moved at  $1.5 \text{ deg s}^{-1}$  across a stationary  $35 \text{ deg} \times 22 \text{ deg}$  random-pixel background. After a random 500–800 ms interval, the background started moving and the pursuit target simultaneously changed speed. No stationary references were visible around the display, although it seems (it is not explicitly stated) that the clipping window around the moving background was stationary and texture disappeared when it moved across this boundary. Observers judged whether the target speed had increased or decreased between the first and second intervals. The target speed in the second interval was adjusted by using a staircase until it appeared equal to that in the first interval; the background speed in the second interval was held fixed within each run.

A purely extra-retinal model of pursuit compensation would predict that perceived target speed would be unaffected by background motion. The simplest purely retinal model, on the other hand, would assume that the background represented a stationary world, and hence would predict that perceived speed should depend only on the relative speeds of target and background (barring any influence of the static clipping window). The prediction of this simple, purely retinal model was fulfilled when target and background moved in opposite directions. When they moved in the same direction, on the other hand, the data fell between the two predictions, asymptoting at  $65\%$ – $70\%$  in favor of the extra-retinal prediction. Brenner and van den Berg concluded that retinal motion signals do contribute to pursuit compensation in the perception of object motion. How similar is that contribution to the one we have found for self-motion perception?

We can compare their results to ours from experiment 3 by noting that simulated pursuit in the same direction as real pursuit in our experiment adds laminar motion (similar to the motion of Brenner and van den Berg's background) in the direction opposite to the eye movement. We can use this similarity to derive an extra-retinal compensatory gain for their data analogous to the one plotted in figure 7. This function has a very simple form: in the conditions corresponding to the portions of figure 7 to the left of the vertical axis (background motion in the same direction as the eye movement), the extra-retinal gain estimated from their data is  $\sim 70\%$ ; in the conditions corresponding to the portions of the figure to the right of the axis (background motion

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in the direction opposite the eye movement), it is zero. These data clearly do not predict our self-motion data in figure 7 quantitatively. It is possible that the prediction for the right side of the graph would have been met if we had been able to use higher pursuit speeds. The prediction for the left side, however, is clearly violated; our results indicate that retinal pursuit-related signals are more important during self-motion than in the perception of frontal plane motion. We speculate that the percept studied by Brenner and van den Berg is more directly related to the perceived lateral head-centric motion of the scene reported by the observers in experiment 3.

Turano and Heidenreich (1999) performed a similar speed-matching experiment to that of Brenner and van den Berg (1994). There were two important differences between the two experiments. First, Turano and Heidenreich's displays were generally considerably smaller (8 deg in diameter, in all but one of the experiments). Second, observers had to judge the speed of motion of the background, not that of the pursuit target. When the background moved in the same direction as the eye, the same objective speed appeared to be slower during pursuit; the background speed had to be increased to match that of the standard. The extent of the decrease in perceived speed is difficult to estimate precisely because of the variability in the data, but in some cases equal retinal speeds were perceived to be equally fast. When the background moved opposite to the pursuit, the effect depended on stimulus size: large backgrounds (38 deg  $\times$  28 deg) generally appeared to be moving slower during pursuit, whereas small ones (8 deg across) generally appeared to be moving faster.

These experiments are more difficult to interpret. When the background target was small, Turano and Heidenreich (1999) found the matched speed to fall between the true speed and the retinal speed of the background, consistent with a purely extra-retinal pursuit-compensation mechanism with a gain considerably less than 100%. This result is qualitatively consistent with our self-motion results in experiment 1. We interpret both results to mean that when the retinal information about pursuit velocity is poor, pursuit compensation is also poor. In the case of Turano and Heidenreich, the retinal information was poor because the background was small and less likely to represent a stationary scene. It was poor in our case because the motion pattern specified self-motion of the observer but did not provide sufficient information to simultaneously determine the translational and rotational velocities, as discussed previously. Turano and Heidenreich's large-background results can be explained by assuming that retinal motion of large backgrounds contributes a retinal signal to pursuit compensation. In order for the retinal motion of the background to provide a valid estimate of pursuit velocity, the background must logically be assumed to be objectively stationary. Thus, any tendency to use the retinal motion of the background as a compensatory signal should decrease its perceived speed.

### 6.7 *What is the retinal stimulus for pursuit compensation?*

We have established that the effect of a prior motion stimulus is overridden in the case of self-motion with respect to floor and ceiling planes, but not in the case of approach to a frontoparallel wall. We pointed out that this difference is probably a consequence of the fact that there is insufficient information in the latter case to estimate pursuit velocity from the retinal motion pattern (Koenderink and van Doorn 1987). We also speculated that the portion of the motion pattern created by distant points in a 3-D scene (in our displays, the horizons) might be important in this regard. This is not a novel notion. Perrone (1992) presented a model of self-motion perception during pursuit that explicitly used the motions of such distant points to derive a retinally based estimate of pursuit velocity. Komatsu and Wurtz (1988) reported that many neurons in cortical area MST respond optimally to pursuit eye movements in one direction and to large-field laminar motion in the opposite direction; this consti-

tutes the desired behavior for integrating extra-retinal pursuit signals with those derived from retinal motions of distant points in the scene. Finally, van den Berg and Brenner (1994) presented evidence that the horizon of a ground plane is important in psychophysical self-motion judgments; they reported that truncating a ground plane closer to the observer (ie removing the dots closest to the horizon) increased errors in self-motion perception during simulated pursuit. This hypothesis suggests that people would try to move the eyes less while moving around in enclosed spaces. However, it should be pointed out that our results can also be explained by assuming that motion parallax (a gradient of motion from one part of the visual field to another, as created by movement through a 3-D scene) is required for there to be a significant retinal contribution to pursuit compensation. The results of Brenner and van den Berg (1994) and Turano and Heidenreich (1999) for frontal-plane motion are not subject to this explanation.

#### 6.8 *Do extra-retinal signals provide metric information about pursuit velocity?*

The results of experiment 3, under conditions where real and simulated pursuits were in the same direction, are consistent with the idea that metric information about pursuit velocity comes primarily from the retinal image, while the extra-retinal signal simply acts as a logical gate; ie it tells the visual system whether or not the eye has moved. However, for reasons discussed above, it is unlikely that the poor pursuit compensation observed during approach to a frontoparallel wall by Crowell et al (1998b) and in our experiment 1 in the 'no prior motion' condition could have had a significant retinal contribution. More concretely, at these display sizes and short durations, the retinal motion pattern is essentially purely radial; there is no laminar component from which to derive an estimate of pursuit velocity. Thus, there must be an extra-retinal signal providing metric information about pursuit velocity. However, it appears to underestimate the actual pursuit speed by roughly half at the short durations we used.

### 7 Conclusions

We examined the effect of prior motion of a retinal stimulus on self-motion judgments during real and simulated pursuit with two types of scenes: a frontoparallel wall and a more 3-D scene consisting of floor and ceiling planes. Our conclusions apply particularly to brief stimulus durations and to responses based on the perceived form of the motion pattern rather than on perceived head-centric motion. We conclude that: (1) prior motion affects pursuit compensation when the scene consists of a wall, but has little effect with a more 3-D scene (consisting of floor and ceiling planes). (2) This effect is mediated by a nonlinear retinal/extra-retinal interaction; the same prior motion has little or no effect during simulated pursuit. (3) Prior motion is probably ineffective with a 3-D scene because the retinal motion pattern caused by self-motion provides sufficient information to support an accurate estimate of pursuit velocity. This retinal pursuit signal overrides the effect of the prior motion stimulus. And, finally, (4) the relative effectiveness of retinal and extra-retinal signals appears to depend in general on their relative informativeness. When there is sufficient retinal information to support accurate estimates of pursuit velocity and self-motion parameters, the extra-retinal signal acts as a simple 'trigger' under many conditions, specifying only that the eye is moving; metric information about pursuit speed may be derived entirely from retinal motion signals. When there is insufficient retinal information to estimate pursuit velocity, however, a purely extra-retinal estimate is used.

**Acknowledgements.** The authors would like to thank observers KVS and JW for contributing their time and irritated eyes to these experiments, and Jim Todd, Del Lindsey, and Johanna Weber for commenting on various drafts of the manuscript. The data presented here were collected in the

Division of Biology at the California Institute of Technology, and the experiments were supported by grants from the National Eye Institute and Human Frontiers to Richard A Andersen.

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## APPENDIX

### Derivation of 'extra-retinal' compensatory gains

We define the compensatory gain as the proportion of the total potential error due to added pursuit-related image motion that is compensated for. We further assume that our observers' performance during purely simulated pursuit represents a complete lack of pursuit compensation, which is reasonable from the point of view of a purely extra-retinal model. We also assume that we can use a line to extrapolate the simulated-pursuit data to higher pursuit speeds; this seems reasonable on the basis of the existing literature, but predictions for this regime (the portion of figure 7 to the right of the vertical axis) may be taken with a grain of salt.

Given these assumptions, the predicted error in the absence of any extra-retinal pursuit compensation ( $E_0$ ) is given by:

$$E_0 = M_{\text{sim}}(V_{\text{sim}} + V_{\text{real}}),$$

where  $M_{\text{sim}}$  is the slope of the simulated-pursuit error function and  $V_{\text{sim}}$  and  $V_{\text{real}}$  are the simulated-pursuit and real-pursuit velocities, respectively (following the convention of figure 6,  $V_{\text{real}}$  was always  $+9 \text{ deg s}^{-1}$  during real pursuit). If, on the other hand, extra-retinal pursuit compensation were perfect, then we would expect the real component of the total pursuit to have no effect on the observers' responses; in other words the predicted error ( $E_{100}$ ) would be given by:

$$E_{100} = M_{\text{sim}} V_{\text{sim}}.$$

All that remains is to fit a line to these two points yielding error  $E$  as a function of gain  $G$ :

$$E = E_0 + G(E_{100} - E_0),$$

which implies that

$$G = \frac{E - E_0}{E_{100} - E_0} = 1 + \frac{MV_{\text{sim}} - E}{MV_{\text{real}}},$$

where  $E$  is the error observed for any given combination of  $V_{\text{real}}$  and  $V_{\text{sim}}$ .