

Temporal contrast sensitivity during smooth pursuit eye movements

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During smooth pursuit eye movements, stimuli other than the pursuit target move across the retina, and this might affect their detectability. We measured detection thresholds for vertically oriented Gabor stimuli with different temporal frequencies (1, 4, 8, 12, 16, 20, and 24 Hz) of the sinusoids. Observers kept fixation on a small target spot that was either stationary or moved horizontally at a speed of 8 deg/s. The sinusoid of the Gabor stimuli moved either in the same or in the opposite direction as the pursuit target. Observers had to indicate whether the Gabor stimuli were displayed 4° above or below the target spot. Results show that contrast sensitivity was mainly determined by retinal-image motion but was slightly reduced during smooth pursuit eye movements. Moreover, sensitivity for motion opposite to pursuit direction was reduced in comparison to motion in pursuit direction. The loss in sensitivity for peripheral targets during pursuit can be interpreted in terms of space-based attention to the pursuit target. The loss of sensitivity for motion opposite to pursuit direction can be interpreted as feature-based attention to the pursuit direction.

Keywords: smooth pursuit eye movements, temporal contrast sensitivity, attention, perception and action

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Introduction

Smooth pursuit eye movements (SPEM) are used to keep the retinal image of a moving object in the fovea, the region with the highest spatial resolution. Numerous studies have investigated how well the visual system can match the speed of the eye movements to the speed of the moving object (Lisberger, Morris, & Tychsen, 1987), but the perceptual consequences of pursuit have been investigated very little. Only few studies have looked at the question how well the tracked objects can be seen during pursuit, as compared to fixation. This can be determined in several ways, for instance by measurements of visual acuity or contrast sensitivity.

Several early studies compared dynamic visual acuity (DVA) during SPEM with static visual acuity (SVA) during fixation of a stationary target. Ludvigh and Miller (1958) showed that DVA is close to SVA for slowly moving targets but declines with increasing target velocity.

They hypothesized that this decline may be caused by imperfect tracking eye movements. If the eyes move slower than the target, as is often reported (Rashbass, 1961; Collewijn & Tamminga, 1984; Heinen & Watamaniuk, 1998), the target will move on the retina and this may go along with decreased visibility. Because Ludvigh and Miller did not record eye movements, they could not test their hypothesis. However, their idea was further investigated in later studies (Brown, 1972a, 1972b; Methling & Wernicke, 1968), where it was found that the decline in DVA in fact corresponds to the extent of eye movement error.

A more complete way to evaluate performance of the visual system during smooth pursuit is to measure contrast sensitivity for gratings of varying spatial and temporal frequency. Several authors (Bedell & Lott, 1996; Flipse, Van der Wildt, Rodenburg, Keemik, & Knol, 1988; Kelly, 1979; Liu & Jiang, 1984; Murphy, 1978) reported that contrast sensitivity was equal during fixation and pursuit, if the retinal-image motion was equal in both observation

conditions. This implies that for spatiotemporal detection, the retinal-image motion determines visibility and the motion of the eye does not matter.

In all of these experiments, the visibility of the tracked object, or of an object spatially coincident with the tracked object, was investigated. For example, in the studies of Flipse et al. (1988) or Murphy (1978), the subjects had to track small spots of light that were superimposed on a large sinusoidal grating. Contrast thresholds were then measured for detection of the grating. In real-world situations, however, smooth pursuit not only keeps the moving target stationary on the fovea. Pursuit has the side effect that nearby targets that are stationary in the world move across the retina. Therefore, we wanted to investigate the effect of SPEM on the detectability of target objects that are not pursued and not located in the fovea. In addition, we were interested whether for moving targets their direction of motion would affect the detectability during SPEM.

Based on previous work, there is good reason to expect an effect of pursuit on the visibility of targets outside the fovea. To track a moving object of interest, the visual system has at first to select and afterward to monitor continuously this object. This is probably accomplished through allocation of attention to the object of interest (Krauzlis & Stone, 1999). Visual attention is known to have beneficial effects on spatial resolution (Yeshurun & Carrasco, 1998) and contrast sensitivity (Carrasco, Penpeci-Talgar, & Eckstein, 2000; Cameron, Tai, & Carrasco, 2002), and SPEM and perception share the same attentional mechanisms (Khurana & Kowler, 1987). The studies mentioned above on contrast sensitivity during smooth pursuit used large stimuli that overlapped the pursuit trajectory in the pursuit condition or the fixation point in the fixation condition. This means that the stimuli were located within the potential attentional spotlight during SPEM, and therefore possible differences between fixation and SPEM due to allocation of attention could not be observed.

Here, we measured contrast sensitivity for stimuli located in the parafovea during fixation and smooth pursuit. The movement direction of the stimuli was either in or opposite to pursuit direction.

Methods

Design

We used a 2AFC paradigm to measure the detection thresholds for Gabor stimuli, consisting of vertically oriented sine wave gratings drifting horizontally at different speeds within a stationary Gaussian window. Three observation conditions were investigated: (1) The observer was fixating a stationary target (FIX); (2) the observer was pursuing a target moving in the same direction as the sinusoid of the Gabor stimulus (MS =

motion same); and (3) the observer was pursuing a target moving in the direction opposite to the sinusoid of the Gabor stimulus (MO = motion opposite). The speed of the moving pursuit target was always 8 deg/s and the spatial resolution of the Gabor stimuli was always 1 cycle/deg. Seven sinusoid speeds of the Gabor stimuli were tested: 1.0, 4.0, 8.0, 12.0, 16.0, 20.0, and 24 deg/s. Because the spatial frequency was 1 cycle/deg, the speed of the Gabor stimuli in degree per second in this case is identical to their temporal frequency in Hz. Because contrast sensitivity of sine wave gratings depends on spatial and temporal frequency (Watson, Ahumada, & Farrell, 1986) rather than speed, we will denote the stimuli in Hz in the following.

Figure 1 illustrates the effect of the various conditions on retinal-image motion. For example, a Gabor stimulus with a sinusoid physical temporal frequency of 8 Hz would be stationary on the retina in the MS condition. However, in the MO condition, it would have a temporal frequency of 16 Hz on the retina. In the MS condition, Gabor stimuli with sinusoid speeds below the pursuit speed are moving opposite to the pursuit direction, and stimuli with sinusoid speeds above the pursuit speed are moving in the same direction as the pursuit target, as can

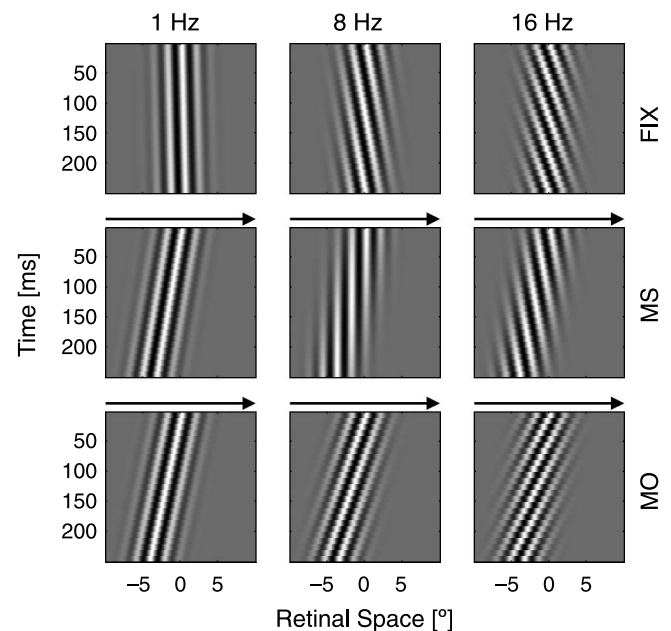


Figure 1. Experiment 1 with stationary Gaussian window and horizontally drifting sinusoid. Retinal space–time plots for three observation conditions (rows) and three temporal frequencies (columns). In conditions MS and MO, the eye moved rightward, indicated by the small arrows above each panel. In condition MS, sinusoids with temporal frequencies below and above 8 Hz differ with respect to their motion direction on the retina. Sinusoids below 8 Hz move opposite to the pursuit direction, and sinusoids above 8 Hz move in the pursuit direction. Sinusoid motion at 8 Hz was stationary on the retina.

be seen in [Figure 1](#). The experiment was separated in 21 blocks; each consisted of one observation condition and one temporal frequency. Two further experiments with Gabor stimuli stabilized on the retina and horizontally oriented Gabor stimuli drifting vertically, respectively, were implemented.

Subjects

The 12 subjects were undergraduate students of the University of Giessen, with a mean age of 27.5 years. Six of them were female. All subjects had normal or corrected-to-normal vision. All subjects were naive with respect to the experiment. Six of the 12 subjects and 1 additional subject participated in the second experiment. Ten of the 12 subjects participated in the third experiment.

Equipment

Subjects were seated in a dimly lit room facing a 21-in. CRT monitor (ELO Touchsystems, Fremont, CA, USA) addressed by an ASUS V8170 (Geforce 4MX 440) graphics board with a refresh rate of 100 Hz non-interlaced. At a viewing distance of 42 cm, the active screen area subtended 51.2° of visual angle in the horizontal direction and 41° vertical on the subject's retina. With a spatial resolution of $1,280 \times 1,024$ pixels, this results in 25 pixels/deg. The subject's head was fixed in place using a chin rest.

Eye movement recording

Gaze 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.

Visual stimuli

A black bull's eye with an outer radius of 0.4° and an inner radius of 0.16° has been used as pursuit target. To measure the spatiotemporal contrast sensitivity, we used small Gaussian vignettted patches of vertical sinusoidal gratings of 1 cycle/deg as detection stimuli. The grating stimuli were achromatic targets modulated around a neutral grey background. The standard deviation of the Gaussian was 1° . The grating drifted horizontally inside the Gaussian window with the respective temporal frequency.

Experimental procedure

At the beginning of each trial, a fixation spot appeared on the horizontal median. The spot was either centered in the fixation condition or shifted about 8° to the left in the two pursuit conditions. The spot had the same properties as the bull's eye but was completely filled. The subject had to fixate the spot and to press an assigned button in order 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. After a successful drift correction, the fixation spot was replaced by the bull's eye. In the fixation condition, the bull's eye appeared at the center of the screen and remained standing still. In the pursuit conditions, the bull's eye appeared 8° left of the center. Two hundred fifty milliseconds later, it started moving according to the step-ramp paradigm (Rashbass, 1961) with a velocity of 8 deg/s. At a step size of 1.2° , the target returned to its initial position within 150 ms. One thousand three hundred fifty milliseconds after trial onset, when the bull's eye reached the horizontal screen center, a Gabor stimulus appeared for 250 ms horizontally centered either 4° above or 4° below the pursuit trajectory. The position of the Gabor stimulus was randomized in each trial. During its presentation time, the Gabor stimulus drifted with the respective frequency. One thousand nine hundred fifty milliseconds after trial onset, the bull's eye disappeared and subjects had to indicate the position of the Gabor stimulus by pressing either an up or a down button. Acoustic feedback was provided if the perceptual decision was wrong. [Figure 2](#) illustrates the procedure for a single trial and [Figure 3](#) shows a video for a sample trial.

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

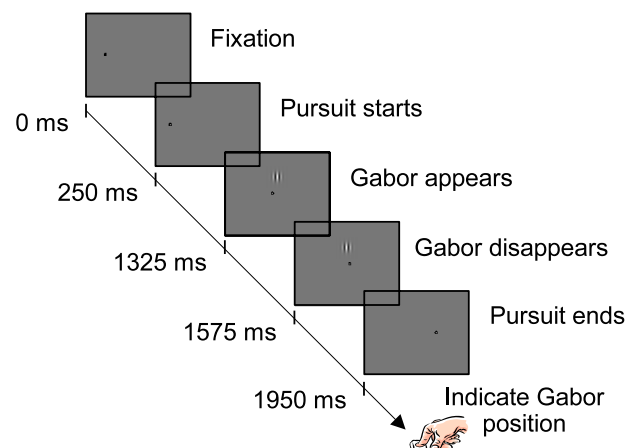


Figure 2. Schematic diagram of one trial.

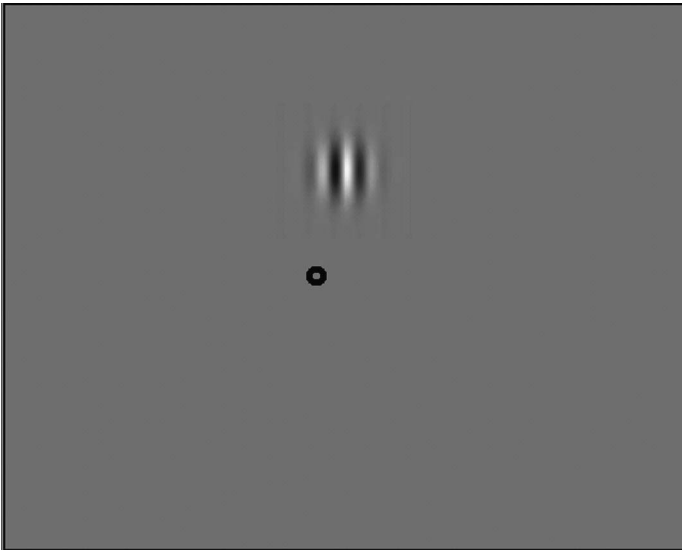


Figure 3. Movie of one pursuit trial with a stationary Gaussian window and sinusoid drifting horizontally in pursuit direction.

over time. The gain of each trace was determined by the average velocity during the period in which the Gabor stimulus appeared divided by the pursuit target velocity. Trials with saccades or eye blinks during Gabor presentation according to the EyeLink detector were excluded from further analysis. This detector uses a velocity threshold of 22 deg/s and an acceleration threshold of 4,000 deg/s² to recognize saccades.

Psychophysical data analysis

The contrast of the Gabor stimuli was adjusted according to a staircase procedure (Levitt, 1971). After a series of three correct responses, the contrast was decreased, and after one incorrect response, the contrast was increased. This procedure leads to a performance target of 79%. The staircase procedure was finished after six reversals. Thresholds were obtained by fitting the percentage of correct answers for the different contrast levels with a logistic psychometric function for a performance level of 75%. The psignifit toolbox in Matlab (Wichmann & Hill, 2001a, 2001b) was used to assess the goodness of fit of the psychometric function. For three subjects, one data point had to be excluded from further analysis because no satisfactory fit of the psychometric function could be obtained. Statistical tests were performed at the 5% significance level.

Experiment 1 with stationary Gaussian window

In the first experiment, the Gaussian window of the Gabor patch was stationary and the sinusoid of

the Gabor drifted horizontally within the Gaussian window.

Experiment 2 with horizontally moving Gaussian window

In the second experiment, the same visual stimuli as in the first experiment were used. However, in the two pursuit conditions, the Gaussian window of the Gabor patch moved along in parallel to the pursuit target. Therefore, as illustrated in Figure 4, Gabor stimuli with a given physical temporal frequency result in approximately the same retinal-image motion of the sinusoid, irrespective of observation condition.

Experiment 3 with vertically drifting sinusoid

In the third experiment, the Gaussian window of the Gabor patch was stationary as in Experiment 1, but the sinusoidal grating was horizontally oriented and drifted vertically. Only six temporal frequencies of the sinusoid were tested: 1, 4, 8, 12, 16, and 24 Hz. As a result of the orthogonal movement directions of the pursuit target and the grating, the distinction between MS and MO was not defined so that only two observation conditions were

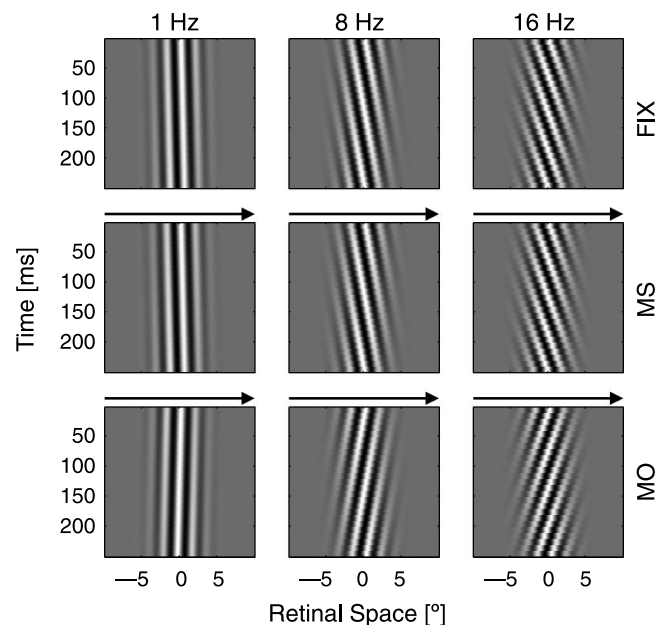


Figure 4. Experiment 2 with horizontally moving Gaussian window and horizontally drifting sinusoids. Retinal space–time plots for three observation conditions (rows) and three temporal frequencies (columns). In the pursuit conditions MS and MO, the sinusoids are stabilized on the retina, by moving the Gaussian window of the Gabor patch parallel to the pursuit target. Therefore, sinusoids with equal physical temporal frequency show the same retinal speed in all three observation conditions.

Experiment	Window speed	Sinusoid speed [Hz]	Sinusoid orientation
Experiment 1	Stationary	1, 4, 8, 12, 16, 20, and 24	Vertical
Experiment 2	8 deg/s (MS and MO) Stationary (FIX)	1, 4, 8, 12, 16, 20, and 24	Vertical
Experiment 3	Stationary	1, 4, 8, 12, 16, and 24	Horizontal

Table 1. Overview of experimental conditions.

tested: fixation of a stationary target and pursuit of a moving target. Table 1 provides an overview about the different stimulus conditions.

Results

Experiment 1 with stationary Gaussian window

Figure 5 shows the mean contrast sensitivity over all subjects as a function of physical temporal frequency for a Gabor patch with a horizontal drifting sinusoid and a stationary Gaussian window. Each panel displays the curve fitting with different models.

The contrast sensitivity function for FIX was fitted by Equation 1, which represents cascaded low-pass exponential and high-pass RC filters and has been frequently used to describe the response behavior of individual neurons (Gegenfurtner, Kiper, & Fenstemaker, 1996; Levitt, Kiper, & Movshon, 1994). In this equation, f stands for the physical temporal frequency, a for the response maximum, b and c determine the behavior of the low-pass part of the function, whereas, d and e characterize the high-pass part.

$$\text{FIX}(f) = a \times \exp\left(-\frac{f}{b}\right)^c \times \left(1 / \sqrt{1 + \left(\frac{d}{f}\right)^2}\right)^e. \quad (1)$$

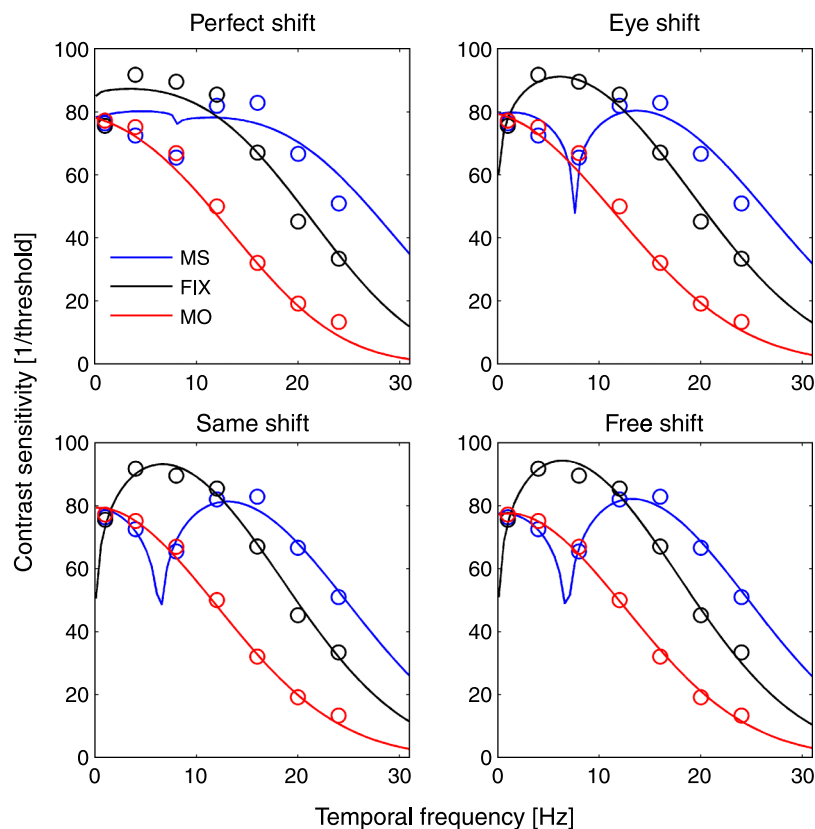


Figure 5. Experiment 1: Mean contrast sensitivity functions for Gabor patches with horizontally drifting sinusoids and stationary Gaussian windows. Each panel shows the data for one shift model. Black circles and lines indicate data and fitted values for fixation (FIX). Blue indicates motion in same direction as pursuit (MS) and red indicates motion opposite to pursuit direction (MO).

As the data for MS and MO could not be expressed in a satisfying manner by Equation 1, these contrast sensitivity functions were shifted along the abscissa and were scaled along the ordinate as in Equations 2 and 3. In these equations, the physical temporal frequency was shifted by the parameter h and the overall sensitivity was scaled by parameter g . The h and g parameters will be reported in hertz and percent, respectively.

$$\text{MS}(f) = \text{FIX}(f + h_s) \times g_s, \quad (2)$$

$$\text{MO}(f) = \text{FIX}(f + h_o) \times g_o. \quad (3)$$

The remaining parameter values were derived from fitting all three data sets simultaneously. For gratings moving in the same direction as the pursuit target but at a slower speed, the resulting retinal motion is actually negative, that is, in the direction opposite to pursuit. Therefore, we used the scaling parameter for MO, g_o , in these cases. For the horizontal shift of the contrast sensitivity functions, we tested four different models:

- Perfect shift model: Because the existing literature shows that contrast sensitivity only depends on retinal temporal frequency, we decided to determine the shift parameters h_s and h_o by the pursuit speed in these conditions. This model is based on the assumption of perfect eye movements with a gain of unity and contains seven free parameters. From Figure 5, it is obvious that the fit still contains a substantial deviation of the empirical data points, wherefore we decided to test three additional models.
- Eye shift model: In this model, the shift parameters were determined by the average eye velocity in the respective conditions. This is a reasonable approach because the average eye gain was not unity but varied between 0.8 and 1.0. Like the perfect shift model, the eye shift model has seven free parameters.

Because our detection targets did not coincide with the pursuit target, we have to consider not only the gain of the smooth pursuit system, but also the gain of the reafferent signals. Because it is known that the reafference gain is imprecise (Aubert, 1886, Fleischl, 1882) and because we did not determine this gain empirically for our observation conditions, we tested two models, in which the shift parameters were determined by the fitting routine.

- Same shift model: In this model, both shift parameters h_s and h_o had to be equal. This model has eight free parameters.
- Free shift model: In the last model, the shift parameters were allowed to differ from each other, so that this model contains nine free parameters.

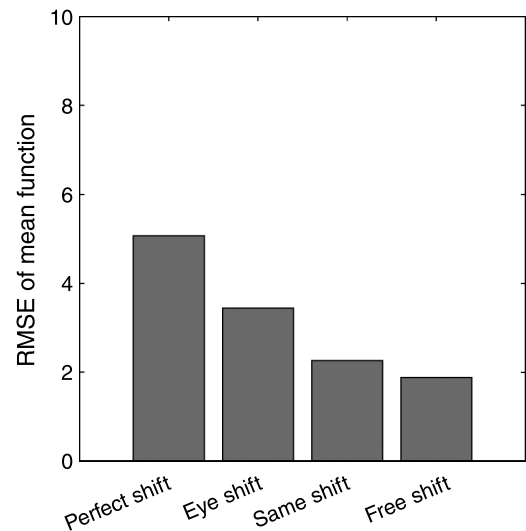


Figure 6. Experiment 1: Root mean square error (RMSE) of the mean contrast sensitivity function for four shift models.

From Figure 5 it seems that the models differ substantially in the deviation from the data. Therefore, we compared the root mean square error (RMSE) of the four models, which is plotted in Figure 6.

The RMSE decreased with weaker assumptions on the shift parameter (8.4, 7.7, 7.1, and 6.7 for perfect shift, eye shift, same shift, and free shift models). As the perfect shift and the eye shift models hold the same number of free parameters, it is quite clear that the eye shift model is superior to the Perfect Shift model. However, the eye shift, the same shift, and the free shift models hold different numbers of free parameters, wherefore a comparison of the RMSE is not sufficient for model selection. To compare these models, we calculated the F ratio of the residual sum of squares (RSS), which takes the number of free parameters in the models into account (Seber & Wild, 1994). The RSS was significantly lower in the same shift model than that in the eye shift model, $F(1,13) = 17.16$, $p < .01$. In the free shift model, the RSS was in turn significantly lower than that in the same shift model, $F(1,12) = 5.36$, $p = .02$. This shows that the alignment of the shift parameters to the eye velocity improves the fitting. Releasing the shift parameters leads to a further improvement of the fits. Figure 7 shows the contrast sensitivity functions for three exemplary subjects, fitted by the free shift model.

Inspection of the contrast sensitivity functions in Figures 5 and 7 suggests that there are differences in peak sensitivity between FIX, MS, and MO. Figure 8 plots the sensitivity for MS versus the sensitivity for MO for all four models.

To evaluate potential differences in sensitivity, we calculated one-way repeated measures ANOVAs for each shift model and t tests for the pairwise comparisons. In the perfect shift model, the sensitivities differed significantly,

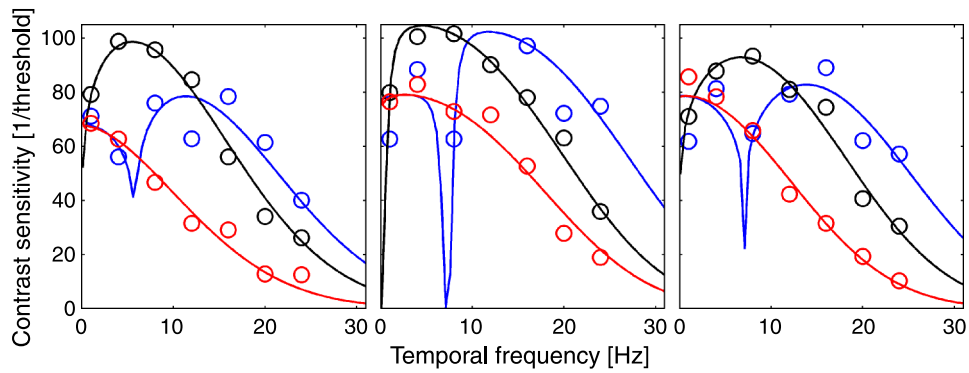


Figure 7. Experiment 1: Contrast sensitivity functions for three exemplary subjects. The fitted values stem from the free shift model. Conventions are the same as in Figure 5.

$F(2, 22) = 7.45, p < .01$. The mean sensitivity for MS was significantly reduced to 91%, $t(11) = 3.70, p < .01$, and for MO sensitivity was reduced to 93%, $t(11) = 2.73, p = .02$. The difference between MS and MO was not significant, $t(11) = 0.85, p = .42$. A similar pattern holds true for the eye shift model (MS = 90%, MO = 89%) and the same

shift model (MS = 90%, MO = 87%). In both cases, the overall one-way repeated measures ANOVA as well as the t tests for the difference between the FIX and the pursuit conditions was significant, but not the t test for the difference between MS and MO. In the free shift model, the mean sensitivity for MS is significantly reduced to

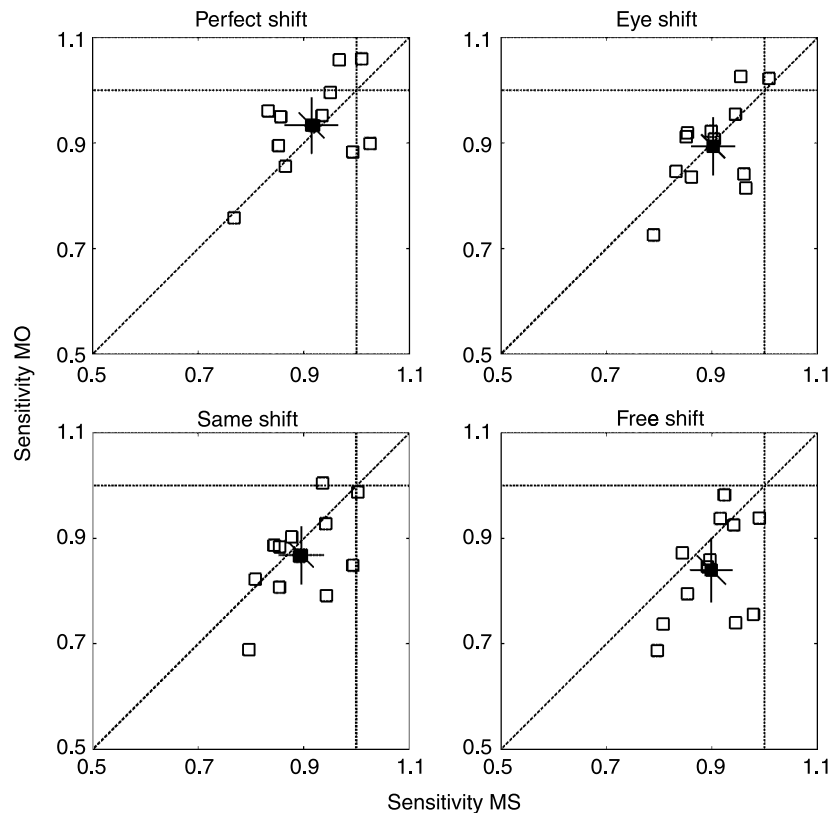


Figure 8. Experiment 1. Sensitivity for motion in pursuit direction (MS) and motion opposite to pursuit direction (MO). Each panel shows the data for one shift model. Open squares indicate values for individual subjects; the filled square indicates the mean sensitivity; error bars denote the 95% confidence intervals of the mean. The diagonal error bar is based on the standard error of the individual sensitivity differences for MS and MO (Loftus & Masson, 1994; Masson, 2003) and has to be tested against the diagonal line, which marks points with equal sensitivity for MS and MO. The horizontal error bar is based on the standard error of the sensitivity for MS and has to be tested against the vertical line, which marks points with equal sensitivity for MS and FIX. The vertical error bar is based on the standard error of the sensitivity for MO and has to be tested against the horizontal line, which marks points with equal sensitivity for MO and FIX.

90%, $t(11) = 5.59$, $p < .01$, and for MO sensitivity is reduced to 84%, $t(11) = 5.77$, $p < .01$. Here the difference between MS and MO is significant, $t(11) = 2.36$, $p = .04$.

There are also differences concerning the horizontal shifts of the contrast sensitivity functions. In the eye shift model, the shifts for MS are significantly reduced on average to 7.56 compared to the pursuit velocity of 8, $t(11) = 3.87$, $p < .01$. The shifts for MO are significantly reduced to 7.45, $t(11) = 4.47$, $p < .01$. The two shifts do not differ significantly from each other, $t(11) = 0.82$, $p = .43$. In the same shift model, the shift is reduced to 6.52, which is also statistically different from 8, $t(11) = 8.75$, $p < .01$. In the free shift model, the shift for MS is significantly reduced to 6.69, $t(11) = 2.91$, $p = .01$, and for MO the shift is reduced to 5.14, $t(11) = 4.96$, $p < .01$. Like in the eye shift model, the shifts for MS and MO differ not significantly, $t(11) = 1.68$, $p = .12$. Figure 9 plots the shifts for MS and MO in the free shift model. To analyze if the shifts in the free shift model depend on smooth pursuit gain, we calculated correlations between shifts and eye gain. The correlations for MS ($r = 0.3$, $n = 12$, $p = .24$) and for MO ($r = 0.16$, $n = 12$, $p = .62$) were low and not significant.

At this point, we have quite strong evidence that the sensitivity is highest for FIX and lower for the two pursuit

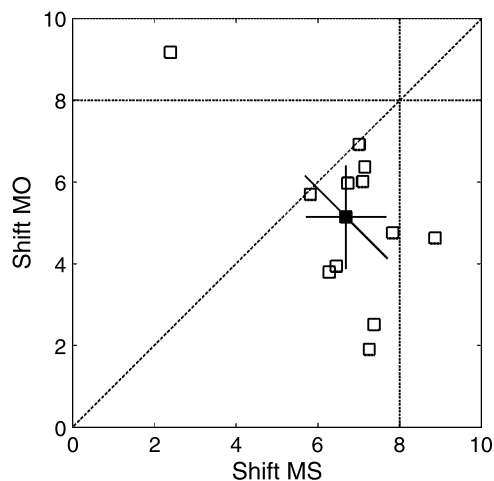


Figure 9. Experiment 1. Shift for motion in pursuit direction (MS) and motion opposite pursuit direction (MO). Open squares indicate values for individual subjects; the filled square indicates the mean shift; error bars denote the 95% confidence intervals of the means. The diagonal error bar is based on the standard error of the individual shift differences for MS and MO (Loftus & Masson, 1994; Masson, 2003) and has to be tested against the diagonal line, which marks points with equal shifts for MS and MO. The horizontal error bar is based on the standard error of the shift for MS and has to be tested against the vertical line, which marks points with shifts that correspond to pursuit target speed. The vertical error bar is based on the standard error of the shift for MO and has to be tested against the horizontal line, which marks points with shifts that correspond to pursuit target speed.

conditions, but there is no clear-cut result for the difference between MS and MO. The ambiguous results for the different shift models suggest that it is difficult to differentiate between horizontal shifts and vertical scalings of the contrast sensitivity functions. Because we cannot resolve this issue by further curve fitting, we ran a second experiment in which the detection target moves along with the pursuit target.

Experiment 2 with horizontally moving Gaussian window

Figure 10 shows the contrast sensitivity functions for the second experiment in which the Gaussian window of the Gabor stimulus moved along in parallel with the pursuit target. This movement approximately stabilized the Gabor on the retina, so that for a given physical temporal frequency the retinal-image motion of the sinusoid should be equal in all observation conditions. This goal was achieved because the contrast sensitivity functions for the two pursuit conditions were no longer shifted along the temporal frequency axis relative to the contrast sensitivity function for the fixation condition. Conceptually, the model corresponds to the perfect shift model in the first experiment.

As before, in the experiment with the stationary Gaussian window, peak sensitivity differed as a function of experimental condition, $F(2,12) = 17.223$, $p < .01$. For MS, sensitivity was significantly reduced to 94%, $t(6) = 2.59$, $p = .04$, and for MO sensitivity was reduced to 88%, $t(6) = 5.01$, $p < .01$. Moreover, in this experiment, the sensitivity for MO was significantly lower than for MS, $t(6) = 4.63$, $p < .01$. Figure 11 shows that this pattern of sensitivities occurred for all subjects except for one.

When we tested the other three models from the first experiment, the same pattern of results occurred. For the eye shift, same shift as well as free shift model, the one-way repeated measures ANOVA was significant, as well as the differences between FIX and MS, FIX and MO, and MS and MO. Thus, in this experiment, sensitivity is highest for FIX, lowest for MO, and in between for MS, regardless of the particular shift model that is used. This is not unexpected because—as already seen in Figure 10—there were no noticeable shifts. In both models, estimated shifts were below 0.5 Hz.

We also performed a nonparametric analysis of the sensitivity differences. To do so, we connected the non-shifted data points for each condition by lines and used the areas under the resulting curves as an estimate of the sensitivity in the respective condition. A repeated measures ANOVA obtained significant differences between the areas, $F(2,12) = 25.834$, $p < .01$. The area below MS was significantly smaller than below FIX, $t(6) = 5.38$, $p < .01$, the area below MO was significantly smaller than below FIX, $t(6) = 5.71$, $p < .01$, and finally the area below MO was also significantly smaller than below MS,

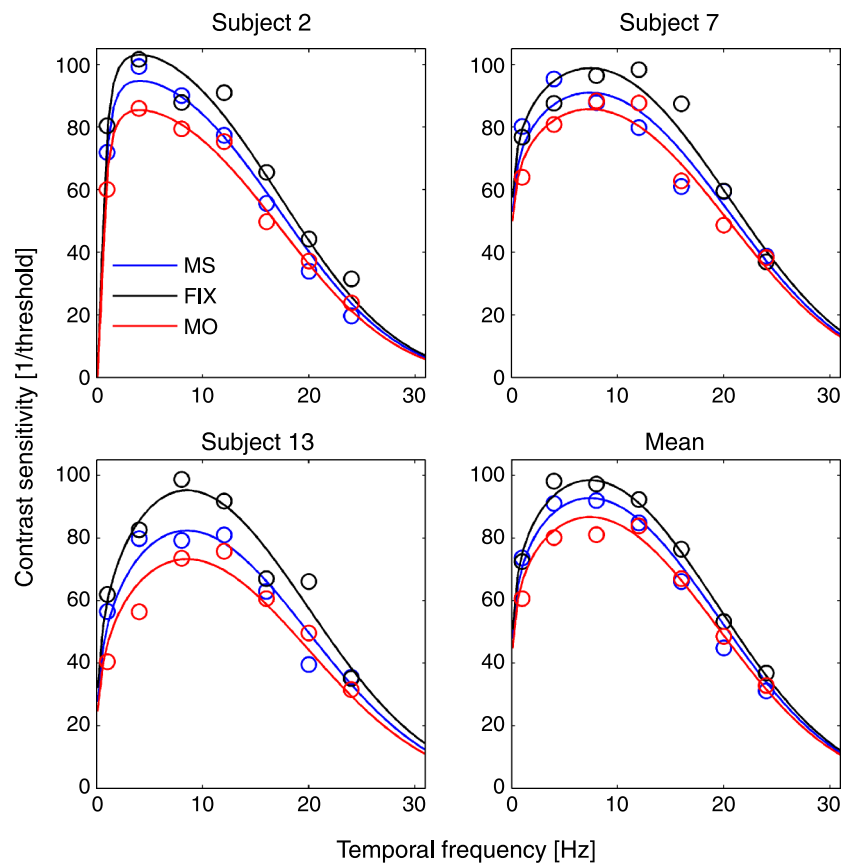


Figure 10. Experiment 2. Contrast sensitivity functions for Gabor patches with horizontally drifting sinusoids and stabilized Gaussian windows. In the top left, the top right, and the bottom left panel, the functions for three subjects are shown. In the bottom right panel, the mean contrast sensitivity function is displayed. Conventions are the same as in Figure 5.

$t(6) = 2.78, p = .03$. Thus, this nonparametric analysis confirmed the results of the previous model analysis that sensitivity was highest for FIX, lowest for MO, and in between for MS.

It is possible that the decline in contrast sensitivity during smooth pursuit is related to the horizontal jitter of the stimuli on the retina, which is caused by small fluctuations of the speed of the eye movements. Any such jitter would basically blur the target on the retina and thereby make it less visible. If there is substantially more such jitter during pursuit than during fixation, this could cause differences in contrast sensitivity. Therefore, we calculated the accuracy of the stabilization of the Gaussian window in the three different conditions. For this purpose, we calculated the RMSE of eye position to pursuit target position in the time interval when the Gabor stimulus was presented. Because the low-frequency trends are not relevant for the jitter, the eye position traces were corrected for a constant lag to the pursuit target. The mean RMSE during the pursuit conditions was 1.2 pixels and during the fixation condition 1.0 pixel. The difference corresponds to 0.008° (approximately 30 arcsec), which can safely be neglected.

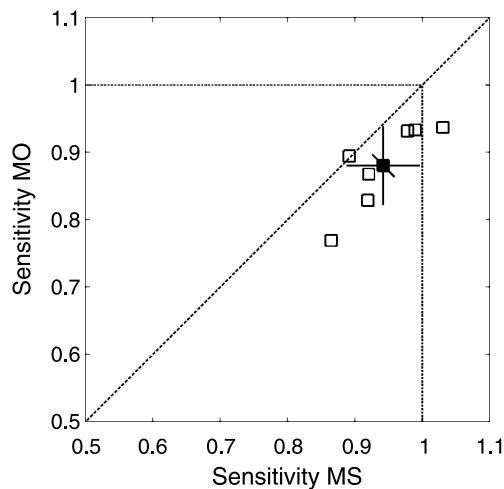


Figure 11. Experiment 2. Sensitivity for motion in pursuit direction (MS) and motion opposite to pursuit direction (MO). Conventions are the same as in Figure 8.

Experiment 3 with vertically drifting sinusoid

We ran a third experiment with vertically oriented stimuli to definitely rule out any explanations for the difference between fixation and pursuit that is not directly

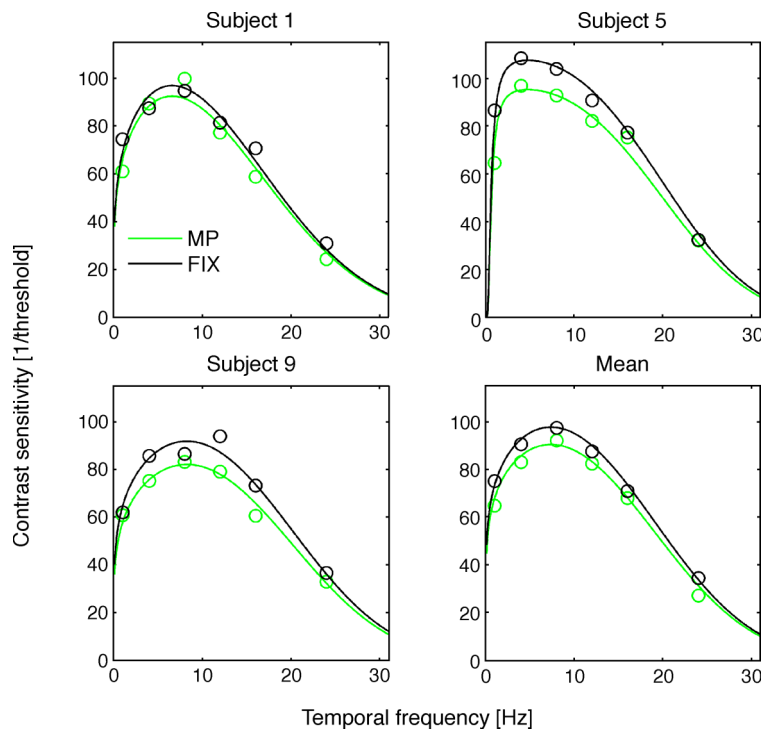


Figure 12. Experiment 3. Mean contrast sensitivity functions for Gabor patches with vertically drifting sinusoids and stationary Gaussian windows. In the top left, the top right, and the bottom left panel, the functions for three subjects are shown. In the bottom right panel, the mean contrast sensitivity function is displayed. Black circles and lines indicate data and fitted values for FIX. Green indicates motion perpendicular to pursuit direction (MP).

related to the eye movements themselves. Because motion of the sinusoid was perpendicular (MP = motion perpendicular) to motion of the pursuit target, the retinal-image motion of the Gabor stimulus was completely independent of the horizontal component of the eye movement.

Figure 12 displays the contrast sensitivity functions for this experiment. In this case, we only tested a model with a fixed shift of zero for the pursuit condition. Again the sensitivity for the pursuit condition (93%) was significantly lower than for the fixation condition, $t(9) = 5.43$, $p < .01$. Figure 13, which plots the peak sensitivity for FIX versus MP, confirms that all but one subject followed this pattern. Furthermore, we performed the nonparametric analysis based on the area below the linearly interpolated curves. This analysis confirmed that the sensitivity for MP was significantly smaller than for FIX, $t(9) = 4.51$, $p < .01$.

Discussion

We investigated the temporal–contrast sensitivity for peripheral targets during SPEM and fixation. In all three experiments, contrast sensitivity was significantly lower during pursuit than during fixation. Because we could not disentangle horizontal shifts and vertical scaling in

our first experiment, we ran two further experiments. Experiment 2 shows not only a significant difference between fixation and pursuit, but also a significant difference between sensitivity for targets moving in the direction of pursuit and targets moving in the opposite direction. Although sensitivity is reduced compared to fixation for both pursuit conditions, it is even more reduced for the detection of targets moving in the direction opposite to the pursuit target. Experiment 3 shows that the difference between fixation and pursuit could not be due to any factors having to do with stimulus jitter on the retina, eye movement gain, or reafferent gain. This leaves attentional factors as a likely cause for the differences in contrast sensitivity.

Pursuit and image coding

These findings may not only have consequences for our understanding of the human visual system. They are also of potential importance for the efficient coding of digital image sequences. Smooth pursuit can be elicited whenever coherent motion signals are present in the input to the visual system, a situation that arises for example during the free watching of movies. The consequence of smooth pursuit is that retinal temporal frequencies may be quite distinct from those expected

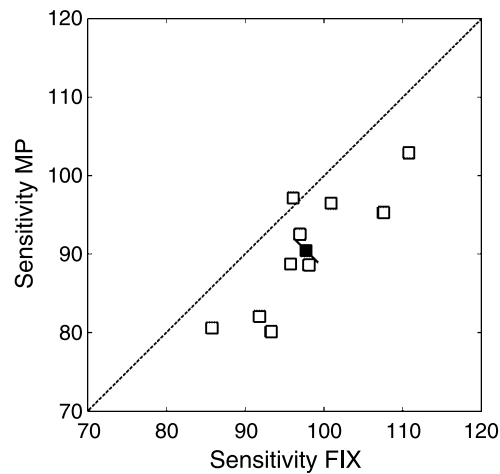


Figure 13. Experiment 3. Peak sensitivity for fixation and motion perpendicular to pursuit direction (MP). Open squares indicate values for individual subjects; the filled square indicates the mean sensitivity; error bars denote the 95% confidence intervals of the means. The diagonal error bar is based on the standard error of the individual sensitivity differences for FIX and MP (Loftus & Masson, 1994; Masson, 2003) and has to be tested against the diagonal line, which marks points with equal sensitivity for FIX and MP. Please note that here peak sensitivity values are shown and not the sensitivity parameters like in Figures 8 and 11.

with an observer who is simply fixating. Eckert and Buchsbaum (1993) showed that the spatial acuity is a function of the ability to pursue moving objects, and therefore fast image motion is not a sufficient precondition to reduce the spatial resolution of the image for efficient coding. This means that pursuit changes the window of visibility and high temporal frequencies, which would be invisible during fixation, could become visible during pursuit. Our results may also be relevant for variable resolution displays. If contrast sensitivity for peripheral targets is reduced in general during smooth pursuit, the spatial resolution in the periphery could be lowered even more than due to cortical magnification. Geisler and Perry (1999) developed Foveated MPEG, an image encoding where the resolution varies across the image. Based on the information about eye movements delivered by an eye tracker, the spatial resolution during smooth pursuit could be lowered even more for peripheral areas. Even without gaze information, spatial resolution in the periphery could be lowered, if smooth pursuit objects can be identified with a high probability.

Comparison to earlier studies

Our results extend several other studies where contrast sensitivity was measured during smooth pursuit. In all of these studies, the detection target overlapped with the

pursuit target. Most of these studies dealt with the sensitivity for moving stimuli. Murphy (1978) compared contrast thresholds for a moving grating viewed during fixation, a stationary grating viewed during pursuit and a moving grating viewed during pursuit. He showed that the contrast sensitivity mainly depends on the retinal-image motion, independent of its source. That means it is irrelevant, if the retinal-image motion is caused by the eyes or the stimulus itself. Flipse et al. (1988) extended these results to a broader range of stimulus velocities, showing again that contrast sensitivity for fixation equals contrast sensitivity for pursuit, if the magnitude of retinal-image motion is equal. More recently, Laird, Rosen, Pelz, Montag, and Daly (2006) determined the two-dimensional spatiovelocity contrast sensitivity function that was first described by Kelly (1979). Laird et al. showed that with eye fixation there was no difference in sensitivity for a sine wave drifting inside a stationary Gabor window compared to a stationary sine wave inside a moving Gabor window as long as the temporal and spatial frequencies were the same on the retina. In both cases, they observed a decline in sensitivity with increasing temporal frequency. This decline did not occur during pursuit of a stationary sine wave inside a moving Gabor window and so they reasoned—consistent with Murphy and Flipse et al.—that eye movements do not affect contrast sensitivity. Similarly, Bedell and Lott (1996) measured the detectability of small peripheral spots in two conditions. The spots were stationary during SPEM or moved during fixation. In both conditions, they were located 0.25° below the pursuit trajectory or the fixation cross. Bedell and Lott obtained no differences in visibility between the two observation conditions. Besides, a single study showed that for a stationary flash no visual suppression occurs during smooth pursuit (Starr, Angle, & Yeates, 1969). In all these studies, the sine wave gratings, Gabor patches, or

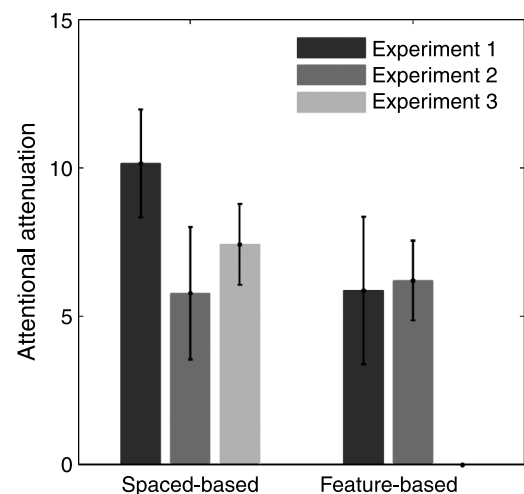


Figure 14. Mean attentional attenuation in all experiments. Error bars denote the standard error of the means.

luminous spots overlapped with the pursuit trajectory or the fixation spot. In contrast, the Gabor patches in the present experiments were located below or above the pursuit trajectory. The eccentricity of the target (i.e., its distance from the pursuit target) may have important implications given recent work on the distribution of attention during smooth pursuit.

A possible reason for the observed sensitivity difference between fixation and smooth pursuit in our data is the concentration of spatial attention on the pursuit target to the detriment of perceptual performance in the periphery. Van Donkelaar (1999) and Van Donkelaar and Drew (2002) showed that the attentional focus is located slightly in front of the pursuit target during SPEM. Further evidence for an involvement of attention during SPEM comes from research on patients suffering from schizophrenia. These patients show impaired shifts of covert attention (Sereno & Holzman, 1996) as well as reduced pursuit gain (Kathman, Hochrein, Uwer, & Bondy, 2003), suggesting a connection between SPEM and attention. Kerzel and Ziegler (2005) observed a similar difference in memory performance during SPEM and fixation. Subjects had to memorize the position of elements presented either in the fovea or in the periphery. Performance for peripheral presented elements was worse during SPEM compared to fixation; performance for foveally presented elements was equal during SPEM and fixation. The other way round, the influence of divided attention on SPEM is currently unclear in the recent literature. Chen, Holzman, and Nakayama (2002) and Hutton and Tegally (2005) showed that a demanding secondary task leads to impaired SPEM. On the other hand, two other studies (Kathman, Hochrein, & Uwer, 1999; Van Gelder, Lebedev, Liu, & Tsui, 1995) observed improved SPEM in a dual task paradigm. It may be that difficult secondary tasks impair, whereas easy secondary tasks facilitate smooth pursuit (Hutton & Tegally, 2005). Garbade and Deubel (2002) showed that a moving distractor influences pursuit velocity. Distractors on the pursuit trajectory were more influential than distractors off the pursuit trajectory, which is an additional indicator for the allocation of attention to the pursuit target.

Many studies also observed space-based attentional modulation in the cortex and showed that attention directed to a location in the visual field attenuates cortical responses to stimuli in unattended locations (for reviews, see Reynolds & Chelazzi, 2004; Yantis & Serences, 2003). For instance, McAdams and Maunsell (1999) measured the influence of space-based attention on responses of single neurons in area V4. For direction-selective neurons in middle temporal and medial superior temporal areas, Treue and Maunsell (1999) observed space-based attentional modulation. Cell responses to the preferred direction were enhanced, if attention was directed to the receptive field of the cell.

In light of these studies, our findings may be interpreted in the following way. During SPEM, attention is bound to

the pursuit target, resulting in an attenuated response to motion in the periphery. In contrast, attention can be easily shifted to peripheral locations during fixation. This explains why contrast sensitivity was reduced in the periphery during SPEM compared to fixation. In most of the previous studies, the smooth pursuit target was presented on a large grating. Therefore, perceptual performance may have been based on foveal signals that were not affected by the coupling of attention to the (foveal) pursuit target. This study disentangles the retinal location of the pursuit and the discrimination targets and reveals a clear reduction in contrast sensitivity during SPEM. Future studies should more closely examine perceptual sensitivity in the fovea during SPEM. Our prediction would be that there are no differences between SPEM and fixation for foveal stimuli because attention is focused on the pursuit target (i.e., in the fovea).

The difference in sensitivity between the two motion directions in Experiment 2 is potentially due to feature-based selective attention which attenuates responses to motion in the direction opposite to the pursuit target. Feature-based attentional modulation has been observed in several brain areas (for a review, see Maunsell & Treue, 2006). For V4 several authors observed feature-based attentional modulation (Haenny, Maunsell, & Schiller, 1988; Motter, 1994). Martinez-Trujillo and Treue (2004) demonstrated that feature-based attention modulates the response of direction-selective neurons in middle temporal. The response of neurons preferring the feature direction was enhanced and the response of neurons preferring the opposite direction was attenuated. Attention to a pursuit target moving to the right would therefore reduce the responses to an object moving to the left, irrespective of its location. These predictions are confirmed by our data, which is summarized in Figure 14. In the first two experiments, the attenuation in the MS condition is attributed to space-based attention, and the additional amount of attenuation in the conditions MO to feature-based attention. Based on the amount of space-based attenuation in Experiments 1 and 2, we conclude that the attenuation of the orthogonal sinusoidal motion in Experiment 3 is mostly due to space-based attention. This in turn means that motion opposite to the pursuit direction is selectively attenuated, leaving other directions unaffected. A similar pattern has been shown for perceived motion smear during pursuit (Bedell & Lott, 1996; Geisler, 1999; Tong, Aydin, & Bedell, 2007; Tong, Patel, & Bedell, 2005). These studies obtained that pursuit attenuates the perceived motion smear only for motion in the opposite direction, leaving motion in orthogonal direction unaffected. We do not argue that the attenuation of motion smear directly influences the temporal contrast sensitivity but suggest a similar mechanism of an extraretinal dichotomic influence on temporal contrast sensitivity.

In sum, this study shows that contrast sensitivity for peripheral stimuli is attenuated during SPEM, possibly as

a result of space-based attention to the pursuit target. Moreover, motion opposite to the pursuit direction was stronger attenuated, which is likely the result of feature-based attention to the pursuit direction.

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