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Precision of speed discrimination and smooth pursuit eye movements

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ABSTRACT

Several studies have shown that the precision of smooth pursuit eye speed can match perceptual speed discrimination thresholds during the steady-state phase of pursuit [Kowler, E., & McKee, S. (1987). Sensitivity of smooth eye movement to small differences in target velocity. *Vision Research*, *27*, 993–1015; Gegenfurtner, K., Xing, D., Scott, B., & Hawken, M. (2003). A comparison of pursuit eye movement and perceptual performance in speed discrimination. *Journal of Vision*, *3*, 865–876]. Recently, Osborne et al. [Osborne, L. C., Lisberger, S. G., & Bialek, W. (2005). A sensory source for motor variation. *Nature*, *437*, 412–416; Osborne, L. C., Hohl, S. S., Bialek, W., & Lisberger S. G. (2007). Time course of precision in smooth-pursuit eye movements of monkeys. *Journal of Neuroscience, 27*, 2987–2998] claimed that pursuit precision during the initiation phase of pursuit also matches the sensory variability, implying that there is no motor noise added during pursuit initiation. However, these results were derived from a comparison of monkey pursuit data to human perceptual data from the literature, which were obtained with different stimuli. To directly compare precision for perception and pursuit, we measured pursuit and perceptual variability in the same human observers using the same stimuli. Subjects had to pursue a Gaussian blob in a step-ramp paradigm and give speed judgments on the same or in different trials. Speed discrimination thresholds were determined for different presentation durations. The analysis of pursuit precision was performed for short intervals containing the initiation period only and also for longer intervals including steady-state pursuit. In agreement with published studies, we found that the Weber fractions for psychophysical speed discrimination were fairly constant for different presentation durations, even for the shortest presentation duration of 150 ms. Pursuit variability was 3–4 times as high for the analysis interval (300 ms) containing the open-loop phase only. For pursuit analysis intervals of 400–500 ms, pursuit variability approached perceptual variability. Our results show that, for the stimuli we used, the motor system contributes at least 50% to the total variability of smooth pursuit eye movements during the initiation phase.

1. Introduction

The processes of transforming a percept into an appropriate action consist of an interwoven sequence of computations in neural networks that are susceptible to noise. Potential noise sources can be classified into sensory estimation at the input stage, central movement planning, and motor noise at the output stage. Several attempts have been made to characterize these noise sources and their relative magnitude for various types of movements, but the results varied considerably, ranging from a dominance of movement execution noise (van Beers, Haggard, & Wolpert, 2004), an emphasis on central planning noise (Churchland, Afshar, & Shenoy, 2006) to sensory signals as the sole noise source (Osborne, Hohl, Bialek, & Lisberger, 2007; Osborne, Lisberger, & Bialek, 2005). Of course, the different studies are difficult to compare, because different types of movements were investigated. But even within the realm of eye movements there has been considerable disagreement between different studies. Eye movements are of particular interest here, because humans continuously move their eyes, and because the eye muscles are among the most densely innervated muscles of the human body, enabling precise control over their movements. The most frequent voluntary eye movements, saccades, direct the fovea onto objects of interest, thus enabling our high resolution foveated vision system. When objects of interest are in motion, humans use slow tracking movements, called smooth pursuit, to continuously keep the projection of the selected object in the fovea.

When the oculomotor system initiates pursuit of a smoothly moving object, a series of computations are triggered. Firstly, the direction and speed of the motion stimulus are estimated, followed by generating the initial motor output to get pursuit going. This in turn leads to feedback and then to locking onto the motion stimulus (Lisberger, Morris, & Tychsen, 1987; Pola & Wyatt, 1991). These computations are influenced by different, interacting factors such

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as the visual stimulus parameters (Braun, Pracejus, & Gegenfurtner, 2006; Braun et al., 2008; Carl & Gellman, 1987; Hawken & Gegenfurtner, 2001; Lisberger & Westbrook, 1985; Spering, Kerzel, Braun, Hawken, & Gegenfurtner, 2005), cognitive expectations (Kowler & Steinman, 1981), or the noise existent in the neural substrate (Kowler & McKee, 1987; Stone & Krauzlis, 2003). Therefore, each single smooth pursuit movement shows a deviation from a hypothetically optimal, noise-free motor response (e.g. Harris & Wolpert, 1998). To characterize the quality of such a smooth pursuit movement, early investigations concentrated on describing pursuit by determining latency, acceleration and average gain. More recently, some investigations have focused on the precision of pursuit by analyzing the variability across trials and comparing it to perceptual measures of variability (Gegenfurtner, Xing, Scott, & Hawken, 2003; Kowler & McKee, 1987; Stone & Krauzlis, 2003). By characterizing variability one can determine the relationship between the precision of sensory coding and the precision of the smooth pursuit response. For that purpose Kowler and McKee (1987) introduced "oculomotor difference thresholds", which is a way of expressing the degree of precision analogous to the use of perceptual difference thresholds.

Kowler and McKee (1987) found that speed discrimination thresholds and steady-state pursuit precision were identical over a large range of conditions. However, they also observed that "[...] there is precise sensory information about the velocity of the target, which is available for perceptual judgments of velocity, but which is not reflected in the early portion of smooth pursuit [...]" (Kowler & McKee, 1987, p. 1012). Thus, given the precise perceptual signal, one possible explanation is that the motor generation of the initial pursuit movement is noisy, but that the amount of noise gradually decreases due to the benefit of feedback. In the study of pursuit precision, the early, open-loop phase is of particular interest, that is the first approximate 120 milliseconds after the onset of the eye movement (e.g. Lisberger & Westbrook, 1985; Priebe, Churchland, & Lisberger, 2001; Tychsen & Lisberger, 1986; Wyatt & Pola, 1983). During this initiation period, the pursuit system has not received feedback from its internal analysis yet. The precision of the pursuit system should therefore reflect the combination of a sensory contribution and an initial motor contribution. Recently, Osborne and colleagues (Osborne et al., 2005, 2007) have investigated the early phase of pursuit in particular, to disentangle the contributions of these two potential noise sources. They argue that the dominant noise source resides in sensory encoding and that the contribution of motor noise is negligible. This viewpoint, which is supported by the recent computational work by Medina and Lisberger (2007), stands in contrast with the conclusions drawn by Kowler and McKee (1987).

There are quite a number of differences between these two studies, which could have led to the differences in results and conclusions. Most importantly, Kowler and McKee (1987) investigated slow speeds (<5 deg/s) only and compared pursuit and perception on different sets of trials. Osborne et al. (2005, 2007) measured pursuit precision for monkeys and only at speeds above 10 deg/s. They compared their results to existing data on speed discrimination, which were obtained with human subjects and different stimuli (De Bruyn & Orban, 1988). Therefore, we decided to resolve some of these issues by measuring pursuit and perceptual precision using the same stimuli and the same human observers.

2. Methods

2.1. Equipment

Subjects were seated in a dimly lit room facing a Sony Triniton F-900 23″ monitor with a refresh rate of 100 Hz. At a viewing distance of 92 cm, the active screen area subtended 29 deg of visual angle in the horizontal direction, and 19 deg vertical on the subject's retina. The screen was viewed binocularly. The subject's head was fixed in place using a bite bar made of dental medical material, two support points at the forehead, and two additional support points at the back of the head. Eye movements of the right eye were recorded using a Dual Purkinje Image Eye Tracker (Fourward Technologies Generation 6.1, Buena Vista, VA; Crane & Steele, 1978). The analog eye position signal was sampled at a frequency of 500 Hz.

2.2. Subjects

The three subjects (DB, CB, NL) were between 24 and 47 years of age and all female. All subjects had normal visual acuity or were slightly myopic. The myope performed the experiments without her optical corrections. Two of the subjects (CB, NL) were naïve with respect to the experiment. Subjects had varying degree of experience with pursuit tasks (much, moderate and none for DB, CB and NL, respectively).

2.3. Stimuli

The motion stimulus consisted of a Gaussian blob with a standard deviation of 0.5 deg moving horizontally across the display using a step-ramp paradigm (Rashbass, 1961). At the beginning of each trial a small red fixation spot was presented for a duration that randomly varied between 500 and 1000 ms. When the fixation spot disappeared, the Gaussian blob appeared to the left or right of fixation position and started to move in opposite direction crossing the center of the screen. The direction of motion was randomly chosen on each trial. The initial step of the Gaussian blob was chosen individually for each subject and condition to prevent initial saccades.

2.4. Experiments

Three different experiments were carried out:

1) *Pursuit-only*: the subjects were asked to fixate the red central fixation spot initially and then to follow the Gaussian blob with their eyes as precisely as possible. Five different motion speeds were used, 8.25, 9.625, 11.0, 12.375, 13.75 deg/s ($s_1, \ldots, s_5$). Ten sessions of 200 trials each were carried out.
2) *Psych*: in addition to performing pursuit with the same motion speeds as in the *pursuit-only*, the subject was asked to give a psychophysical speed discrimination at the completion of each trial: The subject had to judge whether the speed was faster or slower than a standard motion speed (11.0 deg/s). This standard speed was presented 10 times at the beginning of each session, and then throughout the session randomly every 10th trial on average. Trials on which the standard speed was presented were marked by a green fixation spot at the beginning of the trial. No feedback about the correctness of the response was given. Five sessions of 200 trials each were run.
3) *Psych-var*: in this task, we attempted to reduce any cues of position and time by measuring thresholds for three different presentation times (150, 250 and 500 ms) in an interleaved manner. Additionally, each presentation time was slightly jittered by 10–20 ms. Seven different speeds (5.5–16.4 deg/s) were used and the subject had to perform a psychophysical discrimination at the completion of each trial as in Experiment 2, the psych-study. Although it seems that subjects generally make little use of cues about position and time if only a single presentation time is used for differ-

ent target speeds (de Bruyn & Orban, 1988; McKee, Silverman, & Nakayama, 1986), this experiment excluded the possibility that the distance traveled by the target is a helpful cue about speed. Five sessions of 200 trials each were run.

2.5. Eye movement analysis

The position trace was low-pass filtered with a Butterworth filter with cut off frequency of 60 Hz to reduce digitization noise. It was then differentiated to obtain a raw (horizontal) eye velocity using the difference across every 2nd sample. This velocity trace was then low-pass filtered with a Butterworth filter with cut off frequency 40 Hz to reduce tracker noise. This trace is denoted as v_i. An individual eye velocity trace in response to a given stimulus speed (e.g. $v^{s=11.0}$) is denoted as $v_i^{s=11.0}$ The eye velocity traces for a given stimulus speed (e.g. $v^{s=11.0}$) were averaged: $\bar{v}^s = 1/N\sum_{i=1}^{N} v_i^s$. Traces containing a saccade during the analysis interval were discarded as well as traces which showed an absolute velocity value of larger than 2 deg/s during fixation. This served to exclude the rare trials with a saccade during the fixation period. Slow drift movements during fixation typically varied in speed between +1 and -1 deg/s.

2.6. Signal detection analysis

Our goal was to determine how well the different stimulus velocities could be discriminated based on the eye movement records alone. To achieve this, we used the signal detection analysis employed by Osborne et al. (2007). This involves calculating the signal-to-noise ratio, or d', at any instance in time t. d' is given by the average difference between two traces, for two given speeds s_a and s_b, divided by the average standard deviation σ of the same traces:

$$d'_{s_a,s_b}(t) = (\bar{v}^{s_a}(t) - \bar{v}^{s_b}(t))/(\sigma(t)). \tag{1}$$

In our experiments, the standard deviations for the different speeds were quite uniform, as can be seen in Fig. 1b. Therefore we improved our estimate of $\sigma(t)$ by taking the average standard deviation across all speeds.

d' is a measure for the discriminability of two distributions and equals the square root of the signal-to-noise ratio (Green & Swets, 1966). We calculated d' for all combinations of different speeds and at all points in time with respect to stimulus motion onset. For late points in time, the difference in means in eye speed is equal to the difference in stimulus speeds. Since the standard deviation of pursuit is constant during the steady state, d' is therefore proportional to the difference of stimulus speeds, $(s_a - s_b)$. When dividing d' as a function of time by this difference, we obtain a function $K(t)$ that turned out to be equal for all speed combinations. In other words, d' can be approximated by multiplying the function $K(t)$ with the stimulus speed difference: $d'(t) = K(t)(s_a - s_b)$.

Psychophysical threshold is conventionally set to be the point where d' equals unity. Therefore, the speed difference corresponding to threshold at a given point in time t is equal to $1/K(t)$.

Osborne et al. (2007) used an additional method to calculate threshold that takes into account correlations in eye speed error over time. This method involves estimating the inverse of the covariance matrix of eye speed errors, which is numerically unstable because of the high dimensionality of the matrix. Osborne et al. (2007) circumvented this problem by approximating the covariance matrix using its first three principal components. The first step is to obtain the noise vectors, e.g. for a given speed $s = 1$, a noise vector is formed by subtracting the average velocity trace from each individual velocity trace $\delta_i = v_i^{s_a} - \bar{v}^{s_a}$. Then, the covariance matrix of those noise vectors is computed and its principal components are determined. Eigenvectors, $\boldsymbol{u_k}$, and Eigenvalues, λ_k, were then summed as follows, $C_{ij}^{-1} \approx \sum_{k=1}^{3} \mathbf{u}_k\mathbf{u}'_k/\lambda_k$ which then was used to calculate the *SNRe3*:

$$SNRe3_{s_a,s_b}(T) = \sum_{i=0}^{T}\sum_{j=0}^{T} C_{ij}^{-1}\delta_i\delta_j \tag{2}$$

SNRe3 is then used to form K and threshold values as it was done above.

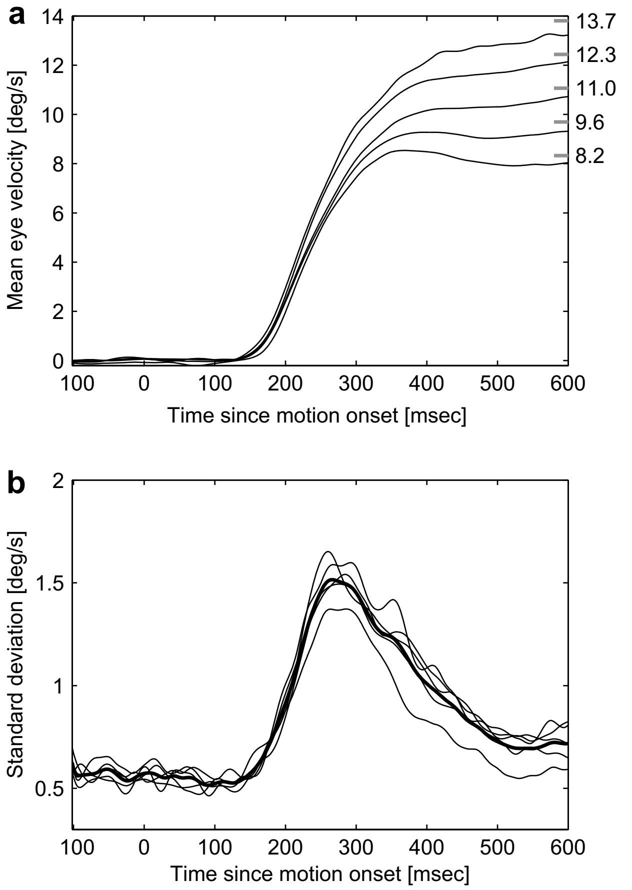

Fig. 1. (a) Mean (horizontal) eye velocities $\bar{v}$ in response to each motion stimulus speed for subject DB for experiment *pursuit-only*. Stimulus onset occurs at $t = 0$ ms. Exact stimulus speeds are indicated by the horizontal gray markers at $t = 600$. (b) Standard deviation for each time unit of the corresponding velocity traces for each stimulus speed. The thick line is the average of the standard deviations.

2.7. Psychometric and oculometric functions

Psychometric functions were estimated by calculating the proportion of "faster" responses for each stimulus speed; functions were fitted with a Gaussian cumulative distribution function (Wichmann & Hill, 2001). The (perceptual) difference threshold was determined as the standard deviation of the fitted cumulative Gaussian, which corresponds to an 84% probability of a faster response. To estimate oculometric functions (Kowler & McKee, 1987), the oculometric discrimination decision was taken at $t_d = 250$, 300, 350, 400, 450, 500, 550 and 600 milliseconds. For such a decision time t_d, the eye velocity $v_i^s(t_d)$ was compared to the average eye velocity $\bar{v}^{s=11.0}(t_d)$ and assigned a "faster" or "slower" response. Functions were fitted analogous to the psychometric functions, and (oculometric) difference thresholds were determined.

2.8. Eye tracker precision

In order to estimate the precision of smooth pursuit eye movements, the amount of variance contributed by the eye tracking equipment has to be estimated and subtracted. We used a model eye (Fourward Technologies, Buena Vista, VA) driven by an analog function generator outputting sinusoidal motion. The model eye moved from +4 deg to −4 deg and thus covered the range of viewing angles used in the experiments. The temporal frequency was set to 1 Hz, which generated eye speeds in the range from −25 deg/s to +25 deg/s. Processing of the artificial eye's traces was identical to ones obtained from the human eyes (see above). For each point of the sinusoidal cycle, the standard deviations of the corresponding eye speeds were determined. Standard deviation was fairly constant for all speeds and varied between 0.061 and 0.171 deg/s with a mean of 0.115 deg/s.

The measurements on the artificial eye present a lower bound on the amount of measurement noise. There are other potential noise sources that are unrelated to pursuit, such as slight head movements of the subjects. We tried to stabilize the observer's head as much as possible, by using a bite bar and a head support (see above). This makes us quite confident that our stability is nearly as good as in primate setups where a headpost is used. A comparison of the standard deviation of the eye speeds during fixation between our present data (see Fig. 1) and monkey data from Osborne et al. (2005), their Fig. 3d supports this view. In both cases, the standard deviation of eye speeds during fixation was about 0.5 deg/s.

2.9. Open-loop interval

We estimated the duration of the open-loop interval using a method introduced by Lisberger and Westbrook (1985) in monkeys. This involved a change in the speed of the pursuit target at the time of pursuit latency. All three subjects underwent two sessions of 200 step-ramp trials each. The paradigm was as above for the *pursuit-only* task, but in about 10% of randomly determined trials the speed of the pursuit target increased from 11 to 22 deg/s 130 ms after its motion had started. A comparison of the perturbed and unperturbed traces then indicates the time it takes for visual feedback to affect the eyes. This was the case 325 ms after stimulus motion onset for subject DB, 300 ms for subject NL, and 275 ms for subject CB. Thus, in close agreement with the data by Lisberger and colleagues (Lisberger & Westbrook, 1985; Tychsen & Lisberger, 1986), the length of the open-loop interval is approximately equal to the latency of pursuit initiation.

3. Results

Fig. 1a depicts the average eye velocity traces for one subject in response to the different stimulus speeds ranging from 8.2 to 13.7 deg/s. The eyes start to move approximately 150 ms after the onset of stimulus motion. There exist only minor differences in latency for this limited range of speeds. Average latencies for individual subjects were 155 ms for DB, 146 ms for NL and 154 ms for CB. The data represented in Fig. 1 were obtained in experiment 1 (*pursuit-only*) where the stimulus speeds were randomly selected within each session. In Fig. 1b, the standard deviation is shown for the same average curves plotted in Fig. 1a. Variability is relatively small during the fixation period before the eyes start to move, and then again after the eyes have reached the phase of steady state during pursuit. If one expected a precise signal, the difference in the average eye-movement traces for the given set of speeds should be large, accompanied by a small standard deviation. Inspection of Fig. 1 indicates such a precise encoding of the stimulus speed from 400 ms onwards. In contrast, during the initiation period, roughly given by the period from 120 to 250 ms after stimulus motion onset, there is hardly any difference in the eye movement traces, whereas the standard deviation is fairly high.

3.1. Signal detection analysis

Fig. 2 illustrates the following steps to calculate exact thresholds. In Fig. 2a the d' values for all the different speed combinations

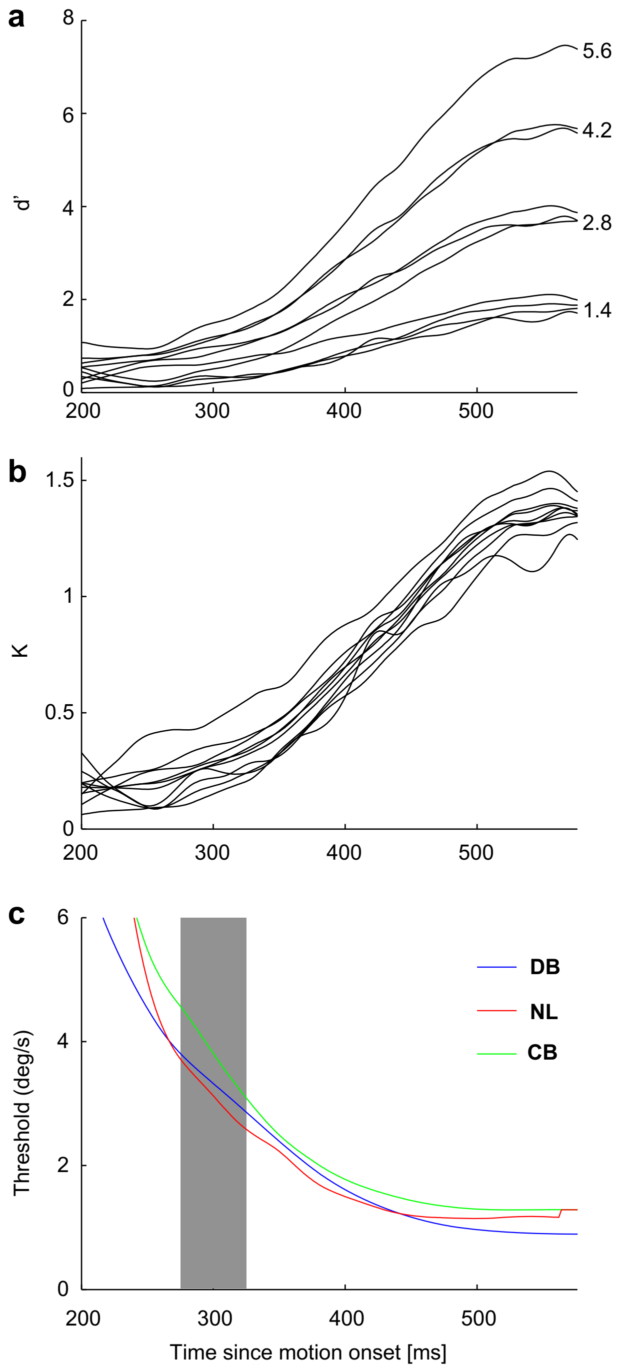

Fig. 2. Obtaining the thresholds. (a) d' For each set of speed pairs (differences of 1.4, 2.8, 4.2 and 5.6 deg/s) for observer DB computed using Eq. (1) (point-wise SNR). (b) The corresponding K values for each speed difference for observer DB. (c) The corresponding thresholds ($1/K$) for all three subjects. The gray shaded bar indicates the end of the open-loop period for our observers.

are shown for observer DB. They start to differ from zero at about 200–250 ms, then increase steadily, and finally saturate at around 550 ms. Of course, discriminability increases with an increasing speed difference. When these values are normalized by the magnitude of the respective speed difference, shown in Fig. 2b for observer DB, the resulting curves overlap to a large degree. Therefore, we averaged these curves to a single estimate of the function $K(t)$, whose inverse then indicates the threshold speed difference, shown in Fig. 2c for all three observers. The estimates using the full covariance matrix did not differ in any systematic way from the simpler estimates and are not shown.

The end of the open-loop interval was between 275 and 325 ms after stimulus motion onset, and between 150 and 200 ms after pursuit onset for our observers. The threshold values obtained for pursuit at that point in time are on the order of 3–5 deg/s. This is substantially higher than reported threshold values for human speed discrimination, which is usually characterized by Weber fractions between 5% and 10% (Liu & Newsome, 2005; Nakayama, 1985; Purushothaman & Bradley, 2005; Sekuler, 1996; Verghese & McKee, 2006). This would correspond to thresholds of 0.55 to 1.1 deg/s for our standard speed of 11 deg/s. Therefore, it seems that in our experiments the precision of smooth pursuit at the end of the open-loop phase is lower than that of perceptual speed discrimination. However, speed discrimination depends on many parameters, and it would be problematic to directly compare thresholds from our pursuit experiments with psychophysical data from the literature. To investigate this issue more thoroughly, we will compare the results of our pursuit analysis with psychometric functions obtained with the same stimuli, and with oculometric functions calculated from the same eye traces as above.

3.2. Oculometric analysis

We analyzed our data using the methods introduced by Kowler and McKee (1987). Here, pursuit traces were used as a basis for so called “oculometric” judgments, which can then be used to construct oculometric functions, analogous to the widely used psychometric functions. Fig. 3 compares the precision of the oculometric

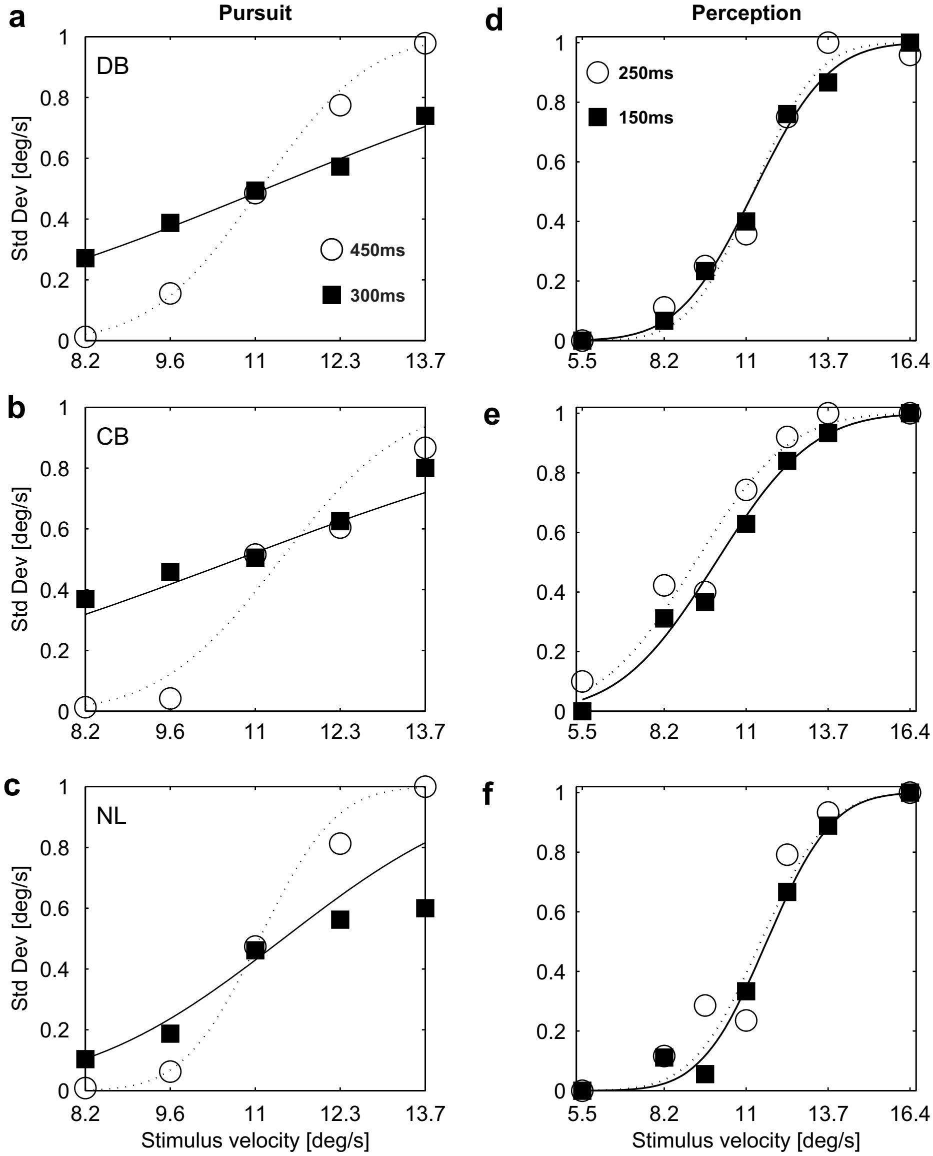

Fig. 3. Comparison of oculometric (left graphs, a–c) and psychometric (right graphs, d–f) functions for Experiment 2 (*psych*) and Experiment 3 (*psych-var*), respectively. Oculometric functions are shown for analysis intervals of 300 ms (filled squares) and 450 ms (open circles), the psychometric functions for a stimulus presentation of 150 and 250 ms (filled squares and open circles): a and d, subject DB; b and e, subject CB; c and f, subject NL.

functions (left column) and psychometric functions (right column). The oculometric functions are shallow for a decision time of $t_d = 300$ ms (filled squares) and evidence the low precision at the end of the open-loop phase. They are steeper for a decision time of $t_d = 450$ ms (dashed) and reflect the high precision during steady-state pursuit, presumably due to the increased use of visual feedback. The psychometric functions for the presentation times of 150 and 250 ms (solid and dashed, respectively) do not differ systematically and have a slope whose magnitude is similar to the slopes of the oculometric functions for longer analysis intervals.

Fig. 4 shows the discrimination thresholds estimated from oculometric functions at different times since stimulus motion onset and from psychometric functions at different presentation durations. In the psychophysical experiments, different presentation durations were used between 150 ms and 1 s. As observed earlier by Kowler and McKee (1987) and de Bruyn and Orban (1988), there is hardly any effect of presentation duration on the psychophysical thresholds.

The oculometric discrimination thresholds start at a value of larger than 5 deg/s at 200 ms after stimulus motion onset and then decrease to about 1 deg/s at 500 ms after stimulus motion onset (about 375 ms after pursuit onset).

There are several noteworthy aspects of the results shown in Fig. 4:

1. For all three observers, the pursuit variability for the initiation period, corresponding to the time period of up to 300 ms since stimulus motion onset, is substantially larger than the psychophysical variability at the shortest presentation duration of 150 ms.
2. For all three observers, pursuit variability does reach psychophysical thresholds for pursuit analysis intervals of 350–450 ms after stimulus motion onset.
3. For longer intervals, pursuit precision becomes even better than perceptual performance, indicating that closed-loop pursuit can be more precise than perceptual judgments.

To discern the detailed dynamics, it is necessary to examine the very early part of the time interval after pursuit onset. During the open-loop phase, the whole pursuit variability is determined by the initial sensory estimate plus the noise added by the motor system. After the open-loop phase, visual feedback about retinal errors becomes available to control eye speed in a closed loop and sensory and motor contributions can no longer be decomposed. For the psychophysical judgments, we will consider only the estimates for the shortest time period (150 ms). In these experiments, no pursuit was initiated, which ensures that the eye speed signal cannot be used to improve the psychophysical judgments. Therefore, during the open-loop phase, the comparison of psychophysical and oculomotor variability allows us to estimate the relative magnitude of those noise sources over time. The observed pursuit variability can be regarded as the sum of three distinct noise sources, the sensory, the motor and the measurement noise source (eye tracker). The psychophysical performance reflects the magnitude of the sensory noise alone, if we assume that decision noise is negligible. The magnitude of the measurement noise was less than 0.2 deg/s, corresponding to a variance of 0.04 deg^2/s^2, which is negligible for our considerations. Fig. 5 shows the magnitude of the motor noise as $N_{\text{motor}}(t) = 1 - \text{Var}_{\text{psycho}}(150)/\text{Var}_{\text{pursuit}}(t)$. $N_{\text{motor}}(t)$ reflects an estimate of the relative contribution of the motor noise to the total pursuit variability at time t. At the end of the open-loop interval, indicated by the vertical short lines, the observed pursuit noise is much higher than the sensory noise. For all three observers, we estimate the motor noise at the end of the open-loop interval to be above 50%. The point where psychophysical and oculometric thresholds are equal, is reached 100–200 ms later.

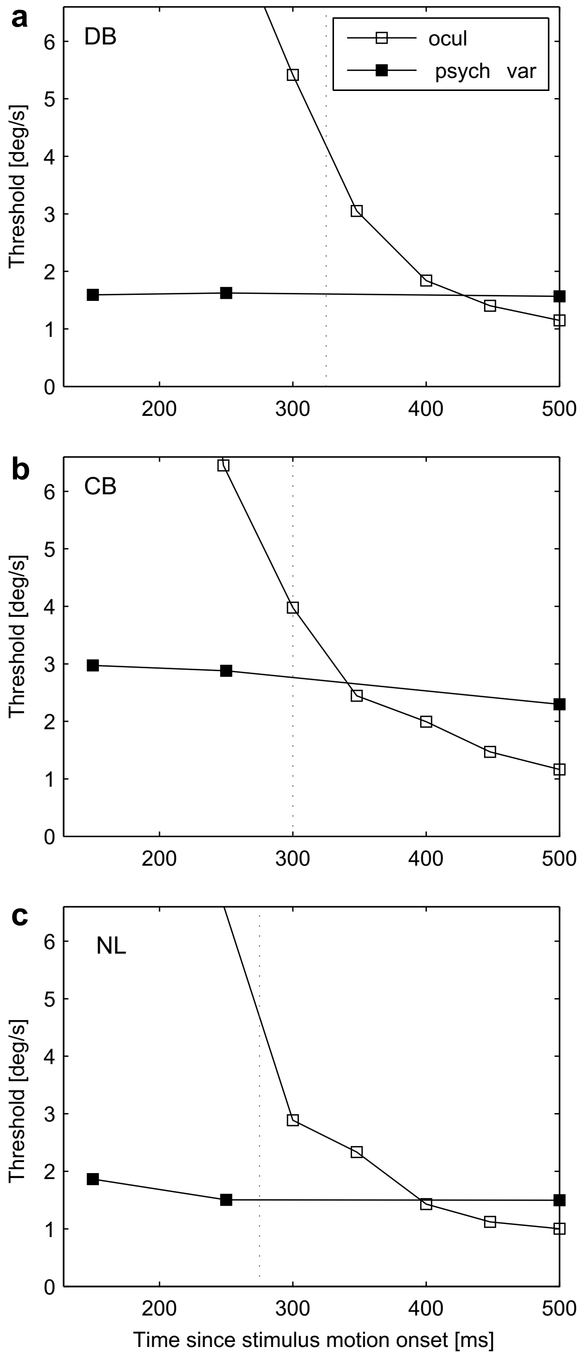

Fig. 4. Difference threshold measures as a function of time since stimulus motion onset for the three subjects. *Pursuit*: difference thresholds based on the oculometric functions from Experiment 1 (*pursuit-only*). *Perception*: difference thresholds based on the psychometric functions from Experiment 3 (*psych-var*): a, subject DB; b, subject CB; c, subject NL.

In Fig. 6 our data are also compared to published data from other labs. The pursuit and perceptual precisions from our study are compared to the pursuit precisions determined by Kowler and McKee (1987), their Fig. 12 and Osborne et al. (2007), their Fig. 12b, and to the psychophysical thresholds measured by de Bruyn and Orban (1988), their Fig. 8. Psychophysical thresholds are plotted as a function of presentation duration. Pursuit precision is plotted relative to stimulus motion onset in Fig. 6a, and relative

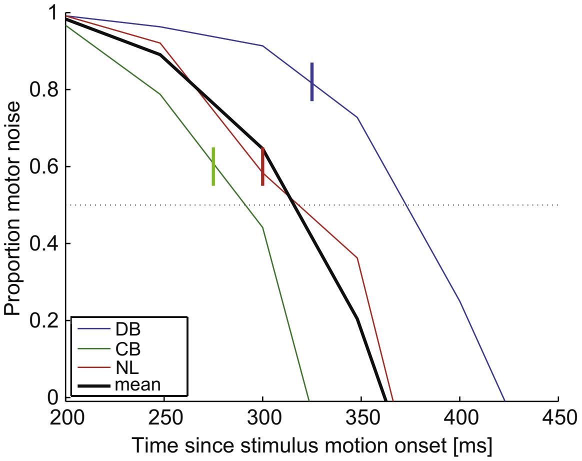

Fig. 5. The proportion of motor noise in dependence of time since stimulus motion onset. Motor variability is 1 minus the variance from the psychometric functions divided by the variance of the oculometric function at the same time. Motor noise is shown for all three subjects, as well as their mean. The short vertical markers indicate the end of the open-loop phase for each observer.

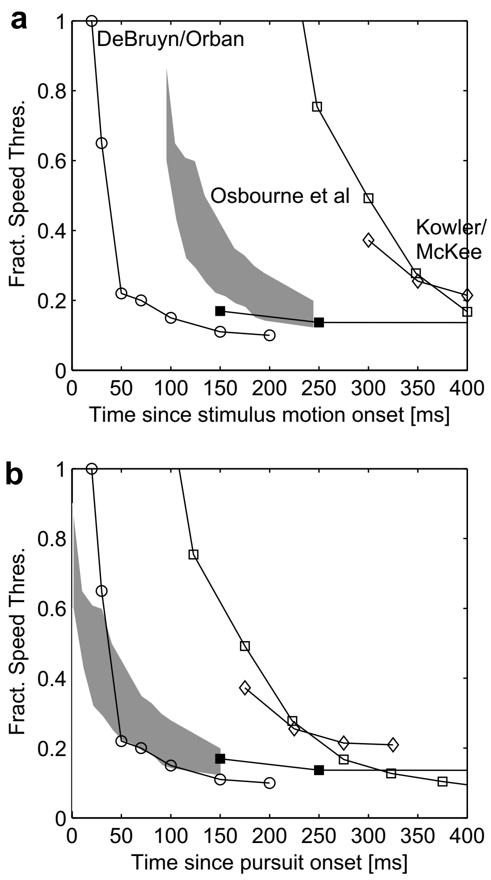

Fig. 6. Comparison of variability measures from various studies expressed as fractional speed thresholds. The open-squares are the oculometric difference thresholds for observer DB from Fig. 4. The filled squares are the psychometric difference thresholds for observer DB from Fig. 4. The open circles describe human perceptual thresholds for a 16 deg/s speed discrimination experiment taken from de Bruyn and Orban (1988). The diamond symbols (on the right) show oculometric difference thresholds from the study by Kowler and McKee (1987), (p. 1010, 3.3 deg/s). The gray shaded area encloses worst and best monkey pursuit difference thresholds for a 20 deg/s stimulus from Osborne et al. (2007), their Fig. 12b. (a) Pursuit precision plotted relative to stimulus *motion* onset. (b) Pursuit precision plotted relative to *pursuit* onset. The pursuit thresholds from panel a were shifted leftwards by their latency.

to pursuit onset in Fig. 6b. All thresholds are expressed as Weber fractions, since the speeds used in the different studies differ to some degree. Our stimuli moved at 11 deg/s (center speed), the ones by Osborne et al. (2007) at 20 deg/s, the ones by de Bruyn and Orban (1988) at 16 deg/s, and the ones by Kowler and McKee at 3.3 deg/s.

There is some agreement and some disagreement between the results from the different studies. Overall, the psychophysical data are in reasonably good agreement with each other and with other published data. For presentation durations of 150 ms or longer, thresholds are stable at a Weber fraction of 10–15%. There is a small increase in thresholds as the duration shortens to 50 ms. Only for extremely short presentations, velocity discrimination deteriorates substantially. There is also reasonable agreement between the asymptotic pursuit precision estimates of all three studies. The threshold values for the Kowler and McKee (1987) study were a bit higher, presumably because the speed used in their experiment was quite low at 3.3 deg/s. Note that we report the data they obtained with a randomized motion direction. Their thresholds are lower for the case where the observer knew the direction of motion ahead of time, but the analysis of the time course of precision is contaminated in this case by anticipatory eye movements. The biggest difference in the data shown in Fig. 6 concerns the Osborne et al. (2007) data. In their study, pursuit precision reached Weber fractions below 20% as early as 100 ms after pursuit onset. For our data, and for Kowler and McKee (1987), this was the case only 200–250 ms after pursuit onset. We will return to this crucial issue in the discussion section.

4. Discussion

Our results show that pursuit precision at the end of the initiation phase is significantly lower than perceptual precision for briefly presented stimuli. This represents strong evidence that pursuit variability during the initiation phase is not only determined by a sensory noise source, but also by a motor noise source to a large degree.

4.1. Comparison to earlier studies

Our experiments are most closely related to the studies by Osborne et al. (2005, 2007), Gegenfurtner et al. (2003) and Kowler and McKee (1987), who all investigated the precision of smooth pursuit eye movements. Most recently, Osborne et al. (2005, 2007) argued that sensory noise alone contributes to the variability of pursuit initiation. Their arguments are based on computational analyses and experimental findings. Analytically, they found three significant eigenvectors for smooth pursuit during the initiation phase, which explain more than 90% of the variance of the pursuit traces in scale, direction and latency. According to Osborne et al.'s viewpoint (2005), these represent "sensory parameters", and therefore little noise is supposed to be added during motor processing. Experimentally, and more importantly, they argue that the variability they observed closely matches sensory variability determined in earlier studies. We think that the argument about speed, direction, and latency being sensory rather than motor by definition cannot be resolved by any of the data at hand.

There are, however, several objections concerning the degree of variability. First, Osborne et al. (2005, 2007) did not measure psychophysical speed discrimination thresholds in their observers for their stimuli. It is always problematic to compare results across conditions from different studies, and in this case it also involved a comparison across species. Second, the agreement observed by Osborne et al. (2005, 2007) appears loose. Human thresholds are typically on the order of 5–15% (e.g. 7% in the study by de Bruyn

& Orban, 1988). The pursuit variability for monkeys measured by Osborne et al. (2005) at the end of the initiation phase was on average 15.4%. This is twice as high as the perceptual thresholds the authors referred to, and the exceeding amount could be interpreted as deriving from a motor source. That there is a possibility of a motor contribution can be seen even in the data presented in Osborne et al. (2007), since the motor variability decreases substantially after the end of the open-loop phase. During the initiation phase (until about 225 ms after target motion onset) of the eye movement traces, they found variability in speed that corresponds to Weber fractions between 11.2% and 18.1%. In Osborne et al. (2007), their Table 2 the analysis was also performed for a larger time interval of 350 ms after target motion onset, for which they observed Weber fractions ranging from 6.3% to 13.3%. On average, there was a reduction in the Weber fraction from 13% to 10% between these two time intervals, indicating that pursuit precision does significantly improve during the period after the end of the open-loop phase. This improvement could be due to sensory feedback, but it could also be a reduction of the motor noise, a reduction in sensory noise, or a combination of everything.

It is true that the time course of the reduction in oculomotor and psychophysical thresholds appears quite similar when looking at Fig. 6. However, it is difficult to evaluate the exact time courses. Both types of thresholds decrease from infinity to their asymptotic values over a short period of time of about 100–150 ms, and it is quite difficult to discriminate between different decay constants. This is particularly true because the steepest part of the decay is based on data points that are associated with a large variability. Furthermore, it is troublesome to estimate the psychophysical speed discrimination thresholds at extremely short presentation durations because stimulus onset and offset transients would dilute the motion signal, while pursuit is only affected by onset transients. This would lead to an underestimation of the perceptual speed discrimination thresholds at short presentation durations.

But the problem is more fundamental. One possibility to achieve such a similarity in time courses is to have sensory noise only, in which case motor noise would be zero. However, the same identical time courses would arise if sensory noise decreases relatively fast to a low value, while motor noise decreases more slowly, but with a similar time course. In other words, since the oculometric thresholds are determined by the sum of sensory and motor noise, it cannot be decided whether any of the two terms is zero. In our opinion, the large delay with which oculometric thresholds are decreasing argue in favor of a significant motor contribution.

Our results do agree quite well with the earlier experiments by Kowler and McKee (1987), as shown in Fig. 5, and with the psychophysical experiments by de Bruyn and Orban (1988). Irrespective of whether the performance of the monkey observers of Osborne et al. (2005, 2007) matches perceptual performance, it is evident that the pursuit variability of monkeys decreases more rapidly than that of the human observers. The curves in Fig. 6 for these two cases are about 100–150 ms apart. There are several possible reasons. We used a single target spot in our study, moving at a speed of 10 deg/s. This is the target speed and stimulus where the monkey observers of Osborne et al. (2007) show major interindividual differences. Thresholds at the end of the open-loop phase are at 15% for one of their monkeys, but fairly high at 30% and 40% for the other two monkeys (their Fig. 10D). This is not very different from our human observers. However, without knowledge of the perceptual thresholds of these monkeys, the whole issue remains very speculative. Another possibility is a species difference between monkeys and humans in the processing time of speed information for pursuit. Alternatively, it could be imagined that the highly practiced monkeys became faster and more precise at their tasks through sensorimotor learning. Setting the correct explanation aside, the discussed issues highlight the need to measure pursuit and perception in the same observers.

4.2. Comparison to other motor tasks

While the above mentioned studies were concerned with pursuit eye movements and speed discrimination, there have been a larger number of studies concerned with other visuo-motor behavior, such as reaching or pointing movements, saccadic eye movements, or the direction of pursuit eye movements.

van Beers et al. (2004) modeled the movement variability of manual pointing movements to visual targets. Most notably, they observed that the direction of such movements varied with the eccentricity of the targets, implying that execution noise rather than planning noise dominates movement variability. Overall, they estimated that sensory noise contributes less than a third of the total variance, with most of it stemming from execution noise. Contrary to that conclusion, Churchland et al. (2006) measured in monkeys that at least 50% of central planning noise contributed to movement speed variability of reaching movements. However, they measured the variability of movement speed with stationary targets. There was no physical variability of the stimulus and consequently no sensory variability. This raises the question why the motor system should minimize the variability of the movement speed for a task for which this quantity is irrelevant. Two other studies compared sensory and motor variability in pointing tasks (Gegenfurtner & Franz, 2007; Ma-Wyatt & McKee, 2006; Ma-Wyatt & McKee, 2007). Both of them show that sensory precision is not the only factor limiting performance in pointing, and that visual feedback during a movement greatly reduces motor endpoint variability. Since movements of the arm and hand take a relatively long time to execute, this feedback might play an important role when executing such movements.

Saccadic eye movements are much faster than hand movement and are truly ballistic. It has been shown by Aitsebaomo and Bedell (1992) that saccades and perception share some common processing when the presentation duration of saccadic targets is changed. Van Beers (2007) modeled saccadic endpoint variability and estimated that about half of the noise is caused by sensory variability.

For pursuit eye movements, not only the speed parameter has been studied, but also the direction parameter. Typically, an excellent agreement has been found for pursuit direction and perceptual direction judgments (Beutter & Stone, 2000, 1998; Krauzlis & Stone, 1999; Osborne et al., 2005; Stone, Beutter, & Lorenceau, 2000; Stone & Krauzlis, 2003). Just as in the case for speed, Osborne et al. (2005, 2007) argue that the precision is determined by sensory noise alone. While the trial-by-trial correlation in pursuit direction and perceived direction observed by Stone and Krauzlis (2003) supports this argument, their analysis was in fact based on the analysis of pursuit during the steady-state interval, starting 300 ms after pursuit onset. They do not report how pursuit thresholds would change at shorter analysis intervals, but inspection of their figures seems to indicate much larger direction thresholds during pursuit initiation. Perceptually, direction thresholds reach asymptotically low values for even shorter presentation durations than velocity thresholds (de Bruyn & Orban, 1988).

4.3. Neural substrates

Both perception and pursuit do rely on the time course by which the relevant information is provided through neuronal computations. It is known that extrastriate cortical area MT is involved in the processing of visual motion, and that signals generated in area MT are used in the control of smooth pursuit eye movements (Lisberger & Movshon, 1999; Newsome & Paré, 1988). It is the first area along the visual pathway to exhibit signs of speed tuning, rather than separable responses to spatial and temporal frequencies that are encountered in *V*1, *V*2 and *V*3 (e.g. Heeger, Simoncelli, & Movshon, 1996; Priebe, Lisberger, & Movshon, 2006). It has also been demonstrated that responses of MT neurons can be used to signal speed differences close to perceptual thresholds (Nover, Anderson, & DeAngelis, 2005). An issue that has not been resolved so far is how much time MT neurons require to signal speed reliably. Since single neurons are not capable to specify speed in a manner that is independent of other stimulus parameters such as contrast or direction, a population response has to be formed and read out (Clifford & Ibbotson, 2002; Lisberger & Movshon, 1999). A further argument for a population code of speed is the time course of information build-up about motion direction in area MT. Osborne, Bialek, and Lisberger (2004) have shown that individual MT neurons can signal very little information about direction of motion, but that most of the information is contained in the first few spikes. Further temporal integration is hampered by strong temporal correlations. While MT neurons do have exceptionally short latencies of 50 ms or less (Lisberger & Movshon, 1999; Vanni et al., 2004), at least one additional processing step is necessary to obtain a precise estimate of speed. Our results in humans suggest that it takes at least 400 ms after stimulus onset until this level of precision is reached in the motor output. The question that is difficult to answer is whether it takes such a long time to reach a precise sensory estimate of speed. To us, this seems unlikely, given that the population response in area MT contains precise speed information at latencies of less than 100 ms. Alternatively, other sources of noise could deteriorate precise motor planning, which in turn would require feedback to achieve maximum precision during motor execution.

Of course, a definitive answer to these questions could only be given if pursuit variability and neuronal variability are compared in the different brain areas which are involved in transforming a sensory speed estimate into a pursuit output. Recently, Lisberger and colleagues (Medina & Lisberger, 2007; Schoppik, Nagel, & Lisberger, 2008) have presented data from recordings in the cerebellum and in the pursuit region of the frontal eye fields. Their result seem to indicate that there is remarkable little noise downstream from the cerebellum, but at the cortical level it is difficult to disambiguate the amount of motor noise from assumptions about the number of neurons involved in controlling pursuit at a particular instance of time.

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