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Localization of speed differences of context stimuli during fixation and smooth pursuit eye movements

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ABSTRACT

The visual system can detect speed changes of moving objects only by means of alterations of retinal image motion, which is also subject to changes induced by head or eye movements. Here we investigated whether smooth pursuit eye movements affect the ability to localize short speed perturbations of large context stimuli. Psychophysical thresholds for localization, discrimination and detection of speed perturbations in one of two context stimuli were measured under two main conditions: in fixation trials subjects fixated a central stationary spot, in pursuit trials they followed a horizontally moving target with their eyes. Context stimuli were vertically oriented sine wave gratings moving simultaneously above and below the fixation or pursuit target for one second in the same direction at the same or a different speed as the pursuit target. During the movement one of the gratings suddenly changed its speed for 500 ms and returned to its original speed. Observers were asked to discern the location of the speed change (two-alternative spatial forced choice task). While detection (two-interval forced choice) and discrimination thresholds for the kind of speed perturbation were in the normal range of Weber fractions of 10–15%, thresholds for the location of the speed perturbation were dramatically increased to 30–50%. Localization thresholds were particularly high when the retinal motion was mainly due to the context movements as during fixation or slow pursuit and significantly reduced when the retinal motion was mainly due to pursuit. This result indicates that the origin of retinal motion, whether it is caused by object motion or by voluntary pursuit is important. We conclude that the localization of speed perturbations affecting one of two peripheral moving objects is exceedingly complicated for the visual system probably due to the dominance of relative motion. During smooth pursuit the ability to localize speed perturbations of non-foveated objects seems to be improved by additional information gained from pursuit such as corollary discharge.

1. Introduction

Visual motion is one of the most important cues for interacting with our environment; it provides essential information about our own movements and the movements of peers, prey, and predators (for review, see Nakayama, 1985). Under natural conditions people or animals often change the direction and speed of their movements so that the ability to analyze the spatial and temporal dynamics of visual object motion is a prerequisite for goal-directed actions and the avoidance of collisions. For example, it is quite important for driving to know the exact positions of speed alterations in traffic. The location of the speed change has to be inferred by comparing the speeds of a selected object over different time periods (speed history) and by comparing its speeds with those of other objects in the near surround. While there has been an enormous amount of work on the detection and discrimination of motion of single objects (for review, see Watson & Ahumada, 1985), much less is known about the perception of motion in environments with several moving objects or surfaces. Here, we address the questions, how well we can localize speed changes in one of two peripheral moving stimuli, and whether this ability is affected by smooth pursuit eye movements to a third moving object.

Several psychophysical studies have suggested that humans are quite sensitive to speed differences of spatially or temporally segregated stimuli, while their perception for continuous speed changes such as acceleration or speed modulations is rather poor (Calderone & Kaiser, 1989; Gottsdanker, 1956; Mateeff et al., 2000; Rosenbaum, 1975; Snowden & Braddick, 1991; Werkhoven, Snippe, & Toet, 1992). The smallest proportional difference between two speeds, the Weber ratio for speed discrimination ($\Delta V/V$), ranges from 5% to 12% when subjects discriminate between constant speeds of stimuli presented one after the other (De Bruyn & Orban, 1988; McKee, 1981; McKee & Nakayama, 1984; McKee, Silverman, & Nakayama, 1986; Orban, De Wolf & Maes, 1984).

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The relationship between velocity and Weber fractions is U-shaped with a minimum of 5% for velocities ranging from 4 to 64 deg/s (De Bruyn & Orban, 1988; McKee, Silverman, & Nakayama, 1986). However, when human observers are asked to detect a speed change of a moving stimulus, thresholds are several times higher, i.e. a 30% difference is needed for the detection of an acceleration (Gottsdanker, 1956) or an oscillation between speeds (Snowden & Braddick, 1991; Bravo & Watamaniuk, 1995). This insensitivity to modest speed changes is explained by the assumption that the visual system integrates speed information and thereby smoothes local variations in velocity over time (Braddick, 1993; Watamaniuk & Duchon, 1992). Also in neurophysiology no evidence for acceleration or deceleration sensitivity was found in individual neurons in the middle temporal (MT) area of awake-behaving monkeys (Price, Ono, Mustari, & Ibbotson, 2005), although, speed changes influenced the neuronal responsiveness. Therefore speed changes may be represented by population activity (Lisberger & Movshon, 1999) and can be explained by combining speed tuning and adaptation behavior of MT-cells (Price et al., 2005).

Under natural conditions the analysis of motion gets further complicated by the fact that neither the eyes within the head nor the head and body are stationary. In order to localize an object in the world, the visual system has to transform its position information from a retino-centric frame of reference into a head-centric or geo-centric frame of reference (see Ilg, Schumann, & Thier, 2004; Souman, Hooge & Wertheim, 2005; Swanston, Wade, & Day, 1987; Wertheim, 1994). Smooth pursuit eye movements alter the perception of spatial position and motion of visual stimuli: flashed stimuli are mislocalized in the direction of pursuit (Brenner, Smeets & van den Berg, 2001; Hazelhoff & Wiersma, 1924; Kerzel, Aivar, Ziegler, & Brenner, 2006; Van Beers, Wolpert & Haggard, 2001) and moving objects appear to move slower when pursued smoothly with the eyes compared to fixation (von Fleischl, 1882 Aubert, 1886, 1887; Freeman & Banks, 1998; Wertheim & Van Gelder, 1990). When pursuit is made in darkness across a small stationary stimulus, it is perceived as moving in the opposite direction to the eyes (Filehne, 1922; Freeman & Banks, 1998; Mack & Herman, 1973; Wertheim, 1987).

For the study of speed perception smooth pursuit eye movements represent an excellent behavioral tool because they depend on visual motion signals and changes of target speeds are followed rapidly by catch-up saccades for correction (Brouwer, de Yuksel, Blohm, Missal & Lefèvre, 2002; Leigh & Zee, 1999; Rashbass, 1961; Robinson, 1965; Segraves & Goldberg, 1994). In their pionieering study Kowler and McKee (1987) investigated human speed discrimination and pursuit eye movement performance in separate experiments. They found that speed discrimination thresholds measured in psychophysical experiments and those reconstructed from the pursuit performance in eye movement experiments, so called oculometric thresholds were very similar. Their results were confirmed by a later study of Gegenfurtner, Xing, Scott, and Hawken (2003) in which subjects followed a horizontally moving target with their eyes and reported after each trial whether the target speed was increased or decreased during a short speed perturbation period. The comparison of thresholds gained from speed judgments and from oculometric functions constructed from ROC analysis of the pursuit velocity traces during the perturbation period revealed similar speed discrimination thresholds for the oculomotor and the perceptual system.

Recently Tavassoli and Ringach (2010) showed that under some conditions the oculomotor system can be even more sensitive to velocity fluctuations than perception. They used small perturbations in target velocity that followed one cycle of a sinusoid, and observers had to judge the polarity of the modulation (first slower then faster or vice versa). The eye was able to follow these perturbations at low amplitudes where perceptual judgments were still at chance level. This is presumably the case because the integration time for perception is longer than for pursuit. A functional dissociation between the processing of motion signals for smooth pursuit and perception in humans was also reported by Spering and Gegenfurtner (2007). Velocities of smooth pursuit responses and perceived velocities of the pursuit targets were measured when either the pursuit target or a visual context surrounding the target briefly changed its velocity. Their results showed that the same motion signals were used differently: to estimate the speed of the pursuit target for a perceptual judgment, context motion was subtracted from the pursuit target motion; to calculate the velocity for the pursuit response to follow the target, both, context motion and target motion were averaged. These opposing context effects indicate different strategies for motion perception and pursuit eye movements: for the estimation of the appropriate pursuit velocity, motion signals are integrated over a larger area (motion assimilation) to improve pursuit precision while for perceptual velocity judgments mainly relative motion signals are used.

Here we wanted to explore the effect of smooth pursuit eye movements on the localization of speed changes in a more general manner. While Spering and Gegenfurtner (2007) focused their study on context effects on pursuit responses, we focused our study on the ability to localize speed perturbations affecting only one of two moving context stimuli. To test whether sensitivity for relative motion is different during steady-state pursuit compared to fixation, we varied eye and context speed independently. Our results show that although smooth pursuit eye movements change the retinal motion, they can improve our ability to localize peripheral speed perturbations of peripheral objects probably by additional extra-retinal information.

2. Methods

2.1. Subjects

Participants of the study were six undergraduate students from the Justus-Liebig-University and one of the authors (DIB). The students were unaware of the purpose of the study and were paid for their contribution. Two of the students and the author had been subjects in other psychophysical eye movement studies. All observers had normal visual acuity or were slightly myopic. The research described here was conducted with the approval of the local ethics committee.

2.2. 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. Subjects viewed the display binocularly from a distance of 47 cm and had their head positioned in place using a chin rest.

2.3. Visual Stimuli and experimental design

Visual stimuli were displayed on a 21-in. CRT monitor (ELO Touchsystems, Fremont, CA, USA) generated by a Nivida Quadro NVS 285 graphics board with a refresh rate of 100 Hz non-interlaced and data collection was controlled by a PC. At a viewing distance of 47 cm, the active screen area subtended 45° horizontally and 39° vertically. The spatial resolution of the screen was set to 1280×1024 pixels, which resulted in 28 pixels per deg.

Context stimuli consisted of two vertically oriented gratings of 0.5 cpd. The gratings were luminance sinusoids modulated symmetrically around a central white point with Judd corrected (Judd, 1951) C.I.E. xyY coordinates (0.32, 0.34, 36.1) and appeared in two rectangular windows (27° long and 9° high) on a uniform gray background with a luminance of (36 cd/m2). The two windows were separated vertically by a 2° gap located along the horizontal screen center (see Fig. 1). A white blob (defined by a generalized Gaussian distribution with a power of 4 and a standard deviation of 0.15°, as specified in Eq. (1)) positioned at the screen center between the gratings was used as a fixation or pursuit target.

$$\mathrm{Contrast}(x,y) = \frac{1}{2 * \pi * SD^2 * e^{-0.5*\left[\left(\frac{x-\mu_x}{SD}\right)^4+\left(\frac{y-\mu_y}{SD}\right)^4\right]}} \tag{1}$$

2.4. Experimental procedure and task

Before each test session, the visual stimuli and task were shown and explained to the observer. Then the observer conducted as many practice trials as he/she wanted. After adjustment of the eye tracker the experimental session started. Before each trial a drift correction was performed: it started with the appearance of a central fixation spot, a black bull's eye with an outer diameter of 0.3° and an inner diameter of 0.15°. The subject had to fixate the bull's eye and press an assigned button to start the trial. This triggered the EyeLink II System to perform a drift correction to correct for errors of headband slippage or other factors. If the drift correction succeeded, the initial bull's eye disappeared and the trial started. In Fig. 1 the sequence of events in a single trial are shown for the two main conditions: fixation and pursuit. At first the two context stimuli and the white blob appeared and remained stationary for 250 ms. In fixation trials the white blob stayed in the screen center during the whole trial, in pursuit trials the blob appeared $-0.75^{\circ}\,^{*}$ pursuit velocity to the left or right. After 250 ms the two context gratings started to move simultaneously in the same direction at the same or a different speed (pedestal speed) as the pursuit target (eye speed). If the pursuit target was initially located to the right (left), it always moved leftward (rightward). After 500 ms one of the gratings suddenly increased or decreased its speed for 500 ms and returned to its original pedestal speed for another 500 ms until the end of the trial. Because of the eye speed dependent horizontal offset of the pursuit target, it reached the screen center always at the middle of the perturbation interval (see Fig. 1). During each experimental session pedestal and eye speed were kept constant; however, the size of the pulse step of the speed perturbation was regulated by an adaptive staircase for speed increments and decrements separately. After each trial the observer was asked to determine whether the upper or the lower grating had changed its speed during the perturbation phase by pressing one of two keys in Experiments 1, 4, 5, 6, 7 and 8. In Experiment 2 we used a two-interval forced choice design and observers had to detect in which interval a perturbation of one of the gratings was presented; in Experiment 3 the speed of both gratings was changed in the same way in the perturbation period and observers had to discern the kind of perturbation (speed increase or decrease). Only in Experiment 5 trials ended right after the perturbation phase. In Experiment 7 the speeds of the two context stimuli differed so that the relative speed difference during the speed perturbation phase was less informative. For all experiments a 2-AFC (or 2-IFC Experiment 2) design and an adaptive staircase procedure was used. On average 80–150 trials were collected for each threshold measurement. For Experiments 1–4 we measured for each observer and condition two thresholds in two separate sessions. For each observer the gain of pursuit eye movements and the eye velocity during fixation trials were calculated in a 700 ms interval, centered on the time period of the speed perturbation. If the pursuit gain was lower than 0.7, the trial was discarded and the subject was informed by a beep of the computer.

Psychophysical data analysis: we used the psignifit toolbox (Wichmann & Hill, 2001) for Matlab to fit cumulative Gaussian functions to the subjectś responses.

2.5. Experiments

2.5.1. Experiment 1 – localization of speed perturbation

The goal of the first experiment was to measure and compare thresholds for the localization of a sudden speed perturbation during steady-state pursuit and fixation. In the pursuit conditions, the pursuit target moved at a constant eye speed and the two context gratings at a constant pedestal speed of 2 or 10 deg/s horizontally in the same direction for 1 s. In the fixation conditions only the gratings moved at 2 or 10 deg/s. Altogether six different conditions were tested (Table 1): two fixation conditions with a pedestal speed of 2 and of 10 deg/s, two pursuit conditions, in which the speed of the pursuit target and context stimuli were the same (eye and pedestal speed = 2 or 10 deg/s; resulting retinal speed: 0 deg/s), one condition, in which the context stimuli moved faster than the pursuit target (eye speed: 2 deg/s and pedestal speed:

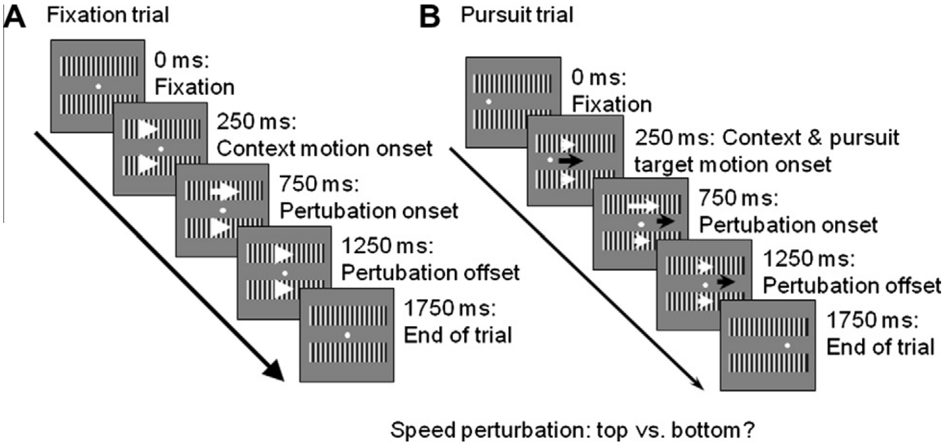

Fig. 1. Experimental paradigms, stimuli, temporal sequence and task. (A) In fixation trials, a white spot appeared in the center on the screen 1° apart from context stimuli above and below. After 250 ms both context stimuli moved in the same direction at the same speed for 500 ms. Then one of them changed its speed for 500 ms and returned to its original speed. Observers were instructed to fixate the central spot during the whole trial and to indicate after each trial which context stimuli had changed its speed during the perturbation phase by key pressing. (B) In pursuit trials, observers were instructed to pursue the white spot, which was initially located to the left or right of the screen center and moved horizontally towards the screen center. The context stimuli moved simultaneously with the pursuit target in the same direction at the same or a different speed. As in A only one context stimulus increased or decreased its speed for 500 ms time and the task was to determine which one.

Table 1
List of conditions used in Experiment 1. Speeds are given in deg/s.

Eye speed	0	2	10	0	2	10
Pedestal speed	2	2	2	10	10	10
Retinal speed	2	0	−8	10	8	0

10 deg/s; resulting retinal speed: 8 deg/s) and one condition, in which the pursuit target moved faster than the context stimuli (eye speed: 10 deg/s and pedestal speed: 2 deg/s; resulting retinal speed: 8 deg/s in the opposite direction). The observeŕs task was to indicate after each trial which context stimulus had changed its speed, i.e. "Top or bottom?". Seven observers were tested including the author DIB.

With four of the observers we measured localization thresholds with additional combinations of eye and pedestal speeds of 2, 4, 8, and 12 deg/s to test at the retinal speeds of 2, 4, 8 and 10 deg/s if it matters whether eye movement or pedestal motion led to the motion across the retina. Also three fixation conditions with pedestal speeds of 2, 4 and 12 deg/s were measured.

2.5.2. Experiment 2 – detection of speed perturbation

In this experiment we measured detection thresholds for speed perturbations with a two-interval forced choice experiment. In a single trial stimuli were presented in two separate time intervals but in only one of them the speed of one of the gratings was changed. In this simple detection task observers had to indicate the interval with the perturbation. For comparison we tested five observers of the first experiment with the same eye and pedestal velocities as in Experiment 1.

2.5.3. Experiment 3 – discrimination of speed perturbation

Here we tested how well observers were able to discriminate the kind of speed perturbation. To prevent relative motion between both gratings during the perturbation phase, they changed their speed simultaneously by the same amount during the perturbation phase. Observers were asked to indicate whether the speed of the gratings had increased or decreased. We tested four observers who participated in Experiments 1 and 2 with the same eye and pedestal speeds as in Experiment 1.

2.5.4. Experiment 4 – localization of speed perturbation of small context gratings

With three observers we tested whether the width of the gratings has an effect on the localization thresholds. The width of both windows was reduced from 27° to 4.5°, but their position remained in the center. We expected that the size reduction of the context stimuli would reduce the effects of pursuit eye movements on localization thresholds, because now the much smaller images of the gratings were projected on the central retina only for a short period during pursuit eye movements. In 10 conditions localization thresholds were measured for a combination of 6 eye speeds (0, 2, 4, 8, 10 and 12 deg/s) and 5 pedestal speeds (2, 4, 8, 10 and 12 deg/s). For comparison the same experimental conditions were tested in Experiments 5–7.

2.5.5. Experiment 5 – localization of single speed step

In the fifth experiment, trials ended after the perturbation phase, i.e. their duration was reduced by 500 ms and the speed of one of the gratings was changed by a single step and remained at this new value until the end of the trial.

2.5.6. Experiment 6 – effect of feedback on localization thresholds

In this experiment we tested the effect of feedback on the ability to localize speed perturbations. The conditions were exactly the same as in Experiment 1, but in the case of a wrong answer the observer was informed by an acoustic signal.

2.5.7. Experiment 7 – reduction of relative motion signals by different pedestal speeds

Here we studied the influence of relative motion cues. To this end, the pedestal speeds of the context stimuli were offset by 1 deg/s. Therefore the motion between both gratings offered no increase in a subject's ability which of the two gratings showed a speed perturbation. The task and the procedure were the same as in Experiment 4, but now for each of the two pedestal speeds a separate staircase was measured. Four (three naïve) observers were tested.

2.5.8. Experiment 8 – effect of depth on localization of speed perturbation

In this last experiment we investigated whether the localization task would become easier during fixation if the two context gratings appeared on different depth planes. By the introduction of spatial depth between the context stimuli we hoped to reduce the effects of relative motion between them during the perturbation phase. Stimuli were displayed on two 19 in. LCD color monitors (Dell™ UltraSharp 1907FP) at a viewing distance of 55.5 cm. The frame rate of the monitors was 60 Hz and screen resolution was 1280 by 1024 pixels. Stimuli for the left eye were presented on the left monitor screen and stimuli for the right eye on the right monitor screen. A Wheatstone mirror stereoscope, consisting of two First Surface Mirrors (169 × 194 mm) was used to bring the two views into alignment. Two spatial conditions were tested randomly intermixed in one session: in the "flat" condition the gratings were presented without spatial offset so that they appeared on the same surface; in the "depth" condition a horizontal offset of 0.4° was added to the gratings, so that one of the gratings appeared to be closer to the observer than the other one. The fixation target appeared to lay between both context stimuli. To enhance the depth impression for the observer, a randomly textured frame of 1.5 deg surrounded the gratings. After a few practice trials all three observers were able to perceive the spatial offset of the two gratings in depth. We measured localization thresholds for four different speeds (2, 8, 10 and 12 deg/s), each twice.

3. Results

In several experiments we investigated the ability to localize brief speed perturbations of drifting context stimuli during steady-state smooth pursuit and fixation. The results of the first experiment are shown in Fig. 2. The leftmost data points in Fig. 2 indicate averaged thresholds for two pursuit tasks, in which the pursuit target was moving at the same speed as the context gratings (eye and pedestal speed were both either 2 or 10 deg/s). In that conditions, both gratings were more or less stabilized on the retina and only the speed perturbation of the affected grating induced retinal motion. In these cases localization thresholds were around 0.5 deg/s, a value found by other investigators for motion detection tasks. The black symbols show data for the two fixation conditions with a retinal (=pedestal) speed of 2 and 10 deg/s. Average localization thresholds were 0.74 deg/s for a retinal speed of 2 deg/s (Weber fraction = 37%) and 3.7 deg/s for a retinal speed of 10 deg/s (Weber fractions = 37%). These localization thresholds were much higher than the typical thresholds measured for speed discrimination ranging between 5% and 12% (De Bruyn & Orban, 1988; McKee, 1981; Orban, De Wolf, & Maes, 1984). In the two other pursuit conditions, the pursuit target moved either faster or slower than the context stimuli: when the pursuit target moved slower (2 deg/s) than the two context stimuli (10 deg/s) the result-

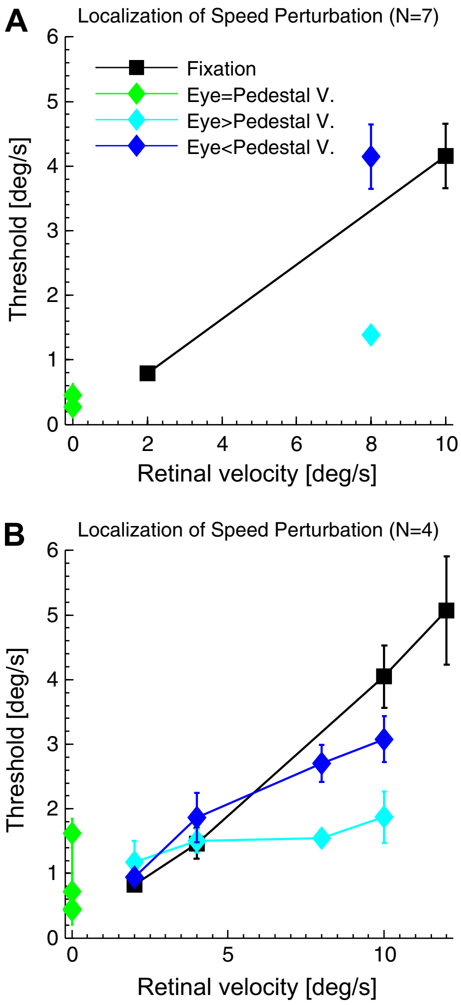

Fig. 2. Results for the first two experiments: mean localization thresholds of short speed perturbations (with standard error of the mean) as a function of retinal velocity during fixation and pursuit. (A) Localization thresholds for seven observers. During fixation (black squares) the context stimuli moved at a pedestal speed of 2 and 10 deg/s. During steady-state pursuit the pursuit target moved either at the same speed as the context stimuli (2 and 10 deg/s – no retinal slip – green diamonds) or the eye speed was higher (light blue diamond) or lower (dark blue diamond) than the pedestal speed so that in both cases the context stimuli moved with a retinal speed of 8 deg/s but in opposite directions. (B) Localization thresholds for the same observers at additional retinal velocities during fixation (black squares) and pursuit with either higher (light blue diamonds) or lower eye speeds (dark blue diamonds). Interestingly, when the eyes moved faster than the context gratings, producing a retinal slip opposite to the direction of pursuit, localization thresholds stayed below 2 deg/s, as during retinal stabilization at equal speeds (green diamonds). Thresholds did not increase with the retinal velocity, as was the case during fixation during slower pursuit.

ing retinal speed for the gratings was about 8 deg/s and observers average localization threshold was 3.45 deg/s (43%). When the pursuit target moved faster (10 deg/s) than the two context gratings (2 deg/s), the resulting retinal speed for the gratings was about 8 deg/s, but in the opposite direction in regard to the pursuit target. Here the average localization threshold was only 1.35 deg/s (17%). The comparisons of localization thresholds for speed perturbations at a retinal velocity of 8 deg/s showed that localization performance was significantly better (paired sample T-test, $t(6) = -3.89$, $p = 0.008$) when the retinal motion was mainly caused by the pursuit eye movements. This was also true when we compared these thresholds to those during fixation and a pedestal speed of 10 deg/s ($t(6) = -4.908$, $p = 0.003$). When the eye speed was much slower than the pedestal speed, thresholds were quite similar to those during fixation ($t(6) = 0.584$, $p = 0.581$).

To study further the influence of eye and pedestal speeds on localization thresholds of speed perturbations, we tested 4 subjects with different combinations of additional pedestal and eye speeds resulting in retinal velocities of 2, 4, 8 and 10 deg/s and during fixation. The averaged thresholds of all 12 conditions are shown in Fig. 2b and in Fig. 3 as a contour plot. Again we found that when the retinal motion was mainly caused by steady-state pursuit, localization thresholds were lower at the retinal velocities of 4, 8 and 10 deg/s than those mainly caused by the context movement. The 2-factorial ANOVA with repeated measures showed no significant main effect for the retinal motion direction for the two pursuit conditions ($F(1,3) = 5.19$; $p = 0.107$), a significant main effect for retinal velocity ($F(3,9) = 12.91$; $p = 0.001$), and a significant interaction ($F(3,9) = 4.587$; $p = 0.033$). The paired T-test showed significant or close to significant differences for a retinal velocity of 8 deg/s ($t(4) = 4.756$, $p = 0.018$) and for 10 deg/s ($t(4) = 2.99$, $p = 0.058$). The effect of steady-state pursuit is quite obvious in the contour plot: localization thresholds increased with increasing pedestal and eye speeds, however, the rise in thresholds was much stronger for increasing pedestal speeds than for increasing eye speeds and highest for fixation where a threshold of 4 deg/s was measured at a pedestal of 10 deg/s (left side of the contour plot). The lowest localization thresholds indicated by the dark blue color were reached when the eye and pedestal speeds were equal or similar, i.e. when the retinal velocity of the context stimuli was close to zero. They ranged between 0.4 and 1.3 deg/s for eye and pedestal speeds from 2 to 12 deg/s. Therefore the origin of retinal motion, whether it was caused by the moving object or the moving eye, seemed to matter.

3.1. Detection and discrimination

Several reasons might explain the relatively bad performance in the localization task during fixation and slow pursuit. First, the observers could simply miss the speed change of one of the context stimuli. To exclude that possibility, we measured detection thresholds for speed perturbations. Five subjects of Experiment 1 were asked to indicate in which of two intervals one of two gratings had changed its speed. Different from Experiment 1, detection thresholds were quite small (10–15% Weber fractions) for all subjects (see Fig. 4), indicating that the perception of the speed perturbation was not difficult. Detection was significantly easier than localization for all but two conditions: 1. when eye and pedestal moved both at 2 deg/s ($t(4) = 2.588$, $p = 0.061$) and 2. when the

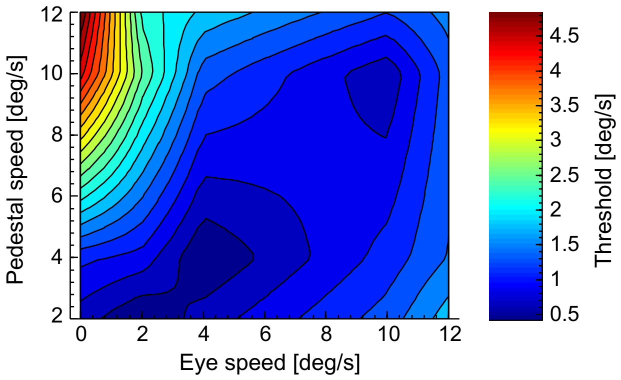

Fig. 3. Contour plot of localization thresholds at different retinal velocities of four observers. Thresholds rose with increasing pedestal speed (y-axis) much faster during fixation (eye speed = 0 deg/s along the x-axis). When eye speed and pedestal speed were equal thresholds were small even for higher speeds (dark blue area in the diagonal direction). The increase in thresholds for higher eye speeds was much smaller than for lower eye speeds or during fixation.

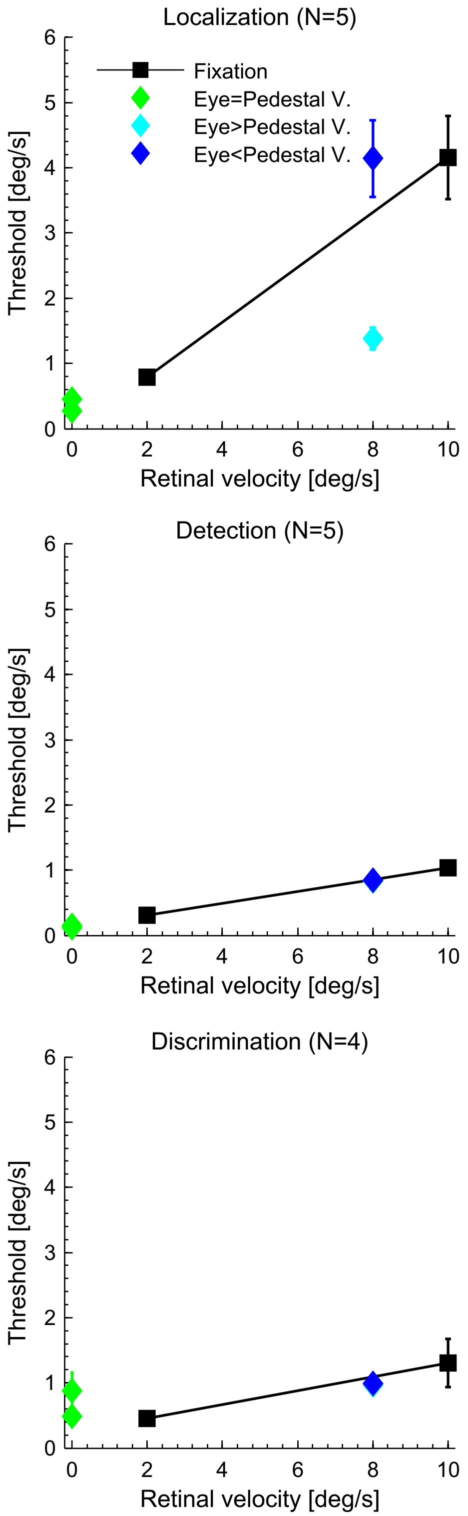

Fig. 4. Comparison of thresholds for localization, detection and discrimination. Thresholds for the detection or discrimination of speed modulation during the perturbation phase rise much less with retinal speed and show no difference for the two pursuit conditions according to the eye/pedestal relationship. In the lower two panels data for eye speed dominating (cyan) are hidden behind data for pedestal dominating (blue).

eyes moved 8 deg/s faster than the context stimuli ($t(4) = 2.158$, $p = 0.097$). Under these conditions also localization thresholds were low, either because the context stimuli were stabilized on retina or because the retinal motion was mainly caused by pursuit.

Second, the observers might have been confused in the perturbation phase by the relative speed. Since a speed change of one of the context stimuli always introduces a relative speed change, i.e. a slowing of the perturbed stimulus causes a relative speeding of the other one, we tested, how well observers could discriminate the kind of perturbation. Therefore both gratings changed their speed during the perturbation phase by the same amount and observers discerned whether the speed of the gratings had increased or decreased. Again for all observers discrimination thresholds were much lower than localization thresholds for speed perturbations (see Fig. 4). For the discrimination of speed perturbations Weber fractions were about 12–13% for all but one condition. (A Weber fraction of 22% was measured during fixation and a pedestal speed of 2 deg/s). No significant difference was found between detection and discrimination thresholds for all 6 conditions.

For the three experiments we also compared the gain of pursuit eye movements during a 700 ms interval, centered on the time period of perturbation because moving textured backgrounds can influence the gain of pursuit (Goltz & Whitney, 2004; Niemann & Hoffmann, 1997; Schwarz & Ilg, 1999; Spering & Gegenfurtner, 2006). Since the pursuit target was spatially separated from each context stimulus by 1°, we expected only small but similar effects for all experiments. On average pursuit gain was close to unity for tasks with equal eye and pedestal speeds. When the pedestal speed was faster (10 deg/s) than the pursuit target (eye speed 2 deg/s) the gain was slightly higher (1.09), when the pedestal speed was slower (2 deg/s) than the pursuit target (10 deg/s) the gain was lower (0.94). Since the effect of context speed upon the pursuit gain was small and similar in all three experiments, we could exclude that differences in gain were causing higher thresholds for localization. For all fixation tasks we measured the mean eye velocity during the same 700 ms interval. As expected we found a small effect of the pedestal speed of the context stimuli on the mean eye velocity: at a pedestal speed of 2 deg/s, the mean eye velocity was on average 0.4 deg/s, at a pedestal speed of 12 deg/s, it increased to 0.6 deg/s.

The results of the first three experiments revealed that during fixation and pursuit the localization of a speed perturbation in one of two context stimuli was far more difficult than its detection or the discrimination of the kind of speed change (Figs. 4 and 5). We also found that the origin of the retinal motion was important: localization thresholds of speed perturbations were much higher

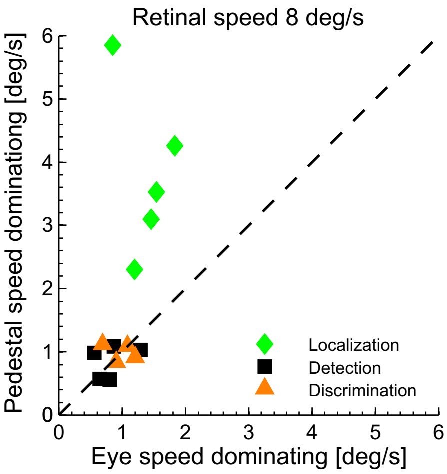

Fig. 5. Influence of pedestal and eye speed on thresholds for localization, detection and discrimination at the retinal speed of 8 deg/s. While the localization thresholds (green diamonds) increased with the dominating pedestal speed, the influence of eye and pedestal was equally low for detection (black squares) and discrimination (orange triangles).

for retinal motion caused only (as during fixation) or mainly (pedestal > eye speed) by object motion compared to retinal motion caused mainly by smooth pursuit eye movements. Therefore smooth pursuit seems to have a positive effect on the ability to determine where a peripheral dynamic object changed briefly its movement speed either by retinal stabilization of the dynamic object or by faster pursuit movements. This advantage may be explained by additional internal motion signals which are only present during the execution of smooth pursuit eye movements: the afferent, proprioceptive signals from the eye muscles (Sherrington, 1918; Wang, Zhang, Cohnen & Goldberg, 2007), and the ‘efference copy’ or ‘corollary discharge’ of the oculomotor command (von Helmholtz, for a review, see Sommer and Wurtz (2008)). Proprioceptive signals and corollary discharge are important for visual stability, motion analysis, calibration and online control of the eye movement system and represent an internal feedback system. Since so far no feedback was provided to the observers about the correctness of their responses, we tested whether feedback would be helpful for the localization of speed perturbations by learning for example to distinguish between the changed speed and the resulting relative speed change of the unperturbed grating. Feedback turned out to have the strongest positive effect for the fixation condition and the pedestal speed of 10 deg/s, resulting in a threshold reduction from 42.4% to 22.24% for the three observers. Feedback during pursuit had no or only small positive effects of up to 5% on localization thresholds. The average thresholds for a pursuit dominated retinal motion of 4, 8 and 10 deg/s were reduced from 1.74 to 1.42 deg/s and for a pedestal dominated retinal motion from 2.98 to 2.48 deg/s. The threshold benefit of about 1 deg/s for retinal motion mainly caused by faster pursuit was still present. To conclude, while feedback helped to localize a limited speed change mainly during fixation, the main effects of the first experiment, i.e. high Weber fractions for localization above 20%, and lower thresholds for retinal motion dominated by pursuit were still present even with feedback.

3.2. Control experiments

The aim of the following three experiments was to find out, why thresholds for localization were much higher than those measured for detection and discrimination. First we tested whether the size of the context stimuli mattered because the width of context windows covered the whole screen so that they could potentially be interpreted as background. Therefore we reduced the width of the context stimuli from 27° to 4.5°. For comparison with the earlier results we measured localization thresholds of three observers during fixation and pursuit at the same eye and pedestal speeds as in Experiment 1 and additional pedestal and eye speeds. We found that for 4.5° context stimuli localization thresholds during fixation and a pedestal speed of 10 deg/s were reduced by 1 deg/s (they stayed the same for a pedestal of 2 deg/s). When the retinal motion was dominated by the pedestal speeds, we found no effect of the smaller window size, however, when the eye speed was the same as the pedestal speed thresholds were on average higher by 0.8 deg/s and also higher by 0.7 deg/s when the retinal motion was dominated by pursuit (Fig. 6). Under this condition, localization thresholds went up for all three retinal speeds (4, 8 and 10 deg/s) tested, on average from 1.74 deg/s for the large 27° window to 2.43 deg/s for the small 4.5° window. This result showed that the benefit of pursuit for retinal motion perception was smaller for the small context objects especially when the eye speed was dominant. Presumable, under these conditions localization became harder because the small context stimuli were mainly projected onto the peripheral retina during the pursuit movement across the screen.

We also tested whether perturbations were easier to localize if the grating velocity was changed by a single step instead of a short pulse. Because of the long integration time of the visual motion system the perturbed speed might be masked if embedded between two periods of the original pedestal speed (Snowden & Braddick, 1991). In general the average thresholds for the localization of single step perturbations were not or only slightly lower during pursuit. During fixation and a pedestal of 10 deg/s localization thresholds were reduced by 1.4–2.8 deg/s. Compared to the average localization threshold at a retinal motion of 10 deg/s mainly caused by pursuit, the benefit of 1 deg/s for dominant eye speed was still present (see Fig. 6).

In all experiments described above the two context gratings moved simultaneously at the same depth plane in the same direction. This might force the visual system to group them into a single moving object. Therefore we performed two experiments where we tried to reduce grouping, either by presenting the context stimuli at slightly different speeds or in different depth planes. To examine the effect of relative speed between the context stimuli in the perturbation phase we tested four observers with the context gratings drifting in the same direction at slightly different

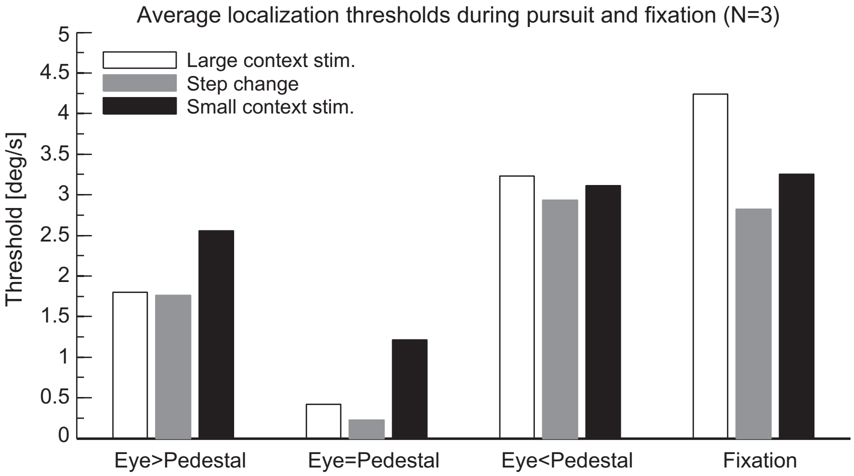

Fig. 6. Comparison of localization thresholds of three experiments for four different retinal motion conditions. During pursuit the retinal motion of 10 deg/s was either dominated by higher eye or higher pedestal velocities, i.e. eye > pedestal, eye < pedestal or it was close to 0 deg/s, when both were 10 deg/s, i.e. eye = pedestal. During fixation the retinal motion was only caused by the context stimuli moving with a pedestal speed of 10 deg/s.

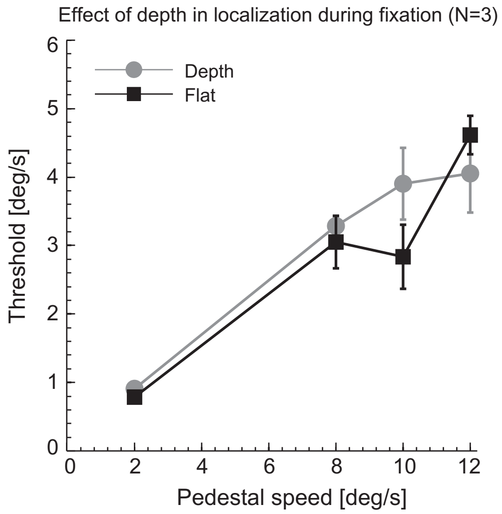

Fig. 7. Average thresholds of three observers for localization of speed perturbations during fixation with or without depth cues at four different pedestal speeds. No threshold differences were found for the two conditions.

speeds (speed difference: 1 deg/s). However, under these conditions localization of speed perturbations became nearly impossible and the results were rather variable.

Therefore we tried to reduce the grouping by presenting the context stimuli in two different depth planes. In a Wheatstone stereoscope observers saw the context stimuli either in a "flat" condition without binocular disparity or in a "depth" condition, where a binocular disparity of 0.4° was introduced so that one grating appeared to be closer to the observer than the other one. Conditions were randomly intermixed and thresholds were measured during fixation at four different pedestal speeds. For both conditions, i.e., with and without binocular disparity localization thresholds were quite similar (Weber fractions between 28% and 41% for pedestal speeds >2 deg/s) and increased with pedestal speed (see Fig. 7). The comparison of the localization thresholds for the four grating speeds tested revealed no difference (paired *T*-test) between the two conditions. We therefore conclude that the impression of different depth planes did not improve the ability to localize speed perturbations during fixation.

4. Discussion

4.1. Summary of the results

We studied the ability to localize, detect and discriminate short speed perturbations affecting one of two moving context stimuli during fixation and steady-state pursuit eye movements. We found that – compared to detection and discrimination – humans were strikingly insensitive to the location of short speed perturbations: localization thresholds were about 3 times higher than detection or discrimination thresholds and reached Weber fractions up to 30–50% during fixation. During pursuit localization thresholds were also in a similar high range when the retinal motion was mainly due to the context motion as throughout slower pursuit velocities. However, localization thresholds for speed perturbations were significantly reduced when the pursuit target and the context stimuli moved at the same speed (no retinal slip) or when the retinal motion was mainly caused by pursuit eye movements; i.e. when the pursuit target moved faster than the context stimuli so that their retinal motion was in the direction opposite to pursuit. Therefore faster ongoing smooth pursuit to a separate target seemed to support the visual system to localize dynamic changes of additional moving objects in the near periphery.

4.2. Motion signals

In our stimulus design different motion signals were present while the observers had to localize a single speed perturbation: first of all, the absolute retinal velocities of the two large context stimuli presented for 500 ms before, during and after the perturbation would be the natural candidate signal to achieve high performance in this task (Masson, Mestre & Stone, 1999). The results in our detection and discrimination paradigm showed that these signals were available and could be used by observers to achieve performance at Weber fractions in the range of 10–15%. Similar Weber fractions were measured by Watamaniuk and Duchon (1992) for a speed discrimination task with random dot stimuli containing a distribution of different speeds. They found that humans were able to integrate different speeds and to arrive at a global speed corresponding to the mean of the distribution, which was as precise as the perceived speed of dots moving at the same speed.

Since detection and discrimination of speed changes were easy, why was it so difficult for the observer to determine which of the two context stimuli had changed its speed? Two possible factors that may be mainly responsible for poor performance on the localization task are temporal integration and relative motion signals. Snowden and Braddick (1991) explored in humans the temporal integration and resolution of velocity signals with horizontally moving random-dot kinematograms. When subjects compared velocities of two temporally separated stimuli, Weber fractions were around 6%, even at very short stimulus presentation times (<200 ms). However, when subjects discriminated between a random-dot pattern moving at a constant speed and a random-dot pattern modulating abruptly between two speeds, at least a 30% speed difference was needed even at a low modulation rate. These authors suggested that the high modulation depth needed for discrimination might be caused by slowly decaying interactions between visual motion detectors. In our experiments the presentation durations of the context stimuli were optimal for speed estimations and comparisons and also the temporal frequency of speed modulation of 1 Hz should be in the optimal range for the visual system leaving enough time for the decay of detector interactions. Since localization thresholds measured after a single step change in speed were only slightly better compared to the original pulse speed change, we conclude that temporal integration is not the decisive issue for the high localization thresholds.

The other possible reason for the difficulty to localize speed perturbations may stem from relative motion signals between the context stimuli. During the perturbation phase, it was very difficult for the observer to determine whether for example the upper context stimulus had increased its speed or whether it appeared faster because the lower one had decreased its speed. This antagonistic speed effect seemed to be the main reason for high localization thresholds during fixation and slow pursuit velocities. Relative motion signals and discontinuities in motion signal distributions resulting from differences in speed, direction or both provide important information for the reconstruction of the three-dimensional structure of objects, for segmentation of visual scenes into component surfaces and the interaction with objects (Nakajama, 1985; Regan, 1986; Britten, 1999; Mestre, Masson, & Stone, 2001). However, it is known that these relative motion signals can be misleading in terms of the cause or origin and they can mask absolute motion signals. Duncker (1929) showed that the motion of a frame relative to a stationary dot is misinterpreted as a dot moving within a stationary frame. Freeman, Champion, Sumnall, and Snowden (2009) found that observers used the sequential relative motion between the pursuit target and the motion stimulus for speed discrimination judgments during pursuit. In this case the relative motion overrides the use of the absolute retinal motion of the stimulus.

4.3. Pursuit and the extra-retinal signal

Why are localization thresholds lower for context stimuli whose retinal motion is mainly caused by pursuit eye movement? In general, pursuit causes a strong change of the retinal image velocities: by stabilizing the tracked object on the fovea, it nullifies the retinal motion of the target object, while it generates retinal motion in the opposite direction for stationary or slower moving objects in the background. Wertheim (1981) suggested that the perception of motion is based on a comparison between the retinal and the extra-retinal signal and that object motion is only perceived when the magnitude between both signals exceeds a threshold. A number of well known misperceptions, such as perceived slowing of pursued objects (Aubert–Fleischl phenomenon (Aubert, 1886; Fleischl, 1882), movement of stationary objects (Filehne illusion (Filehne, 1922)) and trajectory distortions (Souman, Hooge & Wertheim, 2006) can be explained by an underestimation of eye speed (Mack & Herman, 1973; Honda, 1985; 1990) or by a low weighting of eye speed compared to a prior for zero motion, due to the low reliability of the extra-retinal signal (Freeman, Champion, & Warren, 2010).

Those observations indicate that eye movements should make motion estimations even more complex and should lead to higher thresholds. However, the opposite was the case for the localization of a speed perturbation: lowest localization thresholds were found in the case of retinal stabilization when the pursuit target and the context stimuli moved at the same speed and the only retinal motion during the perturbation phase originated from the perturbed context stimulus. When the retinal motion of objects was mainly caused by fast pursuit eye movement, thresholds were significantly lower than during fixation indicating that the visual system can make use of the internal pursuit signal to disambiguate absolute and relative motion cues. Although these retinal motion conditions were quite complex, localization thresholds stayed below 2 deg/s for all retinal velocities measured. A similar asymmetry between motion in- and motion against pursuit direction has been observed for the perception of motion smear, which is selectively reduced for motion opposite to the pursuit direction (Bedell & Lott, 1996; Tong, Aydin, & Bedell, 2007). For motion opposite to the pursuit direction, temporal contrast sensitivity is attenuated (Schütz, Delipetkos, Braun, Kerzel, & Gegenfurtner, 2007) and temporal impulse response is accelerated (Tong, Ramamurthy, Patel, Vu-Yu, & Bedell, 2009), both for luminance stimuli.

This advantage for faster pursuit eye movements may be explained by additional internal motion signals only present during the execution of smooth pursuit eye movements: the afferent, proprioceptive signals from the eye muscles (Sherrington, 1918), and the 'efference copy' or 'corollary discharge' of the oculomotor command (von Helmholtz, 1910/1962; Holst & Mittelstaedt, 1950, for a review, see Sommer and Wurtz (2008)). Proprioceptive signals and corollary discharge are important for calibration and online control of the eye movement system and represent an internal feedback system. While proprioceptive signals can guide the localization of visual targets (Gauthier et al. 1990), extra-retinal signals can contribute to the maintenance of perceptual stability (Stark and Bridgeman 1983), and support motion-in-depth (Welchman, Harris & Brenner, 2009), direction and speed estimations. Haarmeier and Thier (2006) found an improvement for the detection of speed changes of a moving spot during pursuit compared to fixation and recently we found that pursuit has a positive effect on the speed perception of isoluminant targets (Braun et al., 2008). Royden, Crowell, and Banks (1994) found that the estimation of heading in random-dot displays was more accurate during pursuit than during fixation in displays with simulated eye rotations. Similar to Warren and Hannon (1988, 1990), Royden et al. (1994) also observed that at slow eye rotations of <1 deg/s estimates did not differ from the simulated conditions. Turano and Heidenreich (1996) investigated whether speed discrimination of distal grating stimuli was affected by slow eye movements between 0.5 and 3 deg/s. They found that speed discrimination was worse than expected on the basis of retinal motion, when the eyes moved faster than the distal stimuli or in the opposite direction. We did not measure localization thresholds at pursuit below 2 deg/s because of the higher variability of pursuit and the lower pursuit gain. We found that the positive effects of pursuit on localization thresholds were not present at lower retinal motions (<2 deg/s) and for small context stimuli of 4.5°. Therefore we cannot compare our results directly with the study of Turano and Heidenreich (1996).

5. Conclusions

For mobile living organisms the extraction of motion information from the environment is important for the control and guidance of behavior and interactions. Human observers are quite good at detecting changes in the speed of a single moving object. We wanted to explore a more complex situation where several objects are moving while the observer is either fixating or smoothly pursuing a separate target spot. Our results indicate that localization of speed changes was exceedingly difficult probably due to the dominance of relative motion signals when several objects are moving independently. However, when the retinal motion is dominated by pursuit eye movements, localization thresholds for speed perturbation stayed below 2 deg/s and did not increase with retinal speed as during fixation. Therefore smooth pursuit is an effective means to improve localization of peripheral speed perturbations by changing the retinal motion information and providing additional information such as extra-retinal signals and proprioceptive information of the eye position.

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