

Contrast sensitivity during the initiation of smooth pursuit eye movements

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Abstract

Eye movements challenge the perception of a stable world by inducing retinal image displacement. During saccadic eye movements visual stability is accompanied by a remapping of visual receptive fields, a compression of visual space and perceptual suppression. Here we explore whether a similar suppression changes the perception of briefly presented low contrast targets during the initiation of smooth pursuit eye movements. In a 2AFC design we investigated the contrast sensitivity for threshold-level stimuli during the initiation of smooth pursuit and during saccades. Pursuit was elicited by horizontal step-ramp and ramp stimuli. At any time from 200 ms before to 500 ms after pursuit stimulus onset, a blurred 0.3 deg wide horizontal line with low contrast just above detection threshold appeared for 10 ms either 2 deg above or below the pursuit trajectory. Observers had to pursue the moving stimulus and to indicate whether the target line appeared above or below the pursuit trajectory. In contrast to perceptual suppression effects during saccades, no pronounced suppression was found at pursuit onset for step-ramp motion. When pursuit was elicited by a ramp stimulus, pursuit initiation was accompanied by catch-up saccades, which caused saccadic suppression. Additionally, contrast sensitivity was attenuated at the time of pursuit or saccade stimulus onset. This attenuation might be due to an attentional deficit, because the stimulus required the focus of attention during the programming of the following eye movement.

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1. Introduction

Suppression of visual contrast sensitivity is one of the mechanisms of the visual system to prevent spatial instability every time when a saccade causes a rapid large-field movement of the retinal image (Ross, Morrone, Goldberg, & Burr, 2001). In the present study, we investigated whether contrast sensitivity is similarly attenuated by the initiation of smooth pursuit eye movements.

Primates equipped with a fovea use both, saccadic and smooth pursuit eye movements to scan their environment and to track visual targets. Saccades correct position errors by a rapid redirection of the line of sight to the selected target. Smooth pursuit stabilizes the image of the moving

object on the fovea and compensates for velocity errors. Both types of eye movements challenge the perception of a stable world by inducing either rapid retinal image displacements in the case of saccades, or continuous retinal image motion in the case of pursuit. As we usually do not perceive these movements during our eye movements, they have to be compensated by the visual system.

For saccades, perceptual stability seems to be accomplished by a remapping of visual receptive fields before and during the saccade (Colby, Duhamel, & Goldberg, 1995; Duhamel, Colby, & Goldberg, 1992; Merriam, Genovesi, & Colby, 2007; Nakamura & Colby, 2002) and by perceptual suppression of visual stimuli during the saccade (Holt, 1903; Latour, 1962; see Ross et al., 2001 for a review). Saccadic suppression may help to disregard the retinal image motion, which is induced by saccades. This suppressive effect has a duration of about 100 ms and is centered on the saccade onset, where

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suppression is strongest. Burr, Holt, Johnstone, and Ross (1982) showed that the suppression effect is selective for low spatial frequencies. It has been suggested that saccadic suppression only affects the magnocellular pathway, because only the perception of luminance-modulated stimuli is suppressed, while the perception of color-modulated, isoluminant stimuli remains unchanged (Burr, Morrone, & Ross, 1994; Ross, Burr, & Morrone, 1996; Uchikawa & Sato, 1995). The magnitude of the suppression depends on the stimulus contrast, showing a stronger suppression effect for lower contrast stimuli (Michels & Lappe, 2004). Furthermore, the magnitude of suppression also increases with the amplitude of the saccade (Mitrani, Yakimoff, & Mateeff, 1970; Ridder & Tomlinson, 1997; Stevenson, Volkman, Kelly, & Riggs, 1986). It is also known that saccadic suppression is driven by an extraretinal source rather than by simple retinal image motion (Diamond, Ross, & Morrone, 2000). The pre- and perisaccadic remapping of receptive fields may help to compensate the retinal displacement of objects. It was found that saccadic eye movements release a shift of receptive fields in LIP to a coordinate system that is arranged to the post-saccadic center of gaze (Ben Hamed, Duhamel, Bremmer, & Graf, 2002; Duhamel et al., 1992; Heiser & Colby, 2006; Kusunoki & Goldberg, 2003). This remapping has also been observed in other brain areas, for instance in extrastriate visual cortex (Nakamura & Colby, 2002).

For smooth pursuit, less is known about the mechanisms which maintain perceptual stability. There is some evidence that a remapping of visual receptive fields not only happens during saccades, but also during pursuit eye movements. Hartmann, Bremmer, Albright, and Krekelberg (2006) demonstrated a remapping of visual receptive fields during the slow phase of the optokinetic nystagmus, which is comparable to smooth pursuit eye movements (Ilg, 1997; Konen, Kleiser, Seitz, & Bremmer, 2005). This remapping may compensate the effects of the retinal displacement, but it is still unclear, how the visual system compensates the retinal image motion. To investigate this issue we have to differentiate between the initiation of smooth pursuit and the steady state phase. It is commonly assumed that the retinal image motion is canceled by a reafference signal when pursuit is in steady state (von Holst & Mittelstaedt, 1950). However, the Filehne illusion (Filehne, 1922; Mack & Herman, 1973) and the Aubert–Fleischl illusion (Aubert, 1886; Fleischl, 1882; Wertheim & Van Gelder, 1990) show that this extraretinal signal is not exact and therefore the eye velocity is not compensated completely. The contrast sensitivity during steady state of smooth pursuit has been investigated in several studies (Flipse, Van der Wildt, Rodenburg, Keemink, & Knol, 1988; Murphy, 1978; Starr, Angel, & Yeates, 1969; Liu & Jiang, 1984). For targets located in the fovea, no difference was found in contrast sensitivity during fixation and pursuit. Recently, Schütz, Delipetkos, Braun, Kerzel, and Gegenfurtner (2007)

showed that temporal contrast sensitivity for peripheral targets is reduced during smooth pursuit.

The cancellation of the retinal image motion during the initiation of smooth pursuit is a bigger challenge for the visual system. Here, the eyes accelerate and visual background and pursuit stimulus move across the retina until the eye velocity reaches the target velocity and the pursuit stimulus is stabilized on the retina. As these conditions are similar to saccades, it is possible that the compensation of retinal image motion is accomplished by a similar mechanism as during saccades, namely by a suppression of visual sensitivity. Contrast sensitivity during the initiation of smooth pursuit eye movements has not yet been studied, although during this phase of pursuit perception is most similar to saccades. During saccades, the eyes accelerate up to 22,000 deg/s² for a saccade amplitude of 10 deg and during pursuit, peak acceleration goes up to 1000 deg/s² (Leigh & Zee, 1999). Furthermore, the initiation phase of pursuit (between 80 and 120 ms) takes place without visual feedback and operates therefore in the open loop mode (Lisberger & Westbrook, 1985), which is also true for the duration of saccade execution. Based on these similarities between saccades and the initiation of smooth pursuit, we wanted to explore, if the retinal image motion is compensated by a suppression of contrast sensitivity during pursuit initiation as well as during saccades.

Furthermore the contrast sensitivity during pursuit initiation may be influenced by attentional effects. It is well known that spatial attention shifts are closely correlated to eye movements (Moore & Fallah, 2001). For saccades it has been shown that spatial attention is shifted to the future saccade target before the saccade is executed (Deubel & Schneider, 1996; Kowler, Anderson, Doshier, & Blaser, 1995; McPeck, Maljkovic, & Nakayama, 1999). For smooth pursuit it has been shown that attention has to be directed upon the pursuit target in the steady-state phase (Kerzel & Ziegler, 2005; Khurana & Kowler, 1987) but the attentional demand seems to be higher during pursuit onset and offset than during the steady state (Van Donkelaar, 1999). We therefore wanted to investigate if there is some attentional modulation in contrast sensitivity during the initiation of smooth pursuit eye movements.

2. Methods

2.1. Design

We used a 2AFC paradigm to measure the detection thresholds at different points in time during the initiation of pursuit. We presented line stimuli with a fixed contrast at various points in time relative to the pursuit stimulus motion onset. Prior to the experiments, the individual threshold for the target line during fixation was determined. For the actual experiments line contrast was set to a value of 80% detection base rate. Subjects ran the experiments in several blocks of 150 trials. If the average detection rate in one block became too high, possibly due to perceptual learning (Fine & Jacobs, 2002; Sowden, Rose, & Davies, 2002), the line contrast was adjusted to a lower value for the next block. The previous measure-

ments were kept. The contrast was lowered in 5% steps. Such an adaptive change was necessary in all subjects, on average twice. We tested how different motion onset conditions affect detection performance.

2.3. Subjects

The eight subjects were between 22 and 50 years of age ($M = 29 \pm 9$ years). Five of them were female. All subjects had normal visual acuity or were slightly myopic. The myopes performed the experiments without their optical corrections. Five of the subjects were naive with respect to the experiment, two subjects were the authors A.C.S. and D.I.B., and one subject was a colleague experienced in psychophysical experiments. Every experiment was performed by six subjects, four subjects took part in all experiments.

2.4. Equipment

Subjects were seated in a dimly lit room facing a 21-inch CRT monitor (ELO Touchsystems, Fremont, CA, USA) driven by an ASUS V8170 (Geforce 4MX 440) graphics board with a refresh rate of 100 Hz non-interlaced. At a viewing distance of 47 cm, the active screen area subtended 45 deg of visual angle in the horizontal direction and 36 deg vertical on the subject's retina. With a spatial resolution of 1280×1024 pixel, this results in 28 pixel/deg. The subject's head was fixed in place using a chin rest.

2.5. 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. Subjects viewed the display binocularly. Stimulus display and data collection were controlled by a PC.

2.6. Visual stimuli

A black bull's-eye with an outer radius of 0.3 deg and an inner radius of 0.15 deg was used as pursuit and saccade stimulus, respectively. To measure contrast sensitivity, we used a horizontal line, which subtended the whole screen width. The luminance of the line was vertically modulated by a Gaussian distribution with a standard deviation of 0.15 deg.

2.7. Experimental procedure

At the beginning of each trial, a fixation spot appeared in the center of the screen. The fixation spot had the same properties as the pursuit stimulus, but had an inner radius of 0.075 deg. The subjects had to fixate the spot and press an assigned button to start the trial. With pressing the button, the EyeLink II System performed a drift correction to correct errors of headband slippage or other factors. If the drift correction succeeded, the fixation spot was replaced by the bull's-eye. After a randomized delay between 600 and 700 ms the bull's-eye started moving with the respective velocity for 1 s. At a time from 200 ms before motion onset to 500 ms after motion onset, the target line appeared either 2 deg above or below the pursuit trajectory for 10 ms. At the end of the trial, subjects had to indicate the position of the target line by pressing either an "up" or "down" button. The movement direction of the bull's-eye and the position of the line were randomized. Fig. 1 illustrates the procedure for a single trial.

Experiment 1, step-ramp stimulus: In this experiment, we used a step-ramp stimulus (Rashbass, 1961) with a velocity of 10.57 deg/s as pursuit stimulus. At a step size of 2.11 deg to the left or right of the fixation spot, the pursuit stimulus returned to the central position within 200 ms.

Experiment 2, ramp stimulus with 10.57 deg/s: In this experiment, we used a simple ramp stimulus, which started moving from the central position, with a velocity of 10.57 deg/s as pursuit stimulus.

Experiment 3, ramp stimulus with 21.14 deg/s: The only difference to Experiment 2 was that the ramp stimulus moved with a velocity of 21.14 deg/s.

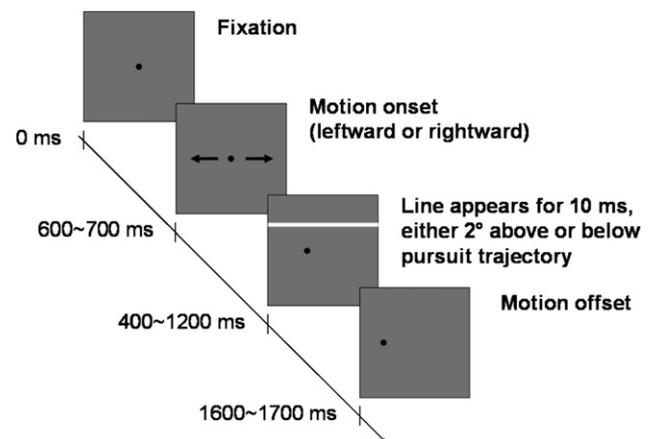


Fig. 1. Schematic diagram of one ramp trial.

Experiment 4, step stimulus: In the last experiment, we tested how saccades affect the detection threshold for the target line. In this case, the bull's-eye did not move at a constant velocity, but disappeared at the center and reappeared immediately at 15 deg eccentricity on the horizontal median, where it remained stationary for 1 s. The line onset was varied between 100 ms before saccade stimulus onset and 400 ms after saccade stimulus onset.

Fig. 2 illustrates the different stimulus motions in the experiments.

2.8. Oculometric analysis

Eye position traces for individual trials were stored on disk for off-line analysis. Eye velocity signals were obtained by digital differentiation of eye position signals over time. The eye position signals were filtered by a second-order Butterworth filter with a cut-off frequency of 30 Hz. The eye velocity signals were filtered by a Butterworth filter with a cut-off frequency of 20 Hz.

The pursuit onset for each individual trial was obtained by determining the best fitting regression line in a specified time interval. In the time interval from 80 ms to 300 ms after pursuit stimulus motion onset, starting with every sample, regression lines with a length of 80 ms were fitted to the velocity trace. The best fitting regression line was selected from all regression lines with a slope between 10 and 200. The interception between the selected regression line and the x -axis was defined as pursuit onset. This procedure led to similar results as the method described by Carl and Gellman (1987), but was more robust. Trials were visually inspected and discarded if the procedure did not lead to a reasonable estimation of pursuit onset (less than 10% of trials). The pursuit gain of each trace was determined as the average velocity during the period from 400 ms to 800 ms after pursuit stimulus motion onset, divided by the pursuit stimulus velocity. Saccades were detected by a cut-off criterion ($75,000 \text{ deg/s}^3$) on the third derivative of eye position (Wyatt, 1998). We used this method, because common velocity based algorithms are often problematic in detecting saccades during ongoing pursuit. In conjunction with the low pass filtering of position and velocity traces and a low cut-off criterion, the used procedure determined saccade onset too early. For horizontal saccades in Experiment 4, the onset difference to the results of a standard velocity based algorithm (Michels & Lappe, 2004) was approximately 34 ms.

In Experiments 1–3, trials with a gain lower than 0.8 were excluded from further analysis (10% of trials in Experiment 1, 20% of trials in Experiments 2 and 3). In all experiments, trials with saccades in a critical interval of 200 ms centered on target line onset were excluded (less than 10% of trials in all experiments). In Experiment 1, trials with saccades during the initiation of pursuit (first 400 ms after pursuit stimulus onset) were also excluded (less than 20% of trials). As a ramp stimulus always elicits initial saccades during the initiation of smooth pursuit, in Experiment 2 and 3 the first two saccades after pursuit stimulus onset were not considered for the exclusion criteria. The first saccade after stimulus onset in Experiment 4 was also not considered.

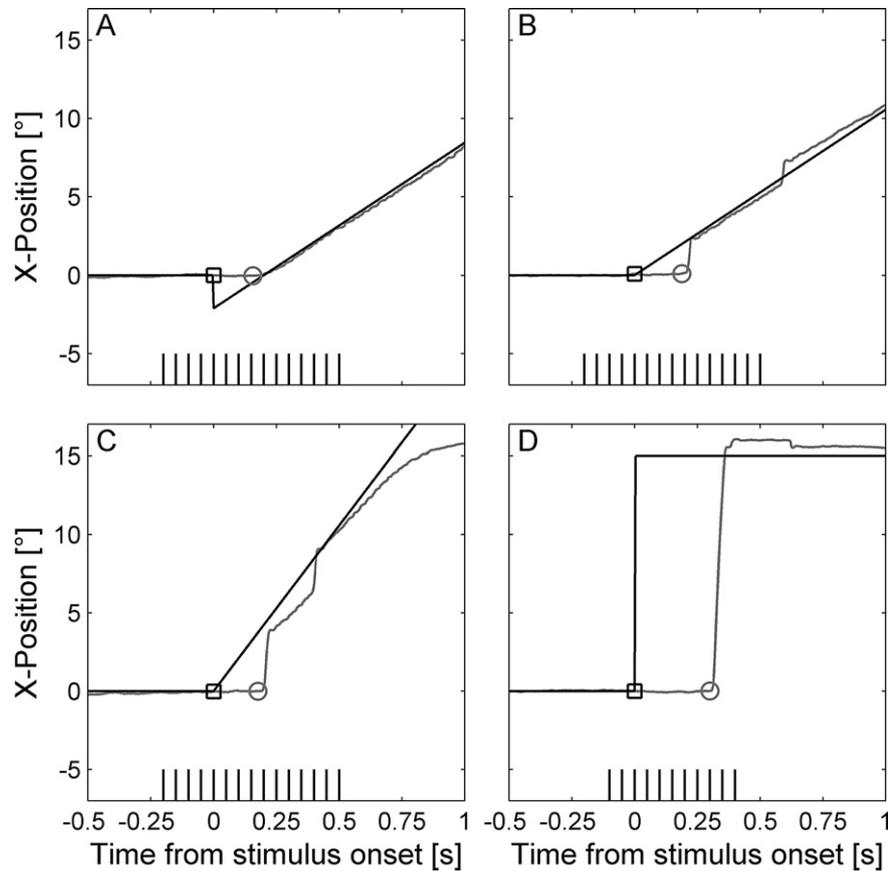


Fig. 2. Timing and position plots of pursuit and saccade stimuli for all four experiments and the resulting typical eye positions. (A) Step-ramp stimulus with 10.57 deg/s (Experiment 1). The black line represents the stimulus position for the eye movements and the gray line the corresponding eye position. The black square marks the stimulus onset and the gray circle the pursuit onset (A) or saccade onset (B–D). The small vertical lines at the abscissa represent points in time at which the target line could appear. (B) Ramp stimulus with 10.57 deg/s (Experiment 2). (C) Ramp stimulus with 21.14 deg/s (Experiment 3). (D) 15 deg step stimulus (Experiment 4).

2.9. Psychophysical data analysis

For each subject, the detection performance over the whole range of presentation times of the target line was determined by calculating a weighted sliding histogram. The optimal bin size bs was calculated for each subject by Eq. (1) (Scott, 1979), in which N is the number of all samples and σ is the standard deviation of the presentation times of the line. The bin size was on average 95 ms, with a standard deviation of 10 ms.

$$bs = 3.49 \times \sigma \times N^{-1/3} \quad (1)$$

This bin was then moved in 4 ms steps, which is the temporal resolution of the eye tracker that we used, over the whole range of line presentation times. Within each bin the proportion of correct responses was calculated. Every response within a bin was weighted by its inverse distance from the center of the bin, which is shown in Eq. (2). Here bs is the bin size, m indicates the center of the bin and t the time of one response.

$$w = \sqrt{|t - m| - 1/2 \times bs} \times 2/bs \quad (2)$$

To quantify changes in detection performance, we decided to use a signal-detection paradigm, similar to the method used by Lindner, Schwarz, and Ilg (2001). As the typical saccadic suppression profile over time resembles a negative valued Gaussian, we fitted Gaussian distributions to time spans of special interest. We selected two regions of 220 ms width, centered either on pursuit stimulus/saccade stimulus onset or pursuit/saccade onset. In both regions, the detection rates were fitted by Eq. (3).

$$a \times G(\mu, \sigma, t) + b \quad (3)$$

G is a standard Gaussian equation, t is the time relative to eye onset, μ determines the location of the Gaussian peak on the time axis and σ determines the width of the Gaussian peak. b stands for the baseline response rate and a reflects the effect size. Only the region within 1.5 standard deviations around μ was fitted. The scaling parameter a was used to quantify the amount of suppression or enhancement in the respective interval. As we did not want to constrain the analysis to suppression effects, the amplitude of the Gaussian was allowed to be positive as well, so that possible enhancements could be approximated, too. This way, random variations in the detection rate would lead to a net amplitude a of zero.

3. Results

3.1. Experiment 1, step-ramp stimulus

Fig. 3 shows the detection rates for the peripheral horizontal target line during pursuit, elicited by a step-ramp stimulus for three exemplary subjects. The line detection rate is plotted relative to the pursuit onset. For all subjects a slight reduction of the line detection rate was found during pursuit stimulus motion onset. The amplitudes of the Gaussian fits (parameter a in Eq. (3)) during pursuit stimulus motion onsets were significantly below zero (mean = $-.20$; student's t -test, $t(5) = 4.11$, $p = .01$), indicating a reduction in detection rate at stimulus motion onset. At pursuit onset, there

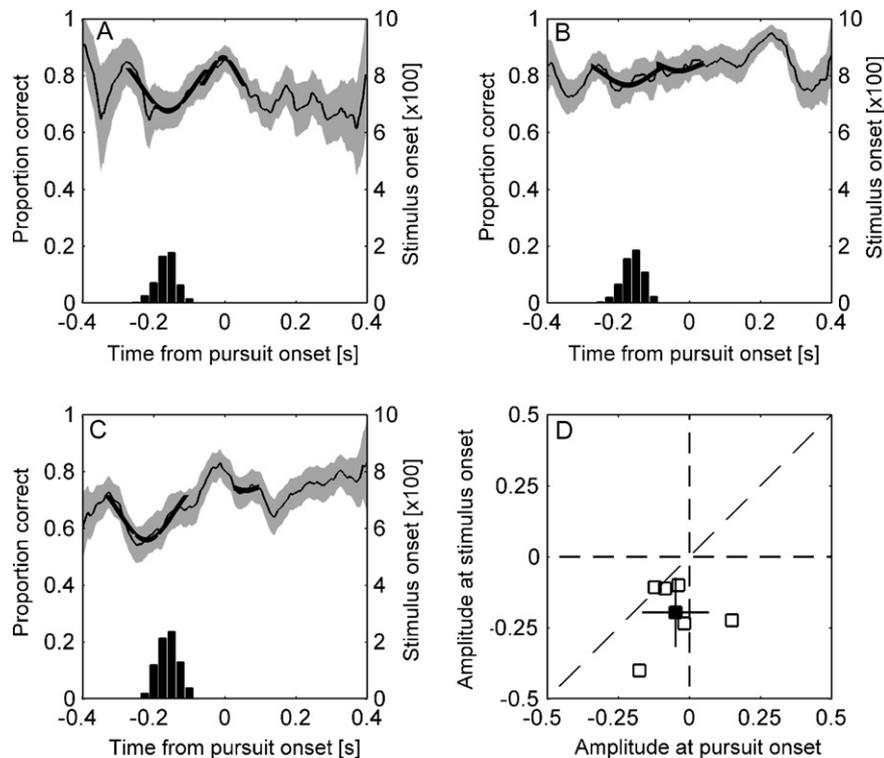


Fig. 3. Experiment 1: Contrast sensitivity during pursuit in response to a step-ramp stimulus with 10.57 deg/s. (A–C) Data for three subjects. The thin black line indicates the detection rate at different presentation times relative to pursuit onset. The gray shaded area represents the standard error of the detection rates. Detection rates are plotted along the left y axis. The black histogram indicates the pursuit stimulus motion onset relative to pursuit onset. Stimulus motion onsets are plotted along the right y axis. The bold black lines show Gaussian fits of the detection performance during stimulus motion onset respective pursuit onset. (D) Amplitudes of the Gaussian fits during pursuit onset and during stimulus onset. Open squares indicate the individual data. The filled square represents the mean value over six subjects, the error bars denote the 95% confidence interval of the mean.

was only a slight trend for suppression of the line. The amplitudes of the Gaussian fits during pursuit onset were not significantly different from zero (mean = $-.05$; student's t -test, $t(5) = 1.05$, $p = .34$), indicating that there was no visual suppression of peripheral targets at pursuit onset.

3.2. Experiment 2, ramp stimulus with 10.57 deg/s

In our second experiment, we investigated a different type of smooth pursuit initiation. Outside the laboratory, a stimulus typically just starts moving, without making a backward step first. In response to such a ramp stimulus, pursuit initiation is accompanied by catch-up saccades. Here we tested if catch-up saccades executed during the initiation of smooth pursuit cause a saccadic suppression effect. To evoke catch-up saccades during pursuit initiation, we used a simple ramp stimulus starting to move from the central fixation point. Fig. 4 shows the line detection rates during pursuit elicited by ramp stimuli for three exemplary subjects. In this graph the line detection rate is plotted relative to the onset of the first saccade after ramp motion onset and like in Experiment 1 the line detection rate was slightly reduced at ramp motion onset. The amplitudes of the Gaussian fits during ramp motion onset were significantly below zero (mean = $-.15$; student's t -test, $t(5) = 3.74$, $p = .01$) which replicates the findings of our first experiment. However, the line detection rates at the

onset of the first saccade after ramp motion onset tended to be attenuated. The amplitudes of the Gaussian fits during saccade onset were just not significant below zero (mean = $-.08$; student's t -test, $t(5) = 2.40$, $p = .06$).

A possible explanation for the lack of saccadic suppression could be that the saccadic amplitudes were too small to produce a significant suppression effect. The size of the saccadic amplitude is known to influence the magnitude of the suppression (Mitrani et al., 1970; Ridder & Tomlinson, 1997; Stevenson et al., 1986). In fact the amplitudes of the first saccades were rather small (average amplitude across subjects: 2.5 deg, standard deviation: 0.6). Moreover, the amplitudes of the first saccades correlated positively with the latency (average correlation across subjects: 0.5, standard deviation: 0.3, all individual correlations were significant at the $p = 0.05$ level). This way, the saccadic amplitude depends on the distance which is covered by the pursuit stimulus during the saccadic latency. Based on this observation, we used a higher pursuit velocity in Experiment 3 to increase the amplitudes of the first saccades. Higher saccadic amplitudes should lead in turn to stronger suppression effects.

3.3. Experiment 3, ramp stimulus with 21.14 deg/s

Fig. 5 shows the target line detection rates during pursuit elicited by a ramp stimulus with a velocity of

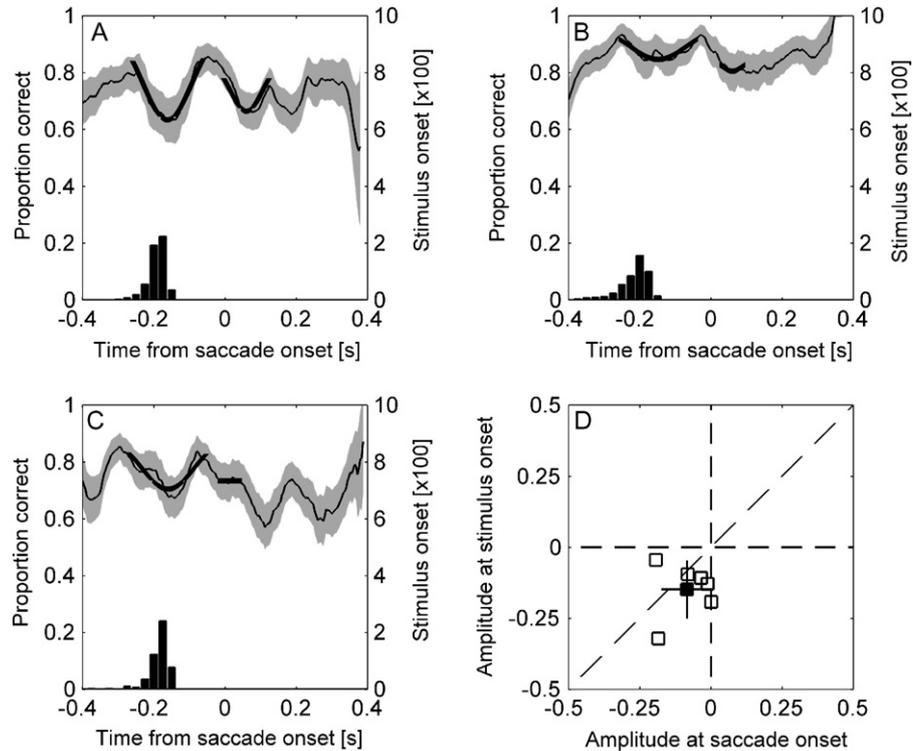


Fig. 4. Experiment 2: Contrast sensitivity during pursuit in response to a ramp stimulus with 10.57 deg/s. The conventions are the same as in Fig. 3. (A–C) Data for three subjects. Here the data is aligned to saccade onset. (D) Amplitude of the Gaussian fits during saccade onset and during stimulus onset.

21.14 deg/s. Like in Fig. 3, the line detection rates are plotted relative to the onset of the first saccade after ramp motion onset. There was a pronounced suppression effect on the detection rate of the line at saccade onset in all subjects. The amplitudes of the Gaussian fits were significantly below zero (mean = $-.15$; student's t -test, $t(5) = 5.06$, $p < .01$). Three of six subjects also showed a reduction of the line detection rate during ramp motion onset. Although, the amplitudes of the Gaussian fits during ramp motion onset were not significantly below zero (mean = $-.04$; student's t -test, $t(5) = 0.57$, $p = .59$), there was a tendency for an attenuation during ramp motion onset.

Our assumption about the amplitudes of the first saccades was correct. Like in Experiment 3, the amplitudes of the first saccades depended on the latency of the saccade (average correlation across subjects: 0.6, standard deviation: 0.3, all individual correlations significant at the $p = 0.05$ level). The higher pursuit velocity led to higher saccadic amplitudes (average amplitude across subjects: 4.8, standard deviation: 1.3) and a stronger suppression of the line detection rate.

3.4. Experiment 4, step stimulus

In the fourth and final experiment, we investigated whether the attenuation of contrast sensitivity at stimulus onset also occurs for saccades without any smooth pursuit initiation. Therefore we measured the detection of a target

line during horizontal saccades of 15 deg. Fig. 6 shows the line detection rates relative to the onset of the saccade. All subjects showed a pronounced suppression effect at saccade onset. The amplitudes of the Gaussian fits were significantly below zero during saccade onset (mean = $-.38$; student's t -test, $t(5) = 7.82$, $p < .01$). The center of the Gaussian fits (parameter μ in Eq. (3)) was shifted on average by 57 ms. This is delayed compared to the values in the literature (Ross et al., 1996; Ross et al., 2001) and is certainly caused by the advance onset determination of the detection algorithm. Using a different saccade detection algorithm (see Section 2) that is suited for this experiment, but not for the detection of saccades in pursuit traces, shifted the peak suppression to 23 ms after saccade onset, which is more in line with the values from the literature. Around saccadic stimulus onset there was also a slight reduction in detection rate. The amplitudes of the Gaussian fits were significantly below zero during stimulus onset (mean = $-.11$; student's t -test, $t(5) = 3.88$, $p = .01$).

4. Discussion

In a series of four experiments, we measured the contrast sensitivity during the initiation of smooth pursuit eye movements and during saccadic eye movements. To do so, we flashed a peripheral target line at different points in time relative to the eye movements. Three main results arise from these experiments, which are illustrated in Fig. 7. First, we found a non-significant trend for suppres-

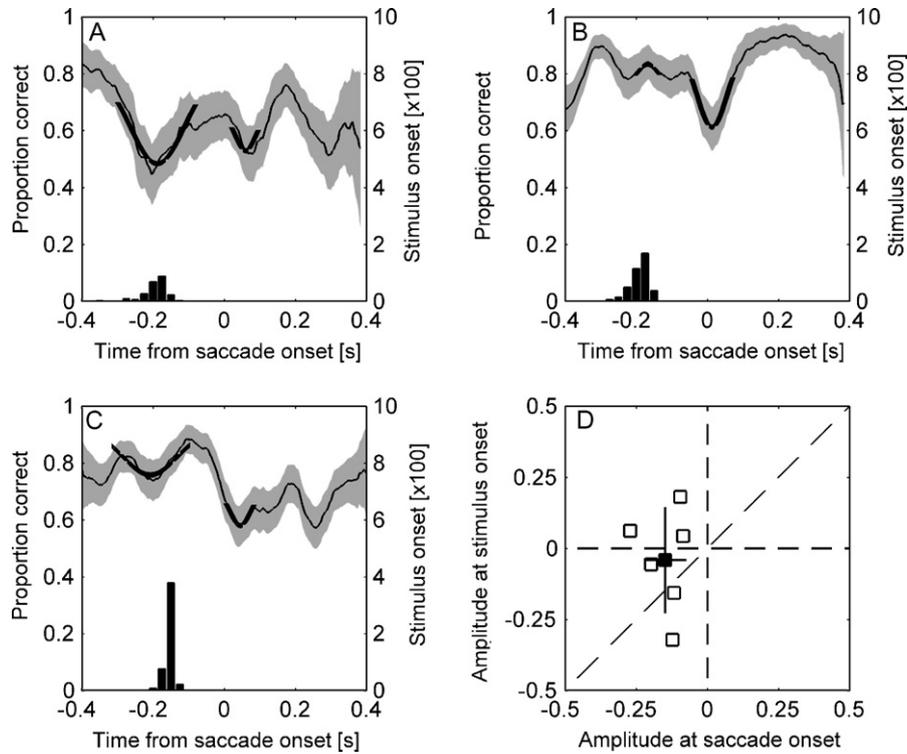


Fig. 5. Experiment 3: Contrast sensitivity during pursuit in response to a ramp stimulus with 21.14 deg/s. The conventions are the same as in Figs. 3 and 4. (A–C) Data for three subjects. (D) Amplitude of the Gaussian fits during saccade onset and during stimulus onset.

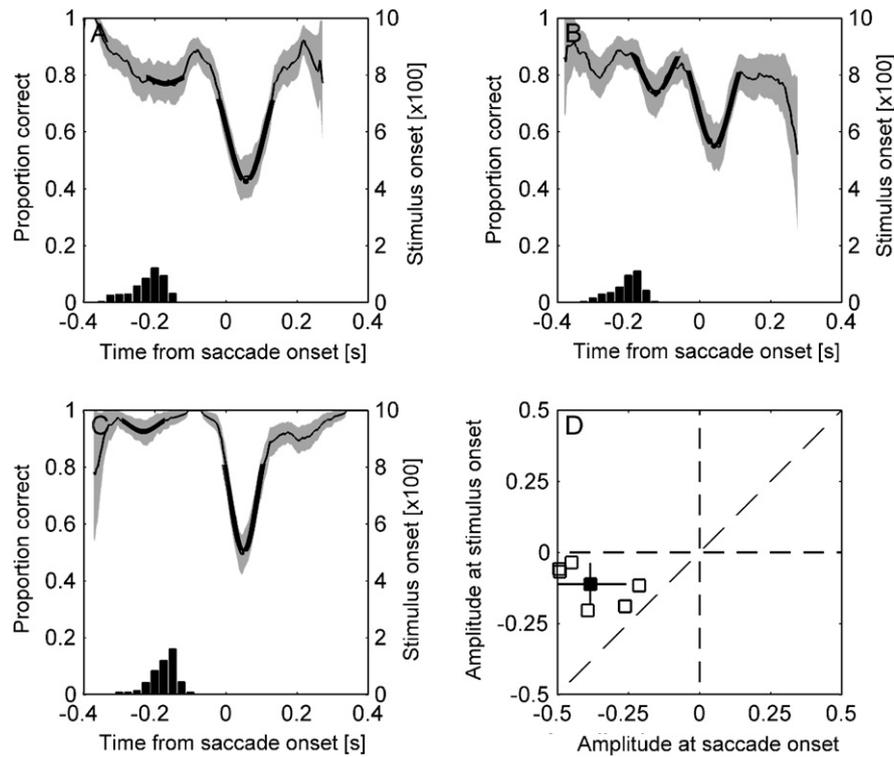


Fig. 6. Experiment 4: Contrast sensitivity during 15 deg horizontal saccades. The conventions are the same as in Figs. 3–5. (A–C) Data for three subjects. (D) Amplitude of the Gaussian fits during saccade onset and during stimulus onset.

sion around the initiation of pursuit elicited by step-ramp stimuli. Second, we obtained saccadic suppression for catch-up saccades during the initiation of smooth pursuit,

if pursuit is elicited by a ramp stimulus. As described before, the size of the saccade was found to be an important factor for contrast suppression. Third, we observed

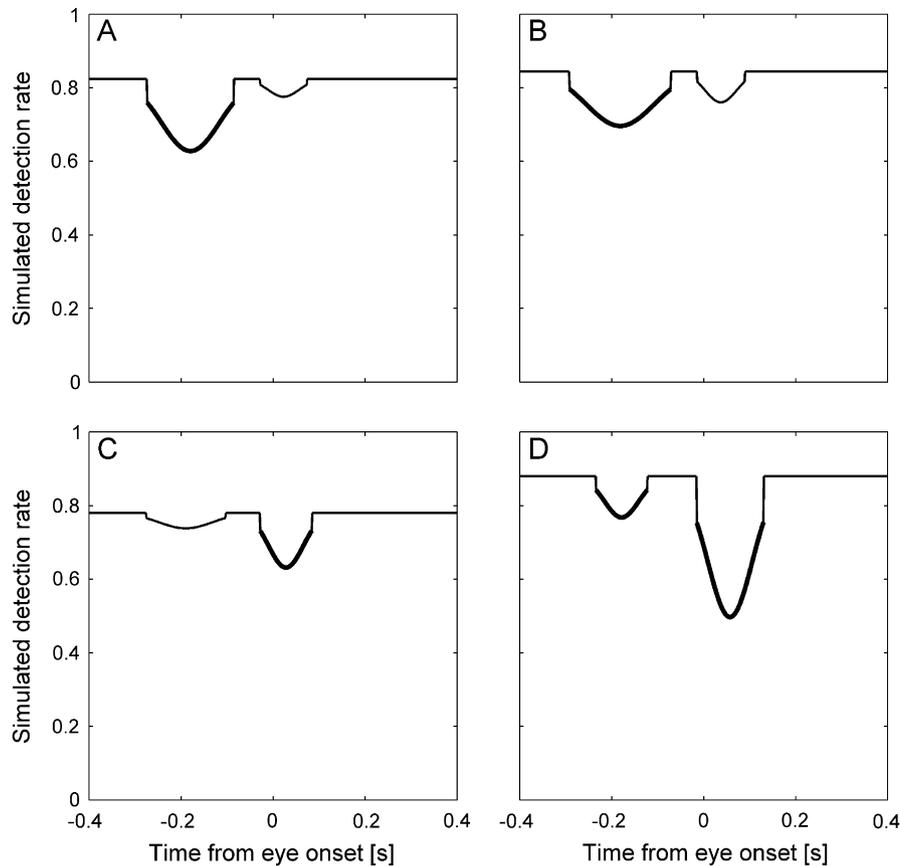


Fig. 7. Fitted detection performance averaged over all subjects, displayed for all four experiments. (A) Detection performance during pursuit in response to a step-ramp stimulus with 10.57 deg/s. The fitted detection performance is calculated by means of the average values of the Gaussian fits during pursuit onset (A) or saccade onset (B–D) and during stimulus onset. The values in between were filled with the baseline value. Significant effects over all subjects are plotted in bold. (B) Detection performance during pursuit in response to a ramp stimulus with 10.57 deg/s. (C) Detection performance during pursuit in response to a ramp stimulus with 21.14 deg/s. (D) Detection performance during 15 deg horizontal saccades.

an attenuation of contrast sensitivity at pursuit respective saccade stimulus onset.

4.1. Eye onset effects

There occurred no significant suppression of contrast sensitivity at pursuit onset if the pursuit was elicited by a step-ramp stimulus and started smoothly without saccades. However, if pursuit was elicited by a ramp stimulus, the first catch-up saccade, executed after motion onset of the pursuit stimulus, caused a mean suppression effect of detection performance of 15%. Saccadic suppression of contrast sensitivity was only observed for the faster ramp speed of 21.14 deg/s as tested in Experiment 3. This relatively high ramp speed triggered larger saccades (average saccadic amplitude 4.8 deg) than the 10.57 deg/s ramp used in Experiment 2 (average saccadic amplitude 2.5 deg). Our finding is in line with the known relationship between the saccadic amplitude and the magnitude of saccadic suppression (Mitrani et al., 1970; Ridder & Tomlinson, 1997; Stevenson et al., 1986). Consistent with this argument, in Experiment 4 the saccadic suppression of detection performance was even more pronounced (38%) during horizontal saccades of 15 deg.

Several aspects may explain why contrast sensitivity was not affected during the onset of smooth pursuit. First, saccades and smooth pursuit serve quite different aims. A saccade is a rapid, discrete movement to foveate an object. Therefore, intrasaccadic perception is not of major interest. Smooth pursuit is a continuous movement to compensate for object movements and to keep the object's image projection in the fovea (Krauzlis, 2004). This means that a continuous perception is an essential prerequisite as well as a goal of the eye movement. A suppression of sensitivity would counteract this purpose and impair the ability to pursue the target. Second, there are some quantitative differences between pursuit initiation and saccades, which could possibly explain why stimuli were not suppressed at the onset of pursuit. The peak velocity and the acceleration of the eyes during the initiation of pursuit are much smaller than during saccades (Leigh & Zee, 1999). This means that the retinal image motion induced by pursuit can be compensated easier than the retinal image motion induced by saccades.

For saccades, it has been shown that the magnitude of saccadic suppression increases with the amplitude of the saccade (Mitrani et al., 1970; Ridder & Tomlinson, 1997; Stevenson et al., 1986). The amplitude of the saccade in

turn determines the peak velocity and the duration of the saccade, a relationship termed main sequence (Bahill, Clark, & Stark, 1975). Possibly the peak velocity and acceleration during pursuit initiation are simply too small, to cause a significant suppression effect. Fig. 8 displays the magnitude of suppression during pursuit onset/saccade onset in dependence of the maximum velocity during pursuit initiation/saccades. The maximum eye velocity and the magnitude of suppression are highly correlated (Pearson correlation, $\rho = -0.8$, $p < .01$) and the regression analysis predicts a suppression magnitude near zero for the eye velocities during pursuit initiation in Experiment 1. While the regression would predict detectable effects at pursuit speeds of 30 deg/s and higher, we could not test such high speeds with our current experimental setup because of the limited size of our CRT screen.

There is a long debate about the origin of saccadic suppression. One model assumes that saccadic suppression is driven actively by an extra-retinal signal (Ross et al., 2001). This extra-retinal signal probably comes from collicular discharge of motor commands. Other models interpret saccadic suppression as a passive process, produced either by metacontrast (MacKay, 1970) or the shearing forces caused by the strong eye acceleration (Richards, 1969). Today there is strong evidence for the extra-retinal model (Diamond et al., 2000). Our results are compatible with both models. Which brain region is responsible for the suppression still remains unclear. Several studies showed that activity in the frontal eye fields, which play a crucial role in the target selection for saccades (Krauzlis, 2005) can

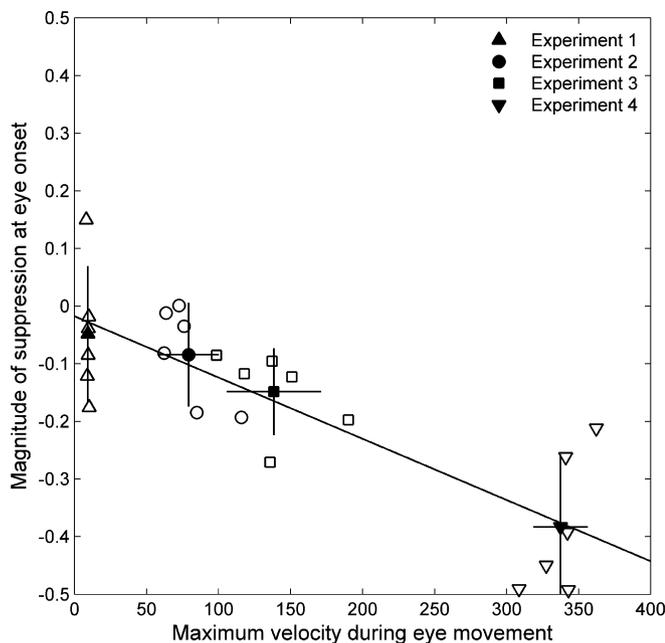


Fig. 8. Magnitude of the suppression effect at eye onset in dependence of the maximum eye velocity during pursuit initiation (Experiment 1), during catch-up saccades while pursuit initiation (Experiments 2 and 3) and during horizontal saccades (Experiment 4). The open markers indicate data for individual subjects; the filled markers indicate the mean for each experiment; the error bars denote the 95% confidence interval. The line represents a robust fit of the individual data.

modulate activity in V4 (Moore & Armstrong, 2003). A transcranial magnetic stimulation study (Thilo, Santoro, Walsh, & Blakemore, 2004) suggests that inhibition occurs very early in the visual pathway, within the thalamus or in the primary visual cortex. Further it is known that neurons in MT/MST, MT+, V1 and V4 show a smaller activity during saccades (Ibbotson, Price, Crowder, Ono, & Mustari, 2007; Kleiser, Seitz, & Krekelberg, 2004; Thiele, Henning, Kubischik, & Hoffmann, 2002; Vallines & Greenlee, 2006).

4.2. Stimulus onset effects

In the first and second pursuit experiment as well as in the saccade experiment, a slight attenuation of detection performance of approximately 12% at stimulus onset could be observed. This effect can be explained by two streams of research, both based on attention. One line of evidence comes from literature about perceptual effects of attention and lack of attention. On the one hand it has been shown that attention can positively influence perceptual performance. This applies to several perceptual dimensions, for example contrast sensitivity (Carrasco, Penpeci-Talgar, & Eckstein, 2000) and spatial resolution (Yeshurun & Carrasco, 1999). On the other hand, the absence of attention can lead to an oversight of salient visual features (O'Regan, Rensink, & Clark, 1999; Chun & Marois, 2002; Mack & Rock, 2000), which has been demonstrated in the inattention blindness and change blindness paradigms. In our case this means that the line was not detected, because attention was bound to the onset of the pursuit respective saccade stimulus.

The second line of evidence for an attentional cause comes from research about the close linkage between visuospatial attention and eye movements. For saccades, it has been shown that it is impossible to perform an accurate and quick saccade to one target and to dissociate spatial attention to another target (Deubel & Schneider, 1996; Kowler et al., 1995). This holds true for pursuit as well (Khurana & Kowler, 1987; Van Donkelaar, 1999). For both, pursuit and saccades it is commonly assumed that attention is needed for the selection of the target and the subsequent target directed eye movements (Krauzlis & Stone, 1999). Liston and Krauzlis (2003) even show that saccades and smooth pursuit share the same processing stages during response preparation. Recent research suggests that the programming of eye movements and the locating of spatial attention share processing (Kustov & Robinson, 1996; Moore & Fallah, 2001). Based on these findings it is probable that the attenuation of contrast sensitivity at stimulus onset for saccades and pursuit is caused by the attentional demands of the eye movement initiation which leads to inattention blindness for the target line.

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