

Directional Asymmetries in Human Smooth Pursuit Eye Movements

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PURPOSE. Humans make smooth pursuit eye movements to bring the image of a moving object onto the fovea. Although pursuit accuracy is critical to prevent motion blur, the eye often falls behind the target. Previous studies suggest that pursuit accuracy differs between motion directions. Here, we systematically assess asymmetries in smooth pursuit.

METHODS. In experiment 1, binocular eye movements were recorded while observers ($n = 20$) tracked a small spot of light moving along one of four cardinal or diagonal axes across a featureless background. We analyzed pursuit latency, acceleration, peak velocity, gain, and catch-up saccade latency, number, and amplitude. In experiment 2 ($n = 22$), we examined the effects of spatial location and constrained stimulus motion within the upper or lower visual field.

RESULTS. Pursuit was significantly faster (higher acceleration, peak velocity, and gain) and smoother (fewer and later catch-up saccades) in response to downward versus upward motion in both the upper and the lower visual fields. Pursuit was also more accurate and smoother in response to horizontal versus vertical motion.

CONCLUSIONS. Our study is the first to report a consistent up-down asymmetry in human adults, regardless of visual field. Our findings suggest that pursuit asymmetries are adaptive responses to the requirements of the visual context: preferred motion directions (horizontal and downward) are more critical to our survival than nonpreferred ones.

Keywords: smooth pursuit, asymmetry, directional anisotropies, catch-up saccades, visual field

Smooth pursuit eye movements, the key response of the eyes to visual motion, serve to keep moving objects of interest close to the fovea. To compensate for retinal image motion, which arises naturally when a moving object is viewed, smooth pursuit must be accurate, with eye velocity closely matching target velocity. An inability to accurately track a moving target and hold it close to the fovea produces motion blur, which may impair visual acuity¹⁻⁵ and debilitate interactions with moving objects in daily activities. Recent studies have shown that accurate smooth pursuit can improve the perception of fine spatial detail,⁴ color,⁵ and motion.^{6,7} Yet, other studies have reported that smooth pursuit accuracy may be highly variable and differ across motion directions. Specifically, four types of directional anisotropies have been reported for smooth pursuit:

1. Cardinal versus diagonal axes: a preference for motion along the cardinal over the diagonal axes, known as the "oblique effect," has consistently been shown in studies assessing perceptual direction discrimination.⁸⁻¹² Some studies report similar oblique effects in smooth pursuit direction,^{12,13} whereas others have found symmetric pursuit responses.⁹
2. Horizontal versus vertical axes: better smooth pursuit performance has consistently been shown along the horizontal rather than along the vertical axes.¹³⁻¹⁹
3. Downward versus upward motion directions: better smooth pursuit for downward than for upward target motion has been found in many studies in infants/

children in humans^{20,21} and monkeys²¹⁻²⁵; however, findings in adults are inconsistent.^{13-16,21,26,27}

4. Centripetal versus centrifugal motion directions: both smooth pursuit and motion perception may benefit from target motion towards the center of the visual field (i.e., straight-ahead eye position) rather than away from the center;²⁷⁻³⁰ but the opposite effect has also been reported.^{31,32}

Results regarding asymmetries along the vertical axis are particularly inconclusive. Such inconsistent findings could be due to many factors, including small sample sizes (most studies used fewer than 10 observers), individual differences between observers, or different levels of training of observers (most studies used highly trained monkeys or laboratory members). Moreover, spatial location within the visual field could have influenced results along the vertical axis. The present study is the first to investigate all four directional asymmetries in one experiment, testing a large sample of mostly untrained human observers. A control experiment examined the possible effects of stimulus location (upper versus lower visual field) on pursuit asymmetries.

METHODS

Observers

Participants were 40 healthy adults (mean age, 23.8 years; SD, 5.1 years; range, 19-34 years; 27 were female); 20 participated

in experiment 1, 22 in experiment 2. Authors SRK and MS participated in both experiments, author JL participated in experiment 1; all other observers were undergraduate or graduate students at the University of British Columbia (UBC) and were unaware of the purpose of the experiment. Data from trained authors and untrained observers were not systematically different. Study procedures followed the tenets of the Declaration of Helsinki and were approved by UBC's Behavioral Research Ethics Board. All observers participated with written informed consent.

Observers were included in the study if they had normal or corrected-to-normal visual acuity; no history of ocular motility abnormality, strabismus, or amblyopia; and no history of any neurologic or psychiatric condition. All observers were screened to confirm normal visual acuity. Monocular and binocular visual acuities were determined using the ETDRS visual acuity chart at 4-m test distance (Original Series Chart "R"; Precision Vision, La Salle, IL). All observers had normal ($n = 19$) or corrected-to-normal visual acuity ($n = 21$) with monocular acuity 20/20 or better in $n = 31$ and 20/40 or better in $n = 9$, and all observers had binocular acuity 20/20 or better; those with refractive errors wore their regular glasses or contact lenses during the study. All observers had normal near stereovision (40 s/arc), as assessed by the Stereo Fly Test at 16-in test distance (Precision Vision). Ocular dominance was determined using the Miles test³³; 25 observers were right-eye dominant, 15 were left-eye dominant. We also tested observers' handedness, using the original Edinburgh Handedness Inventory³⁴; 34 observers were right-handed, 5 were left-handed, and 1 was ambidextrous.

Visual Stimuli and Setup

The visual motion target was a small, white Gaussian spot with diameter 0.5° and luminance 117 cd/m^2 presented on a uniform gray background (70 cd/m^2). The fixation target was a small black square (size, 0.2° ; luminance, 5 cd/m^2). Stimuli were displayed on a calibrated 21-in CRT monitor with dimensions $40.13 \text{ cm} \times 29.85 \text{ cm}$. The display was set to a refresh rate of 85 Hz and a resolution of 1600×1200 pixels. Observers were seated 55 cm away from the monitor with their head stabilized by means of a combined chin and forehead rest with memory-foam padding; to increase horizontal stability observers were instructed to maintain a steady head position.

Design and Procedure

We manipulated stimulus motion direction and speed. In a given trial, the target moved either to the left, right, up, down, or in any of the intermediate diagonal directions at 45° , 135° , 225° , or 315° starting from the screen center; target speed was either 4.5, 11.3, or 22.6 degrees per second (deg/s), resulting in a total of $8 \text{ (direction)} \times 3 \text{ (speed)} = 24$ conditions. Direction and speed were randomized across trials. Each experimental session lasted 60 minutes, during which observers ran 5 to 6 blocks of 96 trials each (each block lasted 6–8 minutes), resulting in a total of 480 or 576 trials per observer (20 or 24 trials per condition). Observers were encouraged to take breaks between blocks of trials, every 7 minutes on average, to prevent effects of fatigue.

Each trial started with a central fixation target. Observers initiated stimulus motion by pressing an assigned button on a gamepad. This gave the observer full control over the pace of the experiment, further preventing fatigue. The stimulus was initially displaced in the direction opposite to the target's velocity (step) before moving back across the fovea (ramp). This step-ramp procedure follows Rashbass³⁵ and is common-

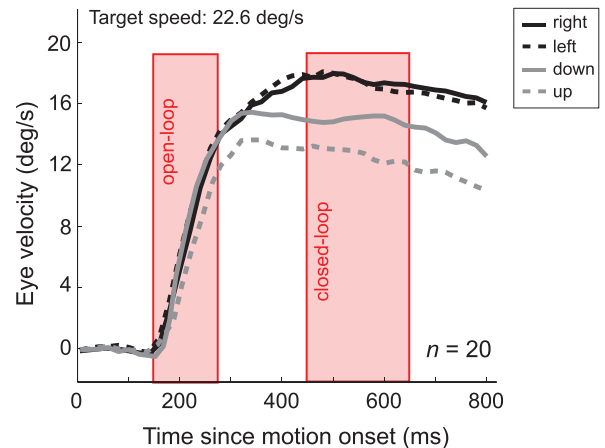


FIGURE 1. Mean eye velocity averaged across 20 observers in experiment 1 for a time period of 800 ms from stimulus motion onset for horizontal (black) and vertical (gray) motion directions. Target speed was 22.6 deg/s. Shaded areas denote analysis intervals for open-loop pursuit (0–140 ms from pursuit onset) and closed-loop pursuit (300–500 ms from pursuit onset), respectively.

ly used to prevent early saccades in smooth pursuit. In a pilot experiment, we optimized the size of the step, tailored to the target's speed, to prevent early saccades in both the direction of the step and the ramp: step sizes were 0.3° , 1.2° , and 4.5° for target speeds 4.5, 11.3, and 22.6 deg/s, respectively, so that the target reached the fovea approximately 200, 106, or 71 milliseconds (ms) after target motion onset. The step was followed by a constant ramp-duration of 800 ms. Observers were instructed to track the moving target with their eyes.

Eye Movement Recording and Analysis

Binocular eye position was measured using the Eyelink 1000 desktop-mount (SR Research, Kanata, ON, Canada) set to a sampling frequency of 1000 Hz. The Eyelink is a remote, video-based eye tracker that is unobtrusive and easy to set up, but it requires use of a chin rest to stabilize head position for high-accuracy tracking. The system reliably tracks observers with glasses or soft contact lenses. Eye movements were analyzed off-line using Matlab (Mathworks, Natick, MA). Eye velocity was obtained by differentiation of eye position signals over time and smoothed with a low-pass Butterworth filter (40-Hz cut off) in Matlab. Saccade onset and offset detection was based on the third derivative of eye position over time (jerk), obtained by differentiating unfiltered eye acceleration. Four consecutive samples had to exceed a fixed criterion of $95,000 \text{ deg/s}^3$ to be counted as saccade samples. For the analysis of smooth pursuit, saccade velocities were replaced by linear interpolation. Smooth eye movement onset was detected in the initial 300-ms interval after stimulus motion onset by fitting each 2-D position trace with a piecewise linear function consisting of two linear segments and one breakpoint. The least-squares fitting error was minimized iteratively (using the function `lsqnonlin` in Matlab) to identify the best location of the breakpoint, defined as the time of pursuit onset. We assessed pursuit quality during the open- and closed-loop phases of the pursuit response. Open-loop responses during the first 100 to 150 ms after pursuit onset reflect an estimate of visual velocity derived from image motion across the retina^{36,37}; closed-loop responses rely on a combination of retinal image motion and extra-retinal feedback. Figure 1 shows mean

TABLE 1. Effects of Speed and Motion Direction on Pursuit Characteristics in Repeated-Measures ANOVA for $n = 20$ Observers

	Speed		Direction		Speed \times Direction	
	$F_{2,38}$	<i>P</i> Value	$F_{7,133}$	<i>P</i> Value	$F_{14,266}$	<i>P</i> Value
Pursuit latency	7.54	0.002	3.50	0.002	0.61	0.85
Acceleration	8.91	0.001	1.72	0.11	1.43	0.14
Peak velocity	17.43	0.001	2.50	0.02	1.71	0.54
Gain	10.77	0.001	17.1	0.001	3.39	0.001
CUS latency	311.52	0.001	4.33	0.001	3.48	0.001
CUS number	88.27	0.001	7.51	0.001	4.04	0.001
CUS amplitude	65.53	0.001	1.17	0.32	0.55	0.90

eye-velocity traces averaged across observers; shaded areas indicate analysis intervals. In the open-loop interval, acceleration and peak velocity were measured during the first 140 ms of saccade-free pursuit with a minimum open-loop window length of 75 ms. Trials in which a saccade occurred within the first 75 ms of pursuit initiation were excluded from open-loop pursuit analysis (<0.1% of all trials). In the closed-loop interval, eye-velocity gain (eye velocity divided by target velocity) was measured in the 300- to 500-ms interval after pursuit onset. We also analyzed the latency of the initial catch-up saccade (CUS) as well as the number and amplitude of catch-up saccades across each trial. Traces with blinks at any time during stimulus presentation were excluded (<0.5% of trials in any experiment).

Statistical Analysis

Pursuit characteristics were compared statistically between conditions using repeated-measures ANOVA with within-subjects factors direction and speed. For each ANOVA, we confirmed the normality of the data and the equality of variances using Mauchly's test for sphericity. Following significant main effects of direction, we compared responses to cardinal-diagonal, horizontal-vertical, and up-down motion directions using 2-tailed *t*-tests at a Bonferroni-corrected α -level of 0.017 (0.05/3); tests were either conducted across speed (if no direction \times speed interaction was found), or separately by speed. All statistical analyses were conducted using SPSS Statistics Release 20 (IBM, Armonk, NY). We normalized pursuit peak velocity, gain, and saccade number by calculating an asymmetry index AI, defined as the difference between the average eye movement response (peak velocity, gain, or saccade number) to horizontal directions and the average eye movement response to vertical directions, divided by the sum (e.g., for peak velocity [pv]):

$$AI_{pv} = \frac{pv_{horiz} - pv_{vert}}{pv_{horiz} + pv_{vert}}$$

Pursuit gain in response to upward versus downward motion was normalized in the same way.

RESULTS

Regardless of eye dominance, we found no significant differences between data collected from either the left or the right eye. We therefore used eye-position data from each observer's dominant eye.

Speed Effects

Target speed significantly impacted pursuit characteristics, as revealed by significant main effects of speed as well as

significant speed \times direction interactions (results of repeated-measures ANOVA in Table 1). Initial eye acceleration and peak velocity increased, and pursuit latency and gain decreased as a function of target speed (see Fig. 2). All three saccade parameters were affected by speed (Table 1): saccade number and amplitude increased with speed, while latency of the first saccade decreased, indicating that pursuit became less smooth at higher speeds (see Fig. 3).

Direction Effects

However, the main focus of the current study was on the effects of motion direction. Mean velocity traces averaged across all observers (Fig. 1) show that pursuit was generally faster along the horizontal than along the vertical meridian (compare black versus gray lines), and faster in response to downward than to upward motion (compare solid-gray versus dashed-gray lines). Statistical results revealed different signatures of motion direction in open-loop and closed-loop pursuit. On the one hand, open-loop pursuit characteristics—latency, acceleration, and peak velocity (Figs. 2A–C)—reflected clear differences between upward and downward motion directions but less between horizontal and vertical motion. On the other hand, closed-loop pursuit gain (Fig. 2D) differed significantly between both horizontal and vertical motion directions and between upward and downward motion.

Open-Loop Pursuit

Pursuit latency (Fig. 2A) was significantly affected by target direction (Table 1) owing to a difference between upward and downward motion. Pursuit was initiated later when target motion was downward (mean [M] = 161.8, SD = 9.69) than when it was upward (M = 156.1, SD = 8.58), corresponding to an increase in latency by 3.5%: $t(19) = 2.31$, $P = 0.03$; nonsignificant at a corrected α -level of 0.017. We observed no difference in latency between horizontal and vertical motion directions, or between cardinal and diagonal motion directions. Whereas direction did not significantly impact initial acceleration (Fig. 2B; Table 1), we observed a significant main effect of direction on peak velocity (Fig. 2C) resulting from an up-down difference across all speeds: peak velocity was significantly higher in response to downward (M = 8.35, SD = 2.33) than to upward motion (M = 7.43, SD = 1.86), corresponding to an increase in peak velocity by 11%: $t(19) = 3.27$, $P = 0.004$ (see Figs. 4A, 5A). None of the other post hoc comparisons were significant.

Closed-Loop Pursuit

Results for closed-loop pursuit gain (Fig. 2D) indicate a horizontal-vertical as well as an up-down asymmetry (statistical results for gain are summarized in Table 2). Gain was

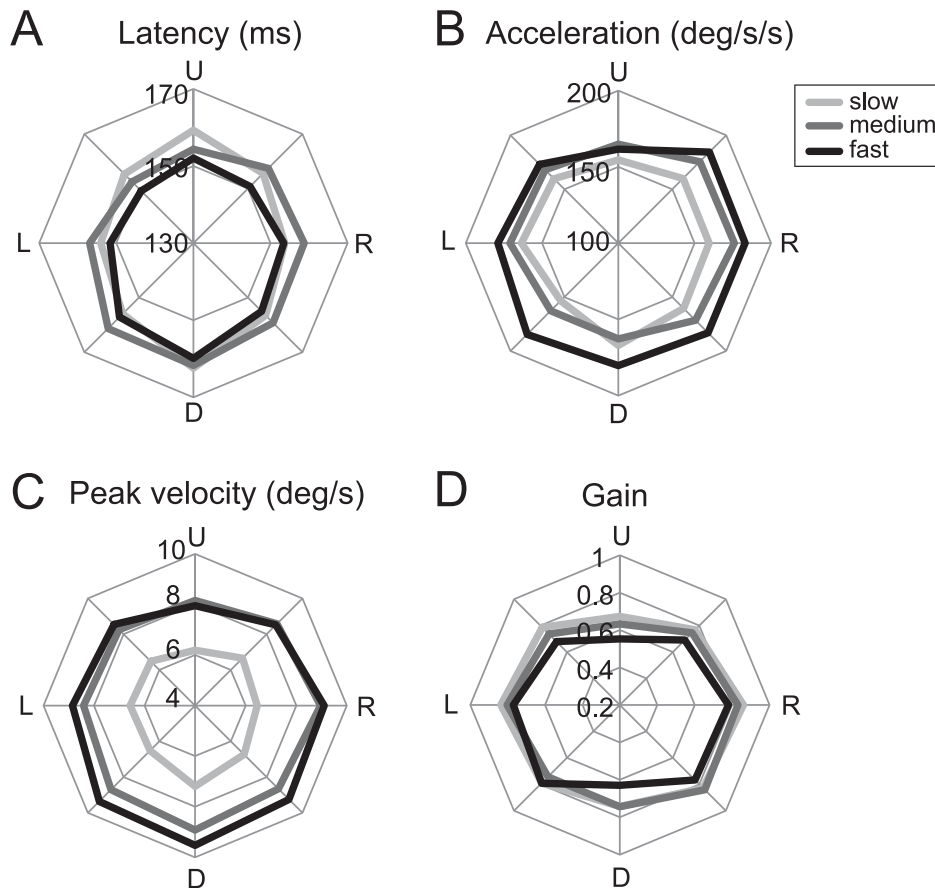


FIGURE 2. Mean pursuit responses in experiment 1 for all eight motion directions. (A) Pursuit latency in milliseconds. (B) Open-loop acceleration in degrees per second squared. (C) Open-loop peak velocity in degrees per second. (D) Closed-loop gain. *Line shades* denote target speeds.

significantly higher in response to horizontal than to vertical motion directions (Figs. 4C, 5C). Gain was also higher in response to downward versus upward motion; this effect was significant for medium and fast speeds (Figs. 4D, 5D), as

reflected in a significant direction \times speed interaction. We found no oblique effect; the gain in response to diagonal motion directions was in between the gains to horizontal and vertical motion directions (Fig. 2D).

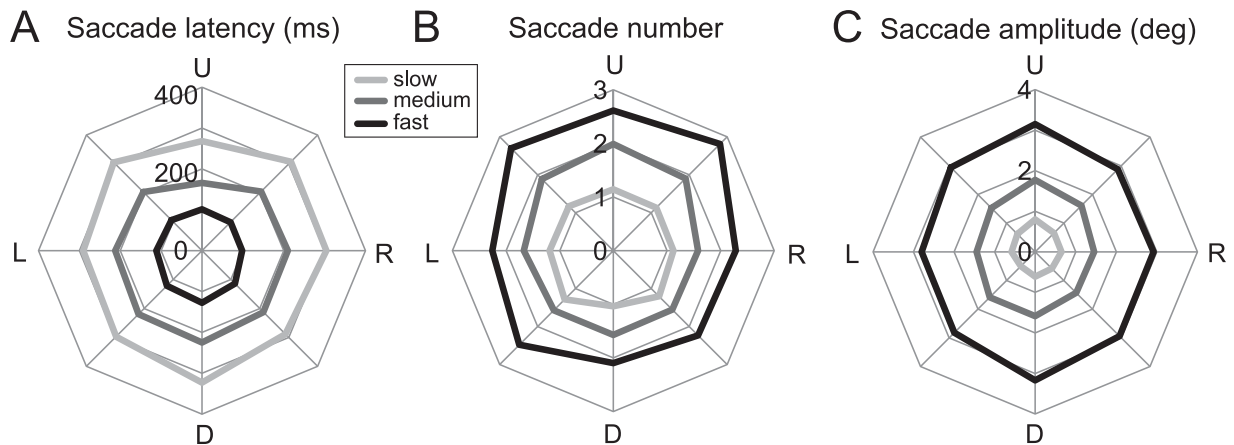


FIGURE 3. Mean CUS characteristics in all eight motion directions. (A) Latency of the initial CUS in milliseconds. (B) CUS number. (C) CUS amplitude in degrees. *Line shades* denote target speeds.

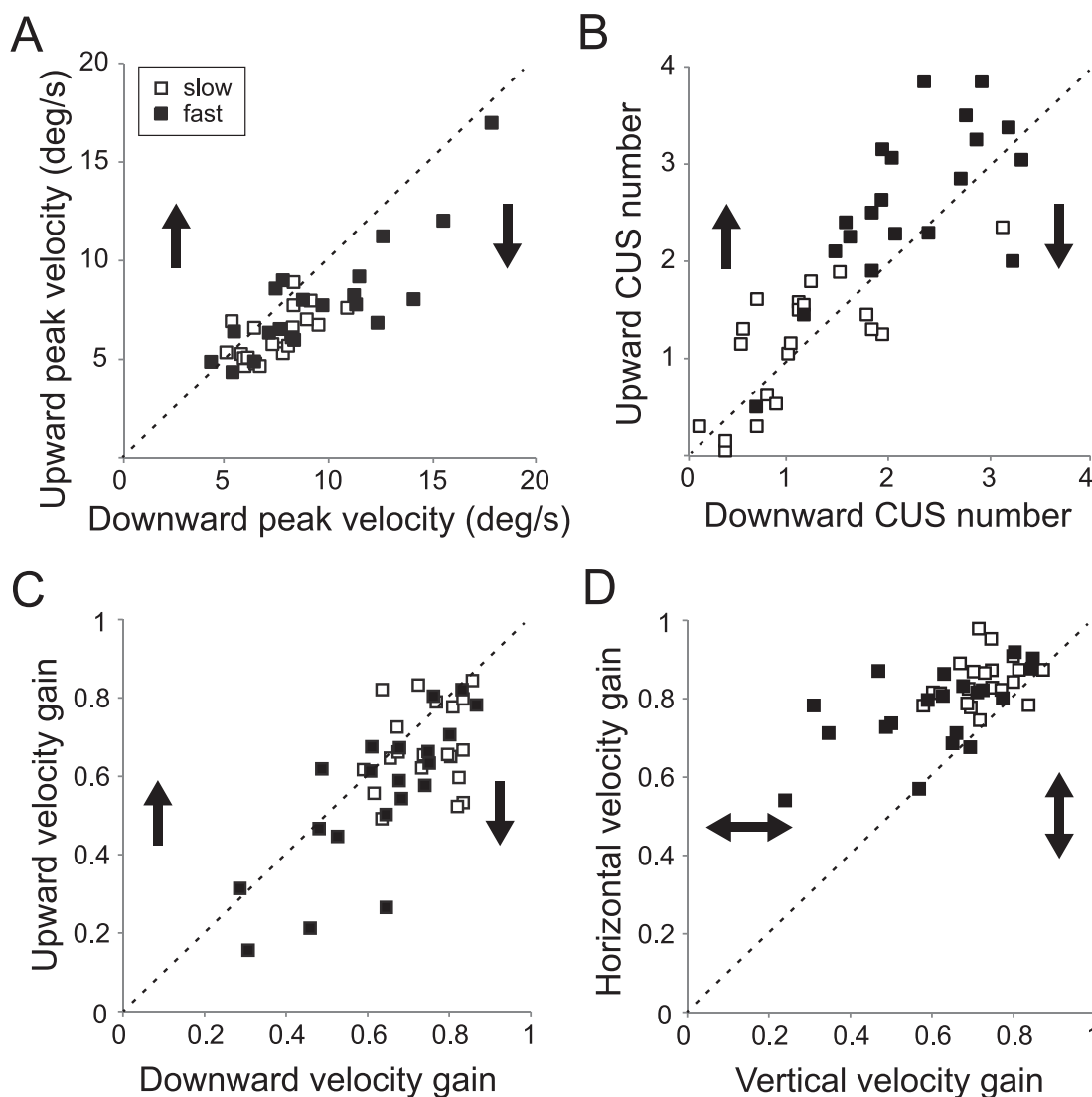


FIGURE 4. Individual observers' data in response to slow (*empty squares*) and fast (*filled squares*) stimulus speeds. Each square denotes mean responses across trials for one observer. (A) Peak velocity to upward versus downward motion. (B) CUS number to upward versus downward motion. (C) Gain to upward versus downward motion. (D) Gain to horizontal versus vertical motion.

Catch-Up Saccades

Smooth pursuit eye movements are never completely smooth; they frequently fall behind the target, and CUS are usually made to compensate for the resulting errors in eye position and velocity.³⁸ We analyzed the latency of the first (initial) catch-up saccade as an indicator of the smoothness of the initial pursuit phase, as well as the number and amplitude of CUS across each trial. Figure 3 shows that CUS, too, reflected an up-down asymmetry (see Table 1). Latency of the initial saccade was significantly shorter in response to upward motion ($M = 179.01$, $SD = 29.54$) than to downward motion ($M = 208.76$, $SD = 44.0$), corresponding to a 14.25% decrease: $t(19) = 3.19$, $P = 0.005$. This finding indicates that pursuit during upward target motion was less smooth than during downward target motion. Correspondingly, more CUS were made in response to upward motion (slow: $M = 1.14$, $SD = 0.63$; medium: $M = 1.99$, $SD = 0.67$; fast: $M = 2.61$, $SD = 0.72$) than in response to downward

motion (slow: $M = 1.04$, $SD = 0.67$; medium: $M = 1.57$, $SD = 0.69$; fast: $M = 2.10$, $SD = 0.70$). The increase in saccade number for upward motion was 9% for slow speed: $t(19) = 0.99$, $P = 0.34$; 21% for medium speed: $t(19) = 4.51$, $P = 0.0002$; and 20% for fast speed: $t(19) = 3.80$, $P = 0.001$. Differences for saccade amplitude were not significant, indicating that CUS to either motion direction were of similar amplitude, regardless of saccade number. None of the catch-up saccade features differed significantly between horizontal and vertical motion directions or between cardinal and diagonal motion directions.

To assess individual differences in asymmetries, Figures 4A to 4C show individual responses to upward versus downward motion for all observers for slow and fast target speeds in open-loop peak velocity (Fig. 4A), catch-up saccade number (Fig. 4B), and gain (Fig. 4C). For peak velocity and gain, the majority of the data points fall below the diagonal, indicating higher eye velocity and gain to downward motion. For the number of CUS, most data points fall above the diagonal, indicating that

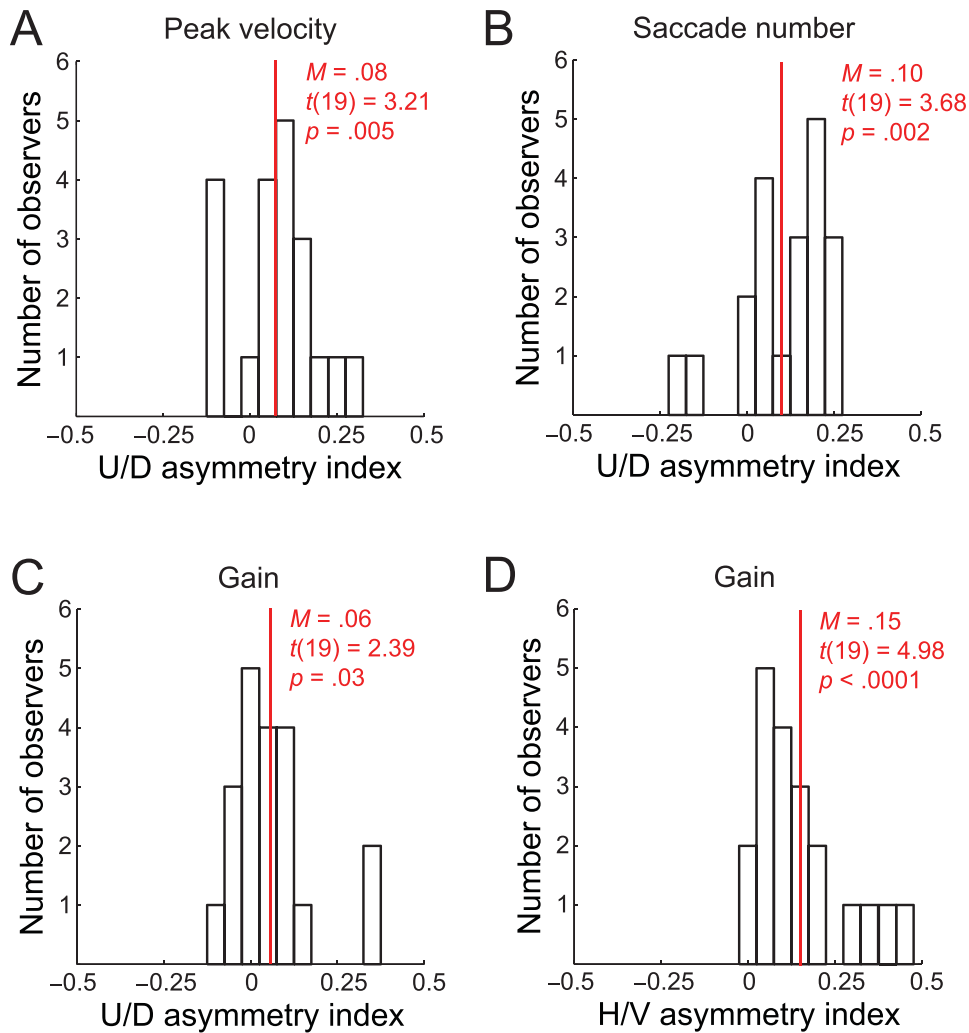


FIGURE 5. Frequency histogram of individual asymmetry indexes for pursuit in response to fast target speed. (A) Peak velocity to upward versus downward motion. (B) CUS number to upward versus downward motion. (C) Gain to upward versus downward motion. (D) Gain to horizontal versus vertical motion. Vertical red line denotes group means; statistical results are for 2-tailed *t*-tests indicating significant differences from zero.

more CUS were made in response to upward motion. Figure 4D shows individual data points for gain in response to horizontal versus vertical motion directions. Here, data points from almost all observers lie above the diagonal, indicating higher gain to horizontal motion.

Figure 5 shows normalized open-loop peak velocity (Fig. 5A), catch-up saccade number (Fig. 5B), and gain (Fig. 5C) to upward versus downward motion, as well as gain to horizontal versus vertical motion (Fig. 5D). Mean asymmetry indexes for

each pursuit measure differed significantly from zero, indicating stable asymmetries despite individual variability in response to horizontal versus vertical (closed-loop) and upward versus downward motion (open-loop and closed-loop pursuit).

Experiment 2

In experiment 1, downward target motion always occurred in the lower visual field, and upward motion occurred in the

TABLE 2. Horizontal-Vertical and Up-Down Differences in Closed-Loop Pursuit Gain*

	Horizontal		Vertical		H-V Difference			Up		Down		U-D Difference		
	M	SD	M	SD	%	<i>t</i> (19)	<i>P</i> Value	M	SD	M	SD	%	<i>t</i> (19)	<i>P</i> Value
Slow	0.85	0.06	0.71	0.07	16.56	7.61	<0.0001	0.67	0.11	0.74	0.10	9.42	2.48	0.02
Medium	0.82	0.08	0.69	0.12	15.67	4.39	0.0003	0.63	0.20	0.74	0.13	14.86	2.95	0.008
Fast	0.78	0.10	0.59	0.11	23.70	5.96	<0.0001	0.55	0.19	0.62	0.16	12.23	2.98	0.007

* All tests for *n* = 20. Significant differences in Bonferroni-corrected *t*-tests in bold.

upper visual field. In experiment 2, we constrained up-down motion directions either to the upper or to the lower visual field. In 22 observers, 20 of them newly recruited and 2 authors (SRK and MS), we varied motion direction (up versus down) and visual field (upper versus lower) by having target motion start either from the center, moving towards the periphery (centrifugal), or by starting in the periphery ($\pm 8^\circ$ from the center), moving towards the center (centripetal). In a given block of trials, upward and downward motion directions were randomly interleaved, but targets were presented only in the upper or in the lower visual field to prevent effects of direction uncertainty when the stimulus started from the center. Observers were randomly assigned to starting either with three blocks of target motion in the upper visual field or three blocks of motion in the lower visual field. Target speed was constant at 11.3 deg/s; step size was 1.2° (as in experiment 1). Target ramp motion after the initial step was 600 ms to prevent the stimulus from crossing into the opposite visual field. Each observer ran 6 blocks of 80 trials each, with a duration of approximately 6 minutes per block, resulting in 480 trials per observer (120 trials per condition). As in experiment 1, regularly scheduled breaks between blocks of trials, every 6 minutes on average, prevented fatigue. We conducted repeated-measures ANOVA and 2-tailed *t*-tests at an α -level of 0.05.

Experiment 2 showed significantly better pursuit in response to downward versus upward stimulus motion in both open-loop and closed-loop responses (Fig. 6) as well as catch-up saccade measures (Fig. 7). Table 3 summarizes results of repeated-measures ANOVA with within-subjects factors direction and visual field.

Open-Loop Pursuit

Pursuit latency was not affected by motion direction but showed a main effect of visual field (Table 3). Latency was significantly shorter in the upper versus lower visual field for downward motion: $t(21) = 2.21$, $P = 0.04$; but not upward motion: $t(21) = 1.75$, $P = 0.09$. Figure 6A shows individual observers' latency (left) and mean latency across 22 observers (right). In contrast, initial acceleration and peak velocity showed significant main effects of motion direction, but not of visual field (Table 3). Acceleration was significantly higher in response to downward motion—most data points in Figure 6B (left) are below the diagonal—but this effect was only significant in the upper visual field: $t(21) = 2.88$, $P = 0.009$; not in the lower visual field: $t(21) = 1.08$, $P = 0.29$ (see Fig. 6B, right). Peak velocity was higher in response to downward motion regardless of visual field (Fig. 6C), both for the upper visual field: $t(21) = 4.61$, $P < 0.0001$; and the lower visual field: $t(21) = 2.18$, $P = 0.04$. For peak velocity, we also found a marginally significant visual field \times direction interaction ($P = 0.05$; Table 3), reflecting a stronger preference for downward motion in the upper than in the lower visual field.

Closed-Loop Pursuit

Pursuit gain was significantly higher in response to downward motion regardless of visual field, reflected in a significant main effect of direction, but not of visual field (Table 3); this difference was significant both in the upper visual field: $t(21) = 3.56$, $P = 0.002$; and in the lower visual field: $t(21) = 2.93$, $P = 0.008$ (Fig. 6D).

Catch-Up Saccades

A main effect of motion direction on initial CUS latency and CUS number (Table 3) indicated that pursuit was smoother in

response to downward versus upward motion direction. Saccade latency was significantly shorter for downward motion both in the upper visual field: $t(21) = 5.64$, $P < 0.0001$; and in the lower visual field: $t(21) = 3.81$, $P = 0.001$. Figure 7A shows individual observers' CUS latency (left), with most data points falling below the diagonal, and mean CUS latency (Fig. 7A, right). Similarly, saccade number was significantly lower for downward motion in the upper visual field: $t(21) = 6.07$, $P < 0.0001$; and in the lower visual field: $t(21) = 4.26$, $P < 0.0001$ (Fig. 7B). We also found a significant main effect of visual field for saccade number, with fewer saccades in the lower visual field for upward motion: $t(21) = 4.51$, $P < 0.0001$; but not downward motion: $t(21) = 0.22$, $P < 0.83$. A significant visual field \times direction interaction for both CUS measures reflects stronger downward preferences in the upper visual field. CUS amplitude was similar across motion directions and visual fields (Fig. 7C).

To summarize, pursuit across the entire response was more accurate and smoother in response to downward versus upward motion. Downward motion was preferred across the visual field, albeit with larger effects in the upper visual field. We found no general preference for the upper or the lower visual field, and no difference between centripetal and centrifugal directions.

DISCUSSION

The present study demonstrates, for the first time, a consistent up-down asymmetry in human adults across the visual field, as well as a horizontal-vertical asymmetry. Our results also confirm the effects of target speed on smooth pursuit—latency decreased and open-loop acceleration and peak velocity increased with speed; closed-loop pursuit gain decreased, and CUS number and amplitude increased with speed; such effects of speed have been discussed in the literature^{27,36,39} and are not the focus of this discussion.

Different Signatures of Asymmetry in Open- and Closed-Loop Pursuit

The preponderance of horizontal over vertical motion directions in pursuit gain is consistent with previous studies in humans^{15,14,17} and monkeys,^{18,19} showing higher gain towards horizontal motion directions (Table 4). While findings are generally consistent for closed-loop velocity gain, results for open-loop pursuit are less clear. Consistent with other studies (e.g., Rottach et al.¹⁵), we did not observe significant horizontal-vertical asymmetries in any of the open-loop measures or CUS. The preference for downward motion in experiments 1 and 2, however, was apparent throughout the entire duration of the response, in open-loop and closed-loop pursuit as well as in CUS. These results are consistent with findings obtained by Grasse and Lisberger²⁵ in a single monkey. They are also in line with up-down asymmetries found in human infants (age, 5–9 months; Grönqvist et al.²⁰), children (age, 9–11 years; Takeichi et al.²¹), and young, trained monkeys (Takeichi et al.²¹; Kasahara et al.²³). Strong up-down asymmetries were also found in untrained monkeys (Akao et al.²²), indicating that asymmetries may lessen with training or experience (although up-down asymmetries may increase with age, as indicated by the faster decrease for upward than for downward gaze with age^{40,41}). In contrast, most studies in human adults have not found systematic patterns of up-down asymmetries in either open- or closed-loop pursuit^{13–15,21,26,27} (see Table 4). Similar inconsistencies exist in perceptual studies, where symmetry along the vertical axis was found in tasks on speed discrimination⁴² and acceleration detection.⁴³

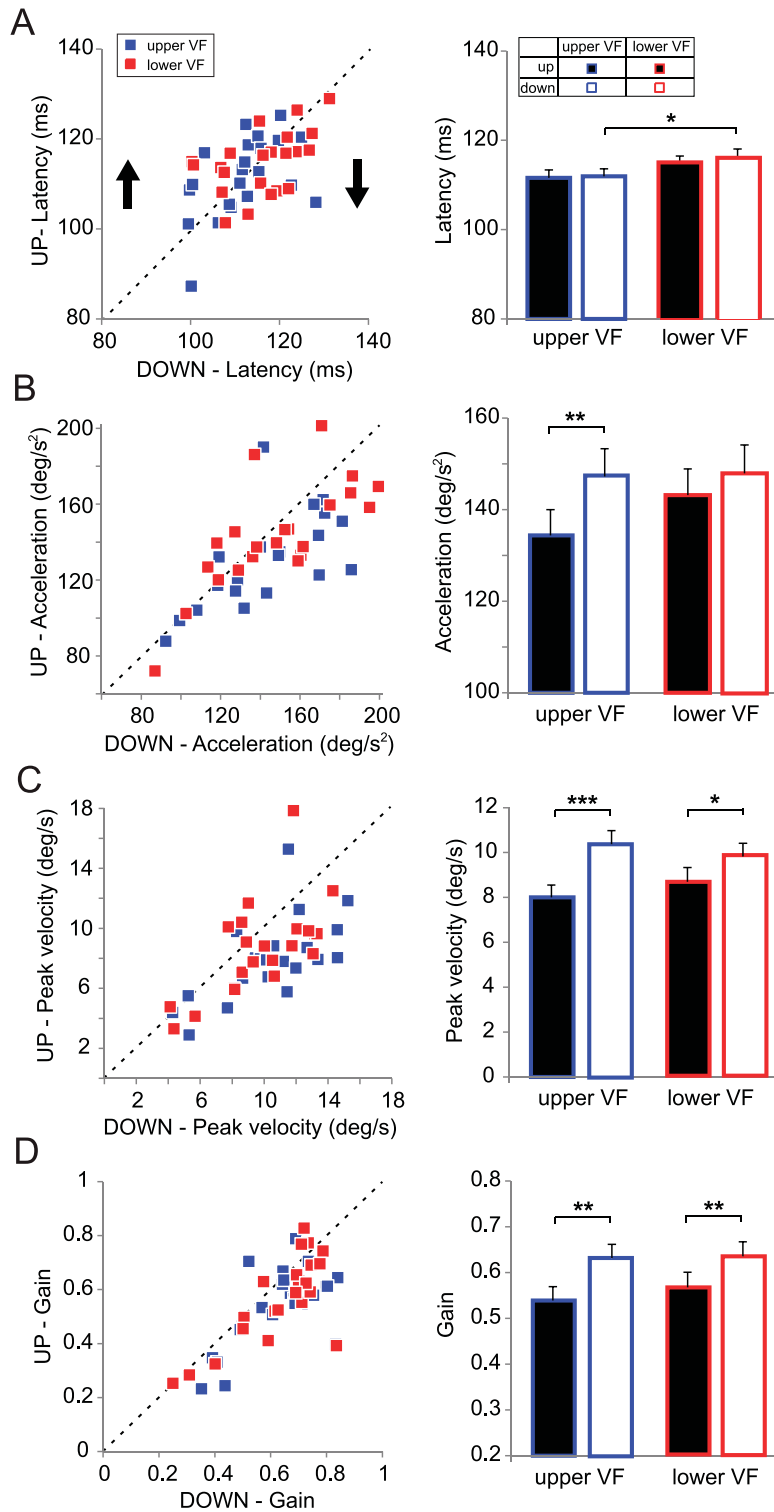


FIGURE 6. Pursuit responses in experiment 2 ($n = 22$). *Left column:* Individual observers' data in response to motion in the upper (*blue*) versus lower (*red*) visual field for upward versus downward motion. Each *square* denotes mean responses across trials for one observer. Data points falling below the diagonal indicate faster/higher responses to downward motion. *Right column:* Means for 22 observers for upward (*black*) versus downward (*white*) target motion in the upper (*blue-framed bars*) versus lower (*red-framed bars*) visual field. *Error bars* denote SEM. *Asterisks* denote significant results in 2-tailed paired-samples *t*-tests, following conventions (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). (A) Pursuit latency. (B) Initial pursuit acceleration. (C) Initial peak velocity. (D) Pursuit velocity gain.

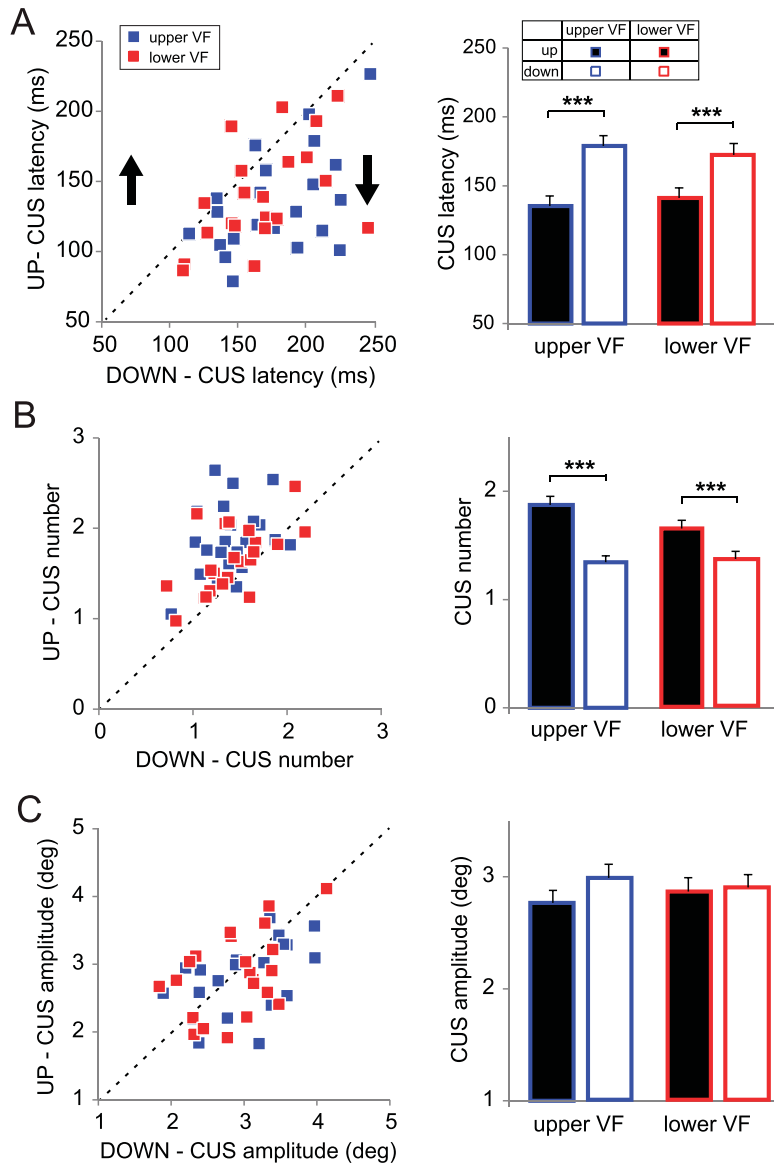


FIGURE 7. CUS results in experiment 2. *Left column:* Individual observers' data in response to motion in the upper (*blue*) versus lower (*red*) visual field for upward versus downward motion. Each *square* denotes mean responses across trials for one observer. Data points falling below the diagonal indicate faster/higher responses to downward motion. *Right column:* Means for 22 observers for upward (*black*) versus downward (*white*) target motion in the upper (*blue-framed bars*) versus lower (*red-framed bars*) visual field. *Error bars* denote SEM. *Asterisks* denote significant results in 2-tailed paired-samples *t*-tests; see Figure 6 legend. (A) CUS latency. (B) CUS number. (C) CUS amplitude.

TABLE 3. Effects of Visual Field and Motion Direction on Characteristics of Pursuit and CUS in Repeated-Measures ANOVA for 22 Observers

	VF		Direction		VF × Direction	
	$F_{1,21}$	<i>P</i> Value	$F_{1,21}$	<i>P</i> Value	$F_{1,21}$	<i>P</i> Value
Pursuit latency	5.88	0.02	0.42	0.53	0.13	0.72
Acceleration	1.63	0.22	5.60	0.03	2.76	0.11
Peak velocity	0.02	0.91	15.01	0.001	4.45	0.05
Gain	0.67	0.42	11.50	0.003	3.20	0.09
CUS latency	0.003	0.96	5.30	0.03	24.83	0.0001
CUS number	6.31	0.02	29.70	0.0001	29.15	0.0001
CUS amplitude	0.008	0.93	1.23	0.28	3.00	0.10

VF visual field.

TABLE 4. Directional Anisotropies in Smooth Pursuit and Motion Perception Reported in 25 Representative Behavioral Studies in Humans and Other Primates*

	>	=	<
Cardinal vs. diagonal	Perception: 8–12; pursuit: 12, 13	Pursuit: 9	
Horizontal vs. vertical	13–19		
Down vs. up	Infants/children: 20–24; adults: 25, 26	Adults: 13–15, 21, 26, 27	16
Centripetal vs. centrifugal	27–30	31	31, 32

* All studies conducted in humans except the following: cats¹⁶; monkeys^{18,19,21–25}; study 21 tested humans and monkeys.

but perceptual estimation of motion duration was better for downward than upward moving targets.⁴⁴ Sample sizes in those pursuit studies reported in Table 4 ranged from 3 to 10 observers, many of them trained laboratory members. Our study provides the first account of a stable up-down asymmetry across the entire pursuit response and across the visual field in a large sample ($n = 40$) of healthy and mostly untrained ($n = 37$) human adults, with no systematic differences in patterns of asymmetry between trained laboratory members and untrained subjects. While training may play a role in diminishing pursuit asymmetries, it cannot eliminate the effects.

Opposite Up-Down Asymmetries in Vertical Pursuit and Optokinetic Nystagmus (OKN)

We have shown better pursuit in response to downward than in response to upward motion direction (see Table 4). Of interest, the majority of studies on OKN report the opposite vertical asymmetry, with higher slow-phase velocities and gain found in response to upward motion in frontal-eyed species such as humans,^{45–50} monkeys,^{51,52} and cats,^{16,53} as well as lateral-eyed animals such as chickens.⁵⁴ Some studies found no vertical asymmetries in OKN.^{55,56} Both smooth pursuit and OKN are visually induced eye movements that are controlled by similar neuronal pathways.⁵⁷ The two types of responses are often distinguished based on the stimulus that elicits them best: smooth pursuit is a continuous, slow response to small targets moving at moderate speeds; OKN responds best to fast motion patterns spanning the entire visual field. But, more important, both systems seem to serve inherently different purposes: pursuit is made to shift and align gaze with a moving object of interest; OKN is a reflexive movement to stabilize gaze on a visual scene.

If we assume that the visual and oculomotor systems are adaptive and have evolved, developmentally and evolutionarily, to optimally respond to the prevailing content of the visual world (e.g., Simoncelli and Olshausen⁵⁸), opposite signatures of up-down motion directions in pursuit and OKN are not surprising. The upward-preference in OKN may be an adaptive response to stabilize gaze during forward locomotion by suppressing or compensating downward optic-flow information. The preference for downward motion in smooth pursuit may partly result from the frequency of exposure to falling (rather than rising) objects owing to gravity, as proposed by studies showing perceptual and motor preference for objects moving in compliance with gravity constraints.^{44,59}

No Vertical-Meridian Asymmetry in Smooth Pursuit

Consistent with other studies on pursuit asymmetries,^{25,27} we found no systematic difference between the upper and lower visual fields. In contrast, many perceptual studies report

vertical-meridian asymmetries, suggesting that humans are better in detecting, discriminating, and segmenting motion direction when the moving object is located in the lower visual field, than when it moves across the upper visual field.^{60–62} However, studies on motor performance yielded inconsistent results. Whereas some studies report a more efficient use of visual feedback when reaching for objects in the lower visual field,^{63,64} as well as higher endpoint precision,⁶⁵ other studies find no differences in movement time and endpoint accuracy of reaching movements to either visual field.^{66,67} Studies on pursuit,²⁵ including the present one, either find a clear downward preference regardless of visual field or a preference for centripetal motion across the visual field (i.e., no general preference for motion in the lower visual field).²⁷

Neuronal Correlate of Pursuit Asymmetries

While asymmetries in smooth pursuit seem to be shaped by prior experience and training, their cause may lie in differences in neuronal processing. Smooth pursuit eye movements are driven by visual motion information, which is mainly transmitted via the cortico-pontine-cerebellar pathway through the middle temporal visual area (MT) to the parietal and frontal cortex and in parallel to the pontine nuclei in the brainstem and the cerebellum for the assembly of motor commands (see detailed reviews in Keller and Heinen⁵⁷; Krauzlis⁶⁸; and Leigh and Zee⁶⁹). Whereas little indication for systematic directional asymmetries has been found in neuronal responses in visual cortical areas such as MT^{9,70} (but see Giaschi et al.⁷¹ for a report of a centripetal-centrifugal asymmetry in human MT), several pursuit-related regions within the cerebellum carry signatures of vertical pursuit asymmetries.

The cerebellar flocculus, mainly involved in the maintenance, but also the initiation, of smooth pursuit, has been described to exhibit an up-down asymmetry in smooth pursuit (for a review, see Ref. 72). The majority of floccular Purkinje cells are active during downward but not during upward pursuit.^{73–75} Using functional imaging of the flocculus, Glasauer et al.⁷⁶ found similar differences in neuronal activity during vertical pursuit in healthy humans. Lesions in the flocculus may result in downbeat nystagmus (i.e., slow upward drifts of the eye followed by downward corrective saccades).^{77,78} This finding, in conjunction with the asymmetry in the activity pattern of floccular Purkinje cells, indicates that the cerebellar flocculus may mediate the preference for downward motion directions in vertical smooth pursuit. Lesions of other cerebellar structures involved in vertical smooth pursuit (e.g., uvula, nodulus) may also result in impaired downward pursuit.⁷⁹ Kurkin et al.²⁴ provide further indirect evidence that the up-down pursuit asymmetry may be mediated downstream from cortical pursuit areas. In two monkeys with up-down pursuit asymmetry, these authors recorded the activity of neurons in the caudal area of the frontal eye fields (FEF), a region that has emerged as one of the

most important cortical pursuit areas.^{68,80} Although behavioral experiments revealed higher downward pursuit gain and peak velocity in these monkeys, the activity of FEF neurons was symmetric.

Neuronal correlates for the horizontal-vertical pursuit asymmetry are less obvious. Pathways for horizontal and vertical pursuit seem to separate in the cerebellum: Purkinje cells in the cerebellar flocculus encode neuronal signals for horizontal and vertical smooth pursuit separately,^{74,81} and projections from the flocculus to the motoneurons go through the superior vestibular nucleus for vertical pursuit⁸² and to the abducens nucleus via the vestibular nucleus for horizontal pursuit.⁵⁷ These separate cerebellar projections may underlie the observed horizontal-vertical asymmetry in pursuit. Such a horizontal preference may be an acquired and adaptive response to the frequency with which we encounter motion along the horizontal axis in our visual environment.

A number of outstanding questions remain, which this study was not designed to address. Smooth pursuit eye movements have consequences for visual perception, and we have recently shown that higher accuracy in pursuit tracking causes an increase in the ability to predict visual motion trajectories.⁸³ Asymmetries in eye-movement accuracy could therefore be responsible for anisotropies observed in many perceptual tasks. While we have assessed naturally occurring asymmetries in healthy adults, eye-movement asymmetries are also present in many disease states, such as strabismus. For instance, infantile strabismus often results in impaired and asymmetric eye movements, (i.e., a nasal-temporal pursuit asymmetry)^{84,85} and occasionally a preference for upward motion,⁸⁵ as well as the loss of visual function. However, vertical asymmetries, in particular, as well as their potential perceptual consequences have not been studied systematically in this or other patient groups nor in the elderly, who may show larger asymmetries owing to a faster decay of upward gaze with age.^{40,41} Our results may serve as a baseline for developmental studies as well clinical studies assessing patients with disorders involving ocular motor asymmetries.

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References

- Methling D, Wernicke J. Visual acuity in horizontal tracking movements of the eye. *Vision Res.* 1968;8:555-565.
- Brown B. Dynamic visual acuity, eye movements and peripheral acuity for moving targets. *Vision Res.* 1972;12:305-321.
- Westheimer G, McKee SP. Visual acuity in the presence of retinal-image motion. *J Opt Soc Am.* 1975;65:847-850.
- Schütz AC, Braun DI, Gegenfurtner KR. Object recognition during foveating eye movements. *Vision Res.* 2009;49:2241-2253.
- Schütz AC, Braun DI, Kerzel D, Gegenfurtner KR. Improved visual sensitivity during smooth pursuit eye movements. *Nat Neurosci.* 2008;11:1211-1216.
- Hafed ZM, Krauzlis RJ. Ongoing eye movements constrain visual perception. *Nat Neurosci.* 2006;9:1449-1457.
- Spering M, Schütz AC, Braun D, Gegenfurtner KR. Keep your eyes on the ball: smooth pursuit eye movements enhance prediction of visual motion. *J Neurophysiol.* 2011;105:1756-1767.
- Ball K, Sekuler R. Models of stimulus uncertainty in motion perception. *Psychol Rev.* 1980;87:435-469.
- Churchland AK, Gardner JL, Chou I, Priebe NJ, Lisberger SG. Directional anisotropies reveal a functional segregation of visual motion processing for perception and action. *Neuron.* 2003;37:1001-1011.
- Dakin SC, Athorp D, Alais D. Anisotropies in judging the direction of moving natural scenes. *J Vis.* 2010;10:1-19.
- Gros BL, Blake R, Hiris E. Anisotropies in visual motion perception: a fresh look. *J Opt Soc Am A.* 1998;15:2003-2011.
- Krukowski AE, Stone LS. Expansion of direction space around the cardinal axes revealed by smooth pursuit eye movements. *Neuron.* 2005;45:315-323.
- Rottach KG, Zivotofsky AZ, Das VE, et al. Comparison of horizontal, vertical and diagonal smooth pursuit eye movements in normal human subjects. *Vision Res.* 1996;36:2189-2195.
- Baloh RW, Yee RD, Honrubia V, Jacobson K. A comparison of the dynamics of horizontal and vertical smooth pursuit in normal human subjects. *Aviat Space Environ Med.* 1988;59:121-124.
- Collewin H, Tamminga EP. Human smooth and saccadic eye movements during voluntary pursuit of different target motions on different backgrounds. *J Physiol.* 1984;351:217-250.
- Evinger C, Fuchs AF. Saccadic, smooth pursuit, and optokinetic eye movements of the trained cat. *J Physiol.* 1978;285:209-229.
- Grant MP, Leigh RJ, Seidman SH, Riley DE, Hanna JP. Comparison of predictable smooth ocular and combined eye-head tracking behaviour in patients with lesions affecting the brainstem and cerebellum. *Brain.* 1992;115:1323-1342.
- Kettner RE, Leung HC, Peterson BW. Predictive smooth pursuit of complex two-dimensional trajectories in monkey: component interactions. *Exp Brain Res.* 1996;108:221-235.
- Leung HC, Kettner RE. Predictive smooth pursuit of complex two-dimensional trajectories demonstrated by perturbation responses in monkeys. *Vision Res.* 1997;37:1347-1354.
- Grönqvist H, Gredebäck G, Hofsten C. Developmental asymmetries between horizontal and vertical tracking. *Vision Res.* 2006;46:1754-1761.
- Takeichi N, Fukushima J, Kurkin S, Yamanobe T, Shinmei Y, Fukushima K. Directional asymmetry in smooth ocular tracking in the presence of visual background in young and adult primates. *Exp Brain Res.* 2003;149:380-390.
- Akao T, Kumakura Y, Kurkin S, Fukushima J, Fukushima K. Directional asymmetry in vertical smooth-pursuit and cancellation of the vertical vestibulo-ocular reflex in juvenile monkeys. *Exp Brain Res.* 2007;182:469-478.
- Kasahara S, Akao T, Fukushima J, Kurkin S, Fukushima K. Further evidence for selective difficulty of upward eye pursuit in juvenile monkeys: effects of optokinetic stimulation, static roll tilt, and active head movements. *Exp Brain Res.* 2006;171:306-321.
- Kurkin S, Akao T, Fukushima J, Fukushima K. Discharge of pursuit-related neurons in the caudal part of the frontal eye fields in juvenile monkeys with up-down pursuit asymmetry. *Exp Brain Res.* 2009;193:181-188.

25. Grasse KL, Lisberger SG. Analysis of a naturally occurring asymmetry in vertical smooth pursuit eye movements in a monkey. *J Neurophysiol.* 1992;67:164-179.
26. Marti S, Bockisch CJ, Straumann D. Prolonged asymmetric smooth-pursuit stimulation leads to downbeat nystagmus in healthy human subjects. *Invest Ophthalmol Vis Sci.* 2005;46:143-149.
27. Tychsen L, Lisberger SG. Visual motion processing for the initiation of smooth-pursuit eye movements in humans. *J Neurophysiol.* 1986;56:953-968.
28. Mateeff S, Hohnsbein J. Perceptual latencies are shorter for motion towards the fovea than for motion away. *Vision Res.* 1988;28:711-719.
29. Edwards M, Badcock DR. Asymmetries in the sensitivity to motion in depth: a centripetal bias. *Perception.* 1993;22:1013-1023.
30. Raymond JE. Directional anisotropy of motion sensitivity across the visual field. *Vision Res.* 1994;34:1029-1037.
31. Dumoulin SO, Baker CL, Hess RF. Centrifugal bias for second-order but not first-order motion. *J Opt Soc Am.* 2001;18:2179-2189.
32. Ball K, Sekuler R. Human vision favors centrifugal motion. *Perception.* 1980;9:317-325.
33. Miles WR. Ocular dominance in human adults. *J Gen Psychol.* 1930;3:412-429.
34. Oldfield RC. The assessment and analysis of handedness: the Edinburgh Inventory. *Neuropsychologia.* 1971;9:97-113.
35. Rashbass C. The relationship between saccadic and smooth tracking eye movements. *J Physiol.* 1961;159:326-338.
36. Lisberger SG, Westbrook LE. Properties of visual inputs that initiate horizontal smooth pursuit eye movements in monkeys. *J Neurosci.* 1985;5:1662-1673.
37. Lisberger SG. Visual guidance of smooth pursuit eye movements: sensation, action, and what happens in between. *Neuron.* 2010;66:477-491.
38. De Brouwer S, Yuksel D, Blohm G, Missal M, Lefevre P. What triggers catch-up saccades during visual tracking? *J Neurophysiol.* 2002;87:1646-1650.
39. Haegerstrom-Portnoy G, Brown, B. Contrast effects on smooth-pursuit eye movement velocity. *Vision Res.* 1979;19:169-174.
40. Clark RA, Isenberg SJ. The range of ocular movements decreases with aging. *J AAPOS.* 2001;5:26-30.
41. Clark RA, Demer JL. Effect of aging on human rectus extraocular muscle paths demonstrated by magnetic resonance imaging. *Am J Ophthalmol.* 2002;134:872-878.
42. Matthews N, Qian N. Axis-of-motion affects direction discrimination, not speed discrimination. *Vision Res.* 1999;39:2205-2211.
43. Calderone JB, Kaiser MK. Visual acceleration detection: effect of sign and motion orientation. *Percept Psychophys.* 1989;45:391-394.
44. Moscatelli A, Lacquaniti F. The weight of time: gravitational force enhances discrimination of visual motion duration. *J Vis.* 2011;11:1-17.
45. Benson AJ, Guedry FE. Comparison of tracking task performance and nystagmus during sinusoidal oscillation in yaw and pitch. *Aerosp Med.* 1971;42:593-601.
46. Garbutt S, Han Y, Kumar AN, Harwood M, Harris CM, Leigh RJ. Vertical optokinetic nystagmus and saccades in normal human subjects. *Invest Ophthalmol Vis Sci.* 2003;44:3833-3841.
47. Murasugi M, Howard IP. Up-down asymmetry in human vertical optokinetic nystagmus and afternystagmus: contributions of the central and peripheral retinae. *Exp Brain Res.* 1989;77:183-192.
48. Ogino S, Kato I, Sakuma A, Takahashi K, Takeyama I. Vertical optokinetic nystagmus in normal individuals. *Acta Otolaryngol.* 1996;522:38-42.
49. Takahashi M, Sakurai S, Kanzaki J. Horizontal and vertical optokinetic nystagmus in man. *ORL J Otorhinolaryngol Relat Spec.* 1978;40:43-52.
50. van den Berg AV, Collewijn H. Directional asymmetries of human optokinetic nystagmus. *Exp Brain Res.* 1988;70:597-604.
51. Matsuo V, Cohen B. Vertical optokinetic nystagmus and vestibular nystagmus in the monkey: up-down asymmetry and effects of gravity. *Exp Brain Res.* 1984;53:197-216.
52. Takahashi M, Igarashi M. Comparison of vertical and horizontal optokinetic nystagmus in the squirrel monkey. *ORL J Otorhinolaryngol Relat Spec.* 1977;39:321-329.
53. Darlot C, López-Barneo J, Tracey D. Asymmetries of vertical vestibular nystagmus in the cat. *Exp Brain Res.* 1981;41:420-426.
54. Wallman J, Velez J. Directional asymmetries of optokinetic nystagmus: developmental changes and relation to the accessory optic system and to the vestibular system. *J Neurosci.* 1985;5:317-329.
55. Knapp CM, Gottlob I, McLean RJ, Proudlock FA. Horizontal and vertical look and stare optokinetic nystagmus symmetry in healthy adult volunteers. *Invest Ophthalmol Vis Sci.* 2008;49:581-588.
56. Knapp CM, Gottlob I, McLean RJ, Rafelt S, Proudlock FA. Effect of distance upon horizontal and vertical look and stare OKN. *J Vis.* 2009;9:1-9.
57. Keller EL, Heinen SJ. Generation of smooth-pursuit eye movements: neuronal mechanisms and pathways. *Neurosci Res.* 1991;11:79-107.
58. Simoncelli EP, Olshausen BA. Natural image statistics and neural representation. *Ann Rev Neurosci.* 2001;24:1193-1216.
59. Senot P, Zago M, Lacquaniti F, McIntyre J. Anticipating the effects of gravity when intercepting moving objects: differentiating up and down based on nonvisual cues. *J Neurophysiol.* 2005;94:4471-4480.
60. Amenedo E, Pazo-Alvarez P, Cadaveira F. Vertical asymmetries in pre-attentive detection of changes in motion direction. *Int J Psychophysiol.* 2007;64:184-189.
61. Lakha L, Humphreys G. Lower visual field advantage for motion segmentation during high competition for selection. *Spat Vis.* 2005;18:447-460.
62. Regan D, Erkelens CJ, Collewijn H. Visual field defects for vergence eye movements and for stereomotion perception. *Invest Ophthalmol Vis Sci.* 1986;27:806-819.
63. Danckert J, Goodale MA. Superior performance for visually guided pointing in the lower visual field. *Exp Brain Res.* 2001;137:303-308.
64. Khan MA, Lawrence GP. Differences in visuomotor control between the upper and lower visual fields. *Exp Brain Res.* 2005;164:395-398.
65. Krigolson O, Heath M. A lower visual field advantage for endpoint stability but no advantage for online movement precision. *Exp Brain Res.* 2006;170:127-135.
66. Binsted G, Heath M. No evidence of a lower visual field specialization for visuomotor control. *Exp Brain Res.* 2005;162:89-94.
67. Brownell K, Rolheiser T, Heath M, Binsted G. Does perception asymmetrically influence motor production in upper and lower visual fields? *Motor Control.* 2010;14:44-58.
68. Krauzlis RJ. Recasting the smooth pursuit eye movement system. *J Neurophysiol.* 2004;91:591-603.
69. Leigh RJ, Zee DS. *The Neurology of Eye Movements.* 4th ed. New York, NY: Oxford University Press; 2006.
70. Maunsell JHR, Van Essen DC. Functional properties of neurons in middle temporal visual area of the macaque monkey. I. Selectivity for stimulus direction, speed, and orientation. *J Neurophysiol.* 1983;19:1127-1147.

71. Giaschi, D, Zwicker A, Young SA, Bjornson B. The role of cortical area V5/MT+ in speedtuned directional anisotropies in global motion perception. *Vision Res.* 2007;47:887-898.
72. Kheradmand A, Zee DS. Cerebellum and ocular motor control. *Front Neurol.* 2011;2:1-15.
73. Fukushima K, Fukushima J, Kaneko CRS, Fuchs AF. Vertical Purkinje cells of the monkey floccular lobe: simple spike activity during pursuit and passive whole body rotation. *J Neurophysiol.* 1999;82:787-803.
74. Krauzlis RJ, Lisberger SG. Directional organization of eye movement and visual signals in the floccular lobe of the monkey cerebellum. *Exp Brain Res.* 1996;109:289-302.
75. Stone LS, Lisberger SG. Visual responses of Purkinje cells in the cerebellar flocculus during smooth-pursuit eye movements in monkeys. I. Simple spikes. *J Neurophysiol.* 1990;63:1241-1261.
76. Glasauer S, Stephan T, Kalla R, Marti S, Straumann D. Up-down asymmetry of cerebellar activation during vertical pursuit eye movements. *Cerebellum.* 2009;8:385-388.
77. Marti S, Straumann D, Glasauer S. The origin of downbeat nystagmus: an asymmetry in the distribution of on-directions of vertical gaze-velocity Purkinje cells. *Ann N Y Acad Sci.* 2005;1039:548-553.
78. Zee DS, Yamazaki A, Butler PH, Gucer G. Effects of ablation of flocculus and paraflocculus on eye movements in primate. *J Neurophysiol.* 1981;46:878-899.
79. Walker MF, Tian J, Shan X, Tamargo RJ, Ying H, Zee DS. Lesions of the cerebellar nodulus and uvula impair downward pursuit. *J Neurophysiol.* 2008;100:1813-1823.
80. Fukushima K. Frontal cortical control of smooth-pursuit. *Curr Opin Neurobiol.* 2003;13:647-654.
81. Krauzlis RJ, Lisberger SG. Simple spike responses of gaze velocity Purkinje cells in the floccular lobe of the monkey during onset and offset of pursuit eye movements. *J Neurophysiol.* 1994;72:2045-2050.
82. Zhang Y, Partsalis AM, Highstein SM. Properties of superior vestibular nucleus flocculus target neurons in the squirrel monkey. I. General properties in comparison with flocculus projecting neurons. *J Neurophysiol.* 1995;73:2261-2278.
83. Spering M, Schütz AC, Braun DI, Gegenfurtner KR. Keep your eyes on the ball: smooth pursuit eye movements enhance prediction of visual motion. *J Neurophysiol.* 2011;105:1756-1767.
84. Mustari MJ, Ono S. Neural mechanisms for smooth pursuit in strabismus. *Ann N Y Acad Sci.* 2011;1233:187-193.
85. Tychsen L, Lisberger SG. Maldevelopment of visual motion processing in humans who had strabismus with onset in infancy. *J Neurosci.* 1986;6:2495-2508.