Dynamics of oculomotor direction discrimination

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Successful foveation of a dynamic target depends on good predictions of its movement direction and speed. We measured and compared the temporal dynamics of directional precision of both saccades and smooth pursuit and their interactions. We also compared the directional precision of both eye movements to psychophysical direction discrimination thresholds. Directional thresholds of pure pursuit responses improved rapidly and reached asymptotic values of 1.5°– 3° within 300 ms after target motion onset, both for trained and untrained observers and irrespective of the speed of the stimuli. Psychophysical thresholds were in the same range. Directional thresholds for saccades in the ramp paradigm were just slightly higher, but these occurred significantly earlier in time at around 200 ms after target motion onset. At the equivalent time during pure pursuit initiation, thresholds were typically higher by 2°–3°. The rise in directional precision—or decrease in thresholds—over time was more pronounced for trials with longer latencies. As an effect, precision depended mainly on time since stimulus motion onset rather than pursuit onset. Directional precision for saccades to static targets was slightly better than to moving targets, at even shorter latencies. We conclude that directional precision is higher for the saccadic system at saccade onset than for the pursuit system, presumably due to additional position signals that are not available to the pursuit system at that point in time. The pursuit response improves rapidly due to refined sensory processing and motor planning. The combination of initial saccades and pursuit to track moving targets is a good strategy for the oculomotor system to reduce directional errors during the phase of initiation. The target speed has very little effects on the directional precision of both eye movements.

Introduction

The human visual system brings together the best of two mutually opposing requirements—high visual acuity and a large field of view. It achieves this feat by restricting the highest visual acuity to a small central region, the fovea, surrounding it with a large field of view at much lower resolution. For such a foveated visual system to be useful, a mechanism is required to move the fovea around in the visual field to sample information at the highest quality. This is done by eye movements, which of course, to be useful have to be quick and precise. Primates coordinate two different modes of voluntary eye movements for tracking at highest acuity: discrete saccades to rapidly (re-)position the fovea onto a target and continuous slow eye rotations, smooth pursuit to stabilize the projection of a moving target on the fovea. In order to plan, initiate, and adjust appropriate eye movements to moving targets, the oculomotor system is dependent on prompt access to precise measurements and predictions of the current and future target trajectories (Becker & Fuchs, 1969, 1985; Bahill & McDonald, 1983; Barnes & Asselman, 1991). When a peripheral target suddenly begins to move, eye tracking is initiated typically with a target-directed saccade to correct rapidly for the position error between target and fovea and then followed by pursuit. Here we measured the time course of the directional precision of both saccadic eye movements and smooth pursuit.

Saccades are very fast voluntary eye movements, characterized by a consistent relationship of peak velocity, duration, and amplitude, the so-called main sequence (Bahill, Clark, & Stark, 1975; Harris & Wolpert, 2006). Despite being fast, they are also quite accurate (Kapoula & Robinson, 1986; Kowler & Blaser, 1995; van Beers, 2007), even in response to moving targets (Heywood & Churcher, 1981; Ron, Vieville, & Droulez, 1989; Keller & Steen Johnsen,

1990; de Brouwer, Missal, & Lefèvre, 2001; de Brouwer, Missal, Barnes, & Lefèvre, 2002; de Brouwer, Yuksel, Blohm, Missal, & Lefèvre, 2002; Eggert, Guan, Bayer, & Büttner, 2005; Guan, Eggert, Bayer, & Büttner, 2005; Etchells, Benton, Ludwig, & Gilchrist, 2010). Depending on many factors such as stimulus characteristics and fixation-target timing conditions, training, and age, it takes about 100–300 ms to initiate a target-directed saccade. Typical mean saccadic latencies are about 180–200 ms in man (Saslow, 1967; Fischer & Ramsperger, 1984; Gellman & Carl, 1991; Munoz, Broughton, Goldring, & Armstrong, 1998). Saccades reflect a more final choice of the oculomotor system, because shortly before their onset about 80–100 ms ("dead time") their amplitude cannot be altered (Wheeless, Boynton, & Cohen, 1966; Becker & Jürgens, 1979; Aslin & Shea, 1987; Ludwig, Mildinhall, & Gilchrist, 2007).

Different from saccades, pursuit movements are continuous slow eye rotations initiated from feed-forward estimates of the direction and speed of a selected moving target (Rashbass, 1961; Lisberger & Westbrook, 1985; Krauzlis & Lisberger, 1994). Pursuit allows to foveate moving targets continuously within a limited range (i.e., optimal velocities are between 4°/s–40°/s). When a target moves toward the direction of gaze and reaches the fixated position within about 200 ms, pure pursuit responses can be initiated into the target movement direction after latencies in the range of 100–180 ms without any saccade (Rashbass, 1961; Carl & Gellman, 1987; Liston & Stone, 2014). However, when a peripheral target suddenly starts to move or if it changes its direction or speed unpredictably during ongoing pursuit, the pursuit system immediately lags behind. This is due to the visual system's inherent processing delay of about 100 ms and the limited capacity of the pursuit system for acceleration. In this case saccades become necessary, which correct for positional errors and to some degree also compensate for the retinal slip (Engel, Anderson, & Soechting, 1999; de Brouwer, Missal, et al., 2002; de Brouwer, Yuksel et al, 2002; Osborne, Bialek, & Lisberger, 2004; Guan et al., 2005; Schreiber, Missal, & Lefèvre, 2006; Orban de Xivry & Lefèvre, 2007).

During initiation, the open-loop phase, pursuit is mainly driven by feed-forward image motion signals and the pursuit response represents a direct visuo-motor transformation of the target movement (Lisberger, Morris, & Tychsen, 1987; Pack & Born, 2001). Depending on the condition (i.e., target speed, contrast, size, and predictability) pursuit accelerates over a time period of up to 300 ms, until the eye velocity has reached the target velocity (Tychsen & Lisberger, 1986; Heinen & Watamaniuk, 1998; Hawken & Gegenfurtner, 2001; Spering, Kerzel, Braun, Hawken, & Gegenfurtner, 2005; Braun et al., 2008; Mukherjee,

Battifarano, Simoncini, & Osborne, 2015). During the closed-loop or steady-state phase the pursuit system stabilizes the target image close to the fovea via a negative feedback mechanism (i.e., corollary discharge or efference copy signal of the oculomotor commands), which minimizes the difference between the eye and the retinal target image velocity (i.e., the retinal slip; Robinson, Gordon, & Gordon, 1986; Lisberger et al., 1987). Retinal image acceleration (Lisberger et al., 1987) and retinal target position relative to the fovea (Blohm, Missal, & Lefevre, 2005) are used as additional signals for pursuit control. Although pursuit velocity oscillates around the target velocity during this phase, image movements are minimized so that object recognition is only slightly reduced compared to fixation (Schütz, Braun, & Gegenfurtner, 2009).

Here we studied and compared directional precision of both types of voluntary eye movements and their interaction. A continuous investigation of the directional precision of tracking eye movements over time was done for macaque monkeys (Osborne, Lisberger, & Bialek, 2005; Osborne, Hohl, Bialek, & Lisberger, 2007). Osborne et al. (2007) analyzed the first 300 ms of monkey pursuit responses to step-ramps varying slightly in movement direction to determine the direction precision of pursuit. After pursuit initiation at about 100 ms after target motion onset, monkeys' direction discrimination thresholds of their pursuit movements remained high and undefined during the first 20–40 ms. Then pursuit discrimination thresholds decreased rapidly and approached their minimum of approximately 3° for spot-like stimuli at the end of the open-loop period, 225 ms after target motion onset, or 125 ms after pursuit onset. According to Osborne and colleagues (Osborne, Lisberger, & Bialek, 2005; Osborne et al., 2007; Osborne & Lisberger, 2009) this rapid improvement of the pursuit direction discrimination thresholds reflected the continuously improving sensory estimates of the target movement direction exclusively. Psychophysical thresholds for direction discrimination were not measured in these monkeys so that a direct comparison of their perceptual and oculomotor thresholds was not available.

Investigations of the directional precision of smooth pursuit were neglected for a long time, maybe because most available eye trackers allowed precise measurements only for the horizontal component of pursuit eye movements while the vertical pursuit component turned out to be more noisy and variable (Collewijn & Tamminga, 1984; Tychsen & Lisberger, 1986; Baloh, Yee, Honrubia, & Jacobson, 1988). Directional precision of human smooth pursuit was measured at fixed points in time in three studies. Watamaniuk and Heinen (1999) used two different kinds of stimuli: a single spot moved at 8°/s into five slightly different directions (6°, 3°, 0°, −3°, −6°) and circular random-dot

kinematograms (RDKs) modified by different levels of directional noise. They limited their analysis and comparison of psychophysical and oculomotor direction discrimination to the late phase of the open-loop period of pursuit and measured their own pursuit eye directions over a 20-ms bin centered 130 ms after pursuit onset, and psychophysical judgments of direction for the same stimuli presented for 140 ms during fixation. Similar to the first psychophysical direction discrimination study in humans by de Bruyn and Orban (1988), psychophysical thresholds for direction discrimination of single spot stimuli during fixation were about 2°. In stark contrast, oculometric thresholds for pursuit responses 130 ms after initiation were about 8°–9° for single spots. However, these measurements were contaminated by initial saccades. For the RDKs, which allow for saccade-free pursuit initiation, one observer had consistently lower thresholds of 3°–4°. A comparison of psychophysical and oculomotor direction discrimination thresholds for the RDKs as a function of added directional noise revealed that oculomotor thresholds were much higher than perceptual thresholds, even though the best fitting functions for both sets of data were quite similar.

A different approach was taken by Stone and Krauzlis (2003). First the authors pursued step-ramps moving along nine different trajectories bracketing the four cardinal axes, and then they gave a binary judgment about the spatial displacement of the ramp trajectory in regard to the cardinal axis. To compare the judgments of displacement perception with pursuit direction of the same trial they converted the filtered pursuit into directional responses and divided them in five different 100-ms time intervals. The oculometric functions for pursuit data during the interval centered around 300 ms after pursuit onset turned out to be quite similar to the psychometric functions for all cardinal directions: The measured perceptual threshold was around 1.3°; the pursuit threshold around 1.6°. More recently, Mukherjee et al. (2015) studied human pursuit direction discrimination with single spot targets or random dot patterns and used step-ramps with unpredictable directions ranging from 9° to −9° and velocities between 10°/s −15°/s. They found that pursuit direction thresholds dropped rapidly after pursuit onset and reached threshold values between 1.5°–1.9° as soon as 240 ms after target motion onset, quite similar to the values they obtained in a perceptual direction discrimination task.

Sudden onsets of object motion are one of the most salient features for our visual system and they can appear anywhere in our visual field (Dorr, Martinetz, Gegenfurtner, & Barth, 2010). Most often movement trajectories are unpredictable, and because objects rarely move toward the position of gaze and because of the limitations of our pursuit system (i.e., inherent

processing delays, limited velocity and acceleration range), pursuit especially depends at target movement onset on the support of the saccadic system. Most pursuit eye movements are initiated by fast target-directed saccades to minimize rapidly the distance between target and fovea, and to prevent that this initial position error grows further over time. Recent studies show that position and motion information are used in the preparation of saccades to moving targets (de Brouwer, Missal, et al., 2002; de Brouwer, Yuksel, et al., 2002; Eggert et al., 2005; Schreiber et al., 2006). Furthermore, after an initial saccade, pursuit speed was higher compared to pure pursuit responses, a phenomenon called postsaccadic enhancement (Lisberger, 1998; Wilmer & Nakayama, 2007). The directional precision of initial saccades and subsequent pursuit has not been studied yet and the postsaccadic enhancement effect itself is poorly understood. Here we were interested in the directional precision of the human oculomotor system during the initiation of tracking either by pure pursuit eye movements or by a combination of initial saccades followed by pursuit. Our main interest was the comparison of the temporal development of directional precision of initial saccades and pursuit eye movements and their interaction.

Methods

Observers

Four (three highly practiced and one untrained) observers, one of them being an author (Do), and six previously untrained observers participated in different sets of experiments. The four observers participated in four experiments—one with a single stimulus speed (20°/s), one with seven different speeds interleaved, one with a static target, and one psychophysical experiment. Three of them were students (mean age: 24 years, one male) of the University Giessen with normal vision. They were naive regarding the purpose of the experiments and they were paid for their participation. Two of them had participated in similar eye movement studies before and one was formerly untrained and became experienced through the large number of trials. One observer was one of the authors, who is slightly myopic. The six additional naive and untrained observers (students, mean age: 25 years, one male) were tested with two different, interleaved speeds (16°/s and 32°/s). They had not participated before in any similar eye movement experiments and were paid. Informed consent was obtained according to the Declaration of Helsinki. Methods and procedures followed the guidelines of the Deutsche Gesellschaft für Psychologie and

were approved by the local ethics committee for proposal number LEK 2009-0008.

Eye movement recording and equipment

For the first sets of experiments with four observers, visual stimuli were presented on a 21-in. SONY GDM-F520 CRT monitor (Sony Electronics, Inc., San Jose, CA), driven by an Nvidia Quadro NVS 290 graphics board (PNY Technologies, Parsippany, NJ) with a refresh rate of 100 Hz non-interlaced. The active screen area on the monitor subtended 43° in the horizontal and 37° in the vertical direction with a spatial resolution of 1280 × 1024 pixels, resulting in 29.79 pixels/degree. In a dark room observers viewed the stimulus display binocularly with their heads stabilized by a chin and forehead rest at a viewing distance of 47 cm. We recorded the eye position signals of the right eye with an EyeLink 1000 Tower Mount, a video-based eye tracker with a sampling rate of 1000 Hz (Eyelink 1000, SR Research Ltd., Osgoode, Ontario, Canada).

Additionally the eye position signals of the right eye of six naive observers were measured with a table mounted Eyelink 1000 and stimuli were presented on a Display++ monitor. The active screen area of this monitor subtended 42.5° in the horizontal and 24.5° in the vertical direction and with a spatial resolution of 1920 × 1080 pixels resulting in 45.2 pixels/degree. The monitor has a refresh rate of 120 Hz noninterlaced (Cambridge Research Systems Ltd., Rochester, UK). The distance between observer and the monitor was 90 cm. Stimulus display and data collection were controlled continuously by a personal computer. Data analysis was done offline.

Procedure

After a short instruction regarding the eye movement task, the position of the observer's head and the eye tracker were adjusted. Calibrations were repeated until the validation score reached gaze-position errors below 0.35°. In rare cases a larger error was accepted when it was caused by a larger gaze deviation of one of the most eccentric positions. In a single session of 1 hr two to three experimental blocks were conducted with longer breaks in between. Each experimental block of either ramps or step-ramps consisted of 150 trials. Each trial was initiated by the observer via button pressing. For each task with a single speed at least six blocks were collected for each observer on different days, for the experiment with seven different speeds three practiced observers participated in 17–22 blocks. For the experiment with two different speeds eye movement data of five blocks were collected each for saccades and pursuit of six untrained subjects.

Paradigms

For the comparison of the directional oculomotor precision we used a ramp paradigm for saccade-initiated pursuit and a step-ramp paradigm for pure pursuit as illustrated in Figure 1. We also measured saccades with static peripheral targets.

Saccades to moving targets (ramp)

Each trial consisted of an initial fixation and a pursuit interval. It started with the appearance of a small black fixation spot (10′) in the center of the gray CT screen (38.86 cd/m²) for a randomized duration between 500–1000 ms. Then the pursuit target, a Gaussian blob ($SD = 17′$, peak contrast: 100%) replaced the fixation spot and moved immediately at a constant speed of 20°/s randomly either to the left or right across the screen for 1 s. None or one out of six different vertical components of ±10°, 5°, or 2° was added unpredictably to the horizontal ramp direction (see Figure 1A).

Smooth pursuit (step-ramp)

As in the ramp experiments, each step-ramp trial started with a fixation period of the central fixation spot for the same randomized duration. After the offset of the fixation spot the pursuit target (a Gaussian blob as above) appeared about 4° (step) to the left or right (step) of the screen center and moved back in the direction of the center at a fixed speed of 20°/s to the right or left (Rashbass, 1961). After crossing the screen center it continued its linear movement for 1 s (see Figure 1D). Seven different vertical components were used in a randomized way: +10°, +5°, +2°, 0°, −2°, −5°, and −10°. The size of the initial position step of the pursuit target was adjusted for each of the observers to minimize the occurrence of early catch-up saccades during the initiation phase of pursuit. Typically, the target reached the screen center after 200–220 ms.

Ramps and step-ramps with different speeds

Three observers (two naive observers and one of the authors) participated in 17–22 separate blocks with ramps and step-ramps in which the seven directions were randomly combined with one of seven (step-)ramp speeds between 14°/s to 43°/s (14.3°/s, 21.4°/s, 25°/s, 28.6°/s, 32.1°/s, 35.7°/s, and 42.8°/s).

For six naive observers saccades and pursuit data were collected in five blocks each in which the (step-)ramp target moved randomly into one of the seven directions and in one of two speeds: 16°/s or 32°/s.
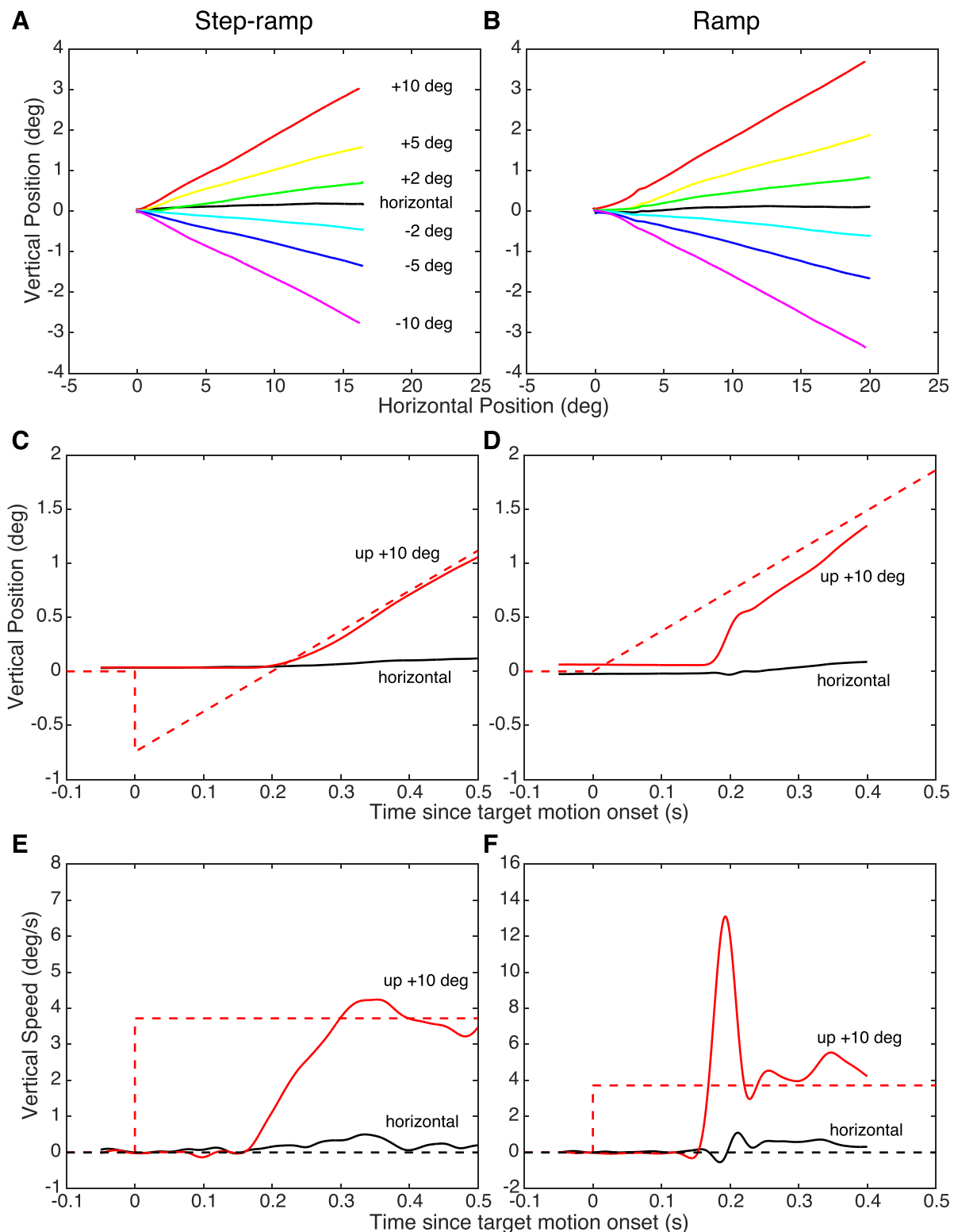
Figure 1. Eye movement responses to step-ramps (left column) and ramps (right column). The first row shows the averaged eye positions a representative observer for all step-ramp (A) and ramp (B) directions in different colors, which indicate the vertical displacement from the horizontal baseline (black). In the second and third row averaged vertical eye positions and eye speeds of the same observer are shown. The continuous red traces show the vertical components of the averaged eye position (C–D) and of the averaged eye speed (E–F) of the eye movements to a 10° upward step-ramp (E) or ramp (F) plotted with a dashed red line. Different from smooth and continuous acceleration of the eye speed until the target speed is reached in the step-ramps condition, initial saccades cause a large up- and downward deflection of the eye speed trace 200 ms after eye movement onset and correct for the increasing position error in the ramp condition.

Saccades to static targets (step)

After the offset of the central fixation spot the Gaussian blob appeared with the same step displacement (20 or 22 according to the step) 4° unpredictably either to the left or right with the same vertical displacements of ±10°, 5°, 2°, or 0°. The observer was asked to make a saccade to the target.

Psychophysical task

We ran a psychophysical direction discrimination experiment with four observers. A fixation target was displayed at the beginning of each trial. Then a small Gaussian blob appeared either at the center and moved with a speed of 20°/s away from it, or appeared 4° peripherally and moved towards the center. Movement duration was 200 ms and the direction was either horizontal or had a vertical component of ±2°, 5°, or 10°. The observer was asked to indicate by button pressing whether the peripheral blob target had moved up- or downward.

Eye movement data analysis

Our aim was to measure and to compare the directional precision of both saccadic and pursuit eye movements to linearly moving targets for each point in time. We constructed oculometric functions from the vertical eye velocity components of each trial for saccades and pursuit. This allowed us to compare the development and dynamics of directional precision—the slope of the oculometric function—of both eye movements at corresponding points in time after target movement onset.

Standard methods were used to process eye position traces (see Braun et al., 2008). In brief, the horizontal and vertical position traces of the right eye of each trial were filtered by a second-order Butterworth filter with a cut-off frequency of 30 Hz. Eye velocities were obtained by digital differentiation of the eye position signals over time.

In our off-line analysis of step-ramp pursuit trials we included only trials in which no catch-up saccade occurred during the fixation period (100 ms before target motion onset) and the initiation phase (the first 300 ms after target motion onset). Saccades were detected using the standard Eyelink criterion, which combines an eye velocity and acceleration threshold of 30°/s and 1000°/s², respectively. For initial saccades we also determined the position error and the retinal slip 100 ms before saccade onset.

Pursuit onset was determined by finding the first 50-ms interval in which eye velocity values were above the average eye velocity during fixation plus 3 times the standard deviation of the velocity during fixation. A regression line was then fitted to the eye velocity trace in that interval. The slope of that line defines the acceleration of pursuit. Trials with latencies shorter than 60 ms or longer than 300 ms, with peak accelerations smaller than 25°/s² and more than 300°/s², or with bad regression fits (r^2 correlation values of less than 0.4) were excluded from the analysis. Ramp-trials were accepted if the first saccade occurred more than 50 ms and less than 300 ms after target motion onset. Typically, 10%–20% of trials had to be excluded in the step-ramp paradigm, mostly due to saccades during the fixation period or problems with the pursuit onset. In the ramp paradigms, fewer trials were excluded, typically between 5%–10%.

Oculometric functions

For each observer we aligned all traces to eye movement onset. To estimate directional sensitivity at any instant t_x we constructed oculometric functions (Kowler & McKee, 1987; Gegenfurtner, Xing, Scott, & Hawken, 2003; Rasche & Gegenfurtner, 2009) based on the average vertical component of the eye movement during a 40-ms window centered on t_x. The median direction of the eye in response to purely horizontal step-ramp (or ramp) stimuli at a given point in time served as the baseline for each observer (see Figure 2A, black histogram). For the other six stimulus directions, the vertical eye speed in each trial was compared to that baseline and the proportions of trials with an upward eye speed larger than baseline were calculated. In Figure 2 frequency histograms for the vertical eye speeds of eye movements to the seven different step-ramp directions measured 200 ms after pursuit onset were plotted in different colors for a typical observer. For horizontal trials the histogram (black color) for the vertical eye speeds is centered at zero. For step-ramps with a vertical component of ±2°, frequency histograms are slightly shifted to the left or right from zero and overlap (i.e., few eye movements are initiated in the opposite vertical direction). For step-ramps with vertical components of ±10°, nearly all eye responses go into the correct vertical direction.

Figure 2B shows how the proportion of upward trials changes over time. The proportions at each point in time were then fitted with a psychometric function, using the software package Psignifit4 (Schütt, Harmeling, Macke, & Wichmann, 2015). A logistic function was fit to the data, with the lapse and guess rate set to 0. The inverse of the resulting slope of this function represents our estimate of the directional precision of the oculomotor system at the selected point in time. It corresponds to the value where the upward judgments are indicated correctly in 73% of the trials. We ran our analyses with many different combinations of filtering,
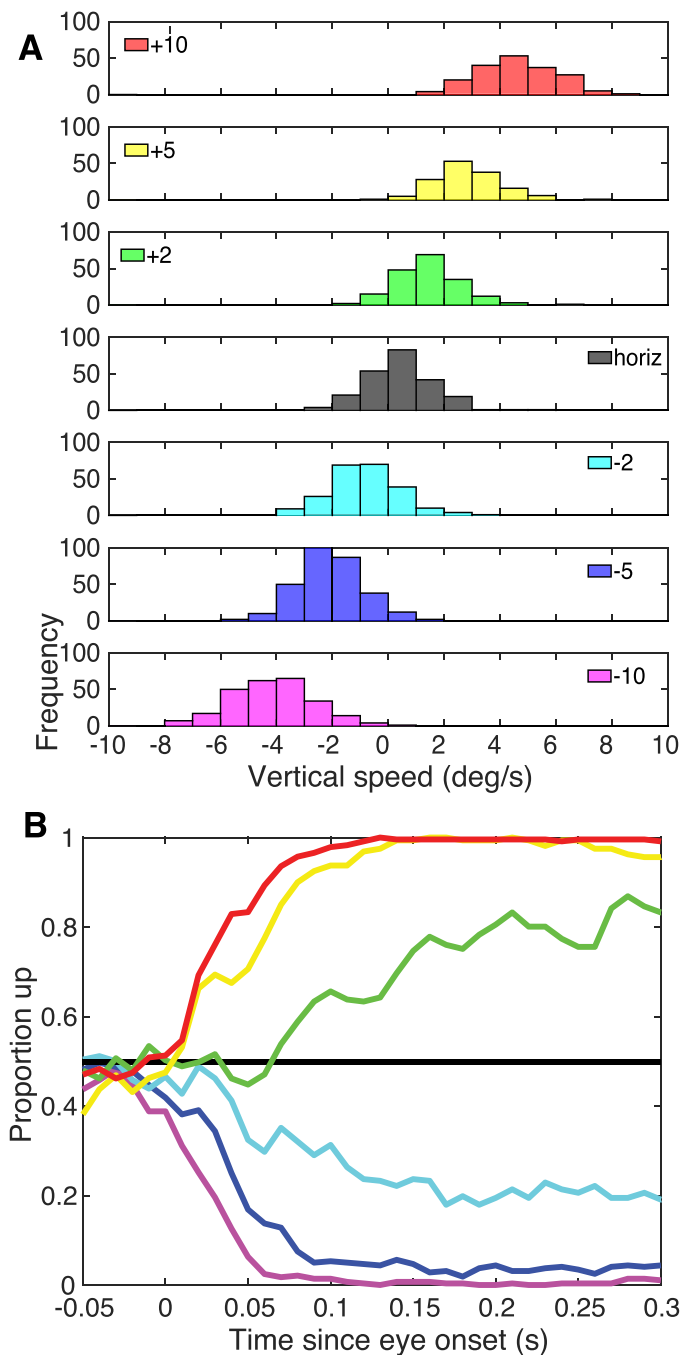
Figure 2. Construction of oculometric functions for pursuit direction discrimination. (A) Frequency histograms of the vertical eye speed over single trials to the different step-ramp directions (shown here in different colors) for observer Do 200 ms after target onset. The black histogram shows the vertical eye velocities of purely horizontal trials, which were used as baseline. (B) For each ramp direction the proportions of trials with an upward eye speed change (*y*-axis) is plotted over time since eye onset for a single observer relative to his/her baseline (black line). Shortly after less than 50 ms proportions of the upward eye speed changes start to deviate according to the ramp direction and asymptote.

averaging windows and both eye direction and vertical position change. In cases where the results were affected by these choices, we make mention of it.

Time course of pursuit precision

To estimate the decay in the oculometric functions over time for each observer, we fitted exponential decay functions to the threshold data:

$$p(t) = a + C*\exp(-t_0/t), \quad (1)$$

where *a* is the asymptotic threshold value reached during steady state pursuit, *C* is a parameter indicating the initial threshold level, and t_0 is the exponential time constant of decay. We chose the time where the threshold first reached a level of twice its asymptote (2*a*) as an indicator of how quickly precision decreased initially.

Latency effects

For three observers a large number of experimental trials were collected in 12–17 blocks, so that we could further divide up trials according to pursuit onset latency. This was done to investigate a potential effect of onset latency on precision during eye movement initiation. The trials were divided into four blocks according to the pursuit latency distribution, using the 25, 50, and 75 percentiles as separators. For each block, termed "very slow," "slow," "fast," and "very fast," the time course of pursuit precision was computed. The resulting curves were generally shifted in time only, and the best fitting shift parameter was compared to the corresponding latency differences.

Results

We first present the results regarding the development of the directional precision of pursuit over time and will compare it with other results in the literature and with our psychophysical results. Then we will compare the directional precision of saccades and pursuit.

Pursuit precision

We used the histograms of vertical eye speed to construct oculometric functions and determined their slopes to measure the directional precision for chosen points in time. Figure 3 shows four oculometric functions of two observers at different points in time
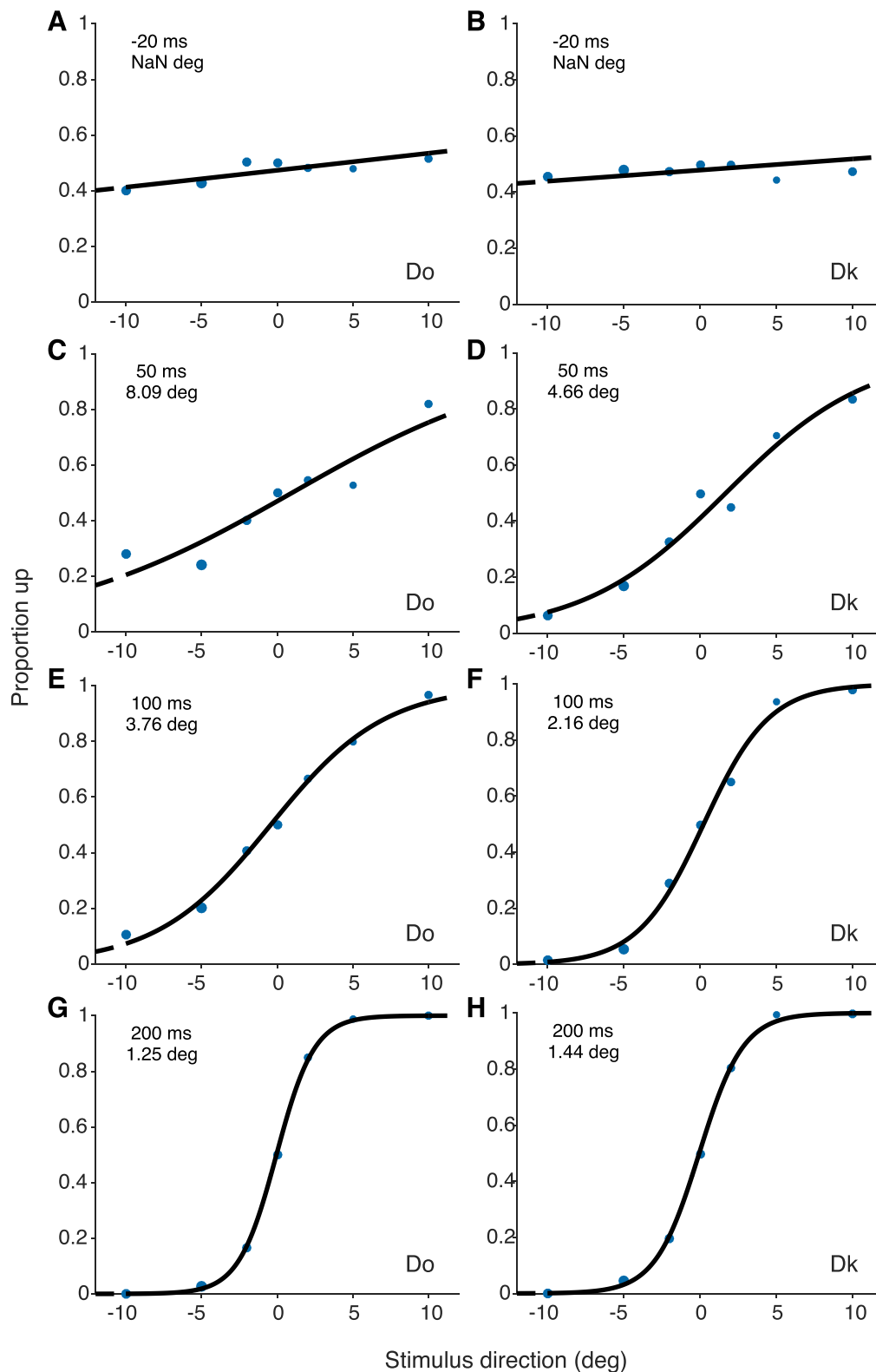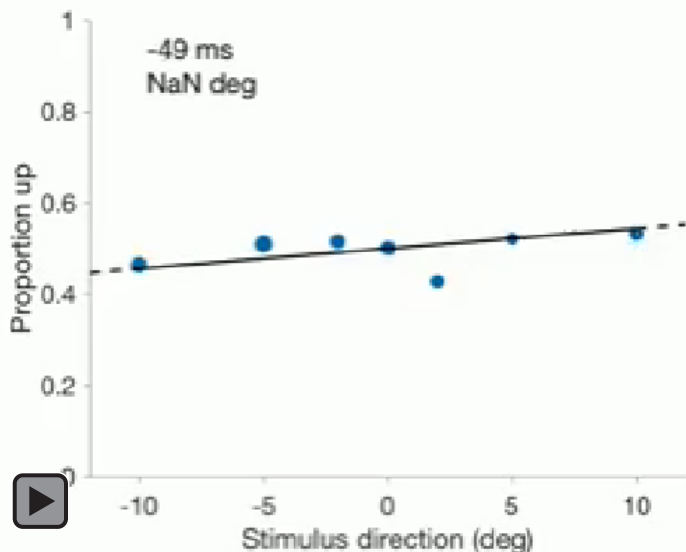
Figure 3. Oculometric functions for the vertical direction constructed at 0, 50, 100 and 200 ms after pursuit onset for two observers. Numbers at the upper left corner of each plot give the point in time relative to pursuit onset and the slope of the oculometric function.

Movie 1: Dynamic of the directional precision of pursuit eye movements for observer Do. Oculometric functions for direction are shown over time after eye movement onset. The slopes of the oculometric functions change rapidly during the first 100 ms after pursuit onset and the n gradually reach an asymptote.

relative to the onset of pursuit. Right before initiation (−20 ms) the oculometric functions of both observers are nearly horizontal and their slopes are very shallow or undefined. Fifty milliseconds after pursuit onset the oculometric functions look different: For observer Dk the function has a well-defined slope, while for observer Do the slope is still shallow. The rapid change of the oculometric functions of both observers continues and the slopes, indicating the directional discrimination thresholds decrease further and reach a minimum at about 200 ms. The differences at early points in time show that the two observers develop their sensitivity to directional differences with different time courses. Observer Dk (left column) reaches a directional threshold of about 2.18° in as little as 100 ms of pursuit, about 2° lower than that of observer Do (right column) but 200 ms after pursuit onset they reach similar low levels of oculometric thresholds below 1.5°. Similar dynamic improvements of pursuit direction discrimination as a function of time were found for the other two observers. The dynamic of the directional precision of pursuit eye movements and the exact time course is shown in Movie 1 for observer Do.

Comparison to psychophysics

We also tested direction discrimination psychophysically for comparison. Figure 4 compares for two subjects the oculometric functions measured 200 ms after target onset with the psychometric functions. For both subjects, the slopes of their psychometric and
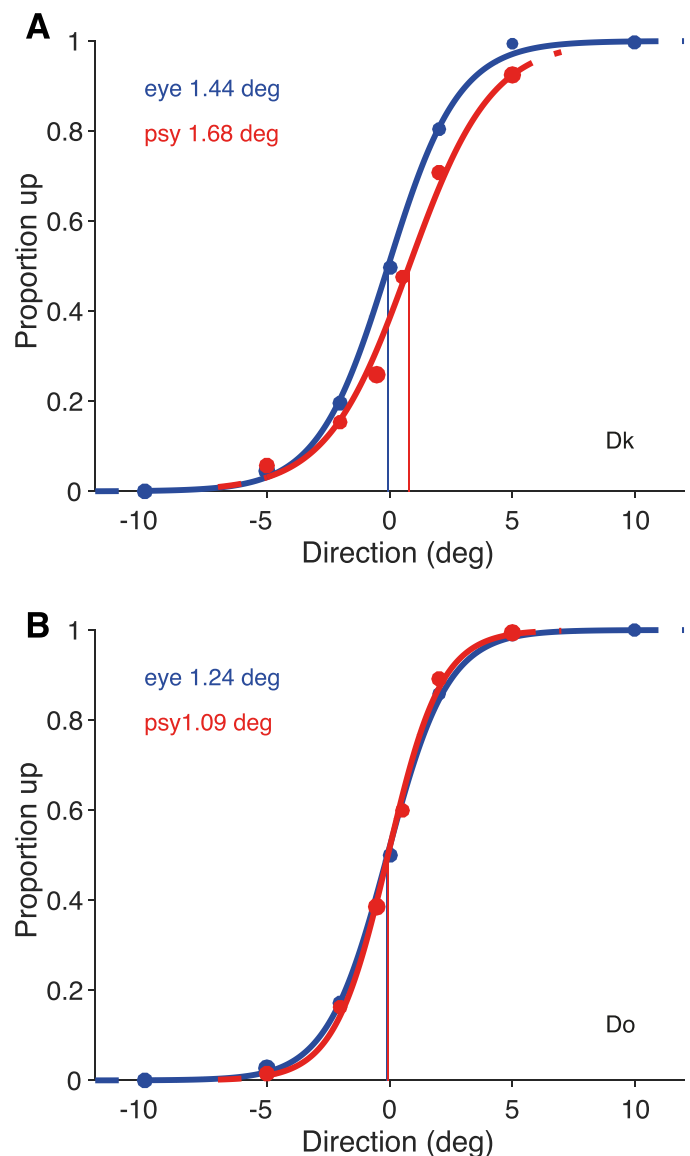

Figure 4. Comparison of oculo- and psychometric functions for two subjects. The psychometric function (red line) is plotted to the data of direction discrimination measured psychophysically during central fixation with ramp stimuli in different directions presented for 200 ms. The oculometric function (blue line) represents the directional precision for pursuit responses to step-ramps measured 200 ms after pursuit onset.

oculometric functions are nearly identical, indicating that psychophysical and oculomotor direction discrimination judgments reach a similar high level of directional precision. There is similar good agreement for the other two observers (see Table 1). Psychophysical direction thresholds of our four subjects were on average 1.60° and therefore very similar to the average oculometric threshold of 1.79°. These results are in excellent agreement with the ones reported earlier for such comparisons under similar conditions (Stone & Krauzlis, 2003; Mukherjee et al., 2015).

Subject	Do	Dk	Fi	Ja	AVG
Pursuit latency (ms)	165	154	148	153	155
Time to threshold (ms)	118	61	88	85	88
Asymptotic threshold (deg)	1.33	1.64	1.71	2.47	1.79
Threshold 200 ms (deg)	1.25	1.44	1.80	2.20	1.67
Psychophysical threshold (deg)	1.09	1.68	1.78	1.84	1.60
Latency initial saccade (ms)	207	171	204	189	193
Amplitude initial saccade (deg)	5.2	3.1	4	4.1	4.1
Saccadic threshold (deg)	2.02	1.79	1.55	2.92	2.07
Equivalent pursuit threshold (deg)	4.46	3.62	4.59	6.43	4.77
Pursuit time to reach saccadic threshold (ms)	150	130	170	140	147.5
Latency saccade stationary target (ms)	184	150	155	178	167
Threshold saccade stationary target (deg)	1.31	1.57	1.52	2.05	161
Amplitude saccade stationary target (deg)	4.5	4.1	4.1	3.9	4.15

Table 1. Summary of statistics for individual observers and their average for a (step-) ramp speed of 20°/s.

The direct comparison between psychophysical and oculometric thresholds is more complicated than the good agreement seems to indicate at first sight. Oculometric thresholds do depend to some degree on the specifics of the filtering used. When the oculometric decisions were based on 10-ms intervals of eye position change, rather than the 40-ms intervals used for Figure 4, thresholds increased up to levels of more than 2°. When a longer averaging window of 100 ms was used, even lower threshold values below 1° were obtained. Note that this is a problem that cannot be completely avoided. The goal of filtering eye tracking output is to avoid the measurement noise introduced by the instrument, without affecting the eye position signal that is being measured. Our choice of a 40-ms averaging window on oculometric decisions agrees well with the velocity filters typically found in the literature, which range between 20 and 25 Hz (Osborne et al., 2005; Osborne et al., 2007; Rasche & Gegenfurtner, 2009; Mukherjee et al., 2015). At the same time, psychophysical thresholds depend on the exposure duration of the stimuli. Here, we chose 200 ms because it approximates the open-loop period of pursuit, and because very short presentation durations lead to a smear of the motion energy due to the onset and offset of the stimulus. Overall, our threshold values are in the same range as what has been observed in the literature (de Bruyn & Orban, 1988; Stone & Krauzlis, 2003; Mukherjee et al., 2015).

Training and experience

Figure 5A shows the complete time course of pursuit precision during the 300-ms interval following pursuit onset for our four practiced observers and for an additional six untrained observers. There is good agreement between all our observers, and it is quite remarkable that thresholds decrease to a relatively low level already 100 ms after pursuit onset. Overall, two untrained observers are basically indistinguishable from the practiced observers, while four untrained observers do have asymptotic threshold values at a level slightly above the ones for the practiced observers. We characterized the shape of these curves by the exponential decay function specified in Equation 1 and we estimated the time it takes to reach threshold as the point in time where the oculometric threshold is at twice the value of its asymptote. These values ranged from 60 ms for observer Dk to 120 ms for observer Do and from 49 to 139 ms for the six untrained observers (see Table 2). Overall, the comparison of our highly practiced observers with previously untrained observers shows that there are differences, but that a few hundred trials suffice to reach an excellent level of performance.

It could be argued that even the previously untrained observers were hardly inexperienced after running several hundred trials. Therefore we compared their performance during the first 150 trials to performance during the last 150 trials. As before, oculometric functions were fitted. We looked at performance at 200 ms after pursuit onset, when thresholds had reached a relatively stable and low level. There was no significant difference between the first and the last set, even though performance correlated quite well across the six individual observers ($\rho = 0.82$, $p < 0.05$), indicating good reliability of our measurements. Average threshold at 200 ms after pursuit onset was 2.34°/s for the first 150 trials and 2.76°/s for the last 150 trials, with performance even slightly declining towards the end. This shows that even naive and unpracticed observers can perform well in this task.

Pursuit precision time course

In Figure 5B the times course of direction discrimination derived from our pursuit data are compared to
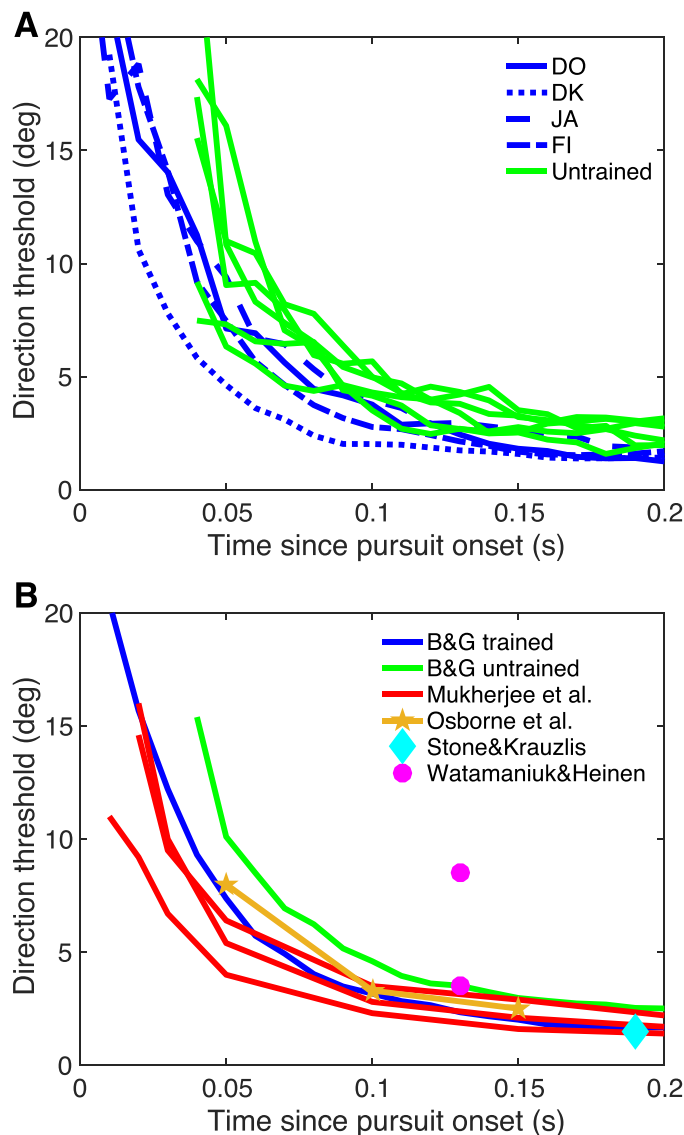
Figure 5. Comparison of the results of our study (A) with three other studies in humans and one in monkeys (B). (A) Time course of direction discrimination thresholds calculated from pursuit eye positions during 300 ms after pursuit onset. Data from four experienced observers are shown in blue, data from six untrained observers in green. (B) Beside our data (blue) from (A) we replotted in red the time course of direction discrimination thresholds for pursuit of a small target moving at 10°/s for the three observers (red) shown in figure 4 of the study of Mukherjee et al. (2015). The green curve represents our approximation of the time course of thresholds for direction obtained from monkeys given in Osborne et al. (2007, their Figure 4A, D, p. 2992) The single data points show the threshold values for direction discrimination of pursuit measured 130 ms after pursuit onset by Watamaniuk and Heinen (1999) and the cyan shows data points during a 100 ms interval centered at 300 ms by Stone and Krauzlis (2003).

existing data from the literature. Watamaniuk and Heinen (1999) measured pursuit direction discrimination thresholds of 4°–9° 130 ms after pursuit onset in two human subjects with RDKs. Stone and Krauzlis (2003) found thresholds of less than 2° 300 ms after pursuit onset when pursuing single dots along the cardinal directions. Recently, Mukherjee et al. (2015) studied human pursuit direction discrimination with a single spot target or random dot patterns and used step-ramps with unpredictable directions ranging from 9° to −9° and velocities between 10°/s–15°/s. Pursuit direction thresholds of their subjects dropped rapidly after pursuit onset and 240 ms after pursuit onset they reached values between 1.5°–1.9°. For the three observers of Mukherjee et al. (2015) we replotted oculometric functions from the pursuit threshold values shown in their figure 4A (page 8521). Similarly, we replotted the results of monkey observers reaching asymptotic thresholds of 2° 125 ms after pursuit onset or 225 ms after target motion onset (Osborne et al., 2007, see figure 4A, p. 2991).

All of these studies used stimuli varying along the cardinal directions only, or even only along the horizontal axis. In another study, Liston and Stone (2014) devised a whole battery of eye movement tests to obtain information from many observers very quickly. They observed higher directional discrimination thresholds for pursuit on the order of 9°, even though the variability between the 41 observers was large. Their observers were previously untrained, but this does not seem to be the crucial difference, since our untrained observers performed quite well. It seems that the higher uncertainty about direction is important, preventing observers from adjusting their sensitivity to discriminating just along one axis (see Jazayeri & Movshon, 2007).

Overall, there is good agreement between the studies using comparable stimuli and paradigms, with only a single data point outside of the typical range of pursuit direction thresholds. However, there is also considerable individual variability between the different observers. Where do these differences emerge? We already noted above that filtering does have an effect on oculometric thresholds. It affects not only the asymptotic thresholds, but also has a dramatic effect on the early threshold values. For example, for observer Do increasing the averaging time interval for oculometric decisions from 40 to 100 ms decreased the time for oculometric precision to reach 5° from 75 down to 60 ms. Note however, that the time to reach a precision equal to twice the asymptotic value was fairly invariant with respect to filtering. For observer Do, it was stable at around 120 ms, the value reported above.

Another source for differences across different studies could be the speed of the pursuit target. We

Subject	As	Mm	Nf	Rd	Rs	Vc	AVG
Pursuit latency (ms)	157	168	152	174	169	159	163
Time to threshold (ms)	58	136	103	73	49	139	93
Asymptotic threshold (deg)	2.94	2.20	1.94	3.78	3.40	1.78	2.67
Latency initial saccade (ms)	186	216	208	266	221	230	221
Amplitude initial saccade (deg)	3.11	3.01	2.78	4.36	2.99	2.53	3.13
Saccadic threshold (deg)	1.64	2.63	3.98	3.00	3.52	5.14	3.32
Equivalent pursuit threshold (deg)	6.56	5.57	3.51	4.99	4.37	6.51	5.25
Pursuit time to reach (ms) saccadic threshold	60	90	100	100	80	80	85

Table 2. Summary of statistics for untrained observers and their average for a (step-) ramp speed of 16°/s.

therefore ran experiments exploring a possible effect of speed on the pursuit dynamics.

Speed invariance of directional thresholds

It is possible that uncertainty about the speed of the stimulus could have an adverse effect on directional thresholds. We therefore tested whether variations of the ramp speed would affect the directional precision of saccades or pursuit. For the directional precision of pursuit and saccades with unpredictable ramp speeds, eye movements of three practiced observers were measured with seven randomly selected ramp speeds ranging from 14°/s to 43°/s and the seven directions ranging from 10° to −10°. In Figure 6A the time courses of directional precision for the seven ramps' speeds are shown for the average of the three practices observers. There were no systematic differences between the different speeds, and the parameters of the exponential decay were quite similar to the ones observed for a single speed. Directional precision of saccades and pursuit was very high (below 2° on average) for all three observers even for the unpredictable ramp speeds. The six naive observers showed similar results. The time courses of oculometric thresholds for the two speeds overlap to a large degree (Figure 6B).

Recently, Mukherjee et al. (2015) suggested that the quality of pursuit initiation might directly depend on the vigor of the pursuit response, as indicated by pursuit acceleration. We explored this hypothesis by dividing up individual observers' pursuit trials into bins of different acceleration or latency to see whether acceleration or latency would have an effect on the time course of the oculomotor precision.

Latency effects on precision

Our observers showed distinct differences in their pursuit responses. This occurred with respect to their onset latencies and with respect to the time duration to reach asymptotic directional threshold values. This raises the interesting question whether the two periods are related. If observers take more time for integrating sensory information and for motor planning before they start moving their eyes, they might exhibit more precise pursuit. For three observers we therefore collected a large number of pure pursuit responses (more than 1,800 trials) and investigated whether a longer preparation time improves the precision of direction discrimination for each observer separately. Our expectation was that in trials with longer onset latencies more sensory information about the target movement could be used, and more time for motor planning was available before pursuit initiation. Our observers initiated their pursuit responses to step-ramps of 20°/s after an averaged onset latency of 155 ms, (range: 148–165 ms). These pursuit onset latencies are similar to the pursuit latencies we have measured before (Spering et al., 2005; Braun et al., 2008) and to those of many other studies (Rashbass, 1961; Robinson, 1965; Tychsen & Lisberger, 1986; Carl & Gellman, 1987) while some authors have reported longer latencies (Liston & Stone, 2014; Mukherjee et al., 2015). Pursuit latencies vary quite a bit with stimulus parameters such as contrast, and they also depend to some degree on the exact method used to estimate them. Here, we are mainly interested in the large spread of latencies across different trials of the same observer. We will use this aspect of natural variability for investigating the contributions of sensory noise, motor planning, and motor execution to pursuit variability.

For three observers we divided the valid data into quartiles based on their onset latencies and analyzed the directional precision of the corresponding pursuit traces. In Figure 7A the time course of directional precision of the latency quartiles is plotted in different colors for observer Fi. In this case, the average onset latencies in the very fast, fast, slow, and very slow quartiles were 123, 140, 155, and 178 ms, respectively. Figure 7A indicates that the onset latency was inversely related to the time it took the eyes to reach asymptotic high directional precision. For pursuit trials with the very fastest onset latencies, it took more than 100 ms to reach a directional precision better than 5°, while for pursuit trials with the longest latencies this was the case in less than 50 ms. This relationship between pursuit
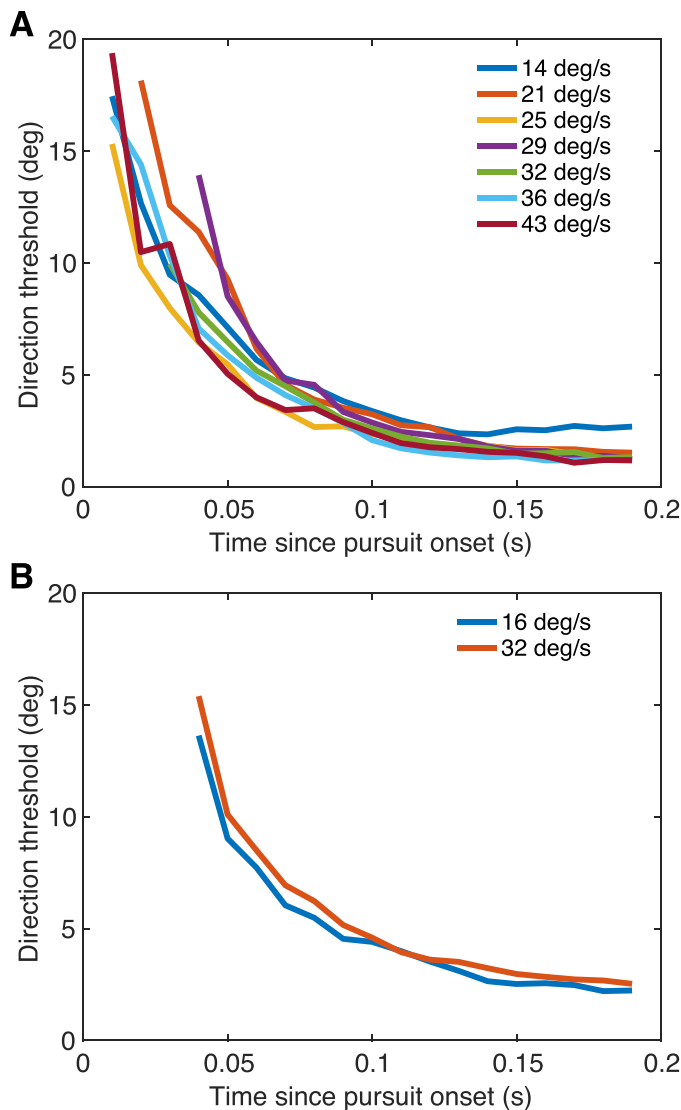
Figure 6. Time course of direction discrimination thresholds at different step-ramp speeds. (A) Average direction discrimination for three practiced observers at seven different speeds. (B) Average direction discrimination for six untrained observers at two different step-ramp speeds

ship holds in all three cases, with the slopes being very close to unity (dashed black line in Figure 7C). This means that the time-to-threshold shift is nearly identical to the change in pursuit latency, indicating a near-perfect balance between preparation and execution of smooth pursuit eye movements. Directional precision of pursuit responses increases with the processing time available to the sensory system for the computation of visual motion, and to the motor system for the planning of the pursuit eye movements. This basically cancels out the latency advantage of faster pursuit responses.

Recently, Mukherjee et al. (2015) suggested that acceleration—the vigor of the pursuit response—might play an important role also for achieving precise pursuit. We therefore repeated the above analyses with acceleration instead of latency to divide up the trials into quartiles. This resulted in different mean accelerations in the four bins ranging from $50°/s^2$ to $150°/s^2$. However, there was little and unsystematic change in the time course of pursuit precision associated with the different acceleration bins. The corresponding fits of lines were flat and nonsignificant, indicating that the degree of pursuit acceleration is not directly related to the precision of the ongoing pursuit response within single observers.

Directional sensitivity of initial saccades

All the data so far were obtained using the step-ramp paradigm introduced by Rashbass (1961), which allows us to exclusively study pursuit initiation without saccadic eye movements affecting the eye movement response. Of course, this paradigm is quite contrived. Targets usually do not step into the periphery before moving centrally across the fovea into the opposite direction. In most cases, a target starts to move somewhere in the visual field and due to the natural delays of the sensory and oculomotor systems, the target moves a short distance before pursuit can be initiated and thus an initial saccade is required to foveate rapidly the target. Here, we want to compare the directional precision of these first initial saccades to the precision of pursuit during the same time interval. We were also interested in comparing pursuit precision with and without preceding saccade, since a positive effect of saccades on motion processing and eye following responses has been reported (Lisberger, 1998; Ibbotson, Price, Crowder, Ono, & Mustari, 2007; Royal, Sáry, Schall, & Casagrande, 2006; Wilmer & Nakayama, 2007).

For three observers we collected data from 12–17 experimental sessions and for a fourth observer six sessions with ramp targets moving at 20°/s (see Figure 1, right column). This data analysis is based on 694–

onset latency and precision was generally the case for all three observers.

We quantified the relationship between onset latency and time to threshold by fitting the precision time courses with exponential functions (Equation 1). The full three-parameter exponential curve was fitted to the complete data set (black curves in Figure 7A and B). For each quartile, as defined by the onset latency distributions, the data were fitted by shifting this template on the horizontal time axis only. Figure 7B shows that the resulting fit was satisfactory, with only minor residual deviations from the template curve. In Figure 7C we plot the resulting relationship between pursuit latency and time to threshold for all three observers. It is quite remarkable that a linear relation-
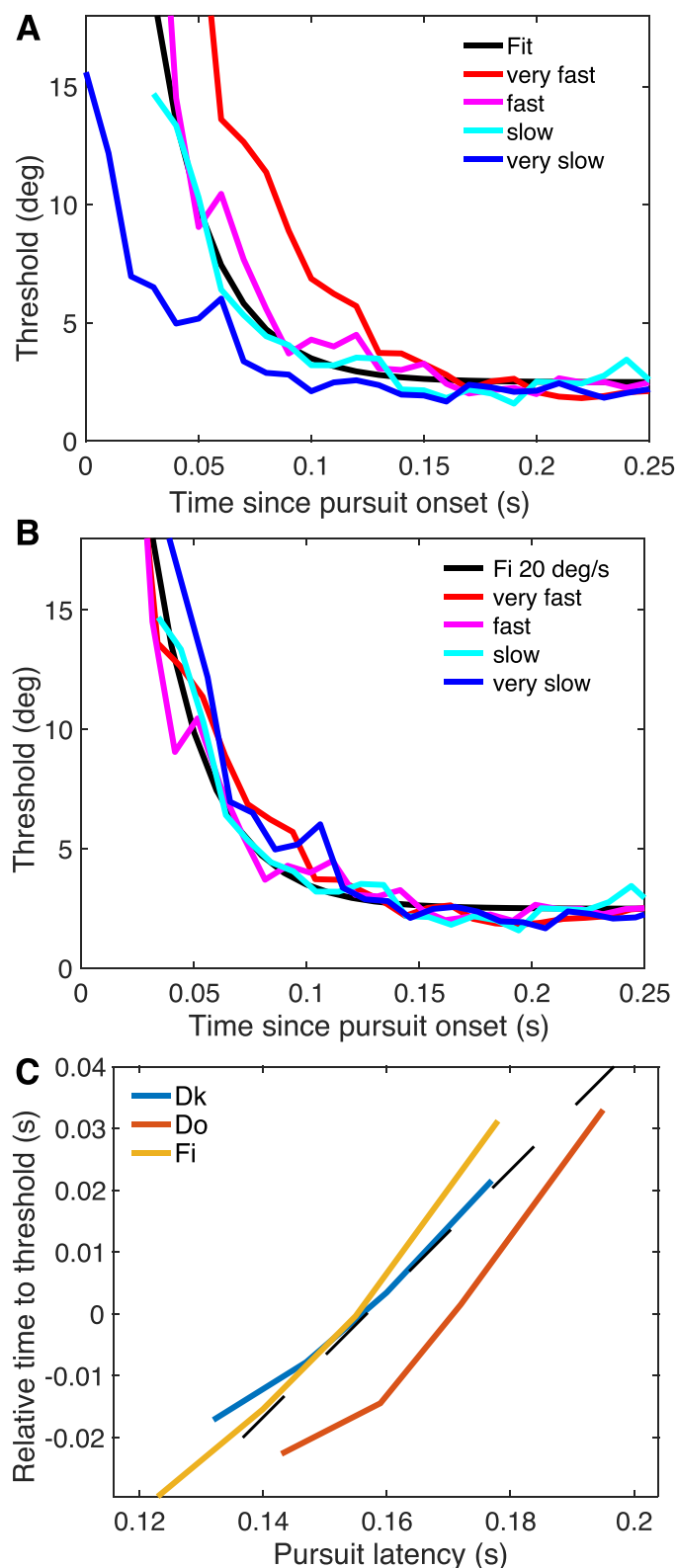
Figure 7. Dynamics of directional precision of pursuit trials with regard to onset latencies. (A) Quartiles for oculometric functions of the fastest, fast, slow and slowest trials for a single subject are plotted in different colors and the corresponding exponential function in black (see Equation 1). (B) To compare the dynamics of the four latency quartiles regarding directional

2,202 valid trials. For each single direction of a single observer the measurement is based on 148–408 saccades. We initially computed the directional precision during the initial saccade using the same procedures as for pursuit precision, as indicated in Figure 2. The green curve in Figure 8A shows the resulting oculometric function for initial saccades to ramp targets for one observer. Saccadic directional precision was fairly high, at or below 2° for three of the observers and 2.92° for the fourth (see Table 1). The saccadic amplitudes were around 4° for subjects Fi and Ja, around 3° for Dk who had the shortest latencies, and around 5° for Do with the longest saccadic latencies.

For comparison to the pursuit responses of the same observers, we looked at the precision during the same time interval since the beginning of stimulus motion in both cases. Saccadic latencies were around 190 ms (171, 207, 204, and 189 ms) for our observers, which is about 40 ms higher than the latencies for pursuit (154, 165, 148, and 153 ms). Of course the easiest way to compare precision would have been to compare trials with the same latencies. However, the latency distributions for saccades and pursuit, even though only 20–50 ms different, did not overlap sufficiently. We therefore computed precision during the pursuit interval corresponding to the time interval equivalent to the saccade. With one exception we found that during that period, pursuit precision was significantly lower than saccade precision, as shown in Figure 8B. Saccade precision was 2.82° on average, while pursuit precision was 5.06° at the equivalent point in time ($t_9 = 4.73$, $p < 0.001$).

A comparison of the whole time course of precision in Figure 9 shows that this benefit of the saccadic system vanishes quickly. In the postsaccadic interval, 50 ms after the saccade, precision of the subsequent pursuit is actually slightly worse than during the saccade and nearly identical to precision of pure pursuit at the equivalent time. Interestingly, the precision of saccades to static targets (red line in Figure 9) was even better and these saccades had shorter latencies as well (see Table 1).

Our results clearly show better precision for the initial saccade than for pure pursuit at the equivalent time. This is the case even though the retinal stimuli in both cases are quite similar. In the step-ramp paradigm, the target starts about 4° eccentric and moves back to the fovea, while in the ramp paradigm the target starts in the fovea and moves by about the same amount away from it. The information contained in both cases is similar. In our psychophysical experiments, we had obtained data for both of these conditions and found no performance difference for motions towards and

precision their functions were shifted horizontally. (C) Relationship between pursuit latency and time to reach threshold for all three observers. The dashed black line indicates unity.
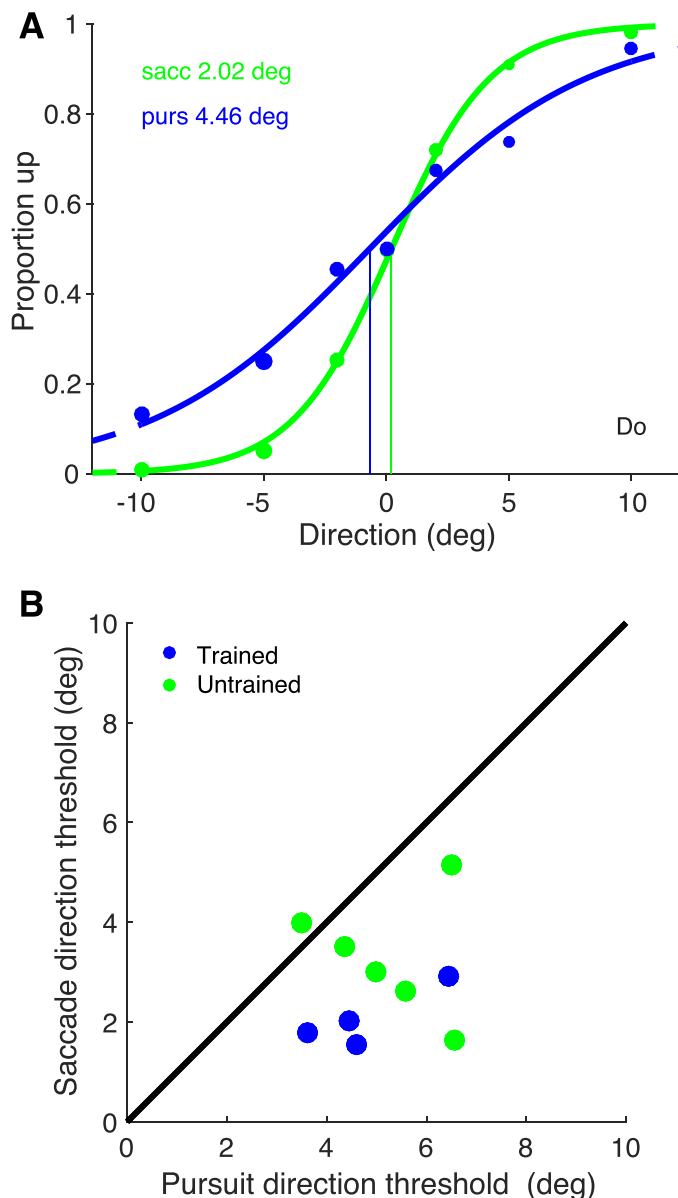
Figure 8. Comparison of direction thresholds of saccades and pursuit. Thresholds were measured for pure pursuit to step-ramps and initial saccades followed by pursuit to ramps at the same point in time after target onset. (A) Oculometric functions of observer Do who initiated pursuit about 80 ms earlier than saccades; however, the directional precision of saccades was better by 2° compared to pursuit at the same point in time. (B) Scatterplot of saccade and pursuit direction thresholds of all our 10 observers. For nine observers pursuit direction thresholds lay below the diagonal, indicating higher thresholds compared to saccades.

away from the fovea. Therefore, it is unlikely that differences in sensory processing contributed much to this effect. The major difference between saccades and pursuit is in the speed of the eye motion (see Figure 1), which is several times higher during saccades. Possibly, a better signal-to-noise ratio can be obtained in the

motor system at higher levels of innervation. Of course, also contributions from measurement noise will be larger at the slower speeds present during pursuit initiation.

Positional information

One major difference between saccadic and pursuit eye movement initiation is that the saccade system does not only have information about visual motion available, but also positional information. At the time when the saccade is planned—about 100 ms after motion onset and 100 ms before saccade onset—the target has moved several degrees away from fixation. In the step-ramp paradigm, the target gets ever closer to fixation and in the end has no significant position error. We investigated whether this could be the major cause of the difference in direction thresholds by comparing the contributions of position and speed errors to the saccades. Previously, Schreiber et al. (2006) had shown that in cases where speed and position errors had nearly orthogonal directions, the fastest saccades were driven by position error while the slowest saccades were curved in the direction of motion and showed a stronger effect of retinal slip (speed error).

For our 10 observers we also found a high correlation between position error at the time when the saccade planning is finished, assumed to be 100 ms before saccade onset. This relationship held both for the magnitude of the position error and the magnitude of the saccade (Figure 10A), and for the direction of the position error and the direction of the saccade (Figure 10B). For the saccade magnitude, ρ was 0.81 for the six untrained observers and 0.74 for the three experienced observers. For saccade direction, ρ was 0.67 for the untrained and 0.57 for the trained observers. Part of that correlation is of course caused by the fact that both the position error and the saccade vector are correlated with the properties of the stimulus itself. But even when stimulus motion and stimulus direction are partialed out of the above relationship, a linear correlation remains, with ρ being equal to 0.63 and 0.31 for saccade amplitude, and 0.22 and 0.25 for saccade direction, for the untrained and trained observers respectively.

We also tested whether the velocity error at this time would have an impact on saccade metrics. Retinal slip was correlated with saccade magnitude ($\rho = 0.68$ and 0.81 for untrained and trained observers, respectively), but these correlations vanished when stimulus speed was partialed out ($\rho < 0.05$ in all cases). There was no correlation between the direction of retinal slip and the direction of the saccade. All of these results held even when we split latencies into different bins. The slight discrepancy to the earlier results by Schreiber et al. (2006) are probably due to the agreement in the
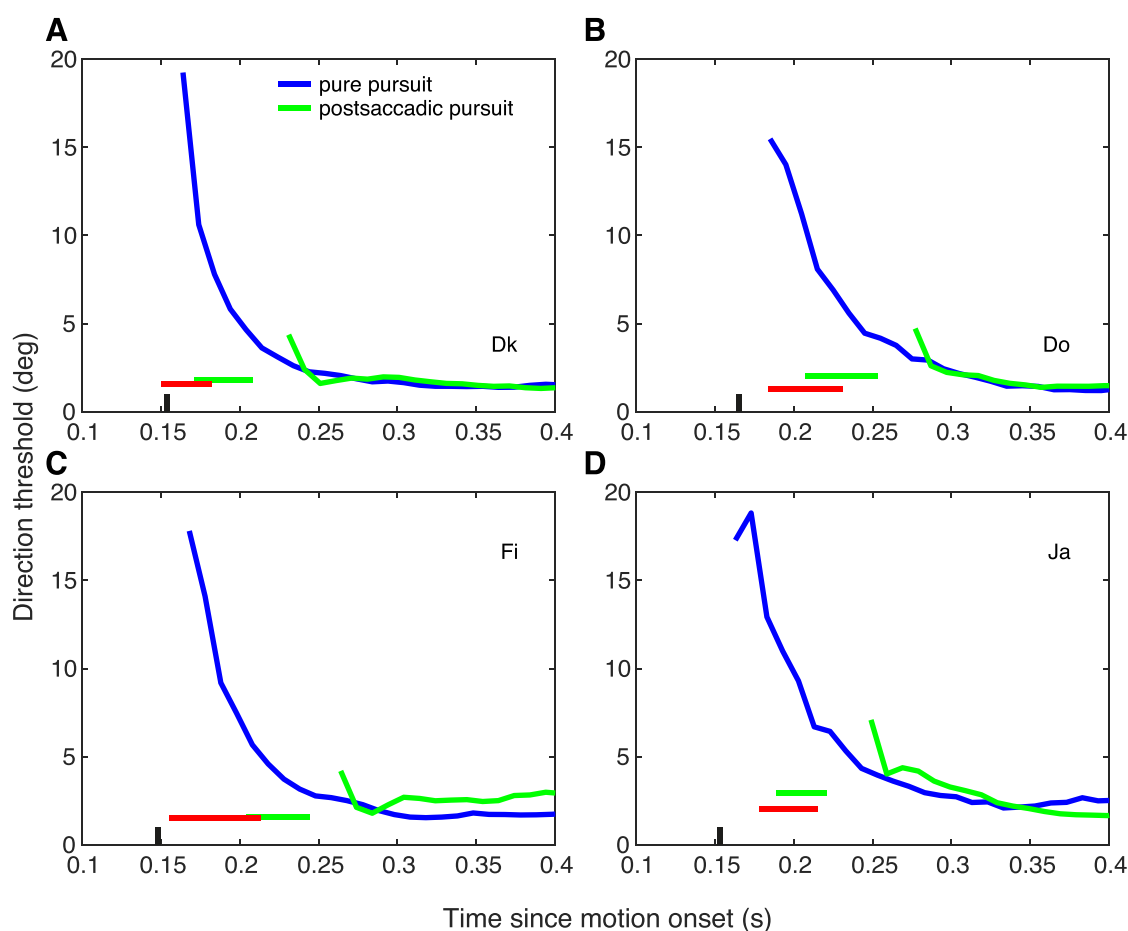
Figure 9. Comparison of thresholds for pursuit and initial saccades for four subjects. The blue curve indicates threshold values in the step-ramp paradigm for pure pursuit. The vertical blue line indicates pursuit onset time. The green curve indicates thresholds for pursuit in the ramp paradigm after the initial saccade. Thresholds during the saccade are indicated by the horizontal green line (latencies were 190 ms on average). Saccadic endpoints indicated target direction with a precision of 1.97°. At this time, about 40 ms after pursuit onset, pursuit oculometric thresholds for the step-ramp paradigm were still above 4° and took at least 150 ms longer to reach values of or below 2°. The red horizontal line indicates results from saccades to stationary targets, which were both faster and more precise than those to moving targets.

direction of position and motion direction in our case, and the fact that in our case the saccades started with a nearly stationary eye, lowering the importance of motion information for saccade programming. Overall, our results indicate that it is positional information that is used to reach a high directional precision for saccades. However, this information is not available to the pursuit system at this point in time (see Segraves & Goldberg, 1994; Orban de Xivry & Lefevre, 2007).

Discussion

Summary

We investigated and compared the directional precision of pursuit and saccadic eye movements over

time in trained and untrained human observers. For pursuit it took only 300 ms after target motion onset until the directional precision reached its asymptotic value of 1.5°–3°, irrespective of the speed of the stimuli or degree of training. An analysis of the time course revealed a quicker improvement of precision for longer pursuit latencies. Only the time available for the accumulation of sensory information about visual motion direction and the planning of the motor command for pursuit was important for the quality of the initial pursuit signal, at least within the bounds of the naturally observed variation in latencies. Therefore high directional accuracy of pursuit is inversely related to the onset latency, indicating that sensory noise and motor planning are responsible for pursuit precision. The directional precision of initial saccades to moving targets was slightly lower than that for saccades to stationary targets but by 2°–3° better than that for

pursuit at the equivalent point in time. This indicates that the positional information mainly used by the saccade system is of higher quality than the motion signal that dominates pursuit. Both the asymptotic precision of pursuit and the precision of saccades were comparable to psychophysical thresholds, possibly due to common limitations in the sensory information processing about target position and movement direction.

Comparison of psychophysical and oculometric direction precision

The comparison between smooth pursuit eye movements and perception of motion is intriguing and has fascinated researchers for decades. However, any direct comparison between pursuit and perception is complicated by several factors.

First of all, pursuit is a gradual slow response with respect to velocity and acceleration but quite fast with respect to onset latency compared to saccades, although experimental conditions have a large influence. Humans typically initiate pursuit after latencies between 100 and 180 ms (Rashbass, 1961; Tychsen & Lisberger, 1986; Carl & Gellman, 1987; Krauzlis, 2004; Spering et al., 2005; Braun et al., 2008; Liston & Stone, 2014; Mukherjee et al., 2015); in the present study we measured average pursuit latencies of 159 ms. During the initiation phase the eye moves roughly into the target direction and adjusts gradually over a period of 150–200 ms to the target direction as we have shown here under conditions similar to Mukherjee et al. (2015). During this initial open-loop phase (up to 150 ms after initiation), the eyes are driven by the initial sensory signal, the movement of the retinal target image. The error signal for the deviation of the eye from the stimulus is not available yet at that point in time due to the visual processing delays.

We found that 100 ms after pursuit onset oculomotor thresholds for direction reached already a level of twice the asymptote, which was finally reached another 50–100 ms later. The ratio of psychophysical precision over pursuit precision at a given time can be used to estimate the relative amount of sensory and motor noise sources to performance. The sensory signal itself can be refined during that period (Pack & Born, 2001; Masson & Stone, 2002). In principle, the pursuit precision at the end of the open-loop period can serve as an estimate of the sensory signals driving pursuit, but this is at a time when pursuit precision changes considerably (see Figure 5). It seems that for pursuit directional precision, different from pursuit speed (see Rasche & Gegenfurtner, 2009), pursuit precision 150–200 ms after pursuit onset does closely approximate the
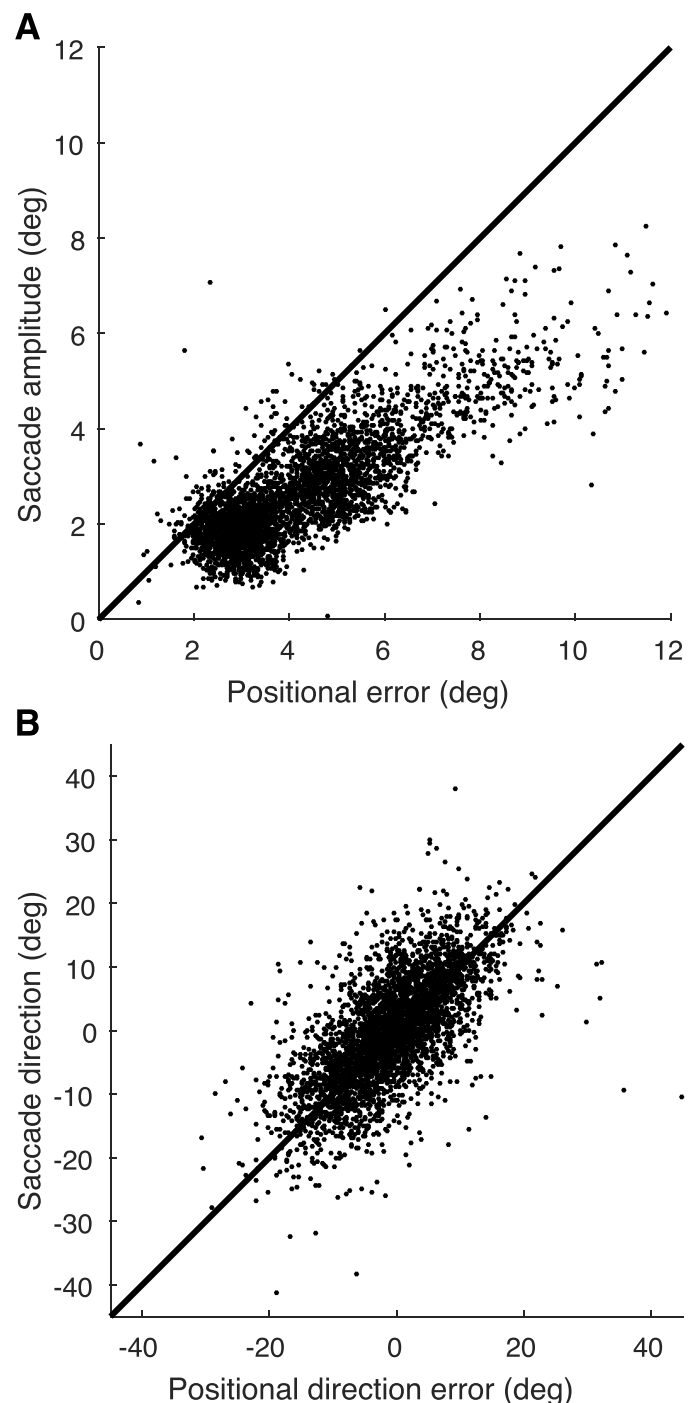

Figure 10. Relationship between position error and saccade metrics for the six untrained observers. (A) The amplitude of initial saccades is highly correlated with the magnitude of the positional error measured 100 ms before saccade onset. (B) The direction of initial saccades is highly correlated with the direction of the positional error.

psychophysical threshold (see Figure 4 and Table 1). Therefore, for direction it could be argued that it is mainly the sensory noise that determines initial pursuit precision (Osborne et al., 2005; Osborne et al., 2007;

Mukherjee et al, 2015). During the closed-loop phase pursuit can reach very high levels of precision for speed and direction by internal feedback signals about velocity errors and the retinal slip is close to zero during steady state (Robinson et al., 1986; Newsome, Wurtz, & Komatsu, 1988; Chukoskie & Movshon, 2009; Schütz et al., 2009).

Second, although under experimental conditions a continuous readout of eye position is possible, measuring this signal is in itself a noisy process. Therefore, eye position signals are usually low-pass filtered. Differentiation, which is necessary to calculate eye speed, amplifies errors, and velocity traces are typically also filtered. The filtering process cannot perfectly discriminate between instrument noise and oculomotor noise, and thus leads to an improvement in precision, irrespective of noise source. We ran our analyses for a whole range of different levels of filtering and averaging, and as expected the choice of filters had a considerable effect on the measured oculomotor precision. For the degree of averaging chosen in Figure 4, psychophysical and oculomotor precisions pretty much agree. If more filtering is chosen, oculomotor thresholds can be lower than psychophysical threshold estimates; with less filtering they end up being higher. The value we chose is comparable with what is used in the literature, but it is still somewhat arbitrary.

Third, the psychophysical judgment has a very different time course. It is usually given at least a second after stimulus presentation, allowing the observer to use all the information available at and after presentation. It is possible to shorten the stimulus presentation to very short durations, similar to the target movement duration relevant for driving pursuit. However, in this case onset and offset transients will reduce the effective magnitude of the visual motion signals. Any potential movement of the eyes during stimulus presentation will also affect the retinal stimulus. For these reasons, a direct comparison of the magnitudes of pursuit and perceptual precision are nearly impossible.

The close relationship between pursuit and perceived rather than physical visual motion was shown first by Spering (1976) with lights fixed to a rolling wheel in the dark and it was confirmed in numerous studies with very different stimuli (for reviews, see Kowler, 2011; Schütz, Braun, & Gegenfurtner, 2011; Spering & Montagnini, 2011). While in general a good agreement between pursuit responses and visual perception was found, the question about the exact relationship between pursuit and perceptual signals is still open. Several answers to that question have been put forward, and the comparison between pursuit and perception has concentrated on the precision of psychophysical and oculometric judgments regarding speed (Kowler & McKee, 1987; Rasche & Gegenfurt-

ner, 2009) and direction accuracy during pursuit initiation (Watamaniuk & Heinen, 1999) or during steady-state (Stone & Krauzlis, 2003; Krukowski & Stone, 2005).

Watamaniuk and Heinen (1999) limited their analysis and comparison of psychophysical and oculomotor direction discrimination to the open-loop period of pursuit, the first 130 ms after pursuit onset. Two different kinds of stimuli were used: a single spot moved horizontally at 8°/s in five slightly different directions (6°, 3°, 0°, −3°, −6°) and circular RDKs, which differed in the levels of directional noise. They measured their own pursuit eye direction over a 20-ms bin centered 130 ms after pursuit onset and psychophysical judgments of direction for the same stimuli presented for 140 ms during fixation. Thresholds of psychophysical direction discrimination for single spot stimuli were about 2°, while those for smooth pursuit during the late phase of initiation about 8°–9°. The comparison of psychophysical and oculomotor direction discrimination thresholds for the RDCs as a function of added directional noise revealed that oculomotor thresholds were much higher, but the best fitting functions describing the effect of noise for both sets of data were quite similar.

Stone and Krauzlis (2003) took a different approach. First they pursued step-ramps moving along nine different linear trajectories bracketing the four cardinal axes, and then they gave a binary judgment about the spatial displacement of the ramp trajectory in regard to the cardinal axis. To compare judgments of the directional perception with the pursuit movement of the same trial they divided the filtered pursuit responses into five different 100-ms time intervals and converted the pursuit directions into oculometric data. The psychometric and the oculometric functions for the data of the interval centered around 300 ms after pursuit onset turned out to be quite similar for all cardinal directions: The measured perceptual uncertainty was around 1.3°; the pursuit uncertainty around 1.6°. Their psychophysical and oculometric thresholds agree very well with our data as shown in Figure 5. Based on the significant covariation of perceptual and oculomotor decisions regarding target direction they concluded that both systems share the same neural machinery for the computation of motion direction and are influenced by the same stochastic noise source.

We also compared our data with the data of Mukherjee et al. (2015) who studied human pursuit direction discrimination abilities with different targets: single spot targets and random dot patterns. For step-ramps with unpredictable directions ranging from 9° to −9° and velocities between 10°/s −15°/s they found that pursuit direction thresholds dropped rapidly after pursuit onset and reached threshold values between 1.5°–1.9° after 240 ms, which is very similar to our data.

To conclude, the thresholds for oculomotor direction discrimination of the discussed literature agree very well. The difference in threshold values depend on the point in time of the pursuit measurements and on the stimuli used but they all show that pursuit precision can reach the accuracy of perception if the pursuit system has enough time (at least 150 ms) for adjustments.

Time course of pursuit precision

It is arguably the major purpose of our sensory systems to guide our actions, whether immediate or delayed via memory (e.g., Goodale & Milner, 1992). Several transformations of the sensory signals are required before arriving at the proper motor command. Each one of these processing steps for visuo-motor control, the initial sensory estimation of the visual signals in visual cortex, the central planning of the movement in motor cortex, as well as the final execution of the motor command are prone to noise (e.g., van Beers, Haggard, & Wolpert, 2004; Osborne et al., 2005; Churchland, Afshar, & Shenoy, 2006; Osborne, Hohl, Bialek, & Lisberger, 2007). Smooth pursuit eye movements offer a unique window into these transformations because the circuits controlling these slow eye rotations are quite well understood at the computational, physiological and anatomical level (for reviews see Robinson, 1965; Keller & Heinen, 1991; Krauzlis, 2004; Lisberger, 2010). They also represent low latency, continuous responses, essentially allowing a continuous readout of the overall level of noise.

As stated above, there has been a consensus for a while now that the human pursuit response is tightly coupled to the sensory processing that ultimately results in conscious visual perception (for reviews, see Kowler, 2011; Schütz et al., 2011; Spering & Montagnini, 2011; Spering & Carrasco, 2012; Gegenfurtner, 2016). Pursuit is prone to the same types of biases as motion perception such as the oblique effect (Krukowski & Stone, 2005) or the motion aftereffect (Braun, Pracejus, & Gegenfurtner, 2006). Overall performance levels, such as thresholds for speed or direction, are highly similar (Kowler & McKee, 1987; Beutter & Stone, 1998; Stone, Beutter, & Lorenceau, 2000; Gegenfurtner et al., 2003; Stone & Krauzlis, 2003; Braun et al., 2006; Tavassoli & Ringach, 2010; Mukherjee et al., 2015). Yet, the exact nature of the noise sources has been elusive, since a comparison of psychophysical and oculomotor judgments at the level of single trials has led to inconclusive results. Some studies have found such a correlation for judgments of direction (Stone & Krauzlis, 2003; Mukherjee et al., 2015) while other studies failed to observe any correlation for judgments of velocity (Rasche &

Gegenfurtner, 2009; Braun et al., 2006), indicating that there might be a fundamental difference in the processing of information about direction and speed in the human visuo-motor system.

Another indicator for such a difference between speed and direction comes from an analysis of the time course of pursuit precision. Osborne and colleagues (Osborne et al., 2005; Osborne et al., 2007) were the first to investigate this in monkey observers. They claimed, based on a comparison of their monkey pursuit responses with human data from the literature, that pursuit precision at the end of the open-loop interval—before any corrections based on visual signals could occur—matches perceptual precision. Two other groups presented contrary evidence that this might not hold for velocity when comparing human perception to human pursuit (Rasche & Gegenfurtner, 2009) or human ocular following responses (Boström & Warzecha, 2010). Recently, Mukherjee et al. (2015) also compared speed and direction judgments in human pursuit and perception. Their evidence is quite convincing for directional responses, and this result is supported by the data presented here. The speed data are noisier and reach asymptotic levels later in time. Like others before, they found trial-by-trial correlation in perceptual and pursuit direction responses. Unfortunately, they did not perform the same experiments and analyses for speed.

Overall, there seems to be consensus that the basic mechanisms of motion processing are shared to a large degree between perception and pursuit. The small degree of covariation for directional judgments and lack of such covariation for speed judgments most likely arises from differences in the readout of information from motion sensitive areas for perception on the one hand and for pursuit on the other hand (Gegenfurtner et al., 2003; Spering & Gegenfurtner, 2008), possibly going along with different populations of motion-sensitive neurons underlying the two tasks (Born et al., 2006; Mukherjee et al., 2015). Unfortunately, it is not possible to resolve these questions through single-unit recordings and modeling, because the behavioral data do not allow a unique specification of the physiological parameters in single brain areas, and because noise sources in different brain regions can be traded off versus each other (Medina & Lisberger, 2007; Schoppik, Nagel, & Lisberger, 2008; Huang & Lisberger, 2009).

It is promising that the data we present here agree quite well with earlier data on directional precision (Figure 5B). For our data, pursuit reaches a precision twice its asymptotic value between 60 and 120 ms after its initiation. This is, on the one hand, remarkably quick; on the other hand, it is still twice as noisy as during steady-state pursuit. We found that the time it took for pursuit to reach these low directional

threshold values depended on the pursuit latency. The later pursuit was initiated, the quicker a high level of precision was reached. This means that for the range of pursuit onset latencies that occurred in our experiments, it does not matter whether to spend more time for the sensory analysis of visual motion and the central motor planning of the eye movements before executing the motor command, or to start the execution earlier.

Interactions between saccades and pursuit

Few studies have looked at the interaction of saccades and pursuit, despite its importance in more natural situations, when objects start to move peripherally or in the fovea. The step-ramp paradigm is really an exception, contrived for the laboratory to study smooth pursuit without any initial saccades. Accurate initial saccades are quite important for target tracking because they reduce the time to intercept the trajectory of a moving target. This allows earlier pursuit periods in which the target can be scrutinized, and it reduces the number of catch-up saccades accompanied by saccadic suppression. For precise initial saccades to moving targets, the saccadic system has also to take into account the target movement during the saccade processing and execution time. If saccades would be based on position error alone they should always severely undershoot a constantly moving target. For accurate saccade generation the system needs to predict where a moving target will be after the saccade has been completed. It also has to take into account the neural delays that occur between movement planning and execution, and the actual saccade movement duration, which depends on the saccadic amplitude (Bahill et al., 1975).

Robinson (1973) suggested that the saccade generator might use retinal velocity errors to extrapolate the future position of a moving target. Gellman and Carl (1991) studied latencies and amplitudes of saccades to different ramp targets. For simple ramp trials they found that target motion had an effect on saccadic latency and accuracy. Although the amplitude of initial saccades was linearly related with the target speed, saccades were not completely accurate and approximated the target position at about 55 ms before saccade onset. They concluded that the saccadic system extrapolated the target position from its velocity but either the target velocity or the saccadic latency was underestimated. Ron et al. (1989), however, found that observers can be accurate when enough time was provided to preview the target motion, so that the saccadic system could better approximate the target position at saccade end by taking the target velocity into account. More recent studies in humans and monkeys investigating saccades to moving targets (de

Brouwer, Missal, et al., 2002; de Brouwer, Yuksel, et al., 2002; Eggert et al., 2005; Guan et al., 2005; Etchells et al., 2010) confirmed that information about the target position and velocity is available during the preparation process of saccades resulting in high accuracy. We measured saccadic latencies to moving and stationary targets and found that latencies were slightly longer (25 ms) for initial saccades to moving ramp targets. This supports the notion that more time is needed to extrapolate the future target position and compute appropriate saccade metrics when saccades direct the eyes to a moving target. Our results show that directional precision for the initial saccades is considerably higher than for pure pursuit responses during the equivalent time interval. Our analysis of saccade amplitudes and directions showed that they were mainly driven by the position error at the time of saccade planning. This indicates that the saccade system is capable of using positional information about the target's trajectory that might not be available to the pursuit system on its own.

Another interesting feature of saccade-pursuit interaction is that after an initial saccade pursuit speed was higher compared to pure pursuit responses (Lisberger, 1998; Wilmer & Nakayama, 2007). However, the directional precision of initial saccades and the subsequent pursuit has not been studied yet and the postsaccadic enhancement effect itself is poorly understood (Wilmer & Nakayama, 2007). In our study we found that the directional precision of initial saccades was two times better than pure pursuit responses at the equivalent point in time. However, after the saccade, directional precision did not improve further and was generally quite similar to that of pure pursuit responses during the equivalent time interval. We found no evidence for postsaccadic enhancement of directional pursuit responses.

Neural substrate

In the past, motion perception and pursuit have been closely related to neural activity in the major motion sensing areas. Direction-selective neurons in primary visual cortex (V1), middle temporal area (MT) and the dorsal part of the medial superior temporal area (MST) of the extrastriate cortex constitute a critical channel linking early cortical mechanisms of spatiotemporal integration of visual inputs to downstream signals commands that underlie motion perception and oculomotor behavior (e.g., Newsome et al., 1985; Dürsteler & Wurtz, 1988; Salzman, Murasugi, Britten, & Newsome, 1992; Pack & Born, 2001; Bair & Movshon, 2004; Chukoskie & Movshon, 2009). Area MT receives a strong direct input from V1 and is rich in motion-sensitive neurons (up to 90%; i.e., neurons respond

selectively to a certain rage of movement directions and speeds; for review see Newsome, Britten, Salzman, & Movshon, 1990; Born & Bradley, 2005). Cells that discharged during pursuit in a specific direction include the fovea and are found in localized regions of MT (MTf) and MST (MSTl & MSTd). Beside difference in receptive field size and stimulus preferences, neurons in area MT stop firing when the eye movement target is briefly blanked during ongoing pursuit, while most MST neurons show continued activity (Komatsu & Wurtz, 1988; Newsome et al., 1988). Pursuit-related activity is also found in other parietal areas (e.g., in the ventral intraparietal area [VIP], the lateral intraparietal area [LIP], and the parietal area [7a]; Bremmer, Distler, & Hoffmann, 1997; Schlack, Hoffmann, & Bremmer, 2003).

Since receptive fields of neurons in area V1 and the foveal representation of MT are small, several processing and integration steps over space and time are required to reconstruct the true movement direction of the target (Adelson & Movshon, 1982; Masson & Stone, 2002; Bayerl & Neumann, 2007). Pack and Born (2001) measured in macaques parallel to the temporal dynamics of MT neuronal responses to bar stimuli also pursuit eye movements as a behavioral correlate. Initially the population of MT neurons responded as local motion detectors primarily to the component of motion perpendicular to the orientation of the bar but over a period of 60 ms their responses shifted to represent the true movement direction independent of the bar orientation. A similar directional change was found in the pursuit responses; pursuit also started out towards the direction orthogonal to the bar and changed within 150 ms into the true direction of motion at the end of pursuit initiation (Masson & Stone, 2002; Wallace, Stone, & Masson, 2005; Born, Pack, Ponce, & Yi, 2006). These temporal changes of motion integration were also found for the initiation of ocular tracking movements (Masson, Rybarczyk, Castet, & Mestre, 2000).

As mentioned earlier, it is not entirely straightforward to relate pursuit responses to the firing of single neurons in various brain areas. As is presumably the case for all behavior, psychophysical decisions or oculomotor behavior such as saccades or pursuit of the visuo-motor computations driving pursuit are performed by populations of neurons in many different regions (Britten, Shadlen, Newsome, & Movshon, 1992; Shadlen, Britten, Newsome, & Movshon, 1996). Still, Lisberger and colleagues (Medina & Lisberger, 2007; Schoppik et al., 2008; Huang & Lisberger, 2009) have tried to use electrophysiology in combination with computational modeling to constrain the potential neuronal circuits. Their results show that at the moment the behavioral data do not allow a unique specification of the physiological parameters in single

brain areas, and because noise sources in different brain regions can be traded off versus each other. Any kind of analysis depends on the size of the pool of neurons involved in a particular decision, on the correlation between these neurons, and on the tuning of each individual neuron. Since pursuit initiation is dynamic, it is not so much the static tuning that is of interest, which is typically measured, but the dynamic emergence of tuning with the first few spikes (see Osborne et al., 2004; VanRullen, Guyonneau, & Thorpe, 2005).

It has become clear that not only motion sensitive areas like MT and MST are of importance for driving pursuit responses. Interestingly, three areas (frontal eye fields [FEF], supplementary eye fields, and area LIP) are active not only during saccades but also during smooth pursuit, which suggests that at the cortical level smooth pursuit and saccades are not strictly separated (for review, see Munoz, 2002; Krauzlis, 2004, 2005). For example, Cassanello, Nihalani, and Ferrera (2008) recorded FEF neurons from awake-behaving rhesus monkeys making saccades to stationary and to moving targets using a step-ramp paradigm. They found that more than 50% of the FEF cells showed significant modulation of firing rate by target velocity during an interval of 100 ms centered on saccade onset. The comparison of the response behavior preceding the onset of saccades to stationary targets and that to moving targets showed that one third of the cells coded better for saccade amplitude in saccades to moving targets and seemed therefore to integrate velocity signals to compensate for the target displacement during the last 100 ms before the onset of the saccade. Therefore FEF neurons encode saccade metrics for position and when a saccade is planned to a smoothly moving target both target position and velocity. The proximity of saccade and pursuit-specific areas such as in the frontal eye field, as evidenced by several studies (Lynch, 1987; Morrow & Sharpe, 1990; Keating, 1991; MacAvoy, Gottlieb, & Bruce, 1991; Tanaka & Fukushima, 1998; Tanaka & Lisberger, 2002), suggests how both oculomotor subsystems interact to allow precise and fast tracking.

Conclusions

Our results establish the precise time course of the directional precision of human observers. Pursuit precision reaches psychophysical thresholds in as little as 150–200 ms after pursuit onset, both for trained and untrained observers, and irrespective of the speed of the stimuli. Variability both between and within observers about the speed with which a high precision is obtained are mainly related to their latencies, indicating that it is sensory noise and motor planning that are responsible for pursuit precision. Precision of initial saccades was

better than pursuit precision at the equivalent point in time after stimulus onset, presumably due to the availability of positional information to the saccade system. Therefore the combination of fast initial saccades and early pursuit responses enables primates to track peripheral objects that start to move rapidly with high directional precision.

Keywords: direction discrimination, oculomotor precision, pursuit saccade interactions

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