

A comparison of pursuit eye movement and perceptual performance in speed discrimination

Karl R. Gegenfurtner

Department of Psychology, Justus-Liebig-University, Giessen, Germany



Dajun Xing

Center for Neural Science, New York University, New York, NY, USA



Brian H. Scott

Center for Neural Science, New York University, New York, NY, USA



Michael J. Hawken

Center for Neural Science, New York University, New York, NY, USA



Currently there is considerable debate as to the nature of the pathways that are responsible for the perception and motor performance. We have studied the relationship between perceived speed, which is the experiential representation of a moving stimulus, and the speed of smooth pursuit eye movements, the motor action. We determined psychophysical thresholds for detecting small perturbations in the speed of moving patterns, and then by an ideal observer analysis computed analogous "oculometric" thresholds from the eye movement traces elicited by the same stimuli on the same trials. Our results confirm those of previous studies that show a remarkable agreement between perceptual judgments for speed discrimination and the fine gradations in eye movement speed. We analyzed the initial pursuit period of long duration (1000 ms) and short (200 ms) duration perturbations. When we compared the errors for perception and pursuit on a trial-by-trial basis there was no correlation between perceptual errors and eye movement errors. The observation that both oculometric and psychometric performance were similar, with Weber fractions in the normal range, but that there is no correlation in the errors suggests that the motor system and perception share the same constraints in their analysis of motion signals, but act independently and have different noise sources. We simulated noise in two models of perceptual and eye movement performance. In the first model we postulate an initial common source for the perceptual and eye movement signals. In that case about ten times the observed noise is required to produce no correlation in trial-by-trial performance. In the second model we postulate that the perceptual signal is a combination of a reafferent eye velocity signal plus the perturbation signal while the pursuit signal is derived from the oculomotor plant plus the perturbation signal. In this model about three times the noise level in the independent signals will mask any correlation due to the common perturbation signal.

Keywords: smooth pursuit, speed perception, perception and action

Introduction

A central goal of sensation and perception is to direct our interactions with the environment. During most voluntary motor actions that are driven by sensory input we consciously experience an internal representation of the visual world. This leads to the question how faithful this internal representation is, and how precise our actions are compared to this reference.

There have been several studies comparing qualitative aspects of perceptual and motor performance in visually driven behavior (Bridgeman et al., 1979; Loomis et al., 1992; Aglioti et al., 1995; Haffenden & Goodale, 1998), in part motivated by the idea of separate systems for action and perception (Goodale & Milner, 1992). The starting point for this study was to ask whether the precise fidelity of the perceptual and motor systems (Kowler & McKee, 1987) is determined by a common signal supplied

by the same neural pathway or similar, yet independent, neural computations by separate neural ensembles. Fidelity as used here can be thought of as the number of different stimuli that lead to a different response. This is equivalent to determining when two stimuli of similar magnitude are just noticeably different (Fechner, 1860). Here, we extend the notion of "just noticeably different" to the motor system by determining when two stimuli lead to just noticeably different actions. On the same trials, we are asking the subject to make a perceptual decision. This allows a direct quantification and a valid comparison of the bandwidth of perception and action for a given task over the combined trials for any condition and on a single trial basis.

In particular, we studied the relationship between perceived speed and the speed of smooth pursuit eye movements. Both speed perception and pursuit require a velocity signal. It is well established that perception and

pursuit share some of the neural signals that are a result of objects moving across the retina (Heywood & Churcher, 1971; Yasui & Young, 1975; Steinbach, 1976; Mack et al, 1979; Dursteler et al., 1987; Dursteler & Wurtz, 1988; Newsome & Pare, 1988; Krauzlis & Stone, 1999). However, it is not clear whether the two systems are noise limited to the same extent by the sensory signals or whether there is additional noise added at stages of the two pathways after they diverge in the brain. Pursuit, for example, has many neural connections that are not part of the perceptual system such as the oculomotor plant (Robinson et al., 1986). For perception, there is strong evidence that a reafferent copy of the eye movement command is used in the computation of perceived speed (Freeman & Banks, 1998; Turano & Heidenreich, 1999, Turano & Massof, 2001), and it seems plausible to assume that a certain amount of noise is generated by the decision-making process.

If velocity perception is determined by a reafferent signal and an error signal, while pursuit is maintained by signals from the oculomotor plant and an error signal, then it is of considerable interest to determine the relationship between the various noise sources. In as much as motion and perception share common signals then it would be expected that discrimination performance of the two systems would be related. This relationship can be determined by measuring the slopes of the discriminability curves and the correlation between speed judgments made by the two systems on a trial-by-trial basis. The degree of correlation between perceptual and motor performance on a trial-by-trial basis will give a measure of the degree that signals with common noise dominate in the neural pathway. If there are completely separate systems for perception and action then the slopes of the discriminability curves would be unrelated to each other, further there would be no correlation between the two sets of measures on a trial-by-trial basis. On the other hand if there are signals with both common and separate noise sources, the degree of correlation will depend on the relative magnitude of the two sets of noise. Here we assess the expected outcome when the noise is common versus the condition when signals and their associated noise are partially independent.

Methods

Equipment

Stimuli were displayed on a Barco RGB monitor (CCID 7351B) by a Cambridge Research Systems VSG 2/3 graphics board with a refresh rate of 60 Hz non-interlaced. Each gun of the CRT was linearized by a look-up table to give 12 bit intensity resolution. A Photo Research Model 703-PC spectroradiometer was used to calibrate the display screen. The display was 17° x 12° at the viewing distance of 117 cm and had a mean

luminance of 57 cd m⁻². Each pixel subtended 1 arc min. Subjects were seated with their heads stabilized with a bite bar.

Subjects

Three of the authors (MH, BS and DX) and two naive observers (SW and LP) were subjects in this study. All procedures were approved by the NYU Human Subjects Committee.

Visual Stimuli

Small Gaussian vignettted patches of sinusoidal grating of 1 c/deg. were used as stimuli. The grating stimuli were achromatic targets modulated around a neutral gray background. The space constant of the Gaussian was 0.5° for all experiments. The contrast was 12.5%, about 10x detection threshold. A schematic diagram of the movement of a standard velocity of the perturbation motion targets is shown in Figure 1A. The onset of base speed of the target begins at t₀ then at time t₁ the stimulus speed is ramped up or down to a new speed (the perturbation speed) that lasts for either 200 ms (short duration) or 1000 ms (long duration) before it is ramped back to the base speed. The ramp, the accelerating phase of the stimulus perturbation, was 3 frames, or about 50 ms. The target appeared either on the left or the right of the screen on the horizontal midline and moved towards the center (Figure 1A) with a speed of 4 deg/s. The observer's task was to follow the target as closely as possible with eye movements and to report, at the end of each trial, whether the target appeared to move faster or slower during the perturbation. In this way we collected psychophysical data and eye movement data on the same trials.

Eye Movement Recording

The position of one eye was measured with a double-Purkinje-image infra-red eyetracker (Crane & Steele, 1978; Fourward Technologies - Generation V). Viewing was binocular with natural pupils; each eye's view was through a 45 degree angled glass plate with greater than 90% transmittance. Details of the eye movement monitoring and data collection are essentially the same as those described in Ringach et al. (1996) and Hawken & Gegenfurtner (2001).

Procedure

Each session consisted of 56 or 84 trials. Within the trials of each session we included all the perturbation speeds and both starting sides (left or right), randomly mixed. One or two sessions were run each day. Two experiments were run. In one experiment two subjects were asked to make binary judgments during each trial. Did the stimulus increase or decrease in speed during the perturbation? Subject BS ran a total of 420 trials while MH ran 672 trials for the binary judgments. In the other

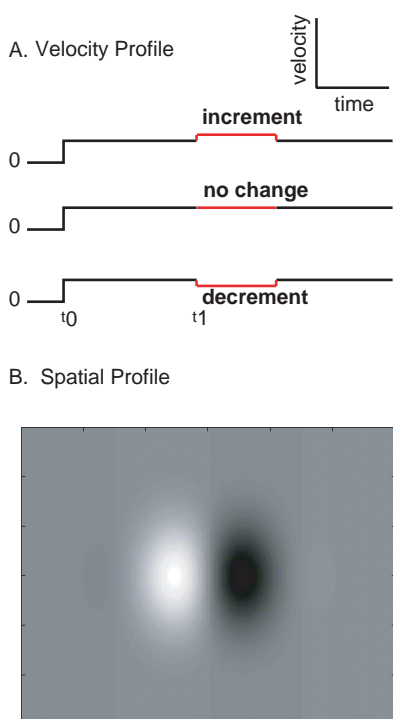


Figure 1. (A) Schematic diagram of the movement of the perturbation motion targets. At motion onset the target moves at the base speed beginning at t_0 , then at time t_1 the speed is ramped up or down to a new speed (the perturbation speed) that lasts for 1000 ms (with a base speed of 4 deg/s) before it is ramped back to the base speed. (B) Small Gaussian vignettted patches of sinusoidal grating were used as the targets. The grating stimuli were achromatic targets modulated around a neutral gray background. The space constant of the Gaussian was 0.5° for all experiments.

experiment subjects were asked to make a category judgment. They were given a 7 point rating scale with 3 slower, 3 faster and one “no change” category. They were asked to make a key press that corresponded to one of these speed ratings on each trial. Three subjects, one author MH and two naive subjects SW and LP ran on the rating experiment for the long duration perturbation. MH ran 504, LP ran 1123 and SW ran 481 trials of which 460, 580 and 410 were used for psychophysical analysis. Two subjects, both authors (MH and DX), ran trials on the rating experiment for the short perturbation. MH ran 790 and DX ran 683 of which 790 (all trials) and 570 respectively were used for psychophysics and pursuit analysis. Note that trials in which the subject gave a “no change” rating could not be used for the construction of the psychometric function. Before and after each session a calibration of the relationship between horizontal eye position and eye tracker output signal was made, which was used later in the analysis of the trials from that session.

Analysis

We recorded position traces for 500 ms prior to the onset of stimulus movement and for 500 ms after the cessation of stimulus motion. The position traces were initially filtered using a 130-point finite impulse response (FIR) filter with a cutoff at 60 Hz. The position signal was differentiated to obtain a velocity trace, which was then smoothed using the same FIR 60 Hz lowpass filter. Saccades were detected in each trace by compiling a histogram of the instantaneous velocities for each trial, and then computing the limits for detection of velocities above and below the dominant velocity distribution (Hawken & Gegenfurtner, 2001). On average, the cutoff velocity was 8.17 ± 1.45 s.d. deg/s. A period of 16 ms before and a period of 70 ms after a saccade were also excluded from further analysis, as were pursuit segments in between saccades that were shorter than 50 ms. We visually inspected all traces to confirm that the algorithm removed all saccades.

Ideal Observer Analysis

The goal of the experiments was to compare the sensitivity of the eye velocity to small changes in stimulus velocity and compare these changes to psychophysical sensitivity. Since the subject was implicitly cued as to the onset and duration of the perturbation period – it was always of the same duration and started at the same time in the trial – we assumed the subjects used all the information during this period. In order to find the period that maximized performance on the pursuit trials the receiver operating characteristic (ROC) based oculometric function was calculated for all time intervals during the perturbation period. For the long perturbation duration trials (1 sec perturbation) the maximal performance was found for intervals beginning 300 ms after the stimulus onset and durations of at least 500 ms. This time window was used for all subsequent single trial pursuit analysis of the long perturbation stimulus condition. For the short duration perturbation a duration of 200 ms was used, maximal performance was found to be at 100–200 ms after perturbation onset (Figure 6). This was the value used in subsequent single trial analysis.

Sensitivity was measured using ROC analysis. Responses from the no perturbation condition were used as the baseline and for 20 criterion speeds we constructed a standard ROC curve for each of the perturbation speeds. Then we measured the area under each of the curves which gives the proportion of “faster” responses, and from these we constructed an oculometric function. The slope of the function gives a measure of discriminability. For the psychophysical responses a standard psychometric function was constructed. The oculometric and psychometric functions were fitted with a cumulative Gaussian. Discrimination thresholds were defined as the standard deviation of the fitted Gaussian. Error estimates were calculated using the bootstrap

procedure. In the analysis of the rating scale data each rating category was assigned to one of the stimulus speeds. In this way the rating scale values were graphed as speed values in Figure 7.

Simulations

We ran computer simulations to determine the effect of uncorrelated noise on the slope of the psychometric and oculometric functions, and on the correlation level between the two types of signals. We started out with the eye speed data for the different observers and set the (hypothetical) perceived speed equal to the observed eye speed; in this case, the signals are perfectly correlated and the slopes for the psychometric and oculometric functions are equal. Then, we added uncorrelated Gaussian noise to evaluate the two models put forward in the introduction. In the first case, noise of a fixed standard deviation σ was added to the eye speed data only, resulting in a difference between perceived speed and eye speed on each trial. An oculometric function was calculated for the noisy data and the procedure was repeated 100 times with new noise samples each time. This way, we determined the average increase in threshold for a range of noise standard deviations varying from a fraction of the observed standard deviation to 10 times the observed standard deviation of the eye speeds.

Similarly, the average correlations between these two simulated signals (eye speed and observed speed) were calculated for each noise standard deviation.

For the second model, uncorrelated Gaussian noise of equal magnitude was added to both eye speed and perceived speed. Again, both the correlation level and the slope of the psychometric and oculometric functions change, but in this case the relative slopes remain constant.

Results

Initially, we developed a method to obtain measures of pursuit performance that were comparable to perceptual performance. In order to compare neural and perceptual performance a number of studies have used ROC analysis to obtain neurometric functions (Parker & Newsome, 1998) that allow a direct comparison to psychometric functions. Analogously, in order to measure pursuit performance an oculometric function (Kowler & McKee, 1987; Beutter & Stone, 1998) was constructed from ROC analysis of pursuit velocity traces during the perturbation period. In Figure 2A the eye speed was averaged over all the trials for each stimulus speed and the resulting traces show that there is a clear separation of average eye speed at all target speeds, but the important question remains whether the differences in eye speed are

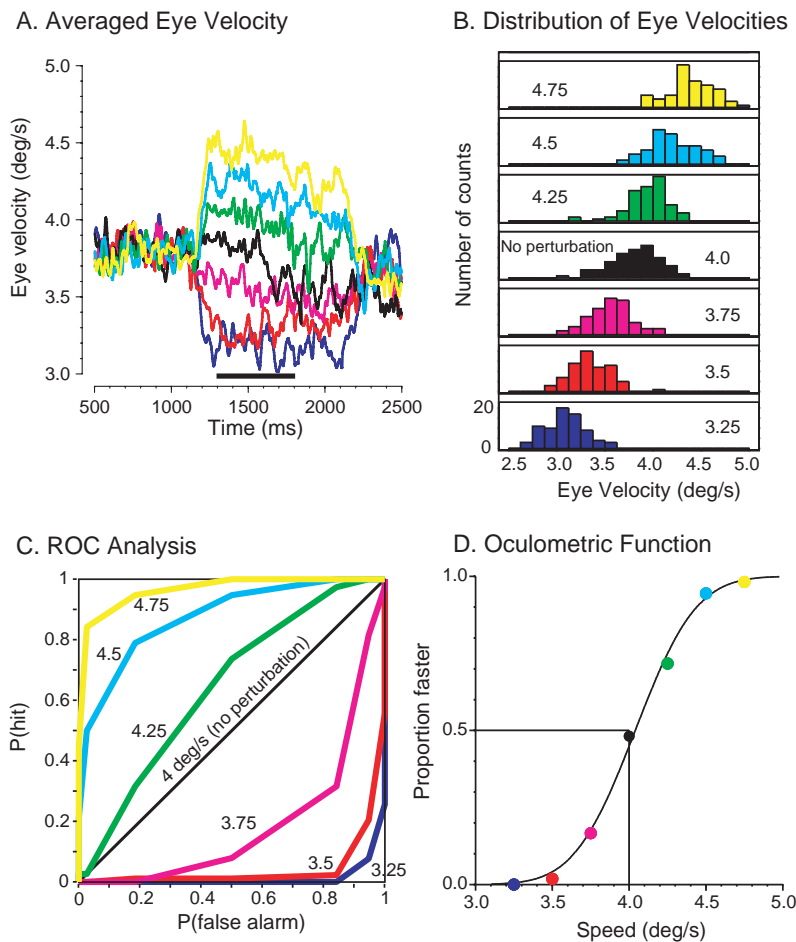


Figure 2. (A) Average eye velocity across all trials for observer MH for stimuli moving at a base speed of 4 deg/s. Different perturbation speeds are indicated by different colors. The black horizontal bar indicates the time window used for the ROC-analysis. (B) Distributions of eye velocities from single trials. The perturbation period target velocity is shown to the left in the first three panels and to the right in the remaining four panels. (C) Responses from the no perturbation condition were used as the baseline and for 20 criterion speeds we constructed a standard ROC curve for each of the perturbation speeds. Again the perturbation speeds are color-coded and labeled as in B. (D) The area under each of the curves gives the proportion of “correct” responses. Each colored point matches the perturbation speed shown in B and C. From the area we constructed an oculometric function. The slope of the function measures discriminability.

as reliable as the differences in perceptual judgments.

To answer this question, we examined the eye velocity during a 500 ms interval starting 300 ms after the start of the perturbation and compiled the resulting speed estimates from individual trials into a histogram (Figure 2B). For each decrement in perturbation speed the resulting histograms are displaced to lower speeds while for each increment the resulting histograms are displaced towards higher speeds, although there is considerable overlap between neighboring histograms. The receiver operating characteristic (ROC) curves were generated by comparing the overlap between the no perturbation condition with each perturbation condition (Figure 2C). The area under each ROC gives the percentages of trials where the eye movements indicated "faster". The percentages were then used to construct the oculometric function (Figure 2D). To obtain the perceptual performance we constructed psychometric functions where the percentage of observed "faster" responses is plotted as a function of perturbation speed. Each set of oculometric and psychometric data was fit with a cumulative Gaussian function. Note that this method fixes the 50%-point for pursuit trials at the base speed of 4 deg/s, while the psychometric function is allowed to vary.

Figure 3 shows the resulting psychometric and oculometric functions for all four observers. Discrimination performance, which indicates the reliability with which each observer can detect the change in speed from the base speed of 4 deg/s, is given by the

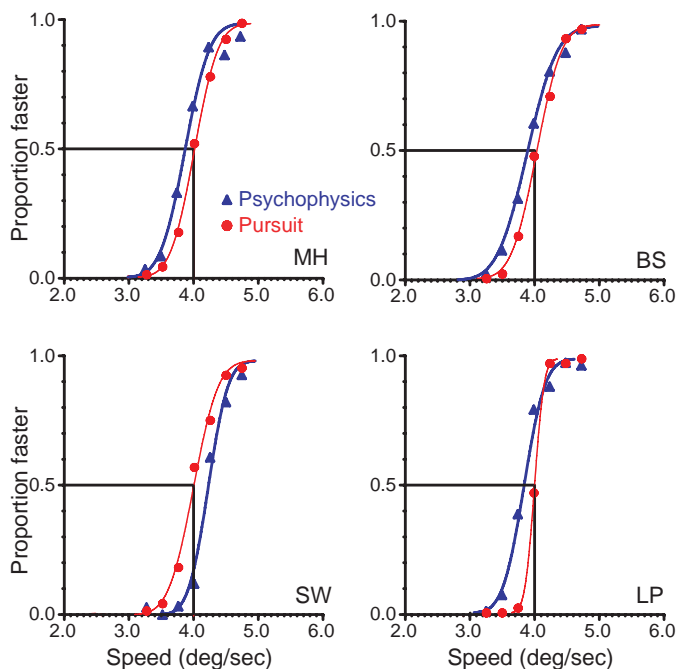


Figure 3. Psychometric (triangles) and oculometric (circles) functions for observers MH, BS, SW, and LP. These were obtained for the long duration perturbation condition.

slope of the psychometric and oculometric functions. Although the perturbations are expressed as changes from the base speed of 4 deg/s this only applies to the stimulus or the observer assuming stationary eyes. Clearly, in the case of a perturbation while the eye is in motion the resulting physical speed change on the retina is dynamically related to the eye speed on a trial-by-trial basis. Nonetheless, the speed change is the same for both perception and pursuit.

Figure 4 compares the discrimination performance for all four observers. For observer MH the slopes of oculometric and psychometric functions are remarkably similar. For observer BS, the psychometric function is slightly shallower, and for observer SW the oculometric function is slightly steeper. None of these differences is statistically significant. The only significant difference we found was the steeper oculometric function of observer LP. LP's eye movement traces were the smoothest of the four observers.

The resulting thresholds for speed discrimination are around 0.28 deg/s, resulting in Weber fractions of about 7%. This is slightly higher than usually achieved for speed discrimination under optimal viewing conditions when the eyes are stationary. Since the eyes are moving together with the stimulus at a high gain, the retinal slip is reduced from 4 deg/s to below 0.5 deg/s.

These results show that the fidelity of the motor system can perfectly match that of the sensory system. An earlier study comparing psychometric and oculometric speed discrimination thresholds had obtained similar results (Kowler & McKee, 1987), but in their experiments different sets of trials were chosen for perceptual and oculometric thresholds. Most importantly, in Kowler and McKee's experiment the eyes were stationary during the perceptual judgments, which results in a different retinal

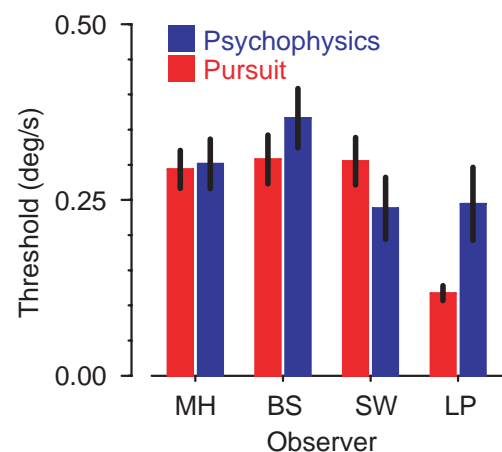


Figure 4. A comparison of discrimination thresholds obtained from the oculometric and psychometric functions for all four observers. The thresholds (slopes of the functions) for pursuit and velocity discrimination are different only for observer LP, who shows superior pursuit performance. The error bars are ± 1 S.D.

stimulus under both conditions. In another experiment, directional sensitivity of smooth eye movements was compared to perceptual judgments (Beutter & Stone, 1998). In these experiments, a qualitative agreement was found between perception and eye movements, but the slopes of the underlying sets of functions differed widely.

Interval Analysis

The time interval used for the pursuit analysis was chosen after comparison of thresholds for different analysis intervals and starting points. The threshold for time intervals of different lengths, centered at different starting points after perturbation onset, shows that the choice of center point has little effect during the interval from 300 ms and 900 ms after perturbation onset (Figure 5). The discrimination thresholds increase when analysis intervals of 120 ms and 250 ms are used. Thus our choice of an interval of 500 ms centered at a time 300 ms after the onset of pursuit gives optimal threshold estimates for all observers. Nonetheless, the analysis is robust over a range of intervals and onset times (Figure 5).

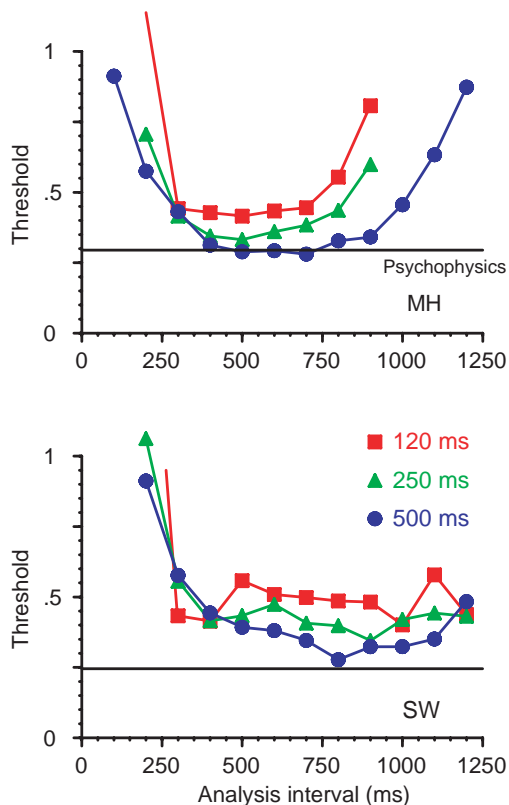


Figure 5. Oculometric thresholds as a function of center of analysis interval since perturbation onset. Three different interval lengths were used, 120 ms (squares), 250 ms (triangles), and 500 ms (circles). Psychophysical thresholds are shown by the solid horizontal lines. Data from two observers (MH and SW) are shown.

Short Perturbation Interval

In the first experiments perturbation duration was 1 sec. It is well established that both an initial motion signal and an internal signal contribute to the maintenance of pursuit eye velocity in the steady state (Pola & Wyatt, 1989). Since we do not know what interval is used to make a perceptual decision we need to determine the effects of different analysis intervals to cover as many of the possible intervals to match with the perceptual decision (Figure 5). We will show later that for the long duration condition, where an internal signal is likely to be used to drive pursuit during the analysis interval, the internal signal derived from the target velocity could not have a significant amount of noise added to it after the sensory motion analysis. Otherwise, the slope of the oculometric function would be considerably shallower and discrimination performance would not match psychophysical performance. A direct way to influence the observer's choice of analysis interval was to use short duration perturbations, where the dominant signal for the change in perceived speed and for the motion signal to drive the change in pursuit speed must come from the speed transients. This would affect mainly the initiation phase of smooth pursuit, which is more likely to be dominated by a sensory motion signal rather than by internal commands.

For two subjects we made the speed perturbation 200 ms in duration. This is long enough to obtain a strongly differential pursuit signal to the perturbation speeds but remain within the usual period whereby the initiation and transition phases of pursuit dominate the response (Krauzlis, 1994). This also makes sure that the same, relatively short interval is used for making the psychophysical judgment.

Under these conditions the thresholds (Figure 6) of the oculometric and psychometric functions are at about twice the level as before. However, the thresholds are still

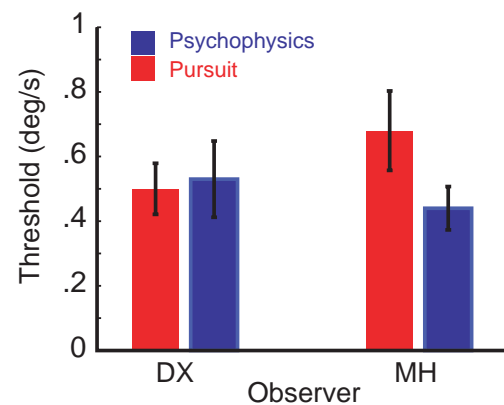


Figure 6. Comparison of oculometric and psychometric performance for short perturbation periods (200 ms) for two observers DX and MH. Thresholds are similar for psychophysical judgments and oculometric performance. Error bars are ± 1 SD.

approximately equal. This makes it quite likely that the same aspects of the stimulus were driving perception and pursuit under both conditions.

Correlation Between Pursuit Speed and Perceptual Speed

At first sight, the results seem to indicate that perception and action may be controlled by one and the same neural computation. However, a perfect agreement in absolute thresholds is difficult to reconcile with a naive model of perception and motor control, where initially the visual system analyzes the speed of moving stimuli, and that speed estimate is then supplied to the motor system to control behavior. It has to be kept in mind that neural computations at all levels are prone to noise.

Our results also rule out the possibility that simple measurement noise of the eye movements may give rise to poorer apparent performance of the oculomotor response. This was suggested as a possible cause of the lack of quantitative correspondence in directional discrimination between perceptual and pursuit judgments (Beutter & Stone, 1998). The results of observer LP clearly place an upper limit on the amount of measurement noise at about 0.11 deg/s. We also performed measurements with a stationary or moving model eye (Fourward Technologies). The output of the stationary model eye had a standard deviation of about 1 mV. With a range of 10 V and a visual field of 20 deg, this corresponds to a standard deviation of slightly less than 10 arc seconds. When the model eye moved at the equivalent speed of 4 deg/s, the standard error of the unfiltered velocity signal over a 500 ms interval was about 0.05 deg/s. This is smaller by a factor of 5 to 10 than any of the other noise sources considered here.

Another source of noise, motor noise from the oculomotor plant, might manifest itself as a reduction in pursuit fidelity compared to the perceptual fidelity (Beutter & Stone, 1998). In our experiments this does not seem to be the case, suggesting that the magnitude of the noise common to both processes, presumably introduced by the analysis of visual motion, is so large that the separate noise sources are negligible. Alternatively, the amount of noise added separately to the two systems could, incidentally or not, be of similar magnitude.

Absolute comparisons between perception and action, such as above, are potentially prone to attentional modulation. Observers might allocate more neuronal resources to one task or the other, thereby affecting absolute levels of performance (Kowler, 1990). This may have caused the small differences between perception and action observed in observers BS and SW. A more direct way to investigate the relationship between the circuits driving perception and action is to look at the correlation between the perceptual and pursuit errors made on individual trials. If faster perceived speed goes along with

faster eye movements on individual trials, this would support the notion that both subsystems are driven by the same circuitry and signals. A lack of correlation would suggest that independent subsystems are responsible for perception and action. To facilitate such a comparison, we ran a sets of trials where the observers gave a category rating (1 = much slower, 7 = much faster) about the perceived speed of the stimuli, while also tracking the target with pursuit eye movements (see methods).

Initially we describe the results for the long perturbation period. The category rating was correlated with the speed of the eyes on each trial (Figure 7A). For subject MH the observed correlation is high ($\rho = 0.70$, $p < 0.0001$), caused by the fact that the eye speed and the category rating correlate highly with the physical speed of

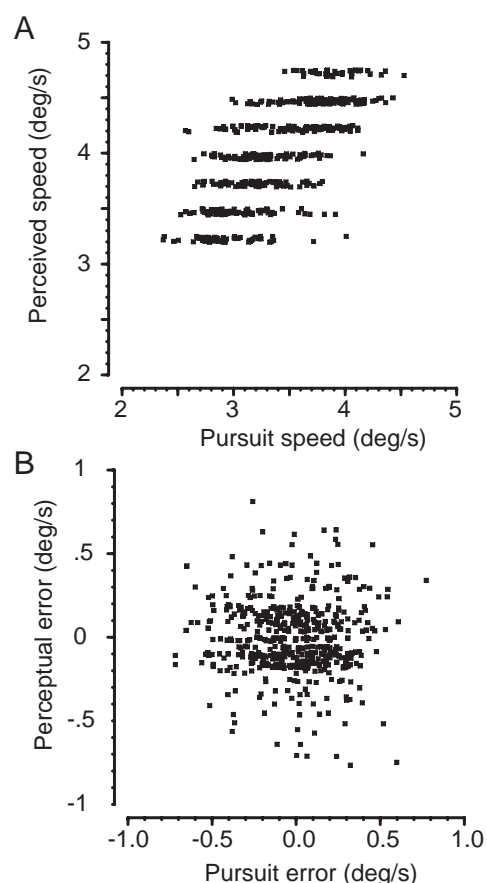


Figure 7. (A) Correlation between pursuit speed and perceived speed on 500 individual trials. Perceived speed was based on a 7-point category rating scale, which was translated into the seven absolute speeds used here. (B) Correlation between pursuit errors and perceptual errors on the same 500 trials. The x-axis (pursuit error) plots the difference between pursuit speed and $0.522 + 0.7227 v$, the y-axis (perceptual error) plots the difference between rated speed and $0.852 + 0.7872 v$, where v is the physical speed of the stimulus. Since the error is the difference between the rating scale value reported by the subject and the regression above, it is a continuous, not discrete, value.

the stimulus ($\rho = 0.82$ and $\rho = 0.87$, respectively, $p < 0.0001$). But when the correlation with physical speed is partialled out, which is equivalent to looking at the error signals, the correlation completely disappears (Figure 7B, $\rho = -0.038$, $p > 0.1$). For the other two observers tested in the rating task (SW and LP), the partial correlation coefficients were also not different from 0 ($\rho = -0.002$ and $\rho = 0.01$, respectively). Additionally, we compared the binary faster/slower perceptual ratings with eye speed on a trial-by-trial basis for the experiments described in Figure 3. There was no correlation between the binary faster/slower ratings and eye speed, once stimulus speed was partialled out. Correlation coefficients were -0.06 and -0.05 for observer BS and MH, respectively, and were not significant ($p > 0.1$). The large number of trials would have enabled us to expose significant correlations as low as 0.1 (Cohen, 1988). This means, if there are both common and separate sources of noise, the separate sources would need to have a variance at least 10 times as high as for the common source, and, since the performance for perception and pursuit are very closely matched, and the separate sources would need to be equal in magnitude.

We did the same correlation analysis for the two observers who were tested with the short perturbation interval. In these experiments categorical judgments were made on the same rating scale as described for the long perturbation interval experiments. In agreement with the results above there was no significant correlation for the error signals (DX $\rho = 0.04$, $p > .1$; MH $\rho = 0.002$, $p > .4$)

This lack of correlation between perceptual and pursuit error held for any time interval during the perturbation period, as is shown in Figure 8 for two representative observers. The large positive correlation between eye speed and psychophysical judgments gradually evolves during the first 500 ms after perturbation onset (Figure 8, squares). At the same time, the correlation with physical perturbation speed partialled out, the error (Figure 8, triangles), remains close to 0 over the whole time period.

Noise Added to the Oculometric and Psychometric Functions.

We simulated two models that combine signals with varying degrees of noise. When internal noise is combined with a signal it reduces the signal effectiveness in a discrimination task. If we consider typical psychometric and oculometric functions for a discrimination task as in Figure 3, then combining additive noise at each speed will have the effect of making the discrimination functions shallower, hence altering the thresholds. In the first simulation we assume that there are two correlated signals that have the same discrimination thresholds. We asked how much noise needs to be combined with either the perceptual or the

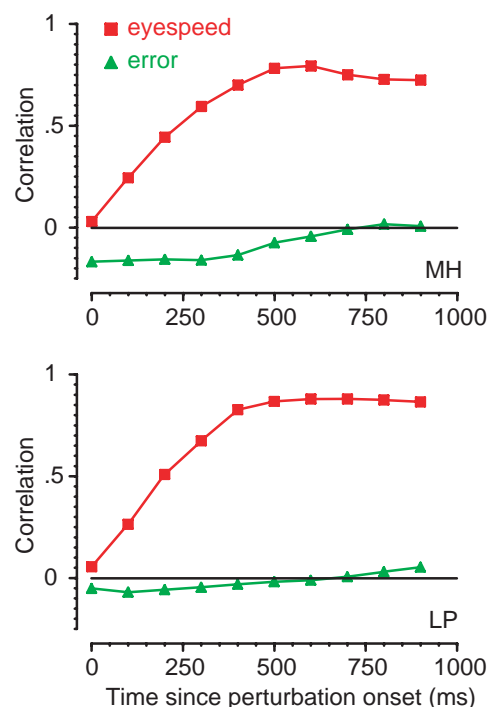


Figure 8. Time course for the correlation between eye speed and perceptual judgment (squares) and the partial correlation between the two, with physical perturbation speed partialled out (triangles). Data for two observers (MH and LP) are shown.

oculomotor signals to reduce the correlation to less than 0.1, a value of correlation that is at the limit of detection using our methods. Initially we assume that the two systems, oculomotor and perceptual, use the same signals. Thus they are perfectly correlated and the internal noise that limits performance is also common. In practice this is likely to be the neural noise introduced in the early stages of the visual pathway.

Figure 9A (squares) shows the effect of adding noise on the correlation between eye speed and perceived speed for the situation where the signals are initially correlated. If the noise is added only to the eye movement signal and this noise has a standard deviation of 10 times the value of the standard deviation of the noise common to the oculomotor and perceptual systems, then the (partial) correlation between eye speed and perceived speed will be reduced to a value of about 0.1. This value, 0.1, is around the limit of the correlation that we could detect in the data.

However, as can be seen in Figure 9B (squares), this added noise has a dramatic effect on the slope of the oculometric function. Adding noise at 10 times the standard deviation of the common noise will decrease the slope by a factor of 10. In fact, just adding noise at the level of the common noise halves the slope of the oculometric function, while the correlation between the two signals would still be relatively high (> 0.5). Neither the slopes of the oculometric nor the psychometric

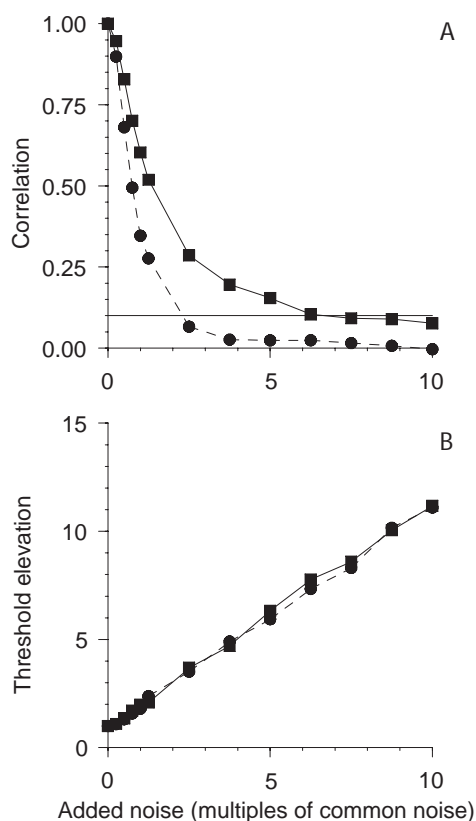


Figure 9. The effects of adding simulated noise to the oculometric function for both models described in the text. (A). Additional noise is added as multiples of the common noise to the oculometric function and the correlation between the two signals is reduced. When noise is added to the eye signal only, it is not until the added noise is 10 times the common noise that the correlation reaches values of around 0.1 or less (filled squares). If the noise is added to both eye and perceptual signals, only 2-3 times the amount of common noise is needed to reduce the correlation (filled circles) (B) The elevation in discrimination threshold as noise is added to the oculometric function. At the levels of correlation that we could no longer detect (0.1) the threshold elevation is greater than five times baseline.

functions for any of the observers are uncharacteristically shallow.

This makes it very implausible that the lack of correlation in our data was due to the addition of either oculomotor or decision noise to a common signal. However, it does not exclude the possibility that uncorrelated noise is added to both variables, pursuit and perception, after an initial common processing stage. These uncorrelated noise sources would have to be of approximately equal magnitude. Furthermore, simulations showed that the standard deviation of the uncorrelated noise would have to be three times larger than the standard deviation of the common noise. This ratio of common versus uncorrelated noise leads to a

reduction of the correlation between pursuit and perception to a level of 0.1, which is the empirically observed value. This is shown by the filled circles in Figure 9A. Adding uncorrelated noise to a common variable (or two initially perfectly correlated variables) rapidly leads to a decrease in the correlation.

The question then arises, where do the independent signals arise. We proposed one such model in the introduction. In this model the perceptual speed signal arises from a combination of a reafferent signal that is the internal representation of eye speed plus the error signal due to the stimulus perturbation. The pursuit signal is due to the signals generated in the oculomotor plant plus the error signal due to the stimulus perturbation. Thus the only common component is the error signal due to the perturbation. In this model the reafferent and oculomotor signals have independent noise and the perturbation signal is common to both. Then, under the assumptions of the simulations the independent signals have more than three times the noise than the common signal.

Discussion

The results show that on the same set of trials the fidelity of the motor system can match perceptual fidelity. For three of the four subjects there was no significant difference between the thresholds for perceptual discrimination of small changes in speed and the oculometric thresholds. For one of the two naive subjects, LP, the oculometric thresholds were about half of the perceptual discrimination thresholds (Figure 4). However this difference in LP's thresholds is not due to an elevated perceptual discrimination threshold, which for LP is about 0.25 deg/s, almost the same as found for the other three subjects. Rather the oculometric threshold appears to be much lower than was found for the other subjects. On inspection of LP's eye movement traces it was soon noticed that there were very few saccades in the pursuit and that pursuit gain appeared to be close to 1. Even though oculometric thresholds were less noise limited than the perceptual thresholds there was no detectable correlation on a trial-by-trial basis for subject LP.

There was no correlation greater than 0.1 between eye speed and the perceptual speed rating for any of the subjects. This indicates that the signals are statistically independent. The simulations based on adding noise to one of the signals adds support to our conclusion that the signals driving perception and pursuit are due to independent processes (Figure 9). If the signals were from a common source but masked by noise in one or both of the processes then the necessary amount of independent noise would have resulted in extremely shallow slopes of the psychometric or oculometric functions. Shallow slopes were not observed in the data.

Of course, smooth pursuit and perceived speed would be independent if completely different motion signals were used for both tasks. Potential signals are the retinal slip of the stimulus with respect to the eye, the speed of the eye itself, the motor signals, any combination of these, and the acceleration of the stimulus. If an acceleration signal was used for making the perceptual judgments we might expect the performance for the long and short interval perturbations to be the same, as the initial acceleration is the same in the two conditions. We found that thresholds were higher for the shorter interval. Other studies have also concluded that acceleration is unlikely to play a major role in perceptual speed judgments (Kowler and McKee, 1987). In addition, as a more direct test we analyzed our short perturbation data for correlation between the relative eye speed signal and the perceptual judgment. The relative signal was taken as the difference in response for 200 ms just before the perturbation and the response during the perturbation. For our short duration data this is close to probing a contribution from acceleration. There was no correlation above 0.1.

Another source of signal independence are the time intervals. Different time intervals of the signals could be used, which would also cause independence. In our experiments and analyses, we carefully tried to exclude possible time interval effects. For the long perturbation interval, we calculated oculometric functions and correlations for a large range of different time intervals, covering all reasonable choices. For none of the intervals, did we observe a correlation. For the short perturbation trials, the only signals really available are the velocity changes at the beginning and at the end of the perturbation period. Since we obtained basically the same results for the long and short perturbations, it is very likely that this aspect of the stimulus was used both in pursuit and perception.

What would be the outcome of our analysis if there was an internal signal that was driving pursuit and perception prior to the perturbation? The total pursuit eye movement signal is due to the signal derived from retinal slip provided by the perturbation added to the internal pursuit signal. The perceptual decision is based on the comparison between an internal eye speed signal alone and the internal signal plus the motion signal from the perturbation (Freeman and Banks, 1998; Turano and Massof, 2001). As discussed earlier, in this case we have a model that has two independent internal signals (one for perception and one for pursuit) plus noise and then a common perturbation signal plus noise that is added to the internal signals. In this case the perturbation signal is common with common noise. In this scenario we postulate that the independent noise from the internal signals masks the noise from the perturbation signal.

As we have shown in the simulations the amount of noise that is required to mask the common signal is about three times the noise of the common signal. The first

conclusion from this analysis is that if the signals driving pursuit are an internal signal plus the perturbation signal then the internal signal must be independent from the reafferent signal that is driving perception. Second, that even though the reafferent signal and the oculomotor signal are independent in this model the noise in the two is comparable. If the standard deviation of the noise in the two independent systems differed by even a factor of two then we would predict that the thresholds for perception and pursuit would differ by an equivalent factor.

Comparison with other Studies

In their pioneering study of the comparison of speed discrimination and pursuit eye movement performance Kowler and McKee (1987) found that performance was similar for perception and for the motor task. Our results confirm Kowler and McKee's findings that speed discrimination thresholds for perceptual judgments and for the pursuit eye movements can be the same. However their experiments were conducted with different sets of trials for the perceptual judgments and for measurement of pursuit performance, therefore they could not compare performance on a trial-by-trial basis. Kowler and McKee argued that dividing resources degrades performance and that thresholds for pursuit and perception are optimal if the observer is only required to make a single judgment. In our experiments the observers were asked to make judgments and move their eyes on the same set of trials. We obtained similar performance when the two tasks were performed simultaneously. Using the same trials for perceptual judgments and pursuit allowed a comparison of performance on a trial-by-trial basis.

Beutter and Stone (2000) made a comparison of the perceived direction of motion and pursuit direction for a parallelogram moving behind a pair of apertures. The retinal motion of the visible portions of the parallelogram is always vertical yet observers tend to report the movement biased toward the global motion rather than the motion of the individual elements. While the psychometric and oculometric functions were similar in form it was found that the slopes of the oculometric functions were generally shallower than the corresponding psychometric functions. A similar finding was reported in an earlier study (Beutter & Stone, 1998). They attributed the difference in slopes, at least in part, to noise in the eye movement recording. To the extent that there are differences in the slopes of the functions that are not due to recording noise it means that in some circumstances the independent signal sources can have unequal noise sources. In our experiments we found that the slopes of the oculometric and psychometric functions were very similar and we do not think that the slopes of the oculometric functions were limited by measurement noise.

Neural Mechanisms

Taken alone the close correspondence between the oculometric and psychometric functions would imply that the two systems share common neural circuitry. However, perceptual and motor performance were uncorrelated on a trial-by-trial basis (Figure 7) which argues strongly against circuitry with a common but performance limiting source of noise (Figure 9). If we consider the model that ascribes the perceptual performance to a reafferent signal plus the error signal and the pursuit performance to a signal from the oculomotor plant plus an error signal then deciding which neural pathways are active requires a more complex analysis. Or does this mean that different neural output pathways (the dorsal and ventral streams) with a common motion input (from MT) are involved (Goodale & Milner, 1992)? While two independent pathways can certainly account for the data, it is instructive to look at the properties of single neurons for a more parsimonious explanation. If pools of neurons in the extrastriate visual motion areas, MT or MST, are responsible for providing signals about the direction and speed of target motion to perception and pursuit (Dürsteler et al., 1987; Dürsteler & Wurtz, 1988; Newsome & Pare, 1988; Newsome et al., 1995, Born et al., 2000), then we need to consider the likely correlation between neurons in the pool. It has been shown that the average correlation between adjacent neurons in the same column of area MT is rather low (mean = 0.143) (Newsome et al., 1995).

Conclusions

In this study we compared the performance of the pursuit eye movement system with the perceptual system on a speed perturbation task. Thresholds for judging increments or decrements in speed were remarkably similar for the two systems. However, a comparison of the errors for pursuit and speed judgments showed no correlation between the two processes. Based on these results we conclude that under the conditions of these experiments the dominant neural signals driving perception and pursuit are independent.

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