

Human discrimination of visual direction of motion with and without smooth pursuit eye movements

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It has long been known that ocular pursuit of a moving target has a major influence on its perceived speed (Aubert, 1886; Fleischl, 1882). However, little is known about the effect of smooth pursuit on the perception of target direction. Here we compare the precision of human visual-direction judgments under two oculomotor conditions (pursuit vs. fixation). We also examine the impact of stimulus duration (200 ms vs. ~800 ms) and absolute direction (cardinal vs. oblique). Our main finding is that direction discrimination thresholds in the fixation and pursuit conditions are indistinguishable. Furthermore, the two oculomotor conditions showed oblique effects of similar magnitudes. These data suggest that the neural direction signals supporting perception are the same with or without pursuit, despite remarkably different retinal stimulation. During fixation, the stimulus information is restricted to large, purely peripheral retinal motion, while during steady-state pursuit, the stimulus information consists of small, unreliable foveal retinal motion and a large efference-copy signal. A parsimonious explanation of our findings is that the signal limiting the precision of direction judgments is a neural estimate of target motion in head-centered (or world-centered) coordinates (i.e., a combined retinal and eye motion signal) as found in the medial superior temporal area (MST), and not simply an estimate of retinal motion as found in the middle temporal area (MT).

Keywords: active vision, motion perception, sensorimotor

Introduction

Is perception different during action than during inaction? More specifically, does perceptual performance during active exploration of the visual scene using eye movements differ from that during passive viewing while fixating? This question is of particular interest in the case of smooth pursuit eye movements and motion perception, because the pursuit response dramatically alters the retinal signal available to perception. In this study, we seek to determine the effect of pursuit on the visual perception of an object's direction of motion. Clearly, the neural signals needed to compute a target's motion are quite different during fixation than during pursuit. During fixation, the object's image drifts across the retina, generating a neural signal related to this retinal slip. Retinal slip alone can then be used directly by

perception to compute object motion. During steady-state pursuit, retinal slip is largely eliminated and the small residual slip is decorrelated with the object's motion. Most of the neural information about the object's motion is then in the efference copy of the pursuit command.

It has long been known that the act of pursuit affects the accuracy of speed perception, as demonstrated by the illusions described by Aubert (1886) and Fleischl (1882). The effect of pursuit on the accuracy of direction perception is less clear. Festinger, Sedgwick, and Holtzman (1976) measured the accuracy of direction perception of a moving target while observers pursued a second target, and found evidence for only minor compensation for pursuit. However, they did not compare perception of a single target during pursuit versus that during fixation, so the impact of pursuit on

the perceived direction of a single moving target remained unresolved.

Instead of examining the effect of pursuit on the accuracy of speed or direction perception, here we measure the precision of perceived target direction during pursuit and during fixation. In particular, we explore the possibility that performance differences between these two conditions might occur at longer stimulus durations, when the difference in the visual signals is large. Finally, it has previously been shown that, during fixation, direction discrimination is more precise for cardinal directions than for oblique directions of motion (e.g., Ball & Sekuler 1987; Heeley & Buchannan-Smith, 1992; Gros, Blake, & Hiris, 1998; Churchland, Gardner, Chou, Priebe, & Lisberger, 2003). Here we measure this motion “oblique effect” during pursuit and fixation. Finding similar anisotropies would provide strong evidence that under these two disparate conditions, performance is limited by the same neural mechanisms. Furthermore, our experiment enables us to examine if the motion oblique effect exists in retinal coordinates, or in head-centered coordinates.

Methods

Visual Stimuli

The stimulus was a single bright spot presented by back-projection of a red laser light source onto a 30 by 40 in. tangent, translucent screen. The position of the spot was controlled using a pair of orthogonal mirror galvanometers driven on a millisecond timescale by a pair of PCs running Tempo software. Observers viewed the stimuli from a distance of 73 cm in a dark room with a white background (~ 13 cd/m²) on the backlit tangent screen. Head movements were minimized by using a bite bar.

Eye-Movement Recording

The position of the observer’s left eye was monitored using an infra-red video-based tracker (ISCAN model RK-726PCI) sampling at 240 Hz. To calibrate the tracker, prior to each run, observers fixated a 3x3 grid of points, -10 to $+10$ deg in azimuth and elevation (for clarity, we use “deg” to denote degrees of visual angle, and $^\circ$ to denote degrees of angular direction). Eye position in tracker coordinates was then converted to eye position on the screen by the best fitting bi-linear function (see Beutter & Stone, 1998). The spatial precision of the tracker was estimated by measuring the SD of eye-position fixations during calibration, typically yielding values < 0.1 deg.

Saccades were detected by thresholding the correlation between the eye-velocity trace and a saccade template, permitting detection and removal of saccades of ~ 0.3 deg or larger. Eye-velocity traces were generated by

low-pass digital differentiation of the eye-position traces (-3 dB at 32Hz).

Experimental Design

The stimulus moved at 10 deg/s along a path tangential to an invisible ~ 5 -deg radius circle (Figure 1a). Observers were presented with two sequential intervals of stimulus motion: a standard at one of eight canonical directions (four cardinals: 0° , 90° , 180° , and 270° , and four primary obliques: 45° , 135° , 225° , and 315°) jittered by $\pm 3^\circ$, and a test differing from the standard by rotations of ± 2 , ± 4 , ± 6 , or $\pm 8^\circ$. The stimulus duration was either short (200 ms) or long (800 ± 50 ms), for a total of 16 types of trials (8 directions x 2 durations). On each trial, the duration and direction were randomly chosen, as was the presentation order of the test and standard intervals.

A number of steps were taken to eliminate extraneous cues that could influence performance. The midpoint of each trajectory was randomized by ± 2 deg in eccentricity and by $\pm 7^\circ$ in radial position about the ideal tangent point on a 5-deg radius invisible circle. Furthermore, to ensure observers were genuinely performing a two-interval forced-choice judgment (2IFC), the directional jitter described above minimized the usefulness of the absolute direction of any single interval. The absolute direction might otherwise have been compared to an internal standard or some visible feature on the screen or in the room.

In Experiment 1, the stimulus trajectory for each interval was a straight line (Figure 1b). Six observers (three naïve) were asked to report, using a button-press, the interval that contained the more clockwise direction of motion (e.g., the blue arrows in Figure 1a). To make the early portion of the stimulus trajectory irrelevant for performing the task and thereby to force observers to make judgments about target direction during ongoing pursuit, we performed a second experiment.

In Experiment 2, the stimulus motion was along a “bent line” that consisted of two sequential and nearly co-linear straight lines separated by a short blank (Figure 1c). Only the long duration condition was run. Four observers (two naïve) were asked to report the interval that contained the more clockwise direction of motion, and to base this judgment only on the late portion of the intervals. After an initial short period of motion along one straight path, the spot was extinguished for 30 ms and, upon reappearance, continued in a slightly different direction along a new straight path. The initial directions for each interval were independently jittered ($\pm 3^\circ$) around the same canonical direction. The final directions for each interval were also independently chosen, in the same fashion as in Experiment 1. Because of the separate jittering of the two initial directions, the size and direction of the bend (and therefore the resulting initial retinal slip) in either interval did not correlate well with the difference in the two final directions (i.e., the task-

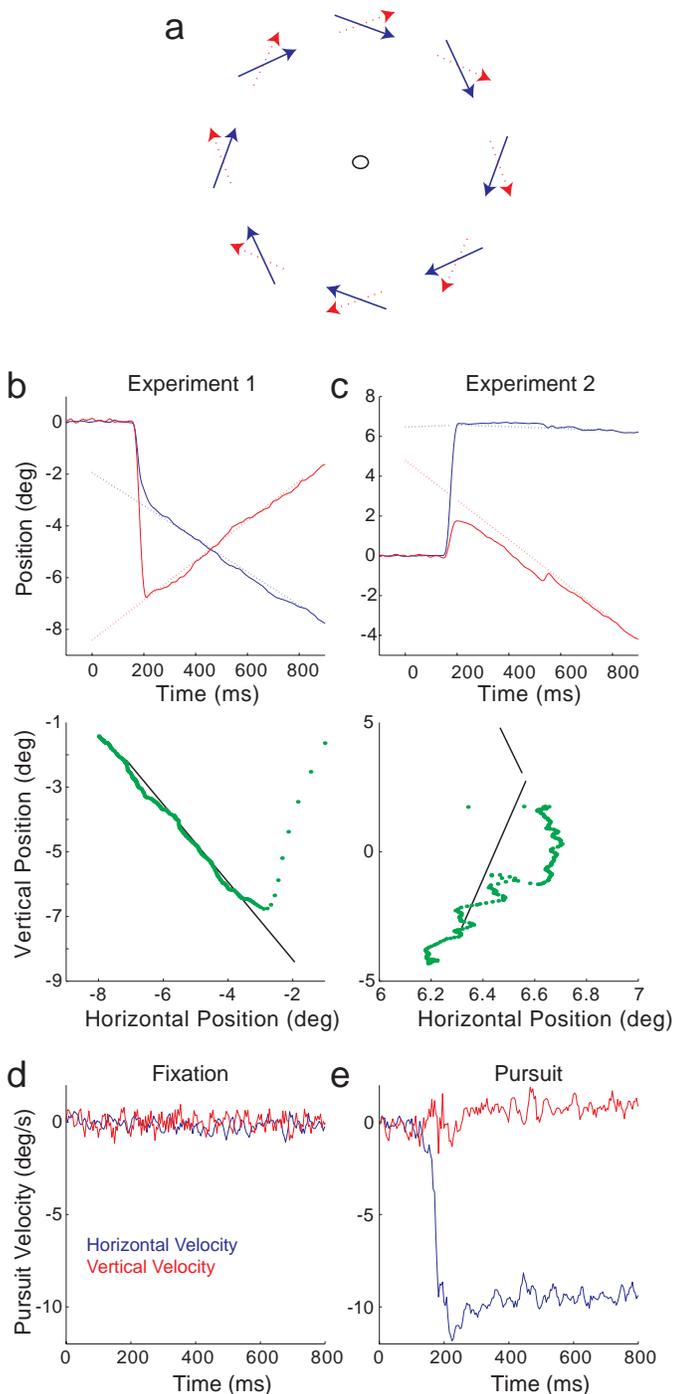


Figure 1. a. Cartoon illustrating the stimulus trajectories of our 2IFC paradigm. For each trial, the pair of trajectories was in one of the eight basic locations, and each followed a tangential patch as described in detail in “Methods.” The psychophysical task was to determine in which of the two sequentially presented intervals the trajectory was more clockwise, or tilted more toward the center of the circle (the blue arrows as opposed to the red arrows). A fixation point appeared before the beginning of each interval at the central location, represented by the open oval, but was extinguished during target motion to minimize relative motion cues. b and c. Sample eye movement traces for naïve observer jj for a single trial from Experiment 1 (b) and Experiment 2 (c). Top panels: eye and target, horizontal and vertical positions shown as a function of time with target position shown in dotted traces and eye position in solid traces (horizontal positions in blue, vertical in red). Bottom panels: horizontal versus vertical position traces (target in black, eye in green). Note the expanded horizontal scale for the bottom panel in c to accentuate the bend in the target and eye trajectories. The blanking and bend in trajectory occurred at the moment of the initial saccade. (d and e) Sample average eye velocity traces for observer jj for fixation (d) and pursuit during leftward horizontal target motion from Experiment 1 (e).

relevant information). The exact time of the change in direction, during the pursuit condition, coincided with **the onset of the initial saccade, determined online** by finding the time point when the eye position left a 2.5-deg radius window around central fixation. This manipulation was done to minimize the salience of the bend by effecting the change of trajectory during a saccade. In the fixation condition, for each observer, individually, the trajectory changes occurred at times matched, for each interval, to the saccadic latencies for trials of corresponding directions. Mean saccadic latencies for the first interval were 181 ± 31 ms (\pm SD across observers) and 158 ± 22 ms for the second interval, which was somewhat shorter presumably because the a priori spatial uncertainty of the stimulus was reduced.

For both experiments, observers were either required to maintain central fixation (Figure 1d) or to pursue the target spot (Figure 1e). The fixation and pursuit conditions were run in separate blocks. In both conditions, a fixation point appeared before the beginning of each interval, but was extinguished during target motion to minimize relative motion cues. When the fixation point reappeared between the two intervals of a trial, observers were required to return to within 0.75 deg of this point before the second interval would begin. In the fixation condition, fixation was monitored online, and the trial was aborted if eye position left a 1.5-deg window around the central location (where the fixation spot had previously been visible) during the stimulus presentation intervals. Despite the lack of a fixation point, observers were typically able to hold fixation throughout the stimulus presentation (Figure 1d). Offline, fixation trials were excluded when observers’ unsuppressed pursuit responses exceeded an average speed of 3.3 deg/s (33% gain) in the temporal windows 250-450 ms or 550-750 ms after target motion onset. In the pursuit condition, observers typically accelerated rapidly up to steady-state speeds (Figure 1e). We ensured that our analysis was restricted to trials with robust pursuit (except for Figure 5) by excluding trials when observers either failed to reach an average eye velocity of 2.5 deg/s early in the trial (300-500 ms after target motion onset) or failed to maintain at least 6.6 deg/s (66% gain) late in the trial (550-750 ms). The percentage of trials that survived these criteria in Experiment 1 was

$89 \pm 11\%$ and $82 \pm 12\%$ (\pm SD across observers) for fixation and pursuit for the short stimulus, and $93 \pm 8\%$ and $86 \pm 15\%$ for the long stimulus. In Experiment 2, $95 \pm 4\%$ of fixation and $87 \pm 22\%$ of pursuit trials were kept. For some observers, the steady-state pursuit gain varied idiosyncratically with direction. However, after the above trial-selection process, average gains for the analyzed trials varied across direction by only $\sim 15\%$. Furthermore, we found no systematic oblique versus cardinal gain asymmetry. The average gains for the cardinal and oblique directions differed by $< 5\%$ for all observers. For Figure 5, the “low-gain” trials are those whose steady-state gains for both the first and second intervals were below the observer’s median gain, and the “high-gain” trials are those whose steady-state gains were above the median.

Psychophysical Data Analysis

Psychophysical curves were generated from the percentage of trials judged to be clockwise for each condition. Because there was typically little difference between performance across the directions within the cardinal and oblique conditions, responses were combined across all four cardinal directions and across all four oblique directions. Psychophysical curves were then fit with a cumulative Gaussian function using Probit analysis (Finney, 1971). The direction uncertainty, or discrimination threshold, was then computed by dividing the best-fitting SD by $\sqrt{2}$ to compensate for the fact that

there were two stimulus intervals. The 95% confidence interval for each estimate of threshold was calculated using chi-squared statistics (Press, Teukolsky, Vetterling, & Flannery, 1992). In Figures 3-5, points were considered significantly different from the line of slope 1 and intercept 0 if the elliptical interpolation of their measured 95% confidence limits did not touch the line.

Results

Experiment 1

Examples of raw psychophysical curves for long duration stimuli are shown for one observer in Figure 2. These data illustrate the two most important findings of this study. First, the psychometric curves during pursuit (Figure 2a and 2b) and fixation (Figure 2c and 2d) were similar. Second, the curves for the cardinal directions (Figure 2a and 2c) were steeper than those for the oblique directions (Figure 2b and 2d). Not shown here is the fact that psychometric curves were somewhat steeper for the longer duration stimuli than for the short duration stimuli. These trends held for all six observers. We performed the standard 3-way ANOVA on the discrimination thresholds appropriate for our $2 \times 2 \times 2$ design. The main direction ($p < .001$) and duration ($p < .003$) effects were highly significant, but the main effect of oculomotor condition was not significant ($p = .773$). The

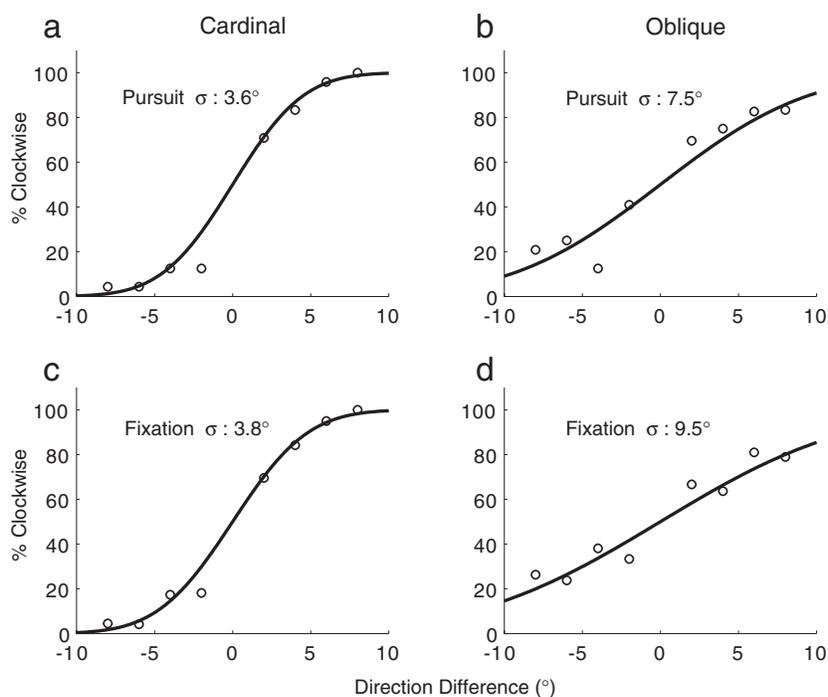


Figure 2. Sample psychophysical curves for observer ak, Experiment 1, long duration. a. Pursuit, cardinal directions; b. Pursuit, oblique directions; c. Fixation, cardinal directions; and d. Fixation, oblique directions. The SD of the best-fitting cumulative Gaussian (σ) is shown in each panel.

effect of duration \times oculomotor-condition was only borderline significant ($p = .044$) and all other cross terms were not significant.

Performance was therefore the same during fixation and pursuit. Figure 3 shows plots of direction discrimination thresholds during fixation versus those during pursuit for both the short (Figure 3a) and long duration (Figure 3b). All data points lie close to the line of slope 1 and intercept 0, with nearly all points not significantly off the line (open symbols). The mean thresholds across all directions for fixation and pursuit were, respectively, $6.2 \pm 2.0^\circ$ and $7.1 \pm 2.0^\circ$ (\pm SD across observers) for the short duration, and $5.7 \pm 2.4^\circ$ and $5.0 \pm 1.9^\circ$ for the long duration.

Figure 3a and 3b also reveal a clear oblique effect in direction discrimination. Thresholds for cardinal directions (green) are lower than those for oblique directions (orange), during both pursuit and fixation. This oblique effect is shown more explicitly in Figure 3c and 3d, where thresholds for the oblique directions are plotted against those for the cardinal directions for pursuit (blue) and fixation (red). All of the points are above the line of slope 1 and intercept 0, with most

points significantly so (solid symbols). The lack of significance of the direction \times oculomotor condition and direction \times duration terms in the ANOVA shows that the size of the oblique effect is not significantly different between fixation and pursuit or between the two stimulus durations. The mean ratios of the oblique to cardinal thresholds for fixation and pursuit were 1.7 ± 0.3 and 1.5 ± 0.2 for the short duration, and 1.9 ± 0.4 and 1.8 ± 0.4 for the long duration.

Unfortunately, it is impossible to determine when, during the stimulus presentation, an observer is culling the information upon which he/she is basing his/her perceptual judgment. There is some improvement in overall performance for the long presentation versus the brief presentation, implying that observers are gathering information throughout the trial and not just relying on the early portion of the trial. Nevertheless, a potential trivial reason for the similarity in performance between the fixation and pursuit conditions for the long stimulus presentation (Figure 3b) could be that observers primarily based their decisions on visual input received at the beginning of the stimulus presentation (i.e., prior to any eye movement response in the pursuit condition), when

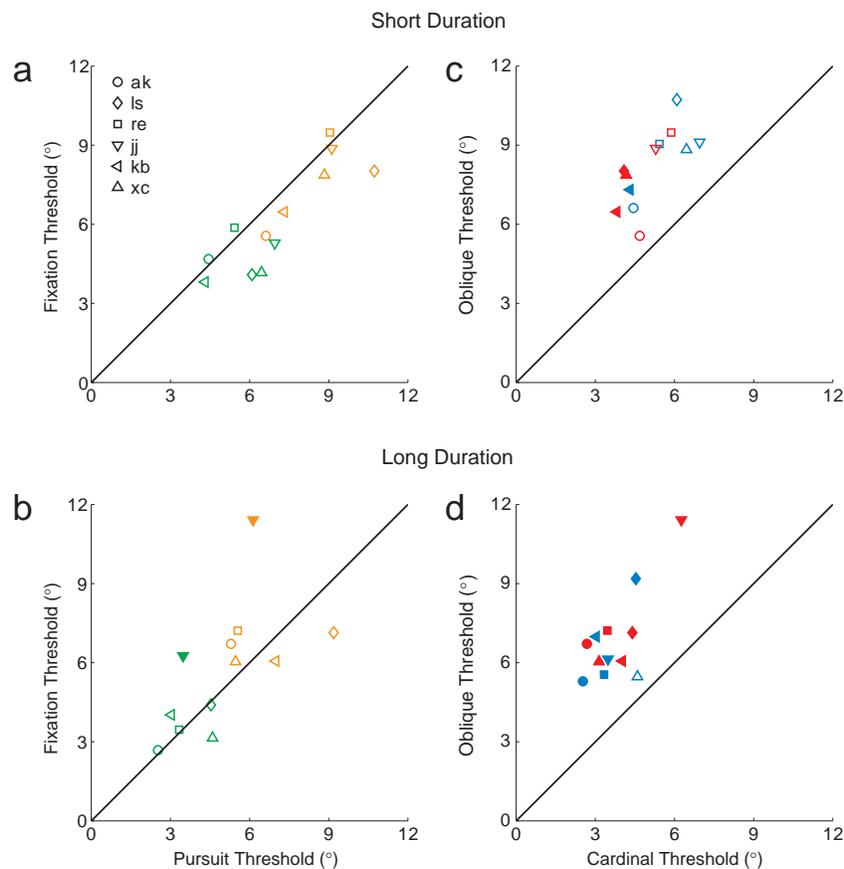


Figure 3. a and b. Discrimination thresholds in Experiment 1 during fixation versus during pursuit. a. Short duration. b. Long duration. Green symbols are for cardinal directions, orange symbols for oblique directions. c and d. The same discrimination thresholds from Experiment 1, now replotted for oblique versus cardinal directions. c. Short duration. d. Long duration. Blue symbols are for pursuit, red symbols for fixation. Filled symbols are used for points that are significantly ($p < .05$) different from the line of slope = 1 and intercept = 0.

the retinal motion under both oculomotor conditions is identical. We therefore ran a second experiment in which observers could not base their responses on the initial stimulus motion.

Experiment 2

In this second experiment, by making the early target motion irrelevant, we forced observers to use information late in long duration trials to achieve reliable performance. In particular, in the pursuit trials, the pre-pursuit target motion was irrelevant and only target motion during ongoing pursuit was useful for performing the task. Observers were asked to discriminate the directions based only on the late portions of test and standard intervals. The standard 2x2 ANOVA reveals a significant main effect of direction ($p < .032$), with no

other terms reaching significance.

Performance was therefore again indistinguishable between the fixation and pursuit conditions. When fixation thresholds are plotted against pursuit thresholds, most points are not significantly different from the line of slope 1 and intercept 0 (Figure 4a). The mean discrimination threshold across all directions was $5.8 \pm 2.1^\circ$ and $4.9 \pm 1.7^\circ$ during fixation and pursuit, respectively. Furthermore, these thresholds are nearly identical to those in Experiment 1, showing that observers followed the instructions and performed the task based on the late portion of the intervals.

Thresholds for oblique motion were again consistently higher than those for cardinal motion (Figure 4b) despite the fact that, in the pursuit condition, observers were required to use information from ongoing pursuit. When oblique thresholds are plotted against cardinal thresholds, all of the points are above the line of slope 1 and intercept 0, with half of them significantly so (solid symbols). During pursuit, the average discrimination thresholds for the oblique directions were 1.8 ± 0.3 times larger than for the cardinal directions, which is similar to the findings in Experiment 1. During fixation, oblique thresholds were 1.3 ± 0.2 times larger than those for the cardinal directions, which is somewhat smaller than that in Experiment 1. Nonetheless, one-tailed paired t tests across observers confirm the fact that the oblique effect was significant during both pursuit ($p < .006$) and fixation ($p < .022$), and the interaction-term in the ANOVA shows that the oblique effects for these two conditions are not significantly different.

One might think that the lack of difference between direction thresholds during fixation and pursuit is happenstance, caused by a fortuitous combination of pursuit and residual retinal motion specific to our task or conditions. To examine this possibility, we reanalyzed the pursuit condition judgments for each observer after separating trials into two groups: one in which pursuit had a gain below the median and another in which pursuit had a gain above the median. Figure 5a plots the thresholds for the higher-gain trials versus those for the lower-gain trials for all four observers, for both the cardinal (green) and oblique (orange) directions. Performance was similar despite the fact that the mean gain was 78% for the lower-gain trials and 101% for the higher-gain trials. None of the points are significantly different from the line of slope 1 and intercept 0. Furthermore, a two-tailed paired t test failed to find a significant difference ($p = .237$) between these thresholds, despite the dramatic difference in the contribution from residual retinal motion.

The oblique effect is preserved, even when we restrict our analysis to either the lower-gain or higher-gain trials (Figure 5b). When thresholds for oblique motion are plotted against those for cardinal motion, all of the points are once again above the line of slope 1 and intercept 0. In particular, for the high-gain trials, three out of four of

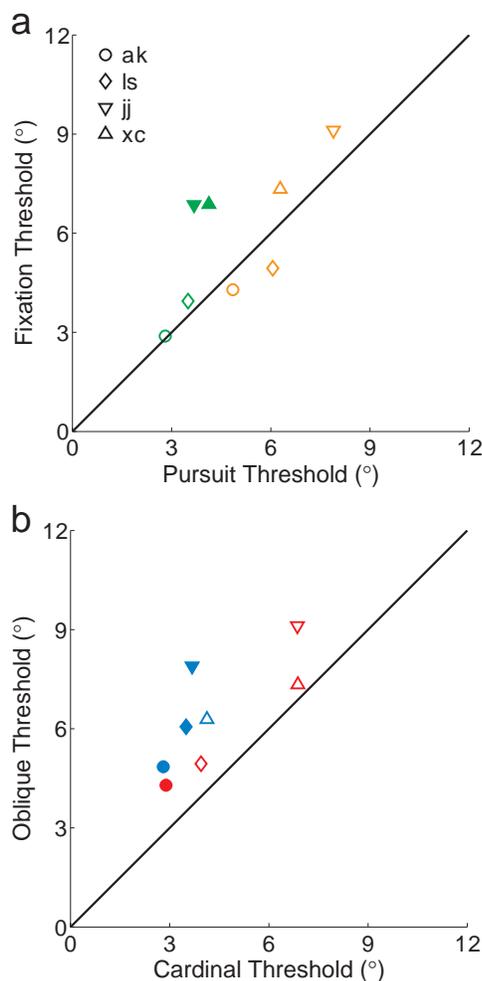


Figure 4. a. Discrimination thresholds for Experiment 2 during fixation versus pursuit. Green symbols are for cardinal directions, orange symbols for oblique directions. b. The same discrimination thresholds for Experiment 2, now replotted for oblique versus cardinal directions. Blue symbols are for pursuit, red symbols for fixation. Filled symbols are used for points that are significantly ($p < .05$) different from the line of slope = 1 and intercept = 0.

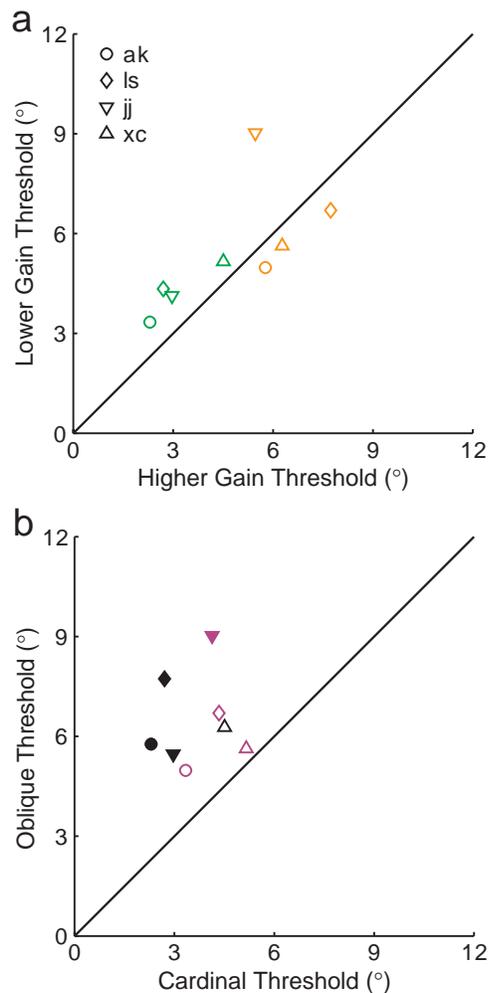


Figure 5. a. Discrimination threshold for Experiment 2 during lower gain pursuit versus higher gain pursuit. Green symbols are for cardinal directions, orange symbols for oblique directions. b. The same discrimination thresholds during high and low gain for Experiment 2, now replotted for oblique versus cardinal directions. Black symbols are for higher gain pursuit, purple symbols for lower gain pursuit. Throughout, filled symbols are used for points that are significantly ($p < .05$) different from the line of slope = 1 and intercept = 0.

the individual points are significantly higher (solid, black symbols). Across observers, a one-tailed paired t test confirms that the oblique effect was significant for the high gain trials ($p < .011$). In this case, given that the steady-state gain is on average perfect, the residual retinal motion is negligible. The motion oblique effect must therefore be based on the direction of eye motion with

respect to the head, and not on the direction of the effectively nonexistent retinal slip. In other words, the oblique effect measured here is related to oblique target motion in head-centered (or possibly world-centered) coordinates.

Discussion

Our results demonstrate that the precision of visual direction discrimination is similar during active (pursuit) and passive (fixation) vision. It would seem common sense that there would be a benefit of actively pursuing a moving target that one is attempting to identify and to interact with. Pursuit has been demonstrated to substantially improve visual acuity for moving objects (Westheimer & McKee, 1975; Haarmeier & Thier, 1999), as well as the detection of coherent motion in the presence of noise (Greenlee, Schira, & Kimmig, 2002). On the other hand, one might expect adverse effects given that pursuit reduces the accuracy of speed perception (e.g., Wertheim & van Gelder 1990; Freeman & Banks 1998; Turano & Heidenreich 1999). In fact, in terms of precisely determining the direction of target motion, our data show that pursuit appears to provide little or no benefit, at least for simple spot stimuli under the conditions we tested. Overall, our discrimination thresholds during both pursuit and fixation are higher than what has been observed previously (e.g., De Bruyn & Orban, 1988; Westheimer & Wehrhahn, 1994). It is likely that this is due to the large amount of spatial and directional uncertainty in our protocol, as our thresholds are comparable to those observed when using a wide range of directions with random dot cinematograms (Gros, Blake, & Hiris, 1998).

Short Versus Long Duration

We have demonstrated that direction discrimination performance is similar during pursuit and fixation for both short (200 ms) and longer (~800 ms) stimulus durations. Not unexpectedly, there was some degree of temporal integration; performance was better for both fixation and pursuit in response to the longer duration stimuli.

In the pursuit condition, the visual signal available to support direction judgments changes over time. At the moment of pursuit initiation the visual input is large (10 deg/s), peripheral, and unaffected by the driven eye movement. Thus, for the short presentation stimuli, it is not particularly surprising that performance was similar during fixation and pursuit, because the visual inputs during pursuit and fixation are identical for most of the stimulus presentation.

The more convincing result is that performance remains the same during pursuit and fixation for the long duration condition. Yet, even for the long duration of Experiment 1, a strategy based on retinal motion that

examines the pre-pursuit stimulus motion could explain our results. Experiment 2, however, rules out this possibility by forcing observers to use information during ongoing pursuit to make their judgments. Nonetheless, it could be argued that during the pursuit condition of Experiment 2, because there remained a small retinal slip signal in the period immediately following the change in direction, one could use this retinal slip to infer the relative direction of the first and second intervals. However, such a strategy would be ineffective and inconsistent with the data. In addition to the directional jitter in the stimulus (see “Methods”), on average, the speed of the residual retinal slip was < 2 deg/s and the variability in retinal (pursuit) direction was $\sim 10^\circ$ in the first 100 ms after the bend. A strategy based exclusively on retinal slip would have produced much worse performance in the pursuit condition than in the fixation condition.

Pursuit and Speed Perception

The study of the effect of pursuit on the perception of speed has a long history (Aubert, 1886; Fleischl, 1882) and has been revisited many times (e.g., Wertheim & van Gelder 1990; Freeman & Banks 1998; Turano & Heidenreich 1999). In general, the perceived speed of a pursued stimulus is slower than the same stimulus perceived during fixation. The degree of this effect depends on several factors, including eye speed (Turano & Heidenreich 1999) and the spatial frequency of the target (Freeman & Banks 1998), which also affects the relative contribution of retinal and efference copy signals to the perception of target speed. Given the existence of pursuit effects on speed accuracy, one might be tempted to expect that pursuit might also affect direction perception. Our results, however, show that at least the precision of direction judgments appears unaffected by pursuit. Furthermore, we examined the possibility that this finding depended critically on the ratio of retinal motion to efference copy in the input signals. We reanalyzed our data for lower and higher gain pursuit separately and found no significant difference between direction thresholds when pursuit gain is nearly perfect or $\sim 20\%$ lower. Our finding of similar thresholds during pursuit and fixation is therefore robust to changes in the ratio of the retinal and efference copy components of the input signals.

Signal Processing for Direction Judgments

During fixation, target motion is largely associated with retinal motion alone. The direction of target motion is encoded in the firing rate of neurons that are tuned to the direction of the retinal slip. Such neurons can be found as early in visual processing as V1 or MT, the latter area being critically involved in direction

perception (Newsome, Wurtz, Dursteler, & Mikami, 1985; Newsome & Pare, 1988). Indeed, many have postulated that perceptual judgments of direction might be performed by simply reading out the population response of MT neurons (e.g., Britten, Newsome, Shadlen, Celebrini, & Movshon, 1996). Especially given MT's organized direction columns (Albright, Desimone, & Gross, 1984), such a mechanism would seem parsimonious.

During steady-state pursuit, retinal motion is dramatically reduced with steady-state errors typically less than a few deg/s. Furthermore, steady-state pursuit is often associated with oscillations back and forth around target speed (Goldreich, Krauzlis, & Lisberger, 1992) such that any residual retinal slip will have only a tenuous correlation with target velocity. Even during perfect pursuit imposed by electronic feedback of eye position or by tracking a retinal afterimage, the target is perceived to move (Wyatt & Pola, 1979; Heywood & Churcher, 1971). These facts demonstrate that efference copy must play a critical role in motion perception. Indeed, an efference-copy signal must be providing the bulk of the direction information used to perform discriminations during steady-state pursuit. Yet, during steady-state pursuit, the ensemble response of the population of MT neurons provides little or no information about the motion of the target, because retinal motion is small and erratic (Newsome, Wurtz, & Komatsu, 1988).

One explanation for our observation that direction precision is largely the same during fixation and pursuit is that a brain area other than MT fortuitously encodes efference-copy direction with the same precision as MT encodes retinal-slip direction. A more parsimonious explanation is that direction discrimination is performed during both fixation and pursuit by the same set of neurons within a single brain area that encodes target motion in head or world coordinates and not in retinal coordinates. The noise in the neural signals in this hypothesized brain area could be affected by a number of factors. In addition to the noise in the input retinal-slip and efference-copy signals, noise can also arise from intrinsic properties of neurons, or local cortical networks, or nonspecific inputs from other sources that are not specifically related to the stimulus parameters. If the noise is dominated by a combination of sources other than the input noise, then our finding of similar direction precision during fixation and pursuit becomes wholly understandable.

Neurons in the MST area combine both retinal slip and efference-copy signals, are active during steady-state pursuit, and may encode target motion in head-centric coordinates (Newsome, Wurtz, & Komatsu, 1988). Given the parallel effects of MST lesions on motion perception and pursuit (Dursteler & Wurtz, 1988; Rudolph & Pasternak, 1999), MST, or an area downstream from it, is a good candidate area for providing the target direction signal (and noise) to

perception during both fixation and pursuit (Stone & Krauzlis, 2003; Stone, Beutter, & Lorenceau, 2000).

The fact that the magnitude of the oblique effect is similar during fixation and pursuit implies that this anisotropy originates in the area where direction precision is limited. Oblique anisotropies have been observed physiologically as early as primary visual cortex in a number of species, including humans (Furmanski & Engel, 2000), and it has been argued that this early physiological anisotropy could account for the oblique effect in the perception of static orientation (Appelle, 1972; Mansfield, 1974). However, the oblique effect for motion perception may have a different physiological origin. A study of the anisotropy in the perception of drifting plaids (Heeley & Buchanan-Smith, 1992) found that directional acuity was worse for plaids that drifted in an oblique direction, even when the components of the plaid were along cardinal axes. This implies that the oblique effect for motion has its origin at the level of the pattern-motion cells of MT (Movshon, Adelson, Gizzi, & Newsome, 1985) or further downstream, and not at the level of V1 or MT component-motion cells. Given that a recent study of MT failed to find an oblique effect in the direction signals of MT neurons (Churchland, Gardner, Chou, Priebe, & Lisberger, 2003), MST becomes the next good candidate for the locus of the direction anisotropy observed here. Furthermore, the view that MST or a cortical area further downstream is the locus of the oblique effect observed here is consistent with the fact that this oblique effect is in head-centered (or world-centered) coordinates and not in retinal coordinates; direction selective receptive fields in MT and earlier in the primate visual pathways are defined in retinal coordinates.

Conclusions

Our results demonstrate that the precision in the target-direction signals supporting perception is the same during pursuit and fixation, even though the visual input is strikingly different under these two oculomotor conditions. This finding suggests that direction perception during both fixation and pursuit is limited by the same ensemble of neurons that responds to a combination of retinal and extra-retinal signals and encodes target motion in head-centered (or world-centered) coordinates.

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