Effects of contrast on smooth pursuit eye movements

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It is well known that moving stimuli can appear to move more slowly when contrast is reduced (P. Thompson, 1982). Here we address the question whether changes in stimulus contrast also affect smooth pursuit eye movements. Subjects were asked to smoothly track a moving Gabor patch. Targets varied in velocity (1, 8, and 15 deg/s), spatial frequency (0.1, 1, 4, and 8 c/deg), and contrast, ranging from just below individual thresholds to maximum contrast. Results show that smooth pursuit eye velocity gain rose significantly with increasing contrast. Below a contrast level of two to three times threshold, pursuit gain, acceleration, latency, and positional accuracy were severely impaired. Therefore, the smooth pursuit motor response shows the same kind of slowing at low contrast that was demonstrated in previous studies on perception.

Keywords: eye movements, smooth pursuit, contrast, motion, spatial frequency

Introduction

Smooth pursuit eye movements serve to center and stabilize the image of selected moving objects on the fovea. The perceptual ability to detect a moving object (Derrington, Allen, & Delicato, 2004) and the oculomotor ability to reliably track its motion with smooth pursuit eye movements (Keller & Heinen, 1991) are closely related. The perceptual and the pursuit system use the same kind of motion information for detection and discrimination of an object's perceived direction and velocity, as indicated by a number of behavioral (Beutter & Stone, 1998, 2000; Hawken & Gegenfurtner, 2001; Krauzlis & Stone, 1999; Stone & Krauzlis, 2003; Watamaniuk & Heinen, 2003), and neurophysiological studies (Lisberger & Movshon, 1999; Newsome & Pare, 1988; Newsome, Wurtz, & Komatsu, 1988; Watamaniuk & Heinen, 1999).

The relationship between physical and perceived speed of an object is modified by stimulus characteristics, such as stimulus contrast, and spatial frequency. Thompson (1982, 1983) reported that the perceived speed of a sinusoidal grating is influenced by its contrast. Low-contrast stimuli consistently appeared slower than the same targets presented at higher contrast. Perceptual slowing holds for luminance, isoluminant, and second-order motion stimuli over a wide range of speeds and contrasts (Blakemore & Snowden, 1999; Gegenfurtner & Hawken, 1996; Hawken, Gegenfurtner, & Tang, 1994; Stone & Thompson, 1992; Thompson & Stone, 1997; Thompson, Stone, & Swash, 1996).

A variety of effects of different spatial frequencies on perceived velocity have been reported. Smith and Edgar (1990) claimed that stimuli with high spatial frequency appear slower than stimuli with low spatial frequency, whereas Diener, Wist, Dichgans, and Brandt (1976) found the opposite pattern. Campbell and Maffei (1981) reported that increasing spatial frequency initially resulted in an increase in perceived velocity, but at spatial frequencies higher than 4 c/deg, perceived speed decreased again.

If the perceptual and the pursuit system indeed use a shared motion signal, stimulus contrast should also affect the velocity of smooth pursuit eye movements. So far, little is known about the effect of contrast on smooth pursuit eye movements. Although it was shown that pursuit latency is markedly reduced with increasing target luminance in the monkey (Lisberger & Westbrook, 1985) and in human subjects (O'Mullane & Knox, 1999), other studies report very small effects over a narrow range of stimulus contrast (Brown, 1972; Haegerstrom-Portnoy & Brown, 1979). However, these studies are difficult to interpret because the visual conditions in the above studies were disparate.

The question we address here is whether changes in stimulus contrast affect smooth pursuit eye movements in the same way as has been reported for the perception of

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velocity. In particular, we explore to what extent quality of pursuit is impaired at very low stimulus contrast. Assuming that a variation in spatial frequency affects the estimation of speed, we also analyzed contrast effects on pursuit for different spatial frequencies.

Methods

We conducted two experiments (the initial experiment to measure contrast thresholds for each observer and the main experiment) with identical subjects, visual stimuli, experimental setup, and eye movement recording procedure. Whenever the procedure of the initial experiment differs from that of the main experiment, it is noted in the text.

Visual stimuli

Stimuli were moving Gabor patches that consisted of a vertical sine wave grating windowed by a Gaussian function with both wavelet components moving together. Targets were presented at a mean luminance of 32 cd/m^{-2}, which matched the homogenous surround of the target. Each patch moved horizontally at one of the velocity/spatial frequency conditions shown in Table 1. Stimulus contrast ranged from below individual thresholds to 100% contrast. Contrast detection thresholds were measured individually for each observer prior to the main experiment. In the initial threshold measure experiment, we used a staircase procedure starting at a stimulus contrast of 40% that moved up or down, according to the observer's response (see Psychophysical data analysis).

		Spatial frequency (c/deg)			
		0.1	1	4	8
Velocity	1	0.1	1	4	8
(deg/s)	8	0.8	8	32	64
	15	1.5	15	60	120

Table 1. Temporal frequencies (Hz) of Gabor patches moving at one of three velocities and one of four spatial frequencies. The condition, spatial frequency = 0.1 c/deg, refers to a stimulus that consists of a Gaussian only. Stimuli with temporal frequencies in those cells marked gray might be outside the window of visibility and are therefore excluded from the analysis of eye movement initiation.

Because it is known that perceived size of a Gabor with a fixed standard deviation varies systematically with contrast (Fredericksen, Bex, & Verstraten, 1997), we used different stimulus sizes (Gaussian *SD*s 0.6, 0.7, and 0.8 deg) in a short preliminary experiment to test for size effects. We found no significant effect of size on pursuit parameters at any contrast level, and therefore used a Gaussian standard deviation of 0.7 deg in subsequent trials.

Experimental setup

Stimuli were displayed on a 21-inch CRT monitor (ELO Touchsystems, Fremont, CA, USA) by an ASUS V8170 (Geforce 4MX 440) graphics board with a refresh rate of 100 Hz non-interlaced. The gamma nonlinearity of the monitor was measured with a Laser 2000 Model 370 Photometer (UDT Instruments, Baltimore, MD, USA) and corrected using a look-up table. The spatial resolution of the monitor was 1280 (H) x 1024 (V) pixels and the screen subtended 39.5 cm (48°) horizontally and 29.6 cm (39°) vertically. At a viewing distance of 47 cm this results in 26 pixels/deg. The monitor had a mean luminance of 32 cd/m^{-2}.

Eye movement recording

Eye position signals were recorded with a head-mounted, video-based eye tracker (EyeLink II; SR Research Ltd., Osgoode, Ontario, Canada) and were sampled at 250 Hz. The apparatus was recalibrated after each block (84 trials at maximum) by instructing the subject to fixate single dots that appeared successively at nine different positions on the monitor. Subjects were seated with their heads stabilized with a chin rest. They viewed the display binocularly through natural pupils. Stimulus display and data collection were controlled by a PC.

Experimental procedure

Each trial started with a fixation bullseye (0.6° diameter) that appeared in the center of the monitor. Observers initiated each trial by pressing an assigned button. The EyeLink II system then performed a drift correction to correct for shifts of the head-mounted tracking system. When the drift correction was successful, the fixation bullseye disappeared. A step-ramp paradigm (Rashbass, 1961) was used to guarantee that the initial pursuit was rarely disturbed by saccades. After a fixed interval of 100 ms, the stimulus appeared to the left or right of the center of the screen. The target then moved in the opposite direction of the step toward the screen center for 1050 ms. The direction of the step was chosen randomly. The size of the step that was used and the time the target needed to return to the center depended on the velocity of the target. Figure 1 depicts a schematic diagram for one trial. In the main experiment, subjects were asked to rate target direction (left or right) and velocity (slow, medium, or fast) by pressing assigned keys on the keyboard at the end of each trial. Contrast thresholds in the initial experiment were measured for left-right motion discrimination. Each observer completed 40-60 test trials before the initial and the main experiment to get used to the procedure and learn to discriminate the stimuli by pressing the correct keys. A correct psychophysical answer in the initial experiment is therefore a correct direction judgment. For an answer to be considered as psychophysically correct in the main experiment, both judgments, direction and velocity, had to be correct. Audible feedback was given after each direction and velocity judgment to indicate an incorrect response in either one.

Psychophysical data analysis

Contrast thresholds for identifying the direction of moving Gabors were established during the full duration of smooth pursuit eye movements using two interleaved staircases in a staircase procedure as described by Levitt (1971). An incorrect response led to an increase of the stimulus contrast on the next trial, and a series of three correct responses led to a decrease. The staircase thus converged to a level where the probability of a correct response was 0.79. The procedure ended automatically after four reversals were reached for each staircase (approximately 500-650 trials). Thresholds were obtained by fitting the percentage of correct answers with a logistic psychometric function for a performance level of 75%. We used the psignifit toolbox in Matlab (Wichmann & Hill, 2001a, 2001b) to assess the goodness of fit of the psychometric function. Summary statistics yielded a good fit between the model and the data.

Mean contrast sensitivity for all subjects is depicted in Figure 2 as a function of spatial frequency for each of the three stimulus velocities. Contrast sensitivity was dependent on target velocity and spatial frequency. Threshold values for the two higher velocities (8 and 15 deg/s) were similar and showed high sensitivity in the low spatial frequency range and low sensitivity in the high spatial frequency range. Contrast sensitivity for slow stimulus velocity (1 deg/s) showed a band-pass pattern with a sensitivity peak at 4 c/deg. The low sensitivity for fast-moving stimuli (velocities 8 and 15 deg/s) with spatial frequency ≥ 4 c/deg points to the fact that those stimuli might be outside the window of visibility. Low spatiotemporal components of the stimulus might actually drive the initiation of the pursuit eye movement. Therefore, we excluded those conditions in the analysis of smooth-pursuit initiation.

Once detection thresholds had been established, the method of constant stimuli was employed. The seven contrast levels employed were derived from the detection threshold by multiplying individual threshold levels by 0.8, 1, 2, 3, 4, and 10. We also used stimuli with 100% contrast.

Design

Sessions were divided into blocks. Within each block of the main experiment, we randomly mixed all types of trials, each of which presented a specific set of stimulus parameters (three velocities times four spatial frequencies times seven contrast levels), resulting in a maximum number of 84 trials per block. The exact number of trials per block varied between observers due to differences in subject's individual threshold values.

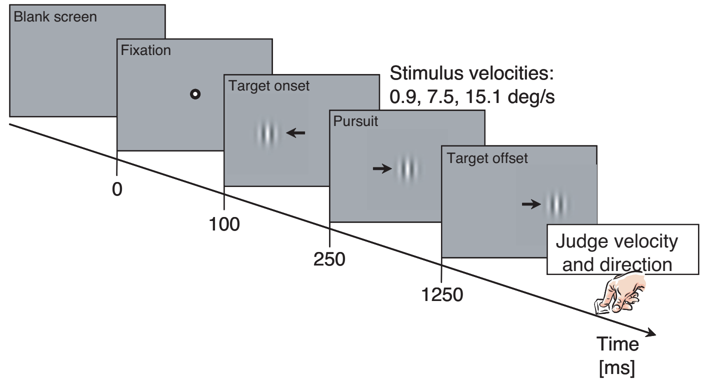

Figure 1. Schematic diagram of one trial. The sequence of the screen images shows the intervals that occurred over the course of one trial. Vertical Gabor patches of varying spatial frequencies moved at different velocities (see Table 1). Stimulus contrast ranged from below individual thresholds to 100% contrast.

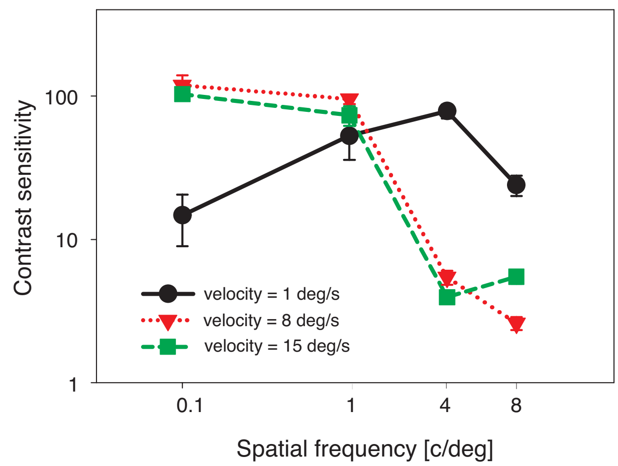

Figure 2. Mean contrast detection thresholds and standard deviations for all subjects.

Subjects

Two of the authors (DK and MS), and four additional observers, two non-naïve (BW and NZ) and two naïve (AO and NB) to the purpose of the experiment, served as subjects for both experiments. All had normal or corrected-to-normal visual acuity. All subjects were highly trained in smooth pursuit tasks and were experienced psychophysical observers. We chose only highly experienced observers to examine as close to optimal human performance as possible by keeping sources of trial-by-trial performance variability (e.g., learning effects and finger errors) to a minimum and to obtain reliable results in subthreshold trials. In the main experiment, data were collected in individual sessions lasting approximately 45 min. Each subject completed one to four sessions of eight blocks resulting in 660 (DK), 1872 (MS), 1771 (BW), 1368 (NZ), 616 (AO), and 2259 (NB) trials. A total of 8546 trials were collected, out of which 7273 (85%) were correct psychophysical answers.

Analysis of eye movements

Eye position traces for individual trials were stored on disk for off-line analysis. We recorded position traces for 220 ms before the onset of stimulus motion and for 600 ms after the cessation of stimulus motion. Eye velocity signals were obtained by digital differentiation of eye position signals over time. Saccades in each trace were detected by using a combined position criterion and fixed-acceleration cut-off that was tailored for the different stimulus speeds (20, 35, and 45 deg/s^2 criterion for stimuli moving at 1, 8, and 15 deg/s, respectively). A period of three samples (12 ms) before and after saccade onset and offset was also excluded. That the algorithm removed all large saccades, the majority of microsaccades, and detected smooth pursuit onset was confirmed by visual inspection of each position and velocity trace along with the stimulus time course. We excluded traces that did not conform to the criteria outlined above or were contaminated by eye blinks from further analysis (n = 40, 0.5% of all trials across all subjects).

Smooth pursuit eye movement responses were analyzed during the initiation and steady-state phase of pursuit (e.g., see Carl & Gellman, 1987; Krauzlis & Lisberger, 1994). Smooth pursuit latency, acceleration, steady-state gain, and position error were determined for trials with correct psychophysical answers on an individual trial basis. Figure 3 gives an overview of smooth-pursuit characteristics that were analyzed.

Initiation phase

The onset of pursuit was defined as the intercept of two sliding regression lines along the position trace. The offset of the regression lines was 200 ms, and there was a window of 40 ms between the two lines. The difference between the slopes of the two regression lines had to exceed a fixed velocity criterion (25% of target velocity) to qualify as smooth pursuit onset. The intersection of the two lines was considered as smooth pursuit onset. Neither this method nor the method introduced by Carl and Gellman (1987) worked well for 1 deg/s targets, because the exact point of initiation was often poorly defined. Any traces where the calculated latency was shorter than 50 ms were not included in the analysis (n = 386, 4.5% of all trials across all subjects), because it was assumed that the subject was making anticipatory eye movements (Kowler & Steinman, 1981). If pursuit onset was detected later than 600 ms, the trial was excluded from further analysis of latency (n = 188, 2.2% of all trials across all subjects).

For analyzing eye acceleration, position and velocity traces were smoothed by a Butterworth filter with a 60-Hz cutoff. Acceleration was analyzed during the first 100 ms following pursuit onset by fitting a regression line to the velocity trace. We chose to use only trials where the fit of the regression was larger than R^2 = 0.4.

Steady-state phase

We calculated pursuit gain and position error (as root mean squared deviation of the eye position from the target

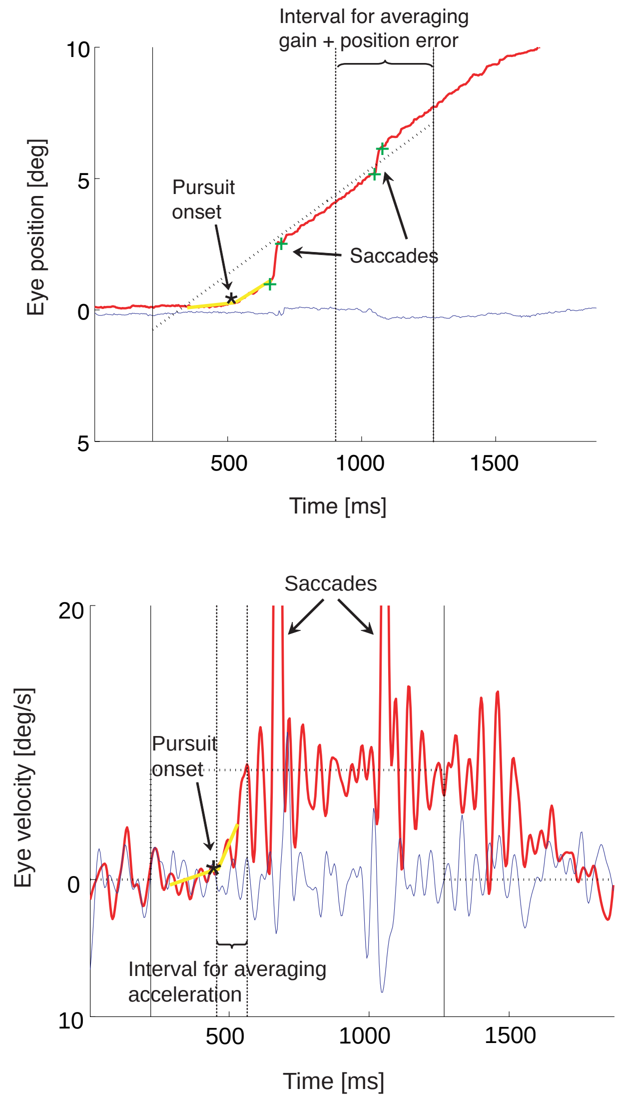

Figure 3. Example position (top) and velocity trace (bottom) to demonstrate time intervals during the stimulus duration that were used for analyzing pursuit characteristics.

position) during the last 400 ms of the stimulus motion in the steady-state phase of pursuit. Using the traces up to the end of pursuit was possible because none of the subjects showed anticipatory slowing. We looked at the pursuit quality of all trials, both with correct and incorrect judgments, to make sure that we did not falsely include trials in which subjects guessed correctly but did not see the stimulus properly. A position criterion was used over the last 400 ms of pursuit. To this end, we calculated an upper (1.5 times target velocity) and a lower bound (0.5 times target velocity) around the target trajectory. If the actual eye position was within those two new trajectories in more than 50% of the samples, the trial was considered as correct pursuit. We then compared this pursuit quality criterion to subjects' psychophysical judgments to test whether subjects tended to pursue a target properly in those trials where they correctly detected the direction and velocity of the stimulus. Table 2 depicts 2 x 2 contingency tables for quality criterion and psychophysical answers for the three stimulus velocities separately (Table 2a-c). Cases with correct psychophysical judgment and an error in pursuit are probably correct guesses, whereas cases with incorrect psychophysical judgment but clean pursuit are likely to be lapses (finger errors). We calculated the Phi coefficient (measuring the degree of association between binary variables) across all observations for each subject. Phi coefficients were Fisher *z* transformed, averaged across all subjects, and then transformed back, resulting in $\Phi = 0.25$, $\Phi = 0.65$, and $\Phi = 0.88$ for the three stimulus velocities, respectively. All Phi coefficients were highly significant ($p < .001$) and point to a positive correlation between pursuit quality as measured by the quality criterion and psychophysical judgment.

A. Stimulus velocity: 1 deg/s

		Psychophysical judgment 0	1	Total
Quality criterion	0	173	484	657
	1	161	2262	2423
	Total	334	2746	3080

B. Stimulus velocity: 8 deg/s

		Psychophysical judgment 0	1	Total
Quality criterion	0	314	179	493
	1	86	2074	2160
	Total	400	2253	2653

C. Stimulus velocity: 15 deg/s

		Psychophysical judgment 0	1	Total
Quality criterion	0	492	58	550
	1	50	2216	2266
	Total	542	2274	2816

Table 2. The 2 x 2 contingency tables for psychophysical answers across all subjects (correct = 1, incorrect = 0) and smooth pursuit quality (criterion satisfied = 1, not satisfied = 0) for velocity: 1 deg/s (A), 8 deg/s (B), and 15 deg/s (C).

The number of correct trials used for calculating acceleration, latency, gain, and position error ranged between 95 and 438 for single stimulus conditions across all subjects. Total numbers of trials used were distributed evenly across all levels of stimulus velocity, spatial frequency, and contrast with the exception of contrast levels below threshold, where the number of incorrect psychophysical judgments was naturally higher than above threshold.

Results

The present study explores the effect of contrast on smooth pursuit eye movements. Six subjects were asked to smoothly track a moving Gabor patch and rate its direction and velocity at the end of each trial. We analyzed the effects of contrast, target velocity, and spatial frequency on pursuit gain, latency, position error, and acceleration in psychophysically correct trials.

Figure 4 shows representative eye movement position (Figure 4, left) and smoothed velocity traces (Figure 4, right) for a stimulus moving at 8 deg/s with spatial frequency = 0.1 c/deg.

Although catch-up saccades occurred even when pursuing high-contrast targets, there were many more saccades during pursuit at low contrast. For contrast at threshold (Figure 4a), most of the foveation was obtained by catch-up saccades. Saccades at low contrast were not very accurate but had roughly the same amplitude, therefore holding the stimulus at a constant peripheral position. Subjects reported that stimuli in that condition did not appear to move continuously across the monitor but that target motion seemed to be rather jerky. Still, at threshold contrast, the gain of the smooth eye movement periods between saccades was significantly different from zero across all subjects ($M = 0.6$, $SD = 0.3$) with $t(655) = 56.2$, $p \leq .001$ (two-tailed).

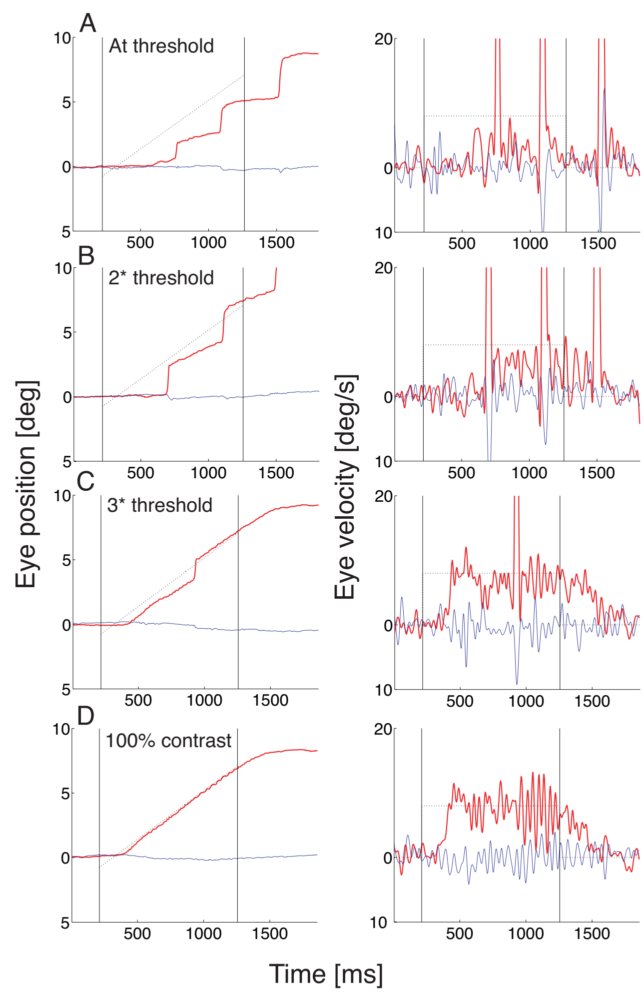

Figure 4. Example position (left) and velocity traces (right) of smooth pursuit eye movements to a stimulus moving at 8 deg/s with a spatial frequency of 0.1 c/deg (subject NZ) for four different contrast levels (a: threshold 1%. b: 2*threshold. c: 3*threshold. d: 100%).

As stimulus contrast increased to two (Figure 4b) and three times threshold (Figure 4c) and up to 100% contrast (Figure 4d), saccade size became smaller and smooth pursuit prevailed.

Our results show that below a contrast level of two to three times threshold, smooth pursuit was severely impaired but improved considerably with increasing contrast. In Figures 5-8, means for pursuit gain, latency, position error, and acceleration are plotted separately for three velocities and four spatial frequencies across all subjects. The data and effects shown were stable across all subjects. Figure 9 summarizes these results across all spatial frequencies showing means for the pooled data. Note that those trials with stimuli outside the window of visibility (conditions marked red in Table 1) were excluded from the analysis of latency and initial acceleration, because the initiation of pursuit might be due to other frequency components.

Gain

Smooth pursuit steady-state gain increased as a function of stimulus contrast (Figure 5 and Figure 9a). At two times threshold, where subjects only made judgment errors in 2.5% of all trials, gain was 0.76 on average across all conditions and reached a maximum of 0.92 compared to an average gain of 0.93 and a maximum gain of 0.97 at 100% contrast. For slow target velocity (1 deg/s), pursuit gain increased linearly with increasing contrast (Figure 5a).

Fitting a regression line for gain for slow stimuli yielded a slope of 0.05. When doubling the contrast from threshold to two times threshold, gain rose by 0.1. For slow stimuli, there was also no influence of spatial frequency on gain, indicating that the pursuit system estimated similar target speeds for all slow-moving stimuli. For stimuli moving at 8 or 15 deg/s, the rise in pursuit gain with increasing contrast was very steep at low-contrast levels, and nearly flat at higher contrast levels above two times threshold. However, when fitting a regression line for gain (velocity = 8 and 15 deg/s, contrast ≥ two times threshold), the slope of the regression line was still larger than zero. Therefore, gain increased significantly even with high-contrast stimuli moving at medium and high velocities. At higher velocities (8 and 15 deg/s), there was also a variability of gain with spatial frequency (Figure 5b and 5c). At spatial frequencies ≤ 1 c/deg and contrasts near threshold, gain rose monotonically. At spatial frequencies ≥ 1 c/deg and two times threshold, gain saturated. There was a similar trend at 15 deg/s velocity (Figure 5c).

A two-way repeated measures ANOVA (contrast x velocity) yielded an overall significant effect of contrast on smooth pursuit gain, $F(6,30) = 170.66$, $p < .001$, and a significant interaction between contrast and velocity, $F(12,60) = 8.91$, $p < .001$. A possible main effect of spatial frequency was tested at three contrast levels (at threshold, two, and three times threshold) using a two-way repeated measures ANOVA (contrast x spatial frequency). We found a significant main effect of spatial frequency for gain, $F(3,15) = 12.33$, $p < .001$.

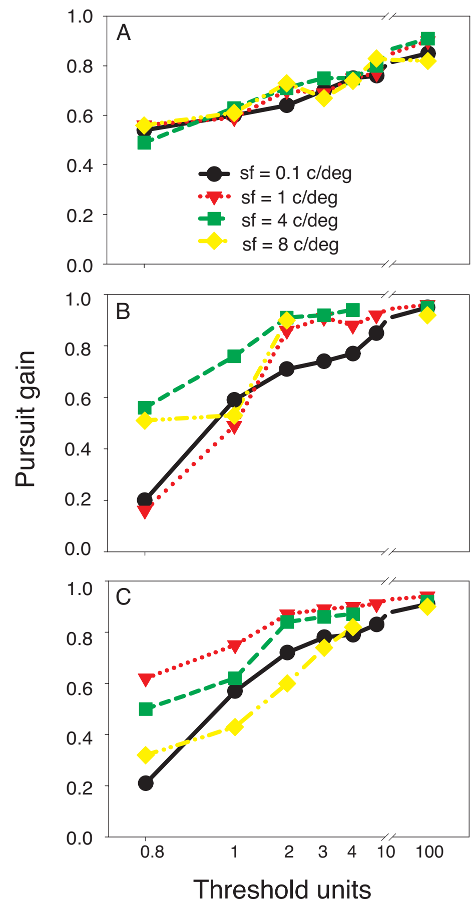

Figure 5. Means for smooth pursuit gain for three stimulus velocities (from a to c: 1, 8, and 15 deg/s) and seven threshold units. Different line colors indicate the four spatial frequencies.

Latency

Smooth pursuit latency decreased with increasing stimulus contrast (Figure 6 and Figure 9b). Concerning pursuit onset at two times threshold, latency was as long as 227 ms on average across all conditions. Pursuit latency normally ranges from 80 to 150 ms after stimulus onset (Ilg, 1997). Pursuit latency at 100% contrast was 135 ms on average.

A two-way repeated measures ANOVA (contrast x velocity) revealed an overall significant effect of contrast, $F(6,30) = 80.99$, $p < .001$, and a significant interaction between contrast and velocity, $F(12,60) = 17.39$, $p < .001$.

There was no effect of spatial structure on latency at a slow velocity of 1 deg/s (Figure 6a). At a velocity of 8 deg/s, at spatial frequency = 0.1 c/deg, and for contrast ≥ threshold, latency decreased monotonically, whereas at spatial frequency = 1 c/deg, latency decreased steeply until it saturated by two times threshold (Figure 6b). At a velocity of 15 deg/s (Figure 6c), again, there was no big effect of spatial

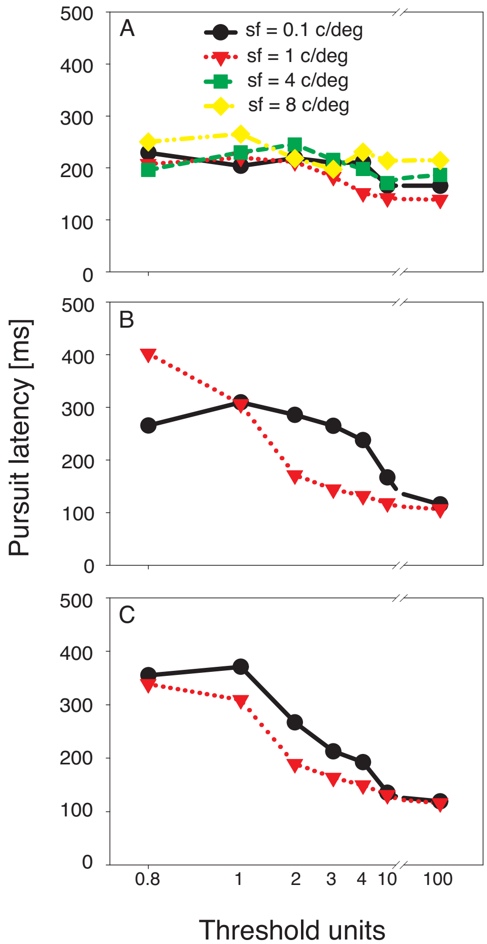

Figure 6. Means for smooth pursuit latency for three stimulus velocities (from a to c: 1, 8, and 15 deg/s) and seven threshold units. Different line colors indicate the four spatial frequencies.

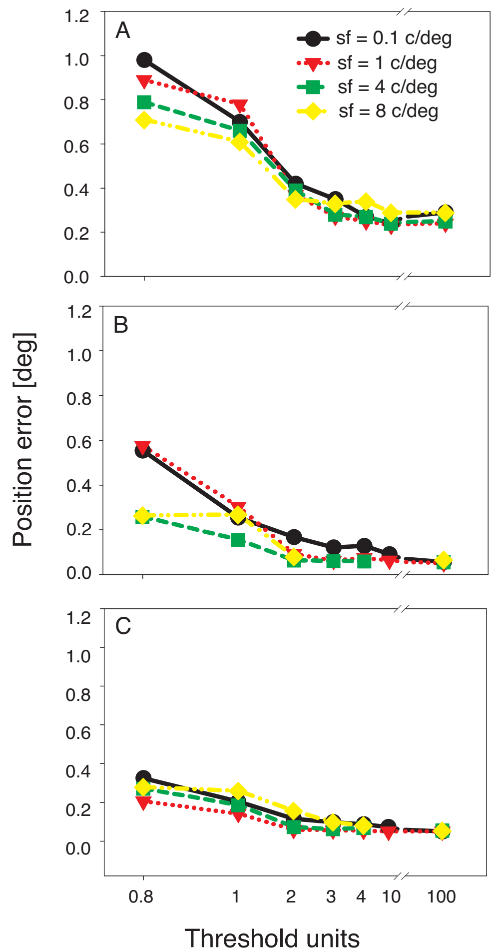

Figure 7. Means for smooth pursuit position error for three stimulus velocities (from a to c: 1, 8, and 15 deg/s) and seven threshold units. Line colors indicate the four spatial frequencies. Position error was calculated as root mean squared deviation of eye position from target position, and was normalized by target velocity.

frequency: Latency decreased monotonically over a range of contrasts from threshold to maximum. Overall, the effect of spatial frequency ≤ 1 c/deg on latency was significant, $F(1,5) = 38.58$, $p < .01$.

Position error

Position error decreased with increasing stimulus contrast (Figure 7 and Figure 9c). For stimuli moving at a velocity of 1 deg/s, the decrease with increasing contrast was steep for lower contrast levels and nearly flat above two times threshold. For stimuli moving at 1 deg/s, position error dropped from 0.84 deg at contrasts below threshold to 0.38 deg at two times threshold, and saturated with yet higher contrasts. The effects of contrast, $F(6,30) = 11.74$, $p < .001$, velocity, $F(2,10) = 92.97$, $p < .001$, and the interaction between contrast and velocity, $F(12,60) = 11.74$, $p < .001$, were significant. Effects of spatial frequency were also significant at threshold, and two and three times threshold, $F(3,15) = 13.19$, $p < .001$.

Acceleration

Initial acceleration increased as a function of stimulus contrast (Figure 8 and Figure 9d) for velocities 8 and 15 deg/s, especially at low contrast. Mean acceleration for velocity = 8 deg/s was 44 deg/s^2 at threshold and increased to 82 deg/s^2 at three times threshold. For velocity = 15 deg/s, mean acceleration at threshold was 107 deg/s^2 and increased to 138 deg/s^2 at three times threshold.

The ANOVA yielded an overall significant effect of velocity, $F(6,30) = 188.7$, $p < .001$. The effect of contrast and the interaction between contrast and velocity were not significant, although there was a clear increase in acceleration with increasing contrast for low-contrast levels, spatial frequency = 0.1 c/deg, and medium and high target speeds. There was no significant effect of spatial frequency on initial acceleration.

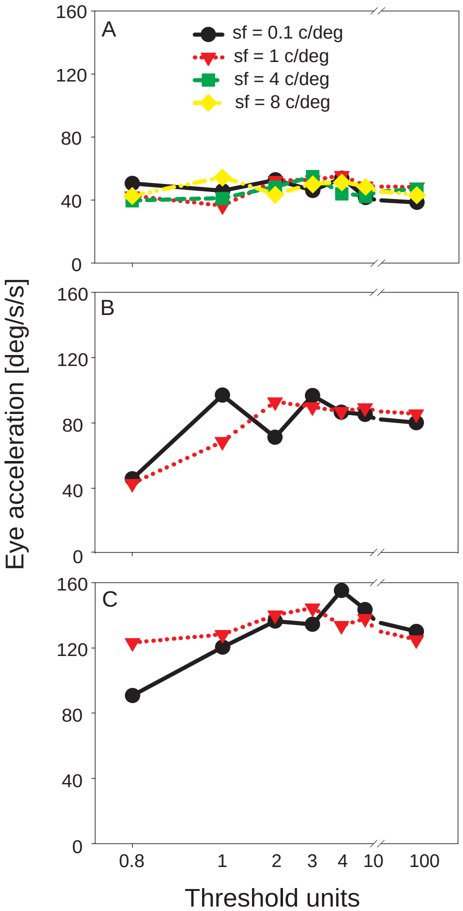

Figure 8. Means for smooth pursuit initial acceleration for three stimulus velocities (from a to c: 1, 8, and 15 deg/s) and seven threshold units. Different line colors indicate the four spatial frequencies.

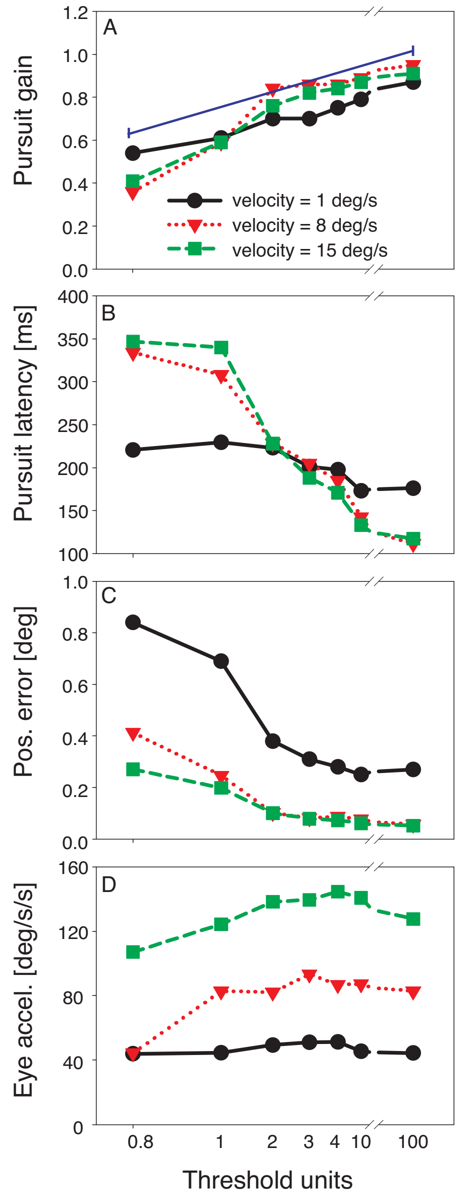

Figure 9. Means for smooth pursuit gain (a), latency (b), position error (c), and initial acceleration (d) for three stimulus velocities (1, 8, and 15 deg/s), as indicated by the line colors, and seven threshold units. The blue regression line in Figure 9a indicates perceptual data from a previous study by Gegenfurtner and Hawken (1996). Depicted is the fitted regression line to mean values (four subjects) for effects of contrast on perceived velocity of gratings moving at 1 Hz.

Discussion

Summary of results

We have shown that smooth pursuit eye velocity gain increased as a function of contrast, but there are different effects of contrast depending on target speed. At a slow target velocity, there is a linear increase in pursuit gain with increasing contrast across all contrast levels. This result is in line with psychophysical effects of relative velocity judgments with contrast at low speeds. For faster target velocities (> 1 deg/s), there is a steep rise in gain as contrast rises above two to three times threshold. The effect of contrast then saturates, but there is still a small increase even at the highest levels of contrast. The effect of contrast is therefore small at higher contrast levels and large at low-contrast levels. Velocity estimation and smooth pursuit eye movement characteristics were also affected by changes in spatial frequency, but the effect was unsystematic.

Comparison with previous studies

Our results are in general agreement with previous studies on the effect of contrast on perception and smooth pursuit. Perceptual slowing has been reported to be more pronounced in slowly moving stimuli (Stone & Thompson, 1992; Thompson, 1982). Hawken and Gegenfurtner (2001) found a reduction in eye velocity with decreasing contrast for first-order motion targets, but only for slow targets moving at 1 deg/s. We also found a small effect at high velocities above two times threshold and a dramatic effect for fast targets at threshold that has not been studied previously. Our results are similar to perceptual data gathered in previous studies (e.g., Gegenfurtner & Hawken, 1996; Hawken et al., 1994; Stone & Thompson, 1992), although different retinal stimuli were used. In the experiment reported here, we used relatively small, moving Gabor patches and asked subjects to track the target, whereas previous psychophysical experiments mostly employed drifting or flickering gratings that were presented foveally or perifoveally while the subject was fixating. The similarity to perceived velocity judgments in a study by Gegenfurtner and Hawken (1996) is shown in Figure 9a. The blue regression line, indicating the dependence of velocity judgments (comparison vs. standard grating moving at 1 Hz) on relative contrast for four subjects (Gegenfurtner & Hawken, 1996, p. 1283, Figure 1) can be compared to the results for stimuli moving at 1 deg/s in the experiment reported here. In this study, we did not directly compare psychophysical velocity judgments and pursuit velocity gain, although this would be desirable. However, a direct comparison on the same trial is difficult to obtain, because smooth pursuit eye movements systematically affect the perceived speed of a stimulus compared to its perceived speed when viewed with a stationary eye (Freeman & Banks, 1998; Turano & Heidenreich, 1999). When a person's eyes move in the same direction as a distal stimulus, the stimulus appears slower than when the person's eyes are stationary.

Recently, Priebe and Lisberger (2004) found that for each of two target velocities (8 and 15 deg/s), eye velocity and acceleration declined with decreasing contrast and as spatial frequency increased from 0.25 to 1 c/deg at 8 and 32% contrast. Furthermore, the authors concluded that the effect of spatial frequency increases with contrast, resulting in a twofold increase in pursuit acceleration for a fourfold increase in contrast for high-contrast targets. Our results for the effect of spatial frequency are inconsistent across velocities, and there is no significant effect of spatial frequency on acceleration. However, our findings are not directly comparable to those obtained by Priebe and Lisberger (2004). In the study by Priebe and Lisberger (2004), only a narrow range of spatial frequencies between 0.25 and 1 c/deg was employed, whereas we used a wide range of spatial frequencies between 0.1 and 8 c/deg. More importantly, Priebe and Lisberger (2004) used absolute contrast measurements, whereas we calculated contrast relative to the perceptual threshold. The use of effective contrast also distinguishes the present study from other studies on the influence of contrast on smooth pursuit eye movements (e.g., Brown, 1972; Haegerstrom-Portnoy & Brown, 1979).

To sum up, we argue that there is no systematic effect of spatial frequency on pursuit per se. Changes in stimulus contrast are changes to the quality of visual information and affect the estimation of target speed by the pursuit system more than changes in spatial frequency. Weiss, Simoncelli, and Adelson (2002) put forward an ideal observer model claiming that perceptual slowing is the result of a coherent computational strategy that is optimal when estimating image velocity under uncertainty (see also Hurlimann, Kiper, & Carandini, 2002). When stimulus contrast is low, local image measurements are noisy and the exact speed of the stimulus is more difficult to determine. Velocity is underestimated because slower velocities are assumed to be more likely to occur than fast ones. Stimuli at low contrast produce small and noisy responses of neurons in the active population. Vector averaging with a bias toward low speeds is employed for target speed estimation (thus resulting in a lower gain at low contrast; Priebe & Lisberger, 2004).

Conclusions

We conclude that poor signal quality at low contrast makes it difficult for the pursuit system to reliably estimate velocity. Apparently, contrast has to be at least twice threshold for the stimulus to be pursued properly. Evidence for the notion that the pursuit system does not engage well near threshold is given by the finding that pursuit is supplemented by saccades to maintain foveation. The internal position signal might be less affected by noise at low contrast, resulting in a pursuit-saccadic trade-off. The similarity between perceptual velocity gain found in previous studies and pursuit velocity gain in our data supports the assumption that perceptual and motor responses are driven by a shared neural signal (Gegenfurtner, Xing, Scott, & Hawken, 2003; Stone & Krauzlis, 2003).

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