Do we have direct access to retinal image motion during smooth pursuit eye movements?

Tom C. A. Freeman   School of Psychology, Cardiff University, UK

Rebecca A. Champion   School of Psychology, Cardiff University, UK

Jane H. Sumnall   School of Psychology, Cardiff University, UK

Robert J. Snowden   School of Psychology, Cardiff University, UK

One way the visual system estimates object motion during pursuit is to combine estimates of eye velocity and retinal motion. This questions whether observers need direct access to retinal motion during pursuit. We tested this idea by varying the correlation between retinal motion and objective motion in a two-interval speed discrimination task. Responses were classified according to three motion cues: retinal speed (based on measured eye movements), objective speed, and the relative motion between pursuit target and stimulus. In the first experiment, feedback was based on relative motion and this cue fit the response curves best. In the second experiment, simultaneous relative motion was removed but observers still used the sequential relative motion between pursuit target and dot pattern to make their judgements. In a final experiment, feedback was given explicitly on the retinal motion, using online measurements of eye movements. Nevertheless, sequential relative motion still provided the best account of the data. The results suggest that observers do not have direct access to retinal motion when making perceptual judgements about movement during pursuit.

Introduction

The information contained in visual images is often distorted by perspective geometry, ambient illumination, and eye movement. When it is, retinal image data needs to be rescaled or transformed in order to recover objective estimates of real-world properties. Classic examples of this process at work are the perceptual constancies of size, speed, lightness, and colour. Given that an objective description of the world is the main goal of visual processing, it is possible that observers are unable to access retinal image data directly. This would appear to be the case for judgements of size. Burbeck ([1987](#)) presented a pair of gratings on two screens separated in depth and found that objective spatial-frequency discrimination was unaffected even though retinal spatial frequency had doubled. McKee and Welch ([1992](#)) added random changes in depth to a retinal size discrimination task and found performance deteriorated even though retinal angular size was unchanged. Bennett and Cortese ([1996](#)) found deterioration in spatial-frequency discrimination was lowest when test stimuli and an interleaved mask shared objective, not retinal, spatial frequency.

Using an analogue of their size constancy experiments, McKee and Welch ([1989](#)) found that binocular depth changes did not affect judgements of retinal speed. Unlike size perception, it appears that observers can directly access measurements of retinal image motion in certain situations. However, depth is not the only dimension along which retinal motion can become distorted and so it is unclear whether this finding is a general one. To investigate, we examined retinal speed discrimination in the presence of smooth pursuit eye movements.

In order to recover objective 'world' motion during pursuit, the observer needs to compensate for the ongoing eye movement. This is because pursuit adds a motion vector to each point in the retinal image, decoupling any straightforward relationship between retinal motion and object motion. To counteract this effect, the observer could use a number of different strategies. Some rely on estimating eye velocity, either by using regularities contained in the patterns of retinal motion (Brenner & van den Berg, [1996](#)) or by using information from non-visual sources, such as extra-retinal signals emanating from the motor system (Freeman, [2001](#); Souman, Hooge, & Wertheim, [2006](#)). Other strategies rely on reasonable assumptions about the statistics of motion, such as the fact that backgrounds are mostly static (Wallach, [1959](#)), that pursuit-related retinal motion is locally smooth (Rieger & Lawton, [1985](#)), or that eye movements and other forms of self-motion yield tell-tale patterns of whole-field motion

(Rushton & Warren, 2005). In the current experiments, we presented random dot planes moving in a dark room and so eliminated most of these strategies, encouraging the observer to rely on extra-retinal information about eye velocity.

Recent work has suggested that under similar constraints, direction discrimination based on extra-retinal information is about as good as that obtained with retinal motion. Krukowski, Pirog, Beutter, Brooks, and Stone (2003) used a single moving point and found direction discrimination thresholds were the same whether the point was tracked by eye or viewed with stationary fixation. They also found similar 'oblique' effects for pursuit and fixation conditions—in both cases, motion sensitivity was best along cardinal directions. On the basis of these results, Krukowski et al. suggested that 'retinal' and 'extra-retinal' motion pathways shared a common noise source, one further along the motion pathway and associated with the mechanism estimating object direction. This suggests that observers do not have direct access to retinal motion.

Other work also questions the generality of McKee and Welch's (1989) findings. Turano and Heidenreich (1996) found that speed discrimination during pursuit was worse than expected on the basis of retinal motion alone. They were able to rule out the use of the relative motion between pursuit target and motion stimulus, an issue that will become relevant to the experiments reported here. Morvan and Wexler (2005) found retinal motion determined the detection of a moving target among moving distractors, but only for briefly presented stimuli (<130 ms). For longer durations, observers used a more object-based world frame, one that incorporated pursuit eye movements. Bedell and Lott (1996) found that the length of motion smear decreased during pursuit. Findings like these suggest that eye-movement compensation may occur quite early on in the processing of retinal motion information. Unlike the combination of retinal motion and depth, therefore, it is possible that observers do not have direct access to retinal motion during pursuit.

Experiment 1: Homogeneous vs. heterogeneous pursuit

Overview

To test this idea, we used a version of the paradigm developed by McKee and Welch (1989, 1992). The technique involved manipulating the correlation between retinal and objective motions. In our task, observers pursued a small moving target while making judgements of the retinal speed of a larger background object (a moving random dot pattern). Target and object moved independently, so that objective motion was the sum of retinal motion and pursuit. The target's speed was changed from trial to trial, allowing us to alter the correlation between retinal motion and objective motion by manipulating how pursuit varied. For an observer without direct access to retinal motion, retinal thresholds should rise as pursuit variability increases.

It is worthwhile understanding why indirect access leads to this prediction. As McKee and Welch (1989, 1992) discuss, one strategy available to the observer is to take an estimate of objective motion and recover retinal motion indirectly by using an estimate of eye speed. Such a strategy is unnecessary when the correlation is high, because both motion cues allow the observer to perform the task well. However, when the correlation is low, the internal noise associated with the estimate of eye velocity is counted twice if an observer uses the indirect strategy. Comparing conditions with high and low correlations therefore reveals the type of strategy the observer is using.

To manipulate the correlation between retinal and objective motions, we varied pursuit target speed from interval to interval. The most obvious conditions to compare are ones containing trials run at a fixed pursuit target speed and another in which target speed varies. Unfortunately, finding elevated thresholds in the latter case could simply reflect general observer uncertainty, fuelled by increased between-trial variation. Hence we used a technique that tried to equate uncertainty while manipulating pursuit noise. In a low-variability 'homogeneous' condition, each trial consisted of two intervals run at one of three pursuit target speeds (P), with the constraint that $P_1 = P_2$ (subscripts denote interval). Target speed varied from trial to trial but was constant within a trial. Figure 1A (top) sketches three possible homogeneous trials, emphasizing that the difference in retinal speed (ΔR) was the same as the difference in object speed (ΔO) (note that each trial shows interval 1 speeds < interval 2 speeds, whereas in the actual experiment interval order was randomized). In a high-variability 'heterogeneous' condition (bottom), each trial contained two *different* pursuit target speeds. These were randomly chosen from the same set of three speeds, with the constraint that $P_1 \neq P_2$. Observers therefore always experienced the same variation of pursuit target speed across trials in both conditions. The key difference was the variation within trials. Unlike the homogeneous condition, the difference in retinal speed (ΔR) was not the same as the difference in object speed (ΔO), as shown in the figure.

We also compared psychometric functions constructed on the basis of ΔR and ΔO. Assuming observers have direct access to retinal motion, performance should be best described by changes in the increment ΔR. This was assessed using both threshold and goodness-of-fit measures. For instance, according to the direct-access hypothesis, the slope of the psychometric function should decrease in the heterogeneous condition when it is determined by ΔO, and its goodness of fit should fall.
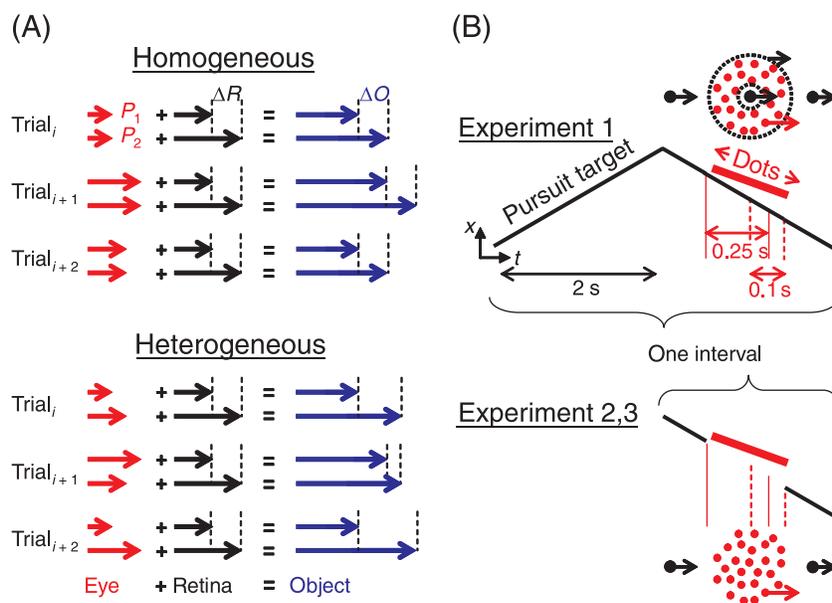
Figure 1. (A) Three example trials containing homogeneous pursuit (top) or heterogeneous pursuit (bottom). Each trial shows interval 1 speeds < interval 2 speeds whereas in the actual experiment, interval order was randomised. (B) Time courses for pursuit target and dot pattern. The inset stimuli show that in Experiment 1, the window (broken outline) moved with the pursuit target whereas in Experiments 2 and 3, neither window nor target appeared when the dots were visible.

Psychometric functions were also constructed for a third motion variable (ΔRel) based on the amount of relative motion between pursuit target and moving stimulus. The use of relative motion turned out to be critical to understanding performance in our 2AFC task. We identify two types. The first is the simultaneous relative motion between a concurrently viewed pursuit target and stimulus. The second is the sequential relative motion between a target and stimulus seen at different times. As will become clear, the use of simultaneous relative motion is relatively easy to control for whereas the use of sequential relative motion is not.

Methods

Stimuli

Each interval consisted of a pursuit target and random dot pattern displayed on the black background of a display screen. The random dot pattern had a density of 1 dot/deg^2 and was displayed through an annulus window (inner radius = 0.5°; outer radius 8°). Dots had a radius of 0.1° and the pursuit target 0.2°. Target, window, and dot stimulus all moved horizontally, with the motion of the window yoked to the pursuit. This ensured that approximately the same portion of retina was stimulated by the dots on each trial. This constraint was changed in later experiments.

In Experiment 1, the pursuit target moved for a total of two horizontal sweeps (left then right or right then left—Figure 1B). The two directions were always the

same for both intervals but alternated from trial to trial. In Experiments 2–3 the initial sweep was removed (bottom of Figure 1B). Each sweep lasted for 2 s. The mean dot duration was 0.25 s, with a random perturbation of 0.1 s added on each interval. This decorrelated retinal speed and the distance traveled by each dot. Prior to each interval, the pursuit target appeared for 0.5 s before moving.

Stimuli were presented on a ViewSonic P225f monitor at a frame rate of 100 Hz. Stimuli were controlled by a Radeon 9800 Pro graphics card using OpenGL. A red gel was placed over the screen to help eliminate phosphor glow and dot trails. All experiments were run in a completely darkened room.

Procedure

To measure retinal speed discrimination thresholds, one interval was randomly selected to display a retinal speed plus an increment ($R_m + \Delta R/2$) while the other displayed a retinal speed minus an increment ($R_m - \Delta R/2$). The speed R_m is sometimes referred to as a 'pedestal'. In the current experiments, it equaled the mean speed across the two intervals. ΔR was controlled by two randomly interleaved 3-down 1-up staircases. Staircases were terminated after 9 reversals, with the step size before the first reversal set to 1 octave and the step size for the last 8 reversals set to 0.5 octaves. Each observer completed at least three replications.

Observers were asked to judge which interval contained the faster retinal speed. Feedback was given following

each trial to help promote retinal speed judgements. In Experiment 1, the feedback assumed accurate pursuit and so in fact promoted judgements of the relative motion between pursuit target and dot pattern. This turns out to be an important feature of our method. In later experiments we sought to eliminate the relative motion cue as well as providing feedback on the actual retinal motion associated with each trial.

In Experiment 1 the retinal motion was always in the same direction as the pursuit target. Homogeneous and heterogeneous conditions were presented in separate sessions in a counterbalanced order. Each session lasted about 30 minutes. Individual trial pursuit target speeds were selected from the three speeds of 4, 8, and 12°/s. Pedestal speeds of 1°/s and 8°/s were investigated. All thresholds for the faster pedestal were collected before the slower.

Eye-movement analysis

In Experiments 1 and 2 an ASL Series 5000 eye-tracker recorded the eye position of the left eye using video-oculography at a sampling rate of 60 Hz. Data were first low-pass filtered and the time-derivative taken. Saccades were then detected using a velocity threshold. A trial was discarded ($\approx 1\%$ of total) if the saccade occurred in either interval during the time the dot stimulus was visible (thick red lines in Figure 1B). The same region of interest was used to determine pursuit performance in the remaining trials. Specifically, mean gain (mean eye velocity/target speed) and standard deviation were calculated within the region of interest, yielding two measures of pursuit performance per interval. Example histograms of these are shown in Figure 2. Trials containing any outliers

$(0.5 < \text{gain} < 1.5$ and $\text{STD} > 2°/s)$ were discarded ($\approx 15\%$ and 30% of total, respectively). The latter exclusion criterion tended to lower thresholds across the board. This suggests a link between the precision of eye movement and the precision of perceived speed, a finding that echoes the work of Gegenfurtner, Xing, Scott, and Hawken (2003) and Kowler and McKee (1987). We hasten to point out, however, that those studies compared the variability of eye movement with the ability to discriminate the speed of the *pursuit target*. Our thresholds, on the other hand, correspond to the precision of motion signals relating to the surrounding stimulus.

Psychophysical analysis

Separate response curves were constructed by plotting the frequency of decisions against the three motion variables of interest: the difference in retinal motion (ΔR), the difference in objective motion (ΔO), and the difference in relative motion (ΔRel). The relative motion is defined here as the difference in speed between pursuit target and dot pattern and is equal to R if pursuit is accurate. The three analyses therefore consisted of exactly the same set of trials but distributed in different ways within the response curve. Retinal speed increments were based on the recorded eye movements. Specifically, each interval's pursuit gain was used to estimate the true mean retinal speed increment (ΔR_{actual}) for each trial. Inevitably this meant that each trial was unique, so a histogram procedure was used to determine threshold. Trials were placed in 2°/s bins and responses coded accordingly. Bins containing 2 trials or less were discarded and then the response frequencies plotted against the mean speed in each bin (for convenience, we used signed increments as
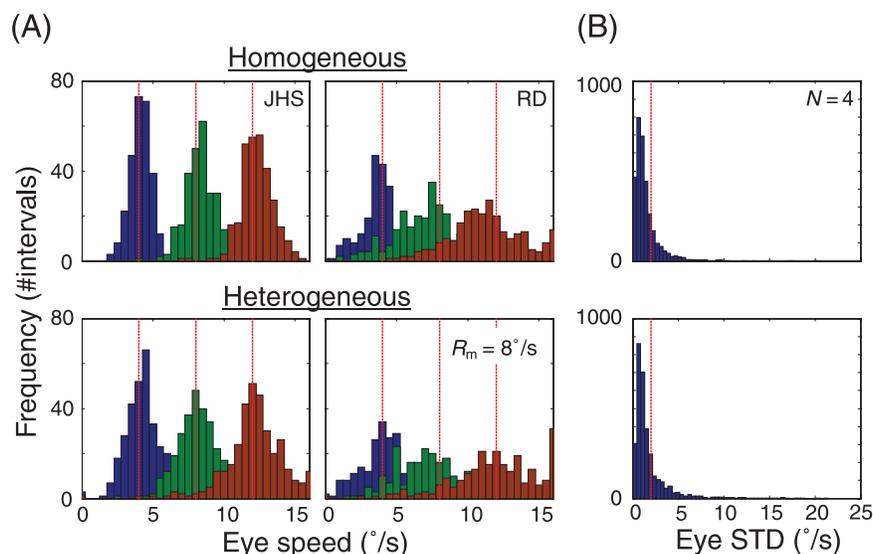

Figure 2. (A) Histograms of eye movement speeds for two observers. Different colours correspond to different pursuit speeds. Vertical dashed lines define target speeds. (B) Histograms of eye movement variability collapsed across all four observers. Vertical dashed line defines exclusion criterion (see text for details).

opposed to collapsing over increments and decrements—see Results section for examples). Psychometric functions were fit using probit analysis. Thresholds were defined as the unsigned speed difference between 75% and 50% points. Deviance was used to assess goodness of fit (Wichmann & Hill, 2001). Higher values mean poorer fits.

Using eye-movement recordings to convert trials into actual retinal motion is a departure from the usual custom of 'trimming'. The latter involves removing trials outside some fixed range of eye-movement accuracy, either at runtime (Crowell & Andersen, 2001) or post experiment (Krukowski et al., 2003). The analysis described here makes fewer assumptions about the accuracy of pursuit contained in each trial. However, it does assume that the eye moved at a constant speed when the dots were visible, an issue discussed further in Experiment 2.

Observers

Two authors (TCAF, JHS) and two naive observers (RD, PJH) took part in Experiment 1. All had normal or corrected vision.

Results

Figure 2A plots example histograms of pursuit speeds for JHS and RD. The vertical red lines define target speeds. The histograms show that different observers and different conditions can change the variability and position of the eye-movement distributions. These would be difficult to account for using standard 'trimming' techniques. Figure 2B summarizes the variability of eye speed across all observers. The distribution is positively skewed. The vertical red line defines the cut-off STD used to reject 'imprecise' trials.

The black points and black curves in Figure 3 show examples of the binning technique for one naive observer at a pedestal of 8°/s. The figure shows responses binned by ΔR_{actual} or ΔO (see labels on *x*-axis).

This makes little difference to the data in the homogeneous condition. Thus the slopes of the curves in the left-hand graphs are similar, as is the goodness of fit. Retinal speed discrimination thresholds are unaffected by pursuit mixture, as demonstrated by the similar slopes for ΔR_{actual} functions (compare first and third graphs). This observer therefore appears to have direct access to retinal motion during pursuit, a conclusion further supported by comparing heterogeneous data binned by ΔR_{actual} or ΔO. The latter is plotted in the right-hand graph and shows a shallower slope and decreased goodness of fit. For this observer, object speed increments do not predict performance nearly as well as retinal speed increments.

Figure 3 also shows psychometric functions fit to the unbinned data (red points and red curves). The thresholds differed little between the two types of analysis—the red curves plot almost exactly on top of the black curves. Our decision to use the binning technique was based on the more meaningful measure of goodness of fit it provides.

Figure 4 summarises thresholds and deviances for the two pedestal speeds, averaged across the four observers. In accordance with the direct-access hypothesis, thresholds obtained using ΔR_{actual} (black bars) are very similar in the homogeneous and heterogeneous conditions, whereas thresholds obtained using ΔO (white bars) increase substantially in the heterogeneous condition. This interpretation is supported by the goodness-of-fit measures shown in the bottom row. Deviance rises substantially for the ΔO thresholds in the heterogeneous condition.

The comparisons between ΔR_{actual} and ΔO data therefore appear to support the idea that observers have direct access to retinal motion. However, the results for the homogeneous condition also show that ΔO thresholds were lower than ΔR_{actual} thresholds, especially at the slower pedestal speed. Why is this? Pursuit target and annulus window were always visible when the dot pattern appeared. Hence the stimuli contained a relative motion cue, specifically the speed difference between dot pattern and the target and window. In the homogeneous condition, the difference in relative motion between the two intervals
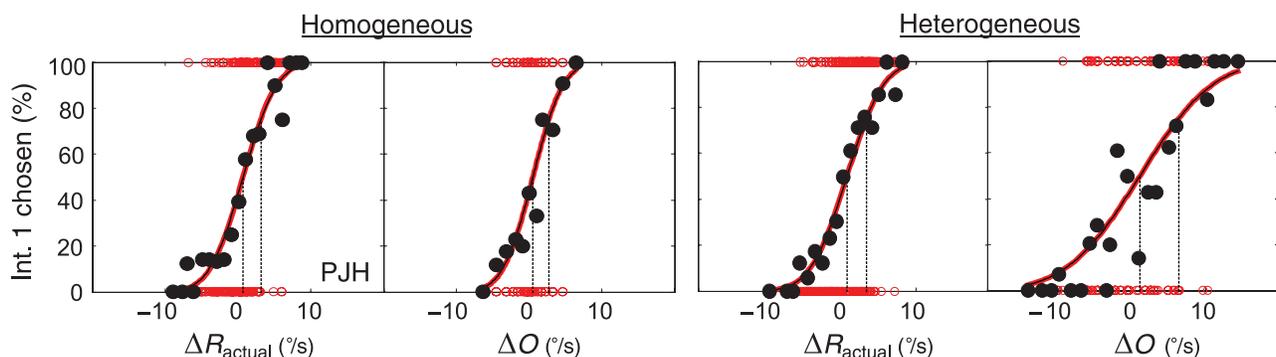

Figure 3. Example psychometric functions for one observer in the faster retinal speed condition ($R_{\text{m}} = 8°/s$). First and third panels show response data plotted against actual retinal speed (ΔR_{actual}) estimated using eye movement recordings. Second and fourth panels show response data plotted against objective speed on the screen (ΔO). Different colours correspond to different analyses (see text for details).
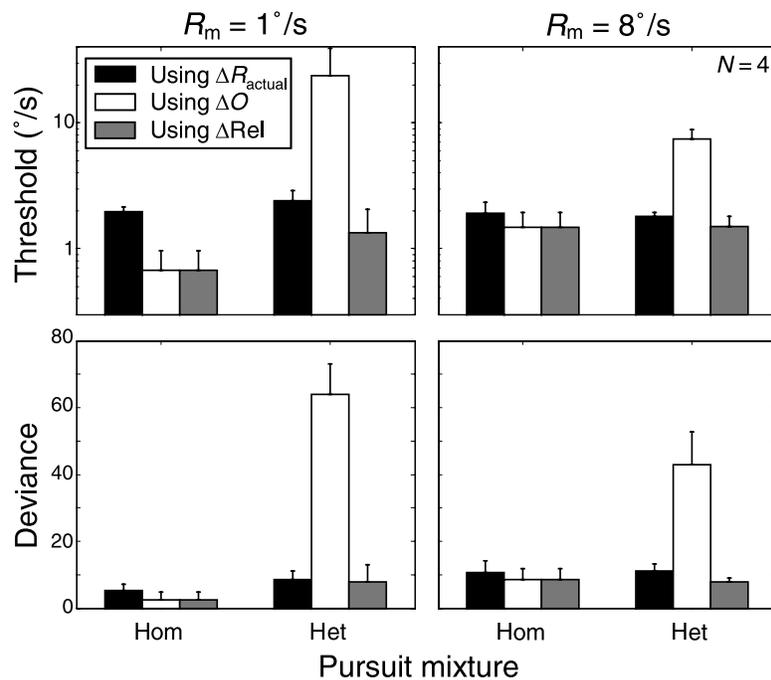
Figure 4. Mean thresholds (top row) and deviances (bottom row) averaged across the 4 observers. Different coloured bars correspond to analyses based on three different motion cues: actual retinal motion (ΔR_{actual}); objective screen motion (ΔO); relative motion (ΔRel). Error bars are +1 *SE*.

is identical to the difference in objective motion (in both cases the speed of the pursuit target is cancelled when calculating the increment). Given that the objective motion provided the poorest explanation of the data in the heterogeneous condition, it seems likely that the lower thresholds and better fits in the homogeneous condition are the result of observers using relative motion. Importantly, the heterogeneous condition decorrelates all three types of motion cue. To obtain a clearer picture, we therefore constructed a third set of response curves by plotting frequency of decisions against the difference in relative motion between the two intervals, ΔRel.

The grey bars in Figure 4 show the result. As expected, ΔO and ΔRel thresholds were identical in the homogeneous condition and lower than the R_{actual} thresholds. More importantly, the ΔRel thresholds gave the best account of the responses in the heterogeneous condition. This is consistent with evidence suggesting that the perceived speed of pursued targets is dominated by relative motion (Brenner & van den Berg, 1994; Spering & Gegenfurtner, 2007). Perhaps the result is not too surprising because the feedback given to observers was based on this cue. To investigate further, the relative motion cue was removed in Experiments 2 and 3. This was achieved by turning off the pursuit when the dots were visible and making the circular window move with the dot pattern. Hence at no point during the motion sequence did the display contain *simultaneous* relative motion between dots and pursuit/window. We hasten to

point out that the relatively brief disappearance of the pursuit target did not seriously disrupt the ongoing eye movement (see below).

The two experiments differed in the type of feedback given. In Experiment 2, the feedback protocol remained unchanged. Because simultaneous relative motion had been removed from the displays, the feedback was therefore defined by the *sequential* relative motion between a pursuit target and dot pattern (i.e., the speed difference between two objects seen at different times). To anticipate, we found that observers based their judgements on this form of relative motion. Hence, in Experiment 3, the protocol was altered so that feedback was determined by the actual retinal motion present in the display. This required on-line analysis of the eye-movement data between each trial, as discussed below.

The direction of retinal motion in Experiment 1 was always the same as the eye movement. Object motion was therefore faster than the pursuit target. Evidence from studies of speed discrimination (Turano & Heidenreich, 1996), temporal contrast sensitivity (Schütz, Delipetkos, Braun, Kerzel, & Gegenfurtner, 2007), and perceived motion smear (Tong, Patel, & Bedell, 2006) suggest a more pronounced influence of eye movement when the retinal motion of the dot pattern moves in the opposite direction to the pursuit target. Direction asymmetries were also reported by Brenner and van den Berg (1994) in a motion perturbation task, although these were more pronounced when pursuit target and background moved

in opposing objective directions. Experiment 2 therefore compared conditions in which the pursuit target moved in the 'same' or 'opposite' direction to the retinal motion.

Experiment 2: Simultaneous relative motion removed

Methods

Stimuli

To remove the simultaneous relative motion between pursuit target and dot pattern, the target was extinguished when the dots were visible (Figure 1B, lower right). To remove the simultaneous motion between dot pattern and window, the latter was made to move with the dots. In other words, the dot stimuli consisted of a circular patch of texture that moved independently of the preceding pursuit target. Unlike Experiment 1, therefore, the part of retina stimulated by the dot pattern depended primarily on its velocity. All other stimulus details were the same as Experiment 1.

Procedure

In Experiment 1, homogeneous and heterogeneous conditions were run in separate blocks. In Experiment 2 they were both included in the same session. One staircase was assigned to each, with an equal probability of appearing in any given trial. This change to the procedure was used to limit any possible changes in strategy that observers might have adopted in Experiment 1 when confronted with homogeneous and heterogeneous conditions. It also equated uncertainty across these conditions (e.g., it was now impossible to predict the pursuit target speed in interval 2 based on the target speed shown in interval 1). Observers carried out 6 replications of 'same' and 'opposite' directions of motion, presented in randomised blocks.

A pedestal speed of 1°/s was chosen because this produced the greatest advantage for thresholds obtained using ΔRel in Experiment 1.

Observers

Two authors (TCAF, RAC) and two naive observers took part (RD, PAW). Two of these (RAC, PAW) had not participated in Experiment 1.

Results

Figure 5 plots the mean thresholds and goodness of fit. As in Experiment 1, objective motion increments ΔO gave the poorest account of the data, with thresholds rising substantially in the heterogeneous condition and goodness of fit declining markedly. Both retinal motion and relative motion increments gave better accounts, with little evidence that the direction of motion affected thresholds based on these motion cues. These thresholds were also similar for homogeneous and heterogeneous conditions,
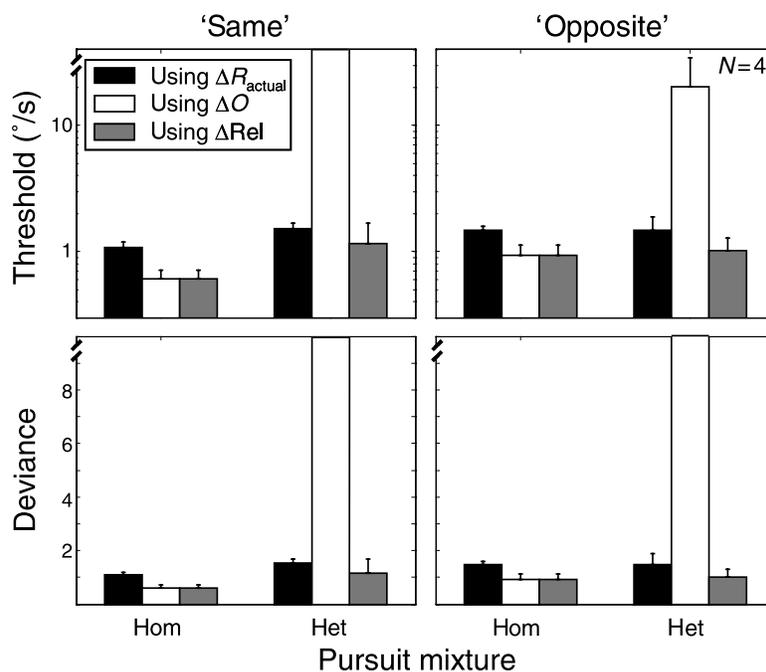

Figure 5. Mean thresholds (top row) and deviances (bottom row) averaged across the 4 observers. The axes limits in three graphs have been truncated and the deviance range is smaller than Figure 4. Error bars are +1 *SE*.
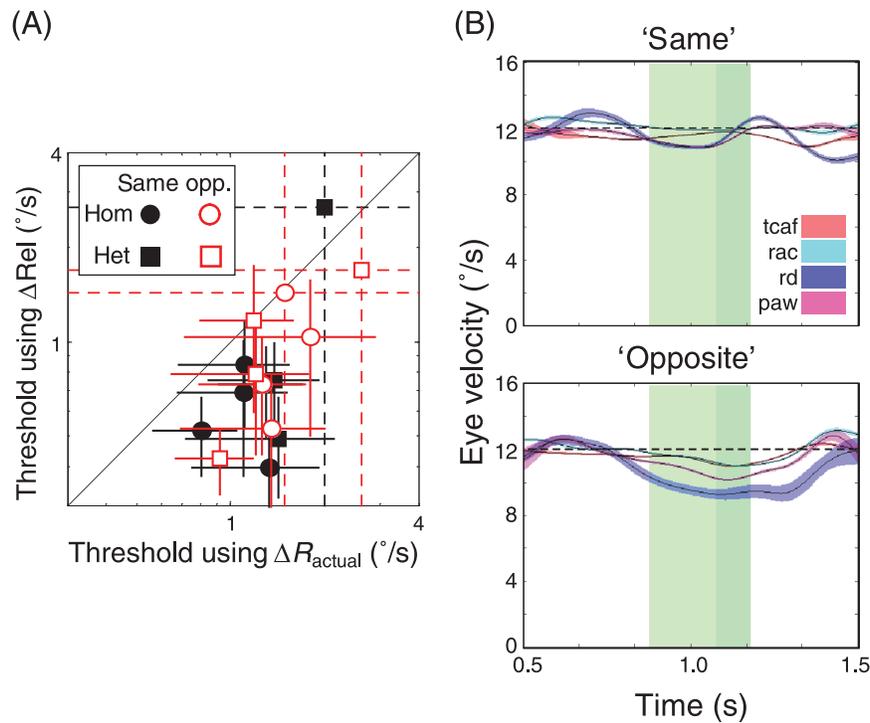
Figure 6. (A) ΔRel thresholds against those obtained ΔR_{actual} thresholds. Error bars correspond to 95% confidence limits (dotted lines indicate limits too large to plot in the log-log space). (B) Average eye movement traces for each observer around the time the dot pattern replaced the pursuit target. The green shaded regions define the period in which the dots were visible, with the darker region corresponding to the minimum and maximum dot duration possible. The horizontal shaded regions denote ±1 *SE* at each time point.

suggesting that observers had direct access to motion information other than the objective movement of the dots.

The lowest thresholds and best fits were obtained when responses were plotted as a function of sequential relative motion, irrespective of whether the retinal motion of the dots was in the 'same' direction as the pursuit target or 'opposite'. This is shown in more detail in Figure 6A, which plots thresholds obtained using ΔRel against those obtained using ΔR_{actual} for each observer. The error bars indicate 95% confidence intervals obtained used a bootstrapping technique (the dotted lines indicate limits too large to plot in the log–log space). All points (except one) lie below the positive diagonal.

The thresholds estimated using R_{actual} assume that eye velocity was constant when the dots were visible. The stimulus configuration used in Experiment 2 is a particularly good test of this assumption because the pursuit target disappeared during this period. Figure 6B shows average eye velocity around this time, for the two directions of motion considered. The traces have been averaged across trials and collapsed across homogeneous and heterogeneous conditions. The vertical shaded regions define the period in which the dots were visible (the darker region corresponds to the minimum and maximum durations possible). The results suggest that the assumption of constant speed is broadly supported. If there is any variation, it appears to be relatively small and quite con-

sistent for each observer. The results agree with previous work on oculomotor control. Pursuit is most affected by changes in background motion some 200–250 ms after background motion is perturbed (Lindner & Ilg, 2006; Spering & Gegenfurtner, 2007).

The feedback in Experiments 1 and 2 was based on relative motion (either simultaneous and/or sequential). Experiment 3 was therefore designed to give feedback specifically on the retinal motion contained in the display.

Experiment 3: Retinal motion feedback

Methods

Stimuli and procedure were similar to those described in Experiment 2. Only the 'same' condition was investigated. The major difference was the manner in which eye-movement recordings were collected and analyzed.

Pursuit was recording using an EyeLink 1000, with samples collected at 1000 Hz. Pursuit data were analyzed online after each trial and feedback given according to the estimate of ΔR_{actual}. Only the period in which the dots were visible was used to make this estimate. Pursuit speed was determined by fitting a straight line of the form
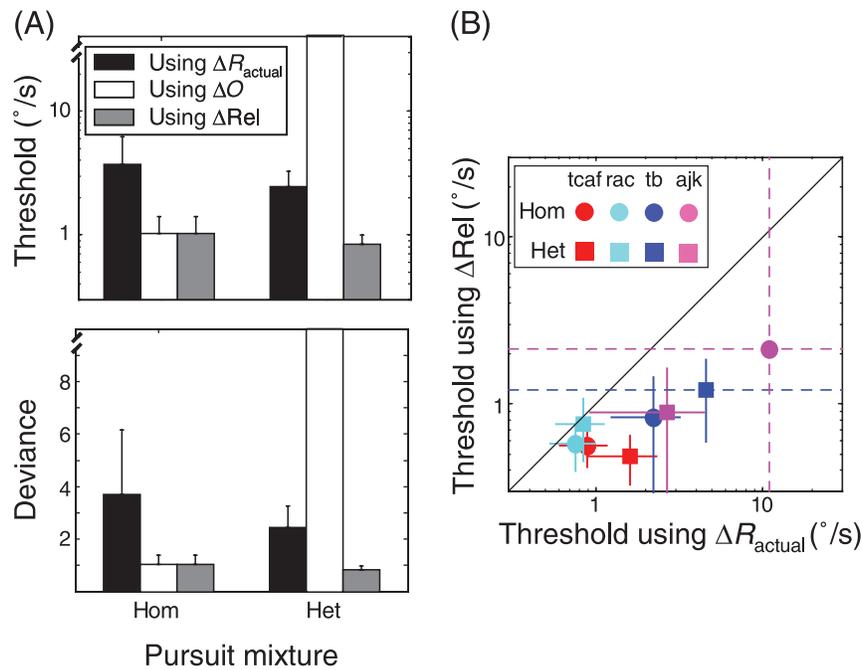
Figure 7. (A) Mean thresholds and deviances averaged across the 4 observers. Error bars are +1 *SE*. (B) ΔRel thresholds against those obtained ΔR_{actual} thresholds. Error bars correspond to 95% confidence limits (dotted lines indicate limits too large to plot in the log-log space).

$y = mx + c$ to the appropriate samples using a least-squares technique. If the observer made an eye-blink during this period, they were informed and the trial was repeated.

Two authors (TCAF, RAC) and three naive observers took part (TB, AJK, EO). EO was unable to perform the task in the heterogeneous condition. However, in the homogeneous condition, her data were similar to those of the other observers. For this reason she was dropped from the analysis.

Results

Figure 7A plots the mean thresholds and goodness of fit. As in previous experiments, the data suggest that observers had direct access to movement information other than the objective motion of the dots. The results show that performance was best described by the sequential relative motion. Thus, despite providing feedback on the retinal motion, observers based their judgements on the sequential relationship between pursuit target and dot speed.

One possible explanation of these results is that observers had learnt to use sequential relative motion in Experiments 1 and 2 and continued to do so in Experiment 3. However, naive observer TB had not previously taken part in any of these experiments and AJK had taken part in an earlier version of Experiment 2, run some months before Experiment 3. Figure 7B shows

individual data, plotting ΔRel against ΔR_{actual} thresholds. For all observers, data points lie below the positive diagonal. The more experienced observers have lower thresholds as one might expect. But qualitatively, the data across observers are in broad agreement.

Discussion

The experiments reported here were designed to test whether observers have direct access to retinal motion during pursuit. To do this, the correlation between objective and retinal motion was varied in a standard speed discrimination task. We found that retinal thresholds did not differ between a homogeneous pursuit condition (where retinal and objective motions where highly correlated) and a heterogeneous pursuit condition (where they were not). However, the same was also true for thresholds based on the relative motion in the display. We identified two types of relative motion—one corresponding to the simultaneous difference in speed between dot pattern and pursuit target and one corresponding to the sequential difference between the two. In the absence of simultaneous relative motion, the final experiment showed that observers used sequential relative motion even when feedback was based explicitly on the retinal motion present. The results therefore suggest that observers do

not have direct access to retinal motion when making perceptual judgements about movement during pursuit.

Relation to previous work

McKee and Welch ([1989](#)) found that retinal speed discrimination did not change when stereo-depth was used to decorrelate retinal and objective motions. On the face of it, their data are very similar to ours. However, they took their results as evidence in favor of the direct-access hypothesis. Importantly, their stimuli contained salient relative motion: a stationary cross was used to control fixation and was visible at all times while observers judged the motion of a moving test line. The fact that disparity failed to alter retinal motion thresholds may therefore have been due to the presence of relative motion. Interestingly, the disparity manipulation was applied to the test line only. As Howard and Rogers ([2002](#)) point out, had the disparity been applied to the fixation cross as well then observers may have scaled the relative motion according to the depth seen in the display. If this were the case, then 'retinal' speed discrimination thresholds would have increased in their heterogeneous condition.

There are a number of reports that the direction relationship between pursuit and retinal motion alters perceived motion. The use of relative motion by our observers goes some way in explaining why we did not find any difference here. Moreover, many of the previous studies used very different tasks and judgements to the one used here. For instance, the work of Bedell and colleagues used an adjustable line to match the length of perceived smear seen with a single point (Tong, Aydin, & Bedell, [2007](#); Tong et al., [2006](#)). Brenner and van den Berg ([1994](#)), on the other hand, had observers detect step changes of the *pursuit* target's speed, with the asymmetry revealed by manipulating the background's motion. Closer to home are experiments by Turano and Heidenreich ([1996](#)). They used a two-interval speed discrimination task to assess the effect of homogeneous pursuit on threshold. Using baseline data from another paper, they found that thresholds departed from those predicted by retinal motion alone. However, this was only the case when retinal motion was relatively slow (as it was in [Experiment 2](#)) and in the opposite direction to pursuit. When retinal motion was fast or in the same direction, the thresholds followed those predicted by their retinal motion model.

The discrepancy between our data and theirs is puzzling. Turano and Heidenreich used data from separate image stabilisation experiments to generate their retinal motion predictions, but it is doubtful this explains the discrepancy, even in the face of evidence that image stabilisation increases speed discrimination thresholds (Heidenreich & Turano, [1996](#)). It is also doubtful that the discrepancy arises from differences in the amount and type of relative motion in the two studies. Their stimuli arguably contained more relative motion than ours,

consisting as they did of gratings presented on a mean luminance background through a fixed circular window. The edges of the screen were therefore clearly visible and, along with the window, did not move with the pursuit target or grating (Turano, personal communication). The relative motion was also simultaneous as opposed to sequential. We suspect the key difference is the fact that their observers were given feedback based on objective motion.

Sequential relative motion

Our experiments show that observers used the sequential relative motion between pursuit target and dot motion to make their speed discrimination judgements. This reveals an intriguing ability to combine motion estimates across time. How might this be achieved? Our speculation is that observers use the 'objective' relative motion between pursuit target and dots. That is, observers estimate the objective motion of the pursuit target and subtract this from an estimate of the objective motion of the dot pattern. Such a strategy would incorporate extra-retinal information about eye velocity, as well as retinal motion related to the dots (and perhaps that of the target as well).

It is intriguing to note that using sequential relative motion is equivalent to encoding the acceleration associated with a step change in speed on each interval. The precision with which observers are able to do this is considerably worse than the ability to discriminate the same two speeds in isolation (Snowden & Braddick, [1991](#)). Nevertheless, even when feedback is provided on the latter, our results show that observers choose to use the step change in speed.

References

Bedell, H. E., & Lott, L. A. (1996). Suppression of motion-produced smear during smooth pursuit eye movements. *Current Biology, 6,* 1032–1034. [PubMed] [Article]

Bennett, P. J., & Cortese, F. (1996). Masking of spatial frequency in visual memory depends on distal, not retinal, frequency. *Vision Research, 36,* 233–238. [PubMed]

Brenner, E., & van den Berg, A. V. (1994). Judging object velocity during smooth pursuit eye movements. *Experimental Brain Research, 99,* 316–324. [PubMed]

Brenner, E., & van den Berg, A. V. (1996). The special rule of distant structures in perceived object velocity. *Vision Research, 36,* 3805–3814. [PubMed]

Burbeck, C. A. (1987). Locus of spatial-frequency discrimination. *Journal of the Optical Society of America A, Optics and Image Science, 4,* 1807–1813. [PubMed]

Crowell, J. A., & Andersen, R. A. (2001). Pursuit compensation during self-motion. *Perception, 30,* 1465–1488. [PubMed]

Freeman, T. C. (2001). Transducer models of head-centred motion perception. *Vision Research, 41,* 2741–2755. [PubMed]

Gegenfurtner, K. R., Xing, D., Scott, B. H., & Hawken, M. J. (2003). A comparison of pursuit eye movement and perceptual performance in speed discrimination. *Journal of Vision, 3*(11):19, 865–876, http://journalofvision.org/3/11/19/, doi:10.1167/3.11.19. [PubMed] [Article]

Heidenreich, S. M., & Turano, K. A. (1996). Speed discrimination under stabilized and normal viewing conditions. *Vision Research, 36,* 1819–1825. [PubMed]

Howard, I. P., & Rogers, B. J. (2002). *Seeing in depth.* Toronto, Canada: I Porteous.

Kowler, E., & McKee, S. P. (1987). Sensitivity of smooth eye movement to small differences in target velocity. *Vision Research, 27,* 993–1015. [PubMed]

Krukowski, A. E., Pirog, K. A., Beutter, B. R., Brooks, K. R., & Stone, L. S. (2003). Human discrimination of visual direction of motion with and without smooth pursuit eye movements. *Journal of Vision, 3*(11):16, 831–840, http://journalofvision.org/3/11/16/, doi:10.1167/3.11.16. [PubMed] [Article]

Lindner, A., & Ilg, U. J. (2006). Suppression of optokinesis during smooth pursuit eye movements revisited: The role of extra-retinal information. *Vision Research, 46,* 761–767. [PubMed]

McKee, S. P., & Welch, L. (1989). Is there a constancy for velocity. *Vision Research, 29,* 553–561. [PubMed]

McKee, S. P., & Welch, L. (1992). The precision of size constancy. *Vision Research, 32,* 1447–1460. [PubMed]

Morvan, C., & Wexler, M. (2005). Reference frames in early motion detection. *Journal of Vision, 5*(2):4, 131–138, http://journalofvision.org/5/2/4/, doi:10.1167/5.2.4. [PubMed] [Article]

Rieger, J. H., & Lawton, D. T. (1985). Processing differential image motion. *Journal of the Optical Society of America A, Optics and Image Science, 2,* 354–360. [PubMed]

Rushton, S. K., & Warren, P. A. (2005). Moving observers, relative retinal motion and the detection of object movement. *Current Biology, 15,* R542–R543. [PubMed] [Article]

Schütz, A. C., Delipetkos, E., Braun, D. I., Kerzel, D., & Gegenfurtner, K. R. (2007). Temporal contrast sensitivity during smooth pursuit eye movements. *Journal of Vision, 7*(13):3, 1–15, http://journalofvision.org/7/13/3/, doi:10.1167/7.13.3. [PubMed] [Article]

Snowden, R. J., & Braddick, O. J. (1991). The temporal integration and resolution of velocity signals. *Vision Research, 31,* 907–914. [PubMed]

Souman, J. L., Hooge, I. T., & Wertheim, A. H. (2006). Frame of reference transformations in motion perception during smooth pursuit eye movement. *Journal of Computational Neuroscience, 20,* 61–76. [PubMed]

Spering, M., & Gegenfurtner, K. R. (2007). Contextual effects on smooth-pursuit eye movements. *Journal of Neurophysiology, 97,* 1353–1367. [PubMed] [Article]

Tong, J., Aydin, M., & Bedell, H. E. (2007). Direction and extent of perceived motion smear during pursuit eye movement. *Vision Research, 47,* 1011–1019. [PubMed]

Tong, J., Patel, S. S., & Bedell, H. E. (2006). The attenuation of perceived motion smear during combined eye and head movements. *Vision Research, 46,* 4387–4397. [PubMed] [Article]

Turano, K. A., & Heidenreich, S. M. (1996). Speed discrimination of distal stimuli during smooth pursuit eye motion. *Vision Research, 36,* 3507–3517. [PubMed]

Wallach, H. (1959). The perception of motion. *Scientific American, 201,* 56–60. [PubMed]

Wichmann, F. A., & Hill, N. J. (2001). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception & Psychophysics, 63,* 1293–1313. [PubMed]