

Perceptual and oculomotor evidence of limitations on processing accelerating motion

Scott N. J. Watamaniuk

Wright State University, Department of Psychology,
Dayton, OH, USA



Stephen J. Heinen

The Smith-Kettlewell Eye Research Institute, San
Francisco, CA, USA



Psychophysical studies have demonstrated that humans are less sensitive to image acceleration than to image speed (e.g., [Gottsdanker, 1956](#); [Werkhoven, Snippe, & Toet, 1992](#)). Because there is evidence that a common motion-processing stage subserves perception and pursuit (e.g., [Watamaniuk & Heinen, 1999](#)), either pursuit should be similarly impaired in discriminating acceleration or it must receive input from a system different from the one that processes visual motion for perception. We assessed the sensitivity of pursuit to acceleration or speed, and compared the results with those obtained in perceptual experiments done with similar stimuli and tasks. Specifically, observers pursued or made psychophysical judgments of targets that moved at randomly selected base speeds and subsequent accelerations. Oculomotor and psychophysical discrimination were compared by analyzing performance for the entire stimulus set sorted by either target acceleration or speed. Thresholds for pursuit and perception were higher for target acceleration than speed, further evidence that a common motion-processing stage limits the performance of both systems.

Keywords: smooth pursuit, eye movements, velocity, acceleration, human

Introduction

To understand the link between perception and smooth pursuit, it is important to know the extent that visual motion processing is shared by these systems. Psychophysical studies have suggested that humans are more sensitive to speed than acceleration (e.g., [Gottsdanker, 1956](#); [Rosenbaum, 1975](#); [Schmerler, 1976](#); [Todd, 1981](#); [Calderone & Kaiser, 1989](#); [Snowden & Braddick, 1991](#); [Werkhoven, Snippe, & Toet, 1992](#)). For example, a 5% difference in the speed of two targets can be detected reliably ([McKee, 1981](#); [Orban, DeWolf, & Maes, 1984](#)); yet, an approximate 30% difference is necessary to detect an acceleration produced by an instantaneous change of speed imposed upon a single target (e.g., [Gottsdanker, 1956](#)). Detection of acceleration when a target changes speed gradually is even poorer (e.g., [Schmerler, 1976](#); [Todd, 1981](#); [Calderone & Kaiser, 1989](#); [Werkhoven et al., 1992](#)). Furthermore, individual neurons in the middle temporal area (MT), a key structure in the cortical motion-processing pathway, do not appear to exhibit acceleration tuning, although an acceleration signal can be mathematically derived from the population response of neurons here ([Lisberger & Movshon, 1999](#)).

High sensitivity of the pursuit system to image acceleration would be in stark contrast to the poor acceleration sensitivity of the perceptual system, and would also be incompatible with previous work indicating that a common motion-processing stage limits pursuit and perception ([Heinen & Watamaniuk, 1998](#), [Beutter &](#)

[Stone, 1998](#); [Watamaniuk & Heinen, 1999](#)). There is evidence that the pursuit system can discriminate acceleration in that the latency of pursuit initiation is different for targets that move with different accelerations ([Krauzlis & Lisberger, 1994](#)). However, this study did not address sensitivity of smooth pursuit to target acceleration after the eyes began to move, important information for understanding how well the pursuit system can follow accelerating targets.

This manuscript describes experiments designed to test the acceleration, as well as speed discrimination ability of the pursuit system and compare it with that of the perceptual system to determine if a common motion-processing stage limits both. The pursuit system was tested by measuring eye acceleration within the second epoch of the open-loop period for pursuit of targets that moved with different base speeds and different subsequent accelerations. The rationale for using eye acceleration is that for accurate pursuit of an accelerating target, the pursuit system must assess and match target acceleration; thus eye acceleration should change systematically with target acceleration. Perceptual discrimination was assessed by having observers make psychophysical judgments of stimuli that moved with the same speeds and accelerations as the pursuit targets. We found acceleration discrimination thresholds obtained in both the pursuit and perceptual tasks to be higher than the speed discrimination thresholds computed from the same data. The results suggest that pursuit and perception of accelerating targets are similar, adding to the growing body of evidence that a common motion-

processing stage limits these two systems. Portions of this work have been presented previously in abstract form.

Method

Subjects

The two authors and two observers naive to the design and purpose of the study served as subjects. During eye movement recording, optics placed between the observers' eyes and the display monitor corrected for individual refractive error. Both of the naive subjects had previous experience with smooth pursuit in the laboratory, but neither had been involved in speed or acceleration discrimination experiments and neither had experience with perceptual motion experiments.

Stimuli

Stimuli were either a single bright dot (0.05-deg diameter) moving horizontally (left or right) against a dark background, or a horizontally moving random-dot cinematogram (RDC) with component dots displayed at a density of 2.0 dots/deg². Dots were presented either on a Tektronix 604 CRT (P4 phosphor) at a rate of 50 Hz (spatial resolution: 204.8 locations/deg) and viewed through a 10-by-10-deg aperture (pursuit data for subject SW, and psychophysics for all of the subjects) or on a 17-in. high-resolution computer monitor (1.76 min arc/pixel) at a rate of 70 Hz and viewed through a 20-deg diameter aperture (open-loop data for subjects JB, YK, and SH). Dot luminance was measured using a Minolta 1° hand-held luminance meter by configuring the dots in a matrix of 16 by 16 dots with the inter-dot spacing being 0.076 deg so that adjacent dots did not overlap. The space-averaged luminance of this dot configuration was 5.4 cd/m². The background luminance was 0.05 cd/m², and all stimuli were viewed from a distance of 57 cm. Luminance values on both the computer monitor and CRT were set to be equal. When the stimulus was an RDC, all dots moved in the same direction and at the same speed and virtually "wrapped around" when a border was reached. All stimuli started at an initial speed between 0 and 8 deg/s and accelerated at a constant rate, ranging from 0-30 deg/s². To put these accelerations into context, from a viewing distance of 50 ft, an automobile that accelerates at a constant rate from 0 to 60 mph in 6 s would produce retinal-image acceleration of about 17 deg/s².

When measuring eye movements, the duration of the stimulus was set to 600 ms, so if the target were a single spot, it would traverse the screen without reaching the edge for all speed and acceleration values. This also required that the initial starting position of pursuit had to be on the left edge of the display for rightward trials and on the right edge of the display for leftward trials. This

meant that target direction was completely predictable on each trial. Although pursuit direction was not the variable of interest, fixation duration was randomized to minimize anticipatory pursuit. When measuring perceptual performance, stimulus duration was set to 140 ms to equate the amount of motion information available to the visual motion system with that available to the pursuit system during the open-loop period of pursuit initiation where our measurements were made (Watamaniuk & Heinen, 1999). The eye movement measures are described in greater detail below.

Procedure

Each block of trials consisted of equal numbers of leftward and rightward stimuli presented in random order. If the target was a single spot, the fixation point appeared at either the left or right edge of the display. The observer fixated the spot, and then pushed a button to initiate an additional random fixation period (200–600 ms), following which the spot began to move. Target motion was always directed opposite the position of the fixation point. At the end of a trial, the observer pushed a button, which, during eye movement experiments, signaled to the computer that the trial had ended. If the target was a field of dots, the same procedure applied except the fixation point appeared in the center of the screen and then disappeared simultaneously with the appearance of the RDC. Perceptual judgments were collected in separate sessions where the stimuli moved in the same fashion as in the eye movement sessions. However, at the end of each psychophysical trial, the observer pushed one of two buttons to indicate whether the stimulus accelerated in that trial more or less than the average acceleration of the stimulus set in accordance with the method of single stimuli (e.g., McKee, 1981; Bravo & Watamaniuk, 1995). In a separate control experiment, observers judged the speed of the accelerating targets.

Eye movement measurement and analysis

Observers viewed the display monocularly while the other eye was patched. Horizontal and vertical eye position was recorded using a Generation V dual-Purkinje-image eyetracker and sampled by computer at 500 Hz. In tests of our instrument with an artificial eye, the overall noise of the system was less than 1 min arc. Eye position was calibrated to tracker output before each session by having the subject fixate several times at each of four 5-deg-eccentric cardinal positions and at the center while offsets and gains were adjusted. Eye velocity signals were obtained by digital differentiation of eye position signals and filtered to reduce 60-Hz noise (2 pole Butterworth filter, cutoff = 50 Hz). Eye acceleration records were obtained by a second differentiation. Saccades were removed from the velocity records by using an eye acceleration threshold (Heinen & Watamaniuk,

1998; Watamaniuk & Heinen, 1999). The records were filtered again with a single pole Butterworth filter (cutoff = 25 Hz) to smooth corners caused by the desaccading algorithm (Heinen & Watamaniuk, 1998; Watamaniuk & Heinen, 1999). Records contaminated by eye blinks were not included in the analyses. Trials in which anticipatory eye movements were present were also excluded. The criterion for exclusion was that eye velocity had to exceed 2 deg/s at the time the target began to move.

Pursuit latency was determined from the eye velocity traces by visual inspection. Average eye acceleration was computed over the second interval of the open loop period (40–140 ms after pursuit onset), which in the past has been used to assess how visual motion-processing guides smooth pursuit eye movements (e.g., Lisberger & Westbrook, 1985; Tychsen & Lisberger, 1986; Heinen & Watamaniuk, 1998). Only horizontal eye velocity and acceleration were used in the analyses.

Results

Open-Loop Eye Acceleration

In the first experiment, we tested the sensitivity of the pursuit system during the open-loop period to target acceleration. In each block of trials, observers tracked targets that moved either left or right with a base speed chosen randomly from a set of five (4, 5, 6, 7, or 8 deg/s) and an acceleration chosen randomly from a set of six (0, 4, 8, 12, 16, or 30 deg/s²). Each block of trials presented all possible stimulus combinations of base speeds and accelerations. Two blocks of trials (6 trials per stimulus per block) were run for each of the single spot and random-dot field conditions. (Subject SW did not perform this experiment with an acceleration of 30 deg/s².) To assess the pursuit response to target speed and acceleration, we sorted the same set of trials across either initial speed or acceleration respectively (see Figure 1). This was done separately for data gathered using the spot and the RDC stimuli.

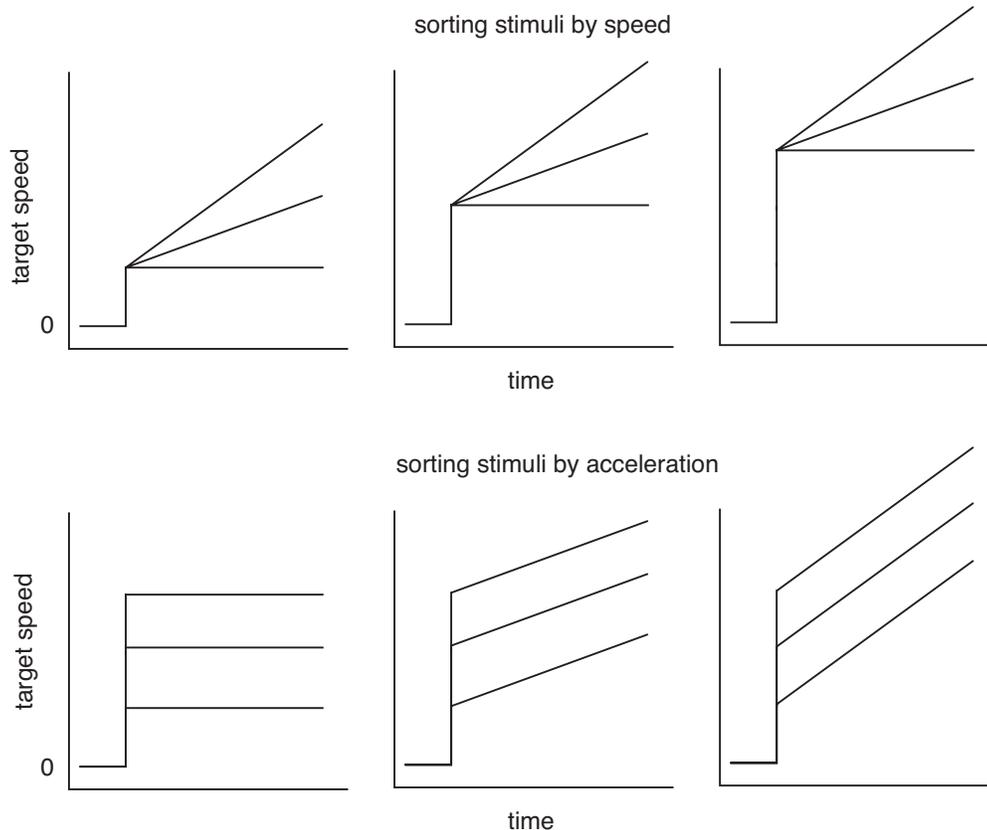


Figure 1. Schematic representations of stimulus motion parameters and how the data were sorted for analysis. Each of the top panels represents stimuli with the same initial speed, but different accelerations. When assessing speed discrimination, data obtained using the stimulus configurations in each panel were grouped together, and compared across base speed. Each of the bottom panels represents stimuli with the same acceleration and three different initial speeds. When assessing acceleration discrimination, data obtained using the stimulus configurations in each panel were grouped together, and compared across acceleration. Note that in the actual experiments, more than three target speeds and accelerations were used.

During the open-loop period, different patterns of responses were observed when the eye traces were sorted as a function of speed and as a function of acceleration. Figure 2. shows representative average eye traces from one block of trials for one observer (rightward trials only). When sorted by speed, the traces appear to be better ordered and more clearly separated than when sorted by acceleration. As can be seen from the traces displayed in the first column, lower eye velocity and acceleration accompanied lower target speeds throughout most of the open loop period when the traces were sorted by speed (Figure 2A and 2C). However, in the second column where the traces are displayed sorted by target acceleration (Figure 2B and 2D), traces do not rank appropriately as a function of acceleration. It may seem

unusual that Figure 2A shows such small differences between the eye traces for the different speeds, but one must keep in mind that while each trace represents the average pursuit to targets that had a starting speed of 4, 6, or 8 deg/s, the targets within a speed accelerated at various rates. For example, for the trace labeled 4 deg/s, there were stimuli that accelerated at 0, 8, and 16 deg/s², so the average speed of the stimulus over the first 140 ms would have ranged from 4 to about 6 deg/s. Thus the average speed of the stimuli that the eye was attempting to follow was higher than the initial starting speed. In addition, we have previously shown that for single spots moving at speeds in the range used here, the difference in eye velocity was not that pronounced (Heinen & Watamaniuk, 1998).

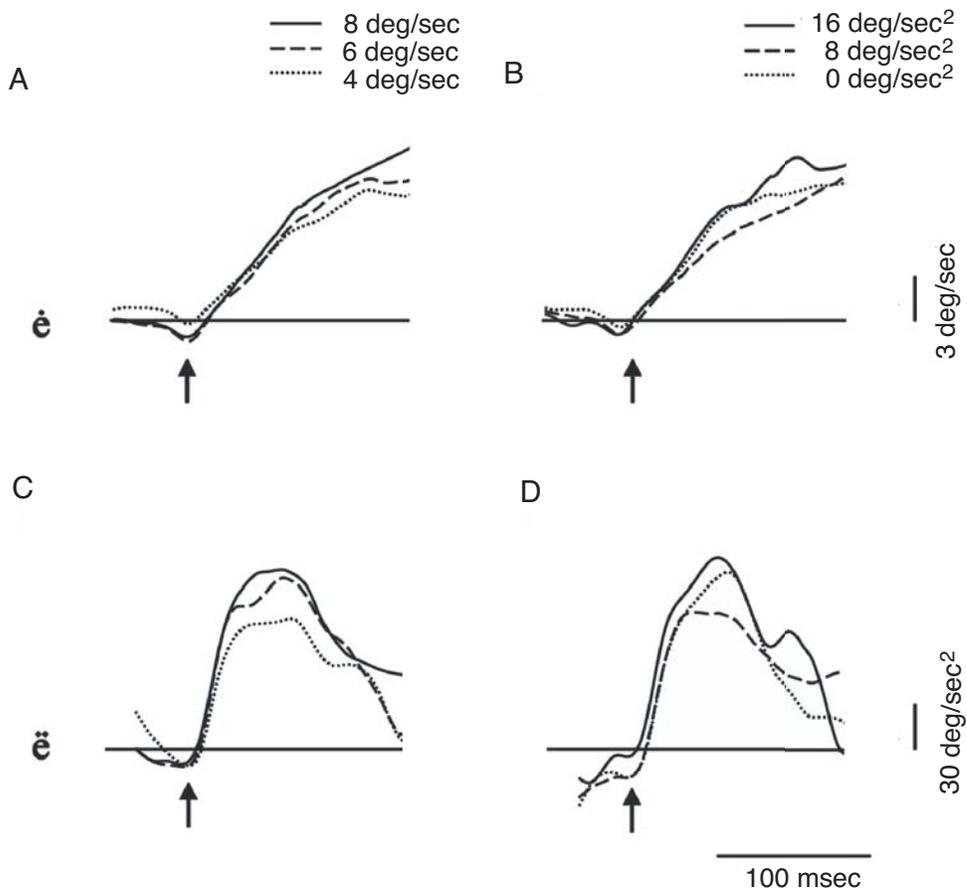


Figure 2. Averaged open-loop eye velocity (\dot{e}) and eye acceleration (\ddot{e}) traces for observer SH. The target was a single spot that moved with a base speed of 4, 6, or 8 deg/s and accelerated at 0, 8, or 16 deg/s². Traces have been sorted by target speed in panels A and C and by acceleration in panels B and D and were aligned on pursuit onset, indicated by the arrows. These are rightward-only traces taken from a single block of trials, so each trace on the left is the average of 18 trials, on the right 15 trials. Notice that when the data are sorted by target speed, eye velocity (A) and acceleration (C) traces diverge appropriately for the different target speeds over most of the open-loop period, with the highest speed target generating the highest eye velocity and acceleration. In contrast, when the data are sorted by target acceleration, eye velocity (B) and eye acceleration (D) traces do not separate appropriately as a function of target acceleration.

In Figure 3, average eye acceleration as a function of target speed and target acceleration is plotted. The data show a tendency for all observers to generate higher eye acceleration with higher target accelerations (Figure 3A), and higher target speeds (Figure 3B). A similar pattern of results was obtained from the two observers tracking RDCs (Figure 3C and 3D). While it appears that eye acceleration increases at a lower rate as a function of target acceleration than it does as a function of target speed, it could be that at the highest target accelerations, eye acceleration saturates. However, Tychsen & Lisberger (1986) showed that human observers' eye acceleration in the open-loop period reached levels in excess of 240 deg/s² for target speeds of 45 deg/s. Eye accelerations in our study reached only about 80 deg/s², far below the accelerations measured in the previous study. Therefore, the range of eye accelerations generated by our observers when they pursued accelerating stimuli appears not to be limited by saturation, rather by a reduced sensitivity of the pursuit system to retinal-image acceleration. We quantify the differences in these functions when we compare oculomotor to perceptual performance.

Perceptual Acceleration Discrimination

To enable a direct comparison of our pursuit data with perceptual performance, we presented observers with stimuli that had the same base speeds and accelerations as were used in the eye movement experiments. Observers were then asked to judge whether the acceleration of each stimulus was higher or lower than the mean acceleration of the stimulus set (see "Methods"). Note that because there were five different rates of acceleration (the 30 deg/s² stimulus was not used in the psychophysical experiments) crossed with five different initial speeds, the distance the target moved was an unreliable cue for making the required perceptual judgments. Stimulus details were the same as those used in the pursuit experiments except that the duration was shortened to 140 ms to make the motion stimulus comparable to the open-loop period of pursuit that we analyzed. Because neither of the naive observers had participated in perception experiments before, each performed 500 practice trials of the acceleration discrimination task prior to the experimental sessions.

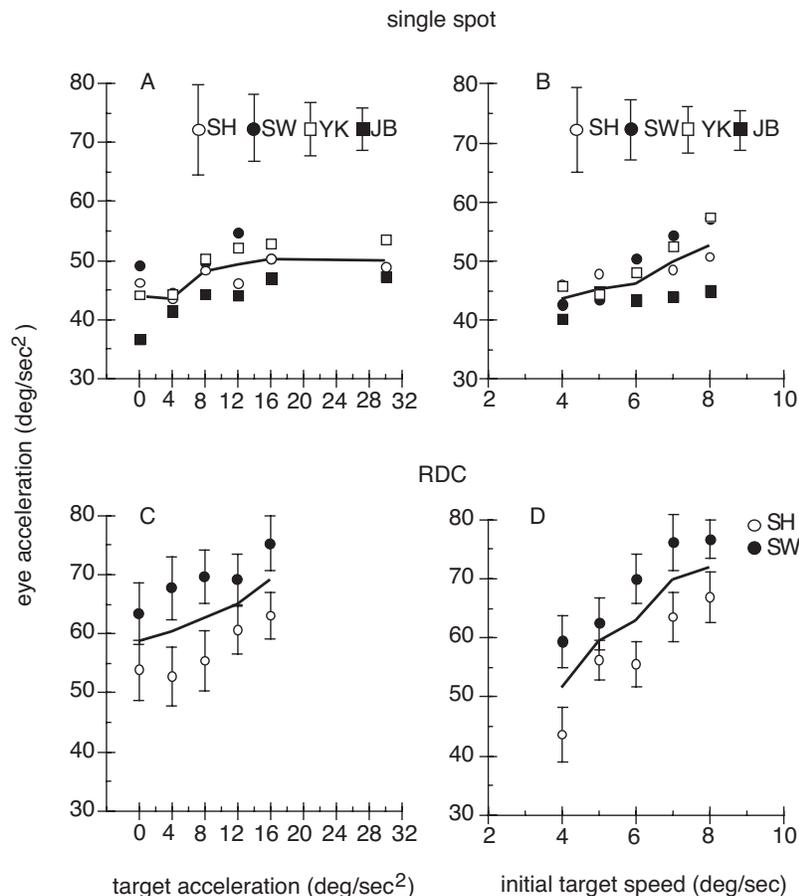


Figure 3. Average eye acceleration during open-loop pursuit initiation (40-140 msec) as a function of target acceleration and initial target speed for single-spot (top panels, four observers) and 200-dot RDC stimuli (bottom panels, two observers). Each data point is the average of 40-72 eye movement trials. For each stimulus type, both graphs plot the same data sorted according to either target acceleration (A and C) or target initial speed (B and D). In A and B, error bars are shown on the legend symbols for clarity and are the average ± 1 SEM for each observer. Error bars in C and D represent ± 1 SEM. Note different scales on the abscissa.

Figure 4 shows perceptual data for all observers for both the single-spot and RDC stimuli. As was done for the eye movement data, results from the same trials are displayed sorted either by acceleration or initial target speed. The line in each plot shows the mean level of performance averaged over observers. In general, observers judged stimuli with higher accelerations as such, although initial target speed also influenced their performance. A similar pattern of results was obtained from the two observers tracking RDCs (Figure 4C and 4D). Thus similar to the pursuit system, it appears that the perceptual system is more sensitive to changes in speed than acceleration. We will quantify these results when we compare perceptual and oculomotor performance. Interestingly, when observer JB's single spot data are sorted by initial target speed (Figure 4B), the trend of his acceleration judgments are opposite that of the other observers. A possible explanation is that this observer overcompensated in his efforts to avoid using

speed as a basis for his judgment, and therefore weighted speed negatively when assessing target acceleration.

An alternative explanation for the perceptual results is that observers were attempting to judge target speed, and not acceleration. This might have occurred if acceleration was difficult to discriminate, and observers made their judgments based upon the more salient speed information. If true, explicitly instructing them to judge target speed should produce identical results. To test this hypothesis, we used the same stimulus set and now asked observers to judge speed (Figure 5). Three observers (JB, YK, and SW) were tested with the single-dot, and one (SH) with the RDC stimulus. So as to not bias the results, the naive observers were not given practice in psychophysical speed discrimination before this control experiment. Performance appears to have greater sensitivity to initial target speed when observers were instructed to judge the speed of the target rather than judge the acceleration. The data for the RDC showed a

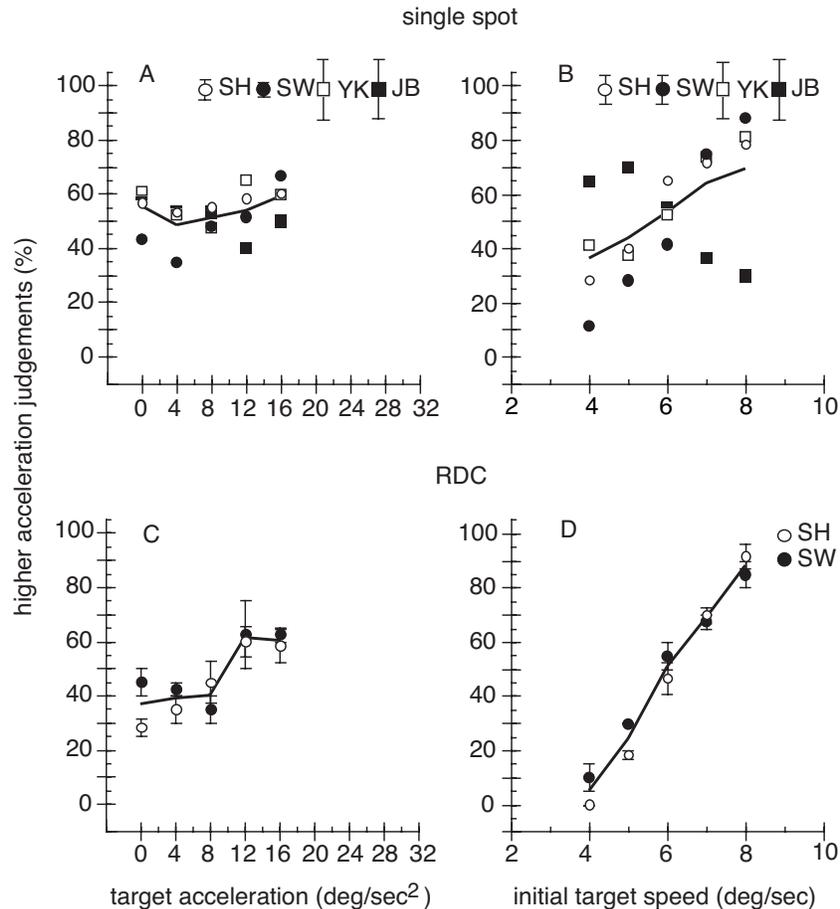


Figure 4. Percent of trials judged to have higher acceleration as a function of target acceleration (A and C) and initial target speed (B and D) for single-spot (top panels, four observers) and 200-dot RDC stimuli (bottom panels, two observers). As in Figure 3, left and right panels plot the same data but sorted according to either target acceleration or initial target speed. The lines through the data represent the average responses over all observers. In A and B, error bars are shown on the legend symbols for clarity, and are the average ± 1 SEM for each observer. Error bars in C and D represent ± 1 SEM. Notice that when the data are sorted as a function of target acceleration, judgments vary little from the 50% point, indicating that observers could not discriminate well the different rates of acceleration. When the data are sorted as a function of target speed, the data now show a noticeable slope. Note that one observer (JB) showed a trend opposite that of the other observers in his single-spot data when sorted by target speed (see text for discussion).

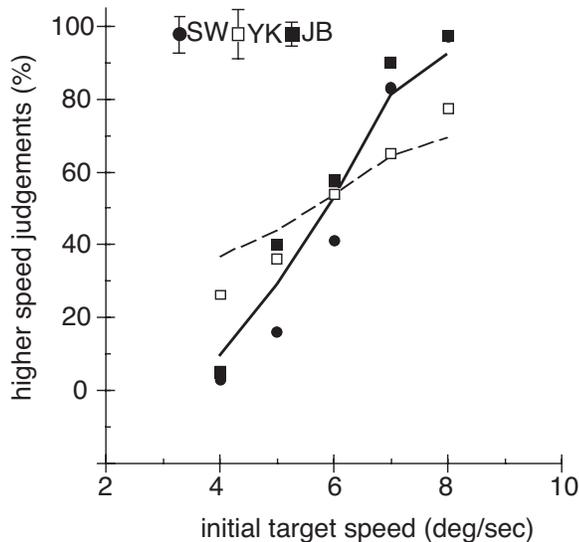


Figure 5. Percent of trials judged to have higher speed for accelerating single-dot targets. The three observers who performed this experiment were instructed to judge target speed and ignore target acceleration. Error bars are shown on the legend symbols for clarity and are the average \pm 1 SEM for each observer. The solid line connects the data averaged over all observers at each initial target speed. The average data from the experiment where observers were asked to judge target acceleration (from Figure 4B) are replotted here as a dashed line to allow comparison with that from the “judge speed” task. Data are sorted by initial target speed, and each point is the result of at least 40 trials.

similar trend. To quantitatively assess this performance difference, we used Probit analysis (Finney, 1971), which allowed us to determine the speed discrimination thresholds for the “judge speed” and “judge acceleration” conditions. A discrimination threshold (Weber fraction) here is the proportional change in target speed required to produce responses that differed from the mean stimulus 75% of the time. Speed discrimination thresholds were lower for the judge speed than the judge acceleration condition ($t(15)=2.21$, $p = .043$), suggesting that observers were not using only speed as a basis for their acceleration judgments in the former experiment.

Comparing Oculomotor and Perceptual Acceleration Discrimination

To compare the eye movement data with the perceptual judgments, it was necessary that the responses of both systems have the same metric. To accomplish this, the eye acceleration data were converted to oculometric functions (analogous to perceptual psychometric functions) in the following manner. For each observer, mean open-loop eye acceleration (40–140 ms) was computed for the middle stimulus (or middle two

stimuli when the number of conditions was even) as a baseline. We then determined whether the mean eye acceleration in the second epoch of the open-loop period (40–140 ms) for each trial was higher or lower than the baseline. This analysis yielded the number of trials where eye acceleration was higher than mean eye acceleration to the middle stimulus, and therefore allowed comparison of this data with the psychophysical data. This procedure is conceptually similar to the method used by Kowler and McKee (1987) and Watamaniuk and Heinen (1999) for creating oculometric functions. This process was performed twice on each set of data, once using the trials sorted by target acceleration and then using the trials sorted by initial target speed. The results of this analysis are shown in Figure 6, now compared directly with the psychophysical data. When plotted together, the mean oculomotor and perceptual behavior of observers appear similar.

To compare quantitatively oculomotor and psychophysical performance, we calculated 75%-discrimination thresholds using Probit analysis for each condition and for each observer (Finney, 1971). Figure 7 plots acceleration and speed discrimination thresholds for eye movements and perceptual judgments, and for both single spot and RDC stimuli. Note that acceleration thresholds above 1.0 and speed thresholds above 0.33 are based on functions extrapolated beyond the data. To compare thresholds among the different conditions, we performed a two-way repeated measures analysis of variance (ANOVA) on the single-spot data and another on the RDC data, the two factors being task (pursuit or perception) and threshold type ($\Delta A/A$ or $\Delta V/V$). Both analyses showed similar results; there were no differences between pursuit and perceptual thresholds (single spot: $p = .81$, RDC: $p = .87$), but there were significant differences between the two threshold types with the acceleration discrimination thresholds ($\Delta A/A$) being larger than the speed discrimination thresholds (single spot: $F(1,3)=24.93$, $p = .016$, RDC: $F(1,1)=929.4$, $p = .021$). The analysis of the RDC data showed no interaction between task and threshold type ($p = .99$). However, a significant interaction was found in the analysis of the single-spot data ($F(1,3)=15.76$, $p = .029$). As can be surmised from the data in Figure 7, the difference between the threshold types ($\Delta A/A$ & $\Delta V/V$) was smaller in the pursuit data (panel A) than it was for the perceptual data (panel B), although speed discrimination thresholds were lower than acceleration thresholds for both pursuit and perception.

We analyzed the pursuit data in the second epoch of the open-loop period so that the transient eye acceleration resulting from the initial step of target speed would not contaminate the response (e.g., Tychsen & Lisberger, 1986). However, because the eyes were stationary at the beginning of the trial, they had to accelerate throughout the open-loop period in order to acquire the target. Thus, the eye acceleration response to the initial target

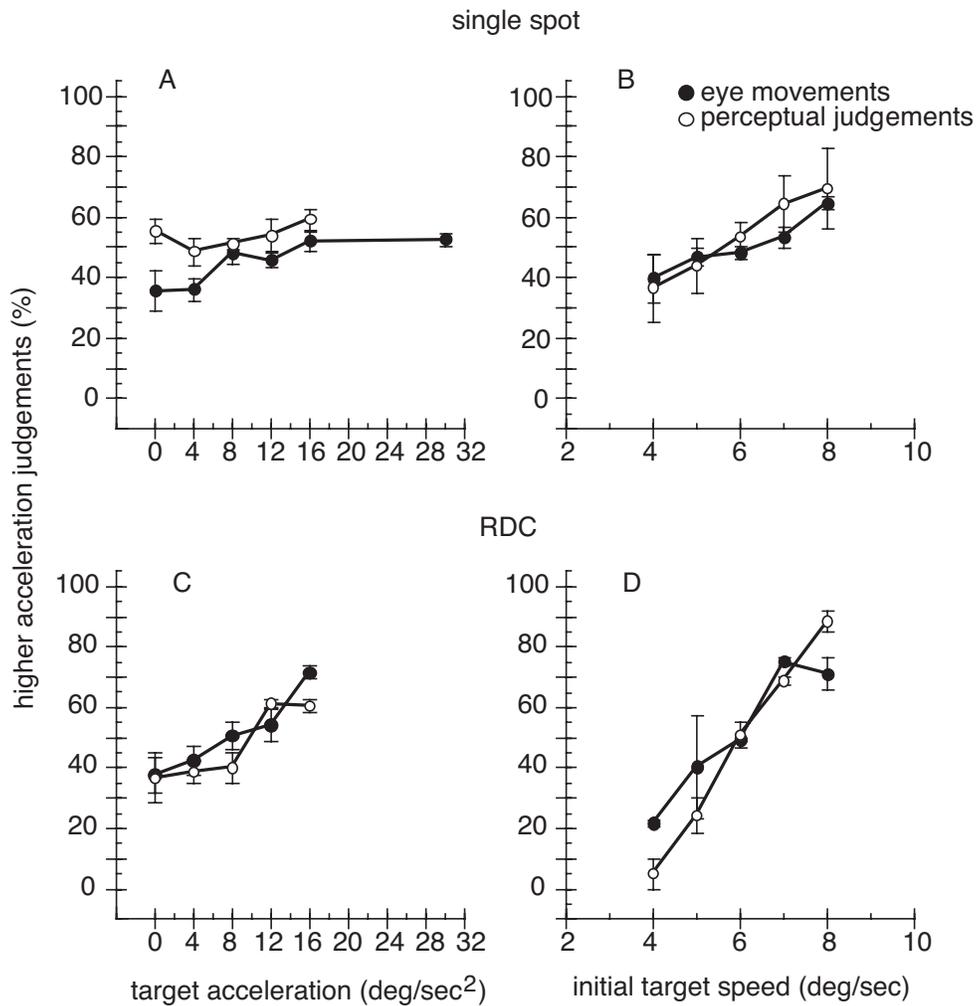


Figure 6. Comparing oculomotor and perceptual behavior. In these plots, the eye movement data have been converted to oculometric functions (see text), and the average over all subjects is plotted and compared with the average performance in the perceptual task. Data are sorted and plotted as a function of target acceleration (A and C) and initial target speed (B and D) for single-spot and 200-dot RDC stimuli. Note that average eye movement and perceptual performance of our observers are strikingly similar.

speed may have obscured or masked the eye acceleration response to target acceleration. To test this, the average eye movement traces from the 0 deg/s²-acceleration condition for each initial target speed were subtracted from each of the individual records for all conditions with that initial target speed. Acceleration 75%-discrimination thresholds for the transformed data were then computed from this data, and are plotted in Figure 8 as Weber fractions along with the original thresholds from Figure 7 for comparison. Notice that the acceleration discrimination thresholds computed before and after the subtraction of the 0 deg/s²-acceleration traces on average are similar. Although SH's threshold dropped and SW's threshold increased, a paired *t* test including both single spot and RDC data showed that acceleration discrimination thresholds overall did not change significantly ($t(5) = -0.004, p = .997$). Therefore, the high acceleration thresholds appear due to a response

to target acceleration, and not by a masking effect of base target speed.

Subtracting 0 deg/s²-acceleration traces from the records should also make the responses less sensitive to speed late in the open-loop period, because the response to speed-only has been subtracted out. This is what was observed in all observers. For single-spot targets, SW's speed threshold went from 0.40 to 1.71, JB's threshold went from 1.36 to 5.51, and YK's threshold went from 0.70 to 0.80. The threshold for observer SH based on the transformed single-spot data could not be calculated because his oculometric function based on target speed had a negative slope and thus could not be extrapolated to 75%. For RDC targets, SW's speed threshold went from 0.32 to 4.28, and SH's threshold went from 0.34 to 0.65. Thus, subtracting 0 deg/s²-acceleration traces from the records had the expected effect and greatly reduced the systematic relationship between the pursuit response and initial target speed.

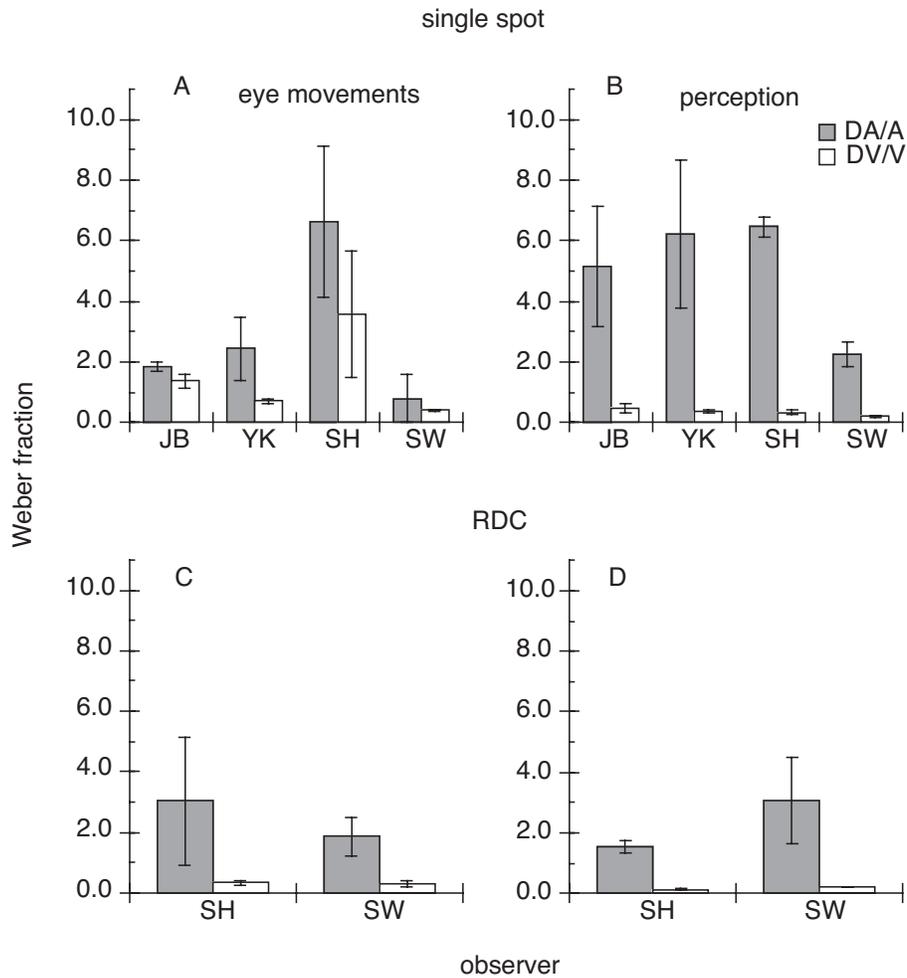


Figure 7. Comparing oculomotor and perceptual thresholds. Eye movement (A and C) and perceptual (B and D) discrimination thresholds plotted as Weber fractions for single-spot (top) and RDC (bottom) stimuli. Each panel plots acceleration discrimination thresholds ($\Delta A/A$) and speed discrimination thresholds ($\Delta V/V$) together for comparison for each subject. Note that acceleration thresholds ($\Delta A/A$) tend to be higher than speed thresholds ($\Delta V/V$) across observers and tasks.

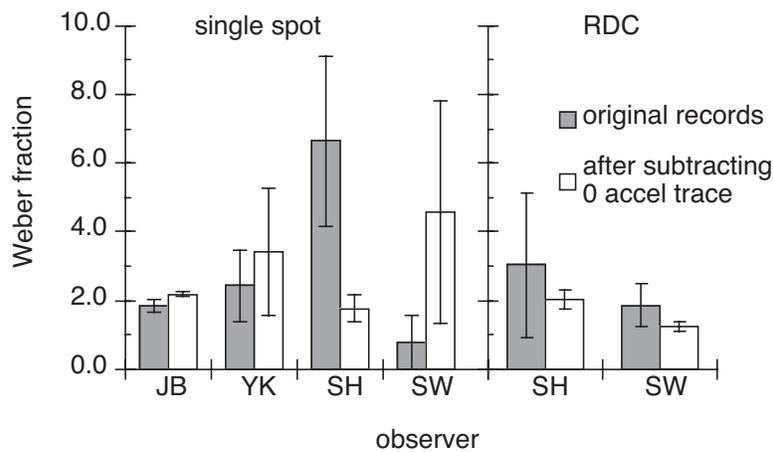


Figure 8. Eye movement discrimination thresholds plotted as Weber fractions for single-spot (left) and RDC (right) stimuli. Each panel plots acceleration discrimination thresholds ($\Delta A/A$) computed from the original eye acceleration traces (Figure 7, filled bars) and from eye traces obtained by subtracting the average eye acceleration trace for the 0 deg/s²-acceleration condition from the original eye acceleration traces for each base speed (open bars). Note that overall, acceleration thresholds changed little as a result of this manipulation.

Discussion

Over the ranges of target accelerations and speeds used here, discrimination thresholds computed from eye acceleration were lower for target speed than for target acceleration for both single spot and RDC stimuli. The same pattern of results was observed in the perceptual data. Moreover, the high acceleration discrimination thresholds were not due to target motion onset or speed masking the pursuit system's response. We interpret these data as support for a common motion-processing stage limiting pursuit and perception. These results are in agreement with previous work demonstrating that observers are poor at processing acceleration (Schmerler, 1976; Calderone & Kaiser, 1989; Snowden & Braddick, 1991; Werkhoven et al., 1992). However, it cannot be concluded that this is the general trend for either system, because speed and acceleration sensitivity may be optimal in different ranges. Perceptual sensitivity for speed is poor for low and high speeds, having an optimum range between 4–64 deg/s (De Bruyn & Orban, 1988). It is possible that there is also an optimal range for discriminating acceleration outside of the range that we tested, and that in that range, discrimination thresholds would be lower.

We are not suggesting humans are blind to image acceleration. All observers in the present study noticed that the speeds of accelerating stimuli increased. However, when asked to judge the rate of the speed change, they performed poorly. These results might be explained if a reliable speed signal was available to observers, but a reliable acceleration signal was not. Work that attempted to determine physiological evidence of acceleration processing in area MT failed to find neurons with responses that varied systematically as a function of image acceleration (Lisberger & Movshon, 1999). However, these authors demonstrated that it is still possible to obtain an acceleration signal by coupling the outputs of a population of MT neurons.

A possible reason that a reliable acceleration signal may not be available to observers is that motion information is integrated over time (e.g., Morgan, 1976, 1980; van Doorn & Koenderink, 1984; McKee & Welch, 1985; De Bruyn & Orban, 1988; Bowne, McKee, & Glaser, 1989; Watamaniuk & Sekuler, 1992; Watamaniuk & Duchon, 1992). Theoretically, by integrating, the visual system averages out neural noise and thereby obtains a better estimate of image velocity. As a consequence, when a moving target changes speed, that speed change is smoothed. Consequently, the perception of the *rate* of change will likely be altered, resulting in poor acceleration discrimination.

Another reason that acceleration discrimination might be poorer than velocity discrimination is if the brain differentiates velocity signals (in a mathematical sense) to obtain acceleration. If the signal and its

associated noise are similar in frequency, the signal to noise ratio (SNR) would change little with differentiation, leaving acceleration discrimination intact. However, a common assumption for neural systems is that the noise has a higher frequency than the signal. Thus differentiation would amplify the noise more and decrease the SNR. Additionally, it may be argued that the poor performance of both pursuit and perception represents the operation of two independent noisy systems similarly affected by differentiation. The expectation then would be that the output of the two systems should be uncorrelated, which is clearly not the case (see Figure 6); the probability that two independent noisy systems produce outputs that are not statistically different is low. Thus if neural noise degrades acceleration discrimination, our results, though not definitive, are consistent with pursuit and perception being limited by a common source.

Previous work has addressed the response of the pursuit system to accelerating stimuli (Krauzlis & Lisberger, 1994). These researchers measured pursuit latency to targets that accelerated at different rates or stepped instantaneously to the same constant speed. They found that the latency of pursuit to targets that took an instantaneous step in speed was shorter than that to targets that accelerated gradually. Furthermore, the slowest accelerations produced the longest latencies. These results show that, using latency as a metric, the pursuit system seems to discriminate target acceleration. Our experiment was different in that we assessed pursuit dynamics as a function of target acceleration. Using this metric, we found poor acceleration discrimination relative to velocity discrimination.

Our data suggest that the smooth pursuit system may not be well designed to pursue accelerating targets. It would be interesting to compare predictions of acceleration discrimination from popular models of smooth pursuit (Robinson, Gordon, & Gordon, 1986; Krauzlis & Lisberger 1989) to the present data. Unfortunately, this cannot be done because both models were designed to describe how accurately the pursuit system follows a target, and not how well it discriminates between targets that move with different speeds or accelerations. Discrimination thresholds are based upon the *precision* of a system, which is limited by noise: internal noise when the stimulus has little or no noise, and external noise when the noise in the stimulus exceeds the noise within the system (e.g., Kowler & McKee, 1987; Geisler, 1989; Watamaniuk, 1993). Our stimuli were constructed without noise, and therefore the limits on the precision of our observers were imposed by internal noise. Neither the Robinson et al. (1986) nor the Krauzlis and Lisberger (1989) models have internal sources of noise, and therefore would respond perfectly to the stimuli that we presented our observers. As a result, discrimination thresholds for speed and acceleration would be minute

for either model. To obtain speed or acceleration discrimination predictions from the models, a source of internal noise would have to be added to them. Our data could be a starting point to establish experimental estimates of internal noise in the pursuit system.

Although not as good as judging speed, observers could still detect and discriminate acceleration to a degree. It is possible that judging acceleration is a cognitive process whereby target speed is compared at various time points during the motion. This process might be capable of providing only a rough estimate of acceleration, but not the fine discrimination afforded by a veridical acceleration signal.

Conclusions

The present data show that observers have relatively poor sensitivity to image acceleration when making perceptual judgments and during smooth pursuit initiation. Although not conclusive evidence, our results are at least consistent with the idea that a common motion-processing stage limits both systems. Previously, we demonstrated that initial eye acceleration increased systematically as the spatial extent of an RDC was increased (Heinen & Watamaniuk, 1998). Perceptual experiments show that at least some aspects of motion perception (e.g., direction discrimination) also improve as the spatial extent of a stimulus is increased (e.g., Watamaniuk & Sekuler, 1992). In addition, the precision of the smooth pursuit response decreases as directional noise is added to a moving stimulus in parallel with psychophysical direction discrimination (Watamaniuk & Heinen, 1999). Smooth pursuit is also subject to the same directional biases as perception when viewing stimuli through elongated apertures (Beutter & Stone, 1998). Finally, directional expectation affects perceptual measures and eye movements similarly by reducing the signal-to-noise ratio needed for detection (Krauzlis & Adler, 2001). These results taken together add to a growing body of literature supporting the notion that the visual motion system subserving human motion perception also limits smooth pursuit. Therefore, it may be appropriate to use the pursuit system as a tool to probe dynamic properties of motion processing that may be inaccessible using other techniques.

Acknowledgments

This research was supported by the National Eye Institute (RO1 EY10838) and The Smith Kettlewell Eye Research Institute. Commercial relationships: none.

References

- Beutter, B. R. & Stone, L. S. (1998). Human motion perception and smooth eye movements show similar directional biases for elongated apertures. *Vision Research*, 38, 1273-1286. [PubMed]
- Bowne, S. F., McKee, S. P., & Glaser, D. A. (1989). Motion interference in speed discrimination. *Journal of the Optical Society of America A*, 6, 1112-1121. [PubMed]
- Bravo, M. J., & Watamaniuk, S. N. J. (1995). Evidence for two speed signals: A coarse local signal for segregation and a precise global signal for discrimination. *Vision Research*, 35, 1691-1697. [PubMed]
- Calderone, J. B., & Kaiser, M. K. (1989). Visual acceleration detection: Effect of sign and motion orientation. *Perception & Psychophysics*, 45, 391-394. [PubMed]
- De Bruyn, B., & Orban, G. A. (1988). Human velocity and direction discrimination measured with random dot patterns. *Vision Research*, 28, 1323-1335. [PubMed]
- Finney, D. J. (1971). *Probit analysis (3rd ed.)*. Cambridge: Cambridge University Press.
- Geisler, W. S. (1989) Sequential ideal-observer analysis of visual discriminations. *Psychological Review*, 21, 267-314. [PubMed]
- Gottsdanker, R. M. (1956). The ability of human operators to detect acceleration of target motion. *Psychological Bulletin*, 53, 477-487.
- Heinen, S. J., & Watamaniuk, S. N. J. (1998). Spatial integration in human smooth pursuit. *Vision Research*, 38, 3785-3794. [PubMed]
- Kowler, E., & McKee, S. P. (1987). Sensitivity of smooth eye movement to small differences in target velocity. *Vision Research*, 27, 993-1015. [PubMed]
- Krauzlis, R. J., & Adler, S. A. (2001). Effects of directional expectations on motion perception and pursuit eye movements. *Visual Neuroscience*, 18, 365-376. [PubMed]
- Krauzlis, R. J., & Lisberger, S. G. (1989) A control systems model of smooth pursuit eye movements with realistic emergent properties. *Neural Computation*, 1, 116-122.
- Krauzlis, R. J., and Lisberger, S. G. (1994). Temporal properties of visual motion signals for the initiation of smooth pursuit eye movements in monkeys. *Journal of Neurophysiology*, 72, 150-162. [PubMed]

- Lisberger, S. G., & Movshon, A. J. (1999). Visual motion analysis for pursuit eye movements in area MT of macaque monkeys. *The Journal of Neuroscience*, *19*, 2224-2246. [PubMed]
- Lisberger, S. G., & Westbrook, L. E. (1985). Properties of visual inputs that initiate horizontal smooth pursuit eye movements in monkeys. *The Journal of Neuroscience*, *5*, 1662-1673. [PubMed]
- McKee, S. P. (1981). A local mechanism for differential velocity detection. *Vision Research*, *21*, 491-500. [PubMed]
- McKee, S. P., & Welch, L. (1985). Sequential recruitment in the discrimination of velocity. *Journal of the Optical Society of America A*, *2*, 243-251. [PubMed]
- Morgan, M. J. (1976). Pulfrich effect and the filling in of apparent motion. *Perception*, *5*, 187-195. [PubMed]
- Morgan, M. J. (1980). Analogue models of motion perception. *Philosophical Transactions of the Royal Society of London B*, *290*, 117-135. [PubMed]
- Orban, G. A., DeWolf, J., & Maes, H. (1984). Factors influencing velocity encoding in the human visual system. *Vision Research*, *24*, 33-39. [PubMed]
- Robinson, D. A., Gordon, J. L., & Gordon, S. E. (1986). A model of the smooth pursuit eye movement system. *Biological Cybernetics*, *55*, 43-57. [PubMed]
- Rosenbaum, D. A. (1975). Perception and extrapolation of velocity and acceleration. *Journal of Experimental Psychology: Human Perception and Performance*, *1*, 395-403. [PubMed]
- Schmerler, J. (1976). The visual perception of accelerated motion. *Perception*, *5*, 167-185. [PubMed]
- Snowden, R. J., & Braddick, O. J. (1991). The temporal integration and resolution of velocity signals. *Vision Research*, *31*, 907-914. [PubMed]
- Todd, J. T. (1981). Visual information about moving objects. *Journal of Experimental Psychology: Human Perception and Performance*, *7*, 795-810. [PubMed]
- Tychsen, L., & Lisberger, S. G. (1986). Visual motion processes for initiation of smooth pursuit eye movements in humans. *Journal of Neurophysiology*, *56*, 953-968. [PubMed]
- van Doorn, A. J., & Koenderink, J. J. (1984). Spatiotemporal integration in the detection of coherent motion. *Vision Research*, *24*, 47-53. [PubMed]
- Watamaniuk, S. N. J. (1993). An ideal observer for discrimination of the global direction of dynamic random dot stimuli. *Journal of the Optical Society of America A*, *10*, 16-28. [PubMed]
- Watamaniuk, S. N. J., & Duchon, A. (1992). The human visual system averages speed information. *Vision Research*, *32*, 931-941. [PubMed]
- Watamaniuk, S. N. J., & Heinen, S. J. (1999). Human smooth pursuit direction discrimination. *Vision Research*, *39*, 59-70. [PubMed]
- Watamaniuk, S. N. J., & Sekuler, R. (1992). Temporal and spatial integration in dynamic random dot stimuli. *Vision Research*, *32*, 2341-2347. [PubMed]
- Werkhoven, P., Snippe, H. P., & Toet, A. (1992). Visual processing of optic acceleration. *Vision Research*, *32*, 2313-2329. [PubMed]