Available online at www.sciencedirect.com
SCIENCE DIRECT®
Vision Research 46 (2006) 1145–1154
Vision Research
www.elsevier.com/locate/visres

Mislocalization of flashes during smooth pursuit hardly depends on the lighting conditions

Dirk Kerzel [a,*], M. Pilar Aivar [b], Nathalie E. Ziegler [c], Eli Brenner [b]

[a] *Faculté de Psychologie et des Sciences de l'Education, Université de Genéve, 40 bd du Pont d'Arve, CH-1205, Genéve, Switzerland*
[b] *Department of Neuroscience, Erasmus MC, 3000 DR Rotterdam, The Netherlands*
[c] *Abteilung Allgemeine Psychologie, Justus-Liebig-Universität, D-35394 Gießen, Germany*

Received 23 May 2005; received in revised form 22 June 2005

Abstract

Targets that are briefly flashed during smooth pursuit eye movements are mislocalized in the direction of motion (forward shift) and away from the fovea (spatial expansion). Hansen [Hansen, R. M. (1979). Spatial localization during pursuit eye movements. *Vision Research 19*(11), 1213–1221] reported that these errors are not present for fast motor responses in the dark, whereas Rotman et al. [Rotman, G., Brenner, E., Smeets, J. B. (2004). Quickly tapping targets that are flashed during smooth pursuit reveals perceptual mislocalizations. *Experimental Brain Research 156*(4), 409–414] reported that they are present for fast motor responses in the light. To evaluate whether the lighting conditions are the critical factor, we asked observers to point to the positions of flashed objects during smooth pursuit either in the dark or with the room lights on. In a first experiment, the flash, which could appear at 1 of 15 different positions, was always shown when the eye had reached a certain spatial position. We found a forward bias and spatial expansion that were independent of the target and ambient luminance. In a second experiment, the flash was always shown at the same retinal position, but the spatial position of the eye at the moment of flash presentation was varied. In this case we found differences between the luminance conditions, in terms of how the errors depended on the velocity and position on the trajectory. We also found specific conditions in which people did not mislocalize the target in the direction of pursuit at all. These findings may account for the above-mentioned discrepancy. We conclude that although the lighting conditions do influence the localization errors under some circumstances, it is certainly not so that such errors are absent whenever the experiment is conducted in the dark.

Keywords: Pointing; Position judgments; Motion; Perception and action; Smooth pursuit

1. Introduction

When making eye movements, retinal motion signals are often considered to be combined with extraretinal signals to achieve stability of the perceptual world (for a review and critical discussion of this issue in relation to saccades see Bridgeman, Van der Heijden, & Velichkovsky, 1994). Although the world does not appear to move around with each eye movement, which shows that the compensation works quite well, a number of systematic errors have been reported. Many of these reports are concerned with the shift and compression of perceived space just before saccades (overviews in Ross, Morrone, Goldberg, & Burr, 2001; Schlag & Schlag-Rey, 2002). However there is also a tendency to mislocalize flashes that are presented during smooth pursuit eye movements in the direction of motion (*forward shift*, Brenner, Smeets, & van den Berg, 2001; Hazelhoff & Wiersma, 1924; Kerzel, 2000; Mateeff, Yakimoff, &

* Corresponding author. Tel.: +41 0 22 3799132; fax: +41 0 22 3799229.
E-mail address: dirk.kerzel@pse.unige.ch (D. Kerzel).
URL: http://www.unige.ch/fapse/PSY/persons/kerzel/ (D. Kerzel).

0042-6989/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2005.06.032

Dimitrov, 1981; Mitrani & Dimitrov, 1978, 1982; Rotman, Brenner, & Smeets, 2004; van Beers, Wolpert, & Haggard, 2001). A possible explanation for this shift is that neuronal delays between retinal and extra-retinal signals are not compensated for (Brenner et al., 2001), so that the flash is mislocalized by a distance that corresponds with the time that it takes for information from retinal stimulation to reach the brain and for oculomotor commands to reach the eye muscles (about 100 ms). At the same time, flashes are localized away from the fovea (*spatial expansion*, Mitrani & Dimitrov, 1982; Rotman et al., 2004; van Beers et al., 2001), such that the forward shift is larger for objects presented ahead of the target (where forward shift and expansion add up) than for ones presented behind the target (where forward shift and expansion cancel). We know of no explanation for the spatial expansion.

1.1. Discrepant results in the literature

The forward shift during smooth pursuit that is observed with perceptual measures was absent in a study in which subjects responded with hammer blows (Hansen, 1979). Recently, Rotman et al. (2004) did find a forward shift when subjects responded with fast tapping movements. A possible key difference between the two studies was the lighting. Hansen's subjects performed in complete darkness, whereas Rotman et al.'s subjects could see their hand and surrounding objects. In the dark, visual references are absent so that localization has to rely on the extraretinal signal only. In contrast, in a lightened room localization can also take place with respect to other objects. Given this additional information, the fact that localization was more accurate in the dark than in the light leads to the rather counterintuitive hypothesis that the extraretinal signal is precise but that relative localization is not (Brenner & Cornelissen, 2000), so that adding retinal references introduces a forward error. This hypothesis is also inconsistent with the notion that the extraretinal signal is sluggish and inaccurate (e.g., Schlag & Schlag-Rey, 2002) and with the fact that previous studies investigating localization during smooth pursuit in the dark with perceptual measures found reliable forward shifts (Brenner et al., 2001; Mitrani & Dimitrov, 1982).

1.2. The role of visual references in spatial expansion

Studies on perisaccadic localization suggest that the lighting conditions can alter the scaling (metric) of space. In particular, targets flashed around saccade onset in the light are often mislocalized toward the saccade target even if this means that the error is in the opposite direction than the saccade. This spatial compression only occurs when visual references are available after saccade offset (Lappe, Awater, & Krekelberg, 2000). These findings may be completely unrelated to the above-mentioned spatial expansion during pursuit, but they suggest that it may be worthwhile examining whether such expansion depends on the lighting conditions.

1.3. Objectives

The goal of the present study was to investigate the effects of lighting conditions on the manual localization of targets presented briefly during smooth pursuit. We sought to clarify why recent studies on manual localization during smooth pursuit found a reliable forward shift, whereas an early study found none. We also examined whether visual references contribute to pursuit-related spatial expansion.

2. Experiment 1

In order to examine the effects of lighting conditions on the manual localization of targets presented briefly during smooth pursuit, targets were either flashed in complete darkness or with full room lighting. They appeared on a 5 deg × 5 deg grid to test for spatial expansion or compression. In particular, we pursued the following questions: First, would localization in the dark be more accurate than localization in the light as suggested by the difference between Hansen's (1979) and Rotman et al.'s (2004) study? Second, would the strength of the expansion of space change with the lighting conditions as is the case for perisaccadic mislocalization? An effect of lighting conditions would indicate that visual references are used to scale the space during smooth pursuit. We instructed our subjects to point as quickly and as accurately as possible to flashes on a computer screen while pursuing a target moving at 7.1 deg/s. A fixation condition was used to detect (and remove) any localization biases that were not related to smooth pursuit eye movements.

2.1. Methods

2.1.1. Participants

Two of the authors (DK, PA) and four naïve students participated in the Experiment. Participants were all right-handed and reported normal or corrected-to-normal vision.

2.1.2. Stimuli and apparatus

The stimuli were presented on a 21 in. (diagonal) CRT-display with a resolution of 1280 (H) × 1024 (V) pixels at a refresh rate of 100 Hz. A photometer confirmed that the monitor had a very low background luminance (less than 0.001 cd/m^2, S370 Optometer, UDT Instruments, Baltimore, Maryland, USA).

Observers' head position was stabilized with a chin rest at 47 cm from the screen. The position of one eye was monitored with a head-mounted, video-based eye tracker at a frequency of 250 Hz (EyeLink II, SR-Research, Osgoode, Ontario, Canada). Pointing movements to the screen were recorded by an ELO Touchsystems (Fremont, California, USA) touch interface at the pixel resolution of the monitor. A key that served as the starting point of the hand's movement was placed on the table in front of the screen centre at a distance of about 25 cm to the screen center. Prior to each session of the experiment, the touch screen was calibrated by determining the relation between the positions of static stimuli presented on the screen and where the subject in question points.

The experiment was run either in complete darkness with a black (<0.001 cd/m^2) background or with room lights on and a gray (7.5 cd/m^2) background. A dark gray bull's eye (diameter 0.3 deg, 0.25 cd/m^2) was used as the pursuit target. A red target with a luminance of either 0.86 cd/m^2 or 11 cd/m^2 and a diameter of 0.5 deg was flashed for one refresh cycle of the monitor. Three conditions were run: First, the 0.86 cd/m^2 flash was presented in the dark (dim flash in the dark). Second, the 11 cd/m^2 flash was presented in the dark (bright flash in the dark). Third, the 11 cd/m^2 flash was presented in the light (dim flash in the light). The use of the term *dim* for the flash in the first and the third condition refers to the percept, which was subjectively similar for the two dim targets, rather than to the luminance. The similarity was not quantified but the 0.86 cd/m^2 flash in the dark and the 11 cd/m^2 flash in the light looked more or less equally bright, whereas the 11 cd/m^2 flash in the dark clearly looked very much brighter.

In two thirds of the trials, the pursuit target moved at a velocity of 7.1 deg/s for 1.5 s. Target motion was either leftward or rightward. In the remaining trials, the bull's eye was stationary on the screen center. In trials in which the pursuit target moved, the trajectory was symmetrical around the screen center and the flash was always presented when the target reached the screen center. The flash appeared equally often at one out of 15 positions in a 5 columns × 3 rows grid. Column spacing was 2.5 deg and row spacing was 4.9 deg.

The frame of the monitor was covered with black cardboard and the room walls were painted black to avoid any illumination by reflected light from the stimulus itself. During the dark conditions of the experiment there were no sources of light apart from the presented stimuli. The flashed light was very dim (again to reduce illumination by the stimulus itself) and red because rods are least sensitive to red light. All these precautions made it impossible for subjects to see any other objects that could serve as reference points for the localization of the flash. However, after about 20 min in the dark, a faint glow of the monitor background illumination became visible. Therefore, the experiment was run in blocks that were shorter than 20 min, and subjects were exposed to daylight between the blocks.

2.1.3. Procedure and design

At the beginning of a trial, the target was at its starting position and observers were asked to fixate it. To initiate a trial, observers put their finger on the key that served as the starting position. This initiated a standard drift correction of the EyeLink II system. One hundred milliseconds later, the target started to move. Observers were instructed to keep their finger on the key until the flash had been presented. The time between flash presentation and release of the key is referred to as the reaction time (RT). The time between flash presentation and contact with the screen is referred to as the total time (TT). Only pointing responses with RTs longer than 100 ms and TTs smaller than 800 ms were considered acceptable. Otherwise, visual error feedback was provided. In addition, pursuit gain had to be between 0.7 and 1.3 (measured 100 ms before flash presentation). Otherwise, the flash was not shown. Trials that did not meet the above-mentioned criteria were repeated later in the block (and the original trial was eliminated from the analysis).

The three luminance conditions (dark/dim flash, dark/bright flash, light/dim flash) were blocked. Each block consisted of the 135 combinations of 3 target directions (left, right, stationary) and 15 flash positions (3 rows, 5 columns), which were randomly interleaved. In each sitting, each luminance condition was administered once (therefore each session consisted of 3 blocks). The order of blocks followed a latin square design. The eye tracker and touch screen were calibrated before each block. Observers worked through 6 sessions for a total of 2430 acceptable trials. About 10% of the trials had to be repeated.

2.1.4. Statistics

The presence of a horizontal shift was established with *t*-tests. Differences between the luminance conditions were tested with within-subject, two-way ANOVAs (luminance condition × flash position) on the individual mean errors and standard deviations for each condition. To correct for the positively skewed distribution of variances, we log-transformed the standard deviations before the ANOVA. The degrees of freedom in the ANOVAs were adjusted using Huynh–Feldt's Epsilon because the number of subjects was small relative to the number of conditions. For clarity, we report the original degrees of freedom and Huynh–Feldt's Epsilon separately. Despite modest deviations from the assumptions of equal variances in our data, we rely on the ANOVAs to give us an indication of significant main effects and interactions, even if the p-values may not be precisely correct. Means of conditions of interest were compared with two-tailed t-tests with df = 5. Only the p-values of the t-tests are reported.

A main effect of luminance condition would indicate that the forward shift depends on the luminance condition. A main effect of horizontal or vertical flash position could indicate that there is a spatial expansion or contraction. For an expansion we expect to find smaller horizontal errors for flashes presented behind the pursuit target, where the forward error and the spatial expansion cancel out, than for flashes presented ahead of the target, where forward error and spatial expansion add up. We also expect to find upward vertical errors for positions above and downward errors for positions below the pursuit target. An interaction between luminance condition and horizontal or vertical flash position would suggest that the expansion depends on the luminance condition.

2.2. Results

Trials in which a saccade occurred within 100 ms of flash presentation (i.e. from 100 ms before to 100 ms after the flash) were excluded from the analysis. This was the case for about 1% of the trials that had passed the online-control during the experiment. An acceleration criterion 4000 deg/s^2 combined with a velocity criterion of 22 deg/s and a distance criterion of 0.2 deg was used to detect saccades.

2.2.1. Localization error

The mean localization bias for each condition was calculated in the following way. First, the difference between the screen location at which the flash was presented and the screen location touched by the subjects (i.e. the error) was determined for each trial. From these values we calculated the mean and standard deviation for each grid position, kind of movement, lighting condition and subject. To eliminate pointing errors that were not related to the eye movement, we subtracted the mean localization bias when fixating the screen centre from the corresponding mean movement endpoint during pursuit, for each grid position, direction of pursuit, subject and luminance condition. There were horizontal biases of up to 1 deg in the fixation condition. Vertical biases were smaller than 0.2 deg. The sign of the horizontal component of the resulting corrected localization error was then reversed for leftward pursuit, so that positive horizontal deviations indicate a forward error (i.e. in the direction of pursuit) and positive vertical deviations indicate an upward error. The grid positions were also flipped horizontally for leftward pursuit so that negative grid positions along the horizontal axis always refer to positions opposite the direction of pursuit. After that the data were averaged across leftward and rightward pursuit. The thus obtained mean corrected localization errors and standard deviations are shown in Figs. 1 and 2.

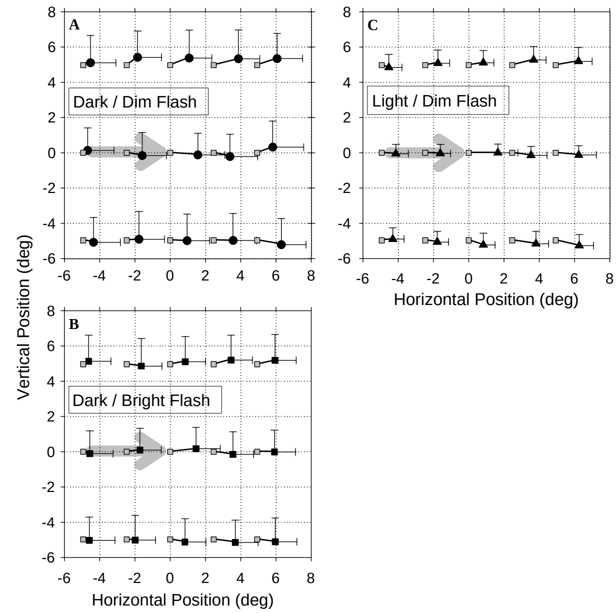

Fig. 1. Localization error as a function of luminance condition and grid position. The real target positions are indicated by gray squares. The solid symbols show the mean pointing endpoints, after eliminating any systematic pointing errors that are not related to the eye movements on the basis of the trials with steady fixation (for details see the Results section). Error bars indicate the trial-to-trial standard deviation averaged across subjects. The arrows indicate the direction of pursuit. The pursuit target was always at $x = 0$, $y = 0$ when the flash was presented. Positive horizontal offsets of the solid symbols relative to the corresponding gray squares indicate that subjects pointed too far in the direction of motion (forward). Positive vertical offsets indicate that subjects pointed too high (up).

2.2.2. Horizontal error

A two-way ANOVA (3 luminance conditions × 5 horizontal flash positions) on horizontal localization error revealed no main effect of luminance condition: $F = 0.28$, $p = 0.62$, $\varepsilon = 0.51$. Separate t-tests showed that the horizontal error was significantly different from zero in the dark with both a dim (0.92 deg, $p < 0.05$) and a bright (0.84 deg, $p < 0.05$) flash, as well as in the light (1.0 deg, $p < 0.01$). There was a main effect of horizontal position: $F(4,20) = 9.3$, $p < 0.01$, $\varepsilon = 0.46$. The forward error was larger for positions that were further in the direction of motion. Inspection of Fig. 2 shows that the effect of flash position was more pronounced behind the pursuit target than ahead of it.

A second two-way ANOVA (3 luminance conditions × 5 horizontal flash positions) on the standard deviations of the error showed that the trial-to-trial variability was larger in the dark (1.47 deg^2 with a dark flash and 1.27 deg^2 with a bright flash) than in the light (0.81 deg^2): $F(2,10) = 39.81$, $p < 0.01$, $\varepsilon = 1.16$. There was a significant effect of horizontal flash position: $F(4,20) = 3.98$, $p < 0.05$, $\varepsilon = 1.13$; as well as an interaction between luminance condition and flash position: $F(8,40) = 4.23$, $p < 0.05$, $\varepsilon = 1.29$.

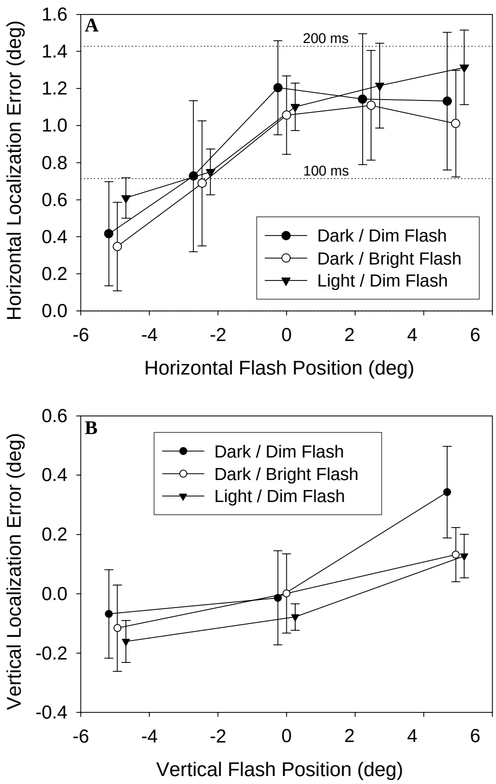

Fig. 2. Mean horizontal (A) and vertical (B) localization error as a function of luminance condition. Error bars indicate the between-subjects standard error. Note that the horizontal positions of the symbols were slightly set apart to allow for better readability. In fact, the same horizontal and vertical positions were used in the three conditions (as specified in the text). The data were averaged across rows for the horizontal displacement and across columns for the vertical displacement. For the horizontal errors, corresponding errors in timing (timing error = localization error/velocity) of 100 and 200 ms are indicated by dashed lines. A positive error in (A) indicates that observers pointed too far in the direction of motion. A positive error in (B) indicates that observers pointed too far up. A positive horizontal flash position indicates a position in the direction of motion relative to the pursuit target. A positive vertical flash position indicates a position above the pursuit target.

2.2.3. Vertical error

A two-way ANOVA (3 luminance conditions × 3 vertical flash positions) on the vertical localization error did not reveal an overall effect of luminance condition, $F = 0.84$, $p = .44$, $\varepsilon = 1.07$. There was a main effect of vertical position, with an upward error for the upper positions (0.2 deg), no bias for the central position (−0.03) and a downward bias for the lower position (−0.12): $F(2, 10) = 9.02$, $p < 0.05$, $\varepsilon = 0.68$. The standard deviation in vertical localization also depended on the luminance condition: it was 1.5 deg^2 and 1.4 deg^2 for the dim and bright flashes in the dark but only 0.7 deg^2 in the light: $F(2, 10) = 70.02$, $p < 0.01$, $\varepsilon = 0.65$. Standard deviations were smaller for the central flash positions (1.05 deg^2) than for the higher (1.27 deg^2) or lower (1.18 deg^2) ones: $F(2, 10) = 7.09$, $p < 0.05$, $\varepsilon = 0.56$.

2.2.4. Reaction and total times

Reaction and total times are shown in Table 1. Reaction and total times were similar in all lighting conditions (perhaps slightly slower with a dim flash in the dark compared to the other lighting conditions; ps < 0.07), but were 20–30 ms shorter when the flash was presented during fixation than when the flash was presented during smooth pursuit (ps < 0.01; see Table 1). To further analyze pursuit-related effects on RTs, we subtracted RTs in the stationary condition from those in the respective pursuit condition. The resulting difference was subjected to a three-way ANOVA (luminance condition × horizontal × vertical flash position). A main effect of luminance condition showed that pursuit-related slowing was more pronounced in the dark (about 30 ms) than in the light (20 ms): $F(2, 10) = 7.63$, $p < 0.01$, $\varepsilon = 1.13$. Pursuit delayed reactions more strongly when the flash was presented below the pursuit target (28 ms) or at the same vertical level (29 ms), than when it was presented above the pursuit target (23 ms): $F(2, 10) = 13.52$, $p < 0.01$, $\varepsilon = 0.99$. There was also a significant interaction between luminance condition and vertical flash position: $F(4, 20) = 4.17$, $p < 0.05$, $\varepsilon = 1.29$. Vertical flash position had the above-mentioned effect on the RT in the dark with a bright flash (from bottom to top: 34, 34, 25 ms) and in the light (20, 23, 16 ms), but not in the dark with a dim flash (29, 30, 28 ms). The total times followed a very similar pattern.

2.2.5. Pursuit gain

Pursuit gain is also shown in Table 1. Pursuit gain was calculated from 100 ms before to 100 ms after the flash. Pursuit gain was around 0.9 in all conditions. It was 0.04 lower in the light than in the dark (ps < 0.02; see Table 1). Correcting the mislocalizations for the differences in gain did not alter the main results. We report the original values without correcting for differences in gain.

2.3. Discussion

The main result of the experiment was that neither the forward shift, nor the spatial expansion was modi-

Table 1
Mean reaction time, total time to reach the target (both in ms) and smooth pursuit gain (eye velocity/target velocity) as a function of luminance condition and target motion (stationary or moving)

Room/target	Reaction time		Total time		Gain
	Stationary	Moving	Stationary	Moving	Moving
Dark/dim	294	324	658	681	0.93
Dark/bright	285	315	645	669	0.93
Light/dim	287	307	659	671	0.89

Between-subject standard errors ranged between 6 and 9 for the reaction time, between 21 and 27 for the movement time, and were about 0.03 for the gain.

fied by the luminance condition. Regardless of whether the target was presented in the dark or light, the flashes were mislocalized in the direction of motion and away from the fovea (as evident in the effects of horizontal/vertical flash position). The invariable mislocalization in the direction of motion shows that visual references do not make localization less accurate, as the discrepancy between Hansen (1979) and Rotman et al. (2004) suggests. The invariable expansion is unlikely to be related to the compression of space right before saccades. Not only is the error in the opposite direction, but perisaccadic compression is very sensitive to the presence of visual references, amounting to about 25% of the distance to the saccadic target with visual references but less than 5% in the dark (e.g., Lappe et al., 2000).

We found forward displacement in all luminance conditions, which is hard to reconcile with the results of Hansen (1979) who reported accurate motor localization during smooth pursuit in the dark. To further examine this discrepancy we conducted a second experiment in which we tried to reproduce more aspects of Hansen's experiments. Given the very different experimental setup (Hansen used analog displays and hammer blows) and some missing information in Hansen's study (e.g., no information on flash luminance), we had to restrict ourselves to a replication of several possibly relevant aspects of Hansen's study.

3. Experiment 2

One evident difference between Hansen's (1979) study and our Experiment 1 is that in Hansen's study the flash was always presented at the fovea but at a random position along a 10 deg trajectory. The orientation of the eye at the moment that the flash was presented varied between trials and the timing of the flash was unpredictable, but the retinal position was always the same. In contrast, in our Experiment 1 the retinal and spatial positions of the flash were unpredictable, but the timing of the flash and the eye's orientation when the flash was presented were predictable. As previous studies have shown that target predictability can affect localization (Brenner & Smeets, 2000; Müsseler & Kerzel, 2004; Rotman, Brenner, & Smeets, 2002) this could be a crucial difference.

Other differences include the fact that the target in Hansen's study oscillated continuously between the endpoints of the trajectory (±5 deg), moved at velocities between 0.25 and 30 deg/s and had to be hit with a hammer. We see no reason to expect a fundamentally different response when hitting an object with a tool than when hitting it with a finger, and did not want subjects to hit our screen with a hammer. It seems too unlikely that people would be able to perform almost perfectly with a hammer but would fail systematically when pointing with their own finger. We also considered it unlikely that the oscillating pursuit is critical, because we know that flashed targets are mislocalized in the direction of pursuit when the pursuit target is oscillating in complete darkness (Brenner et al., 2001). The fact that we only used one target velocity could be an issue, although again we would expect better performance with less variability, not worse performance. However varying the velocity has the additional advantage of revealing the extent to which neuronal latencies are involved in the mislocalization. For errors caused by constant neuronal delays one can expect a linear increase of the localization error with increasing velocity. Thus, in the second experiment we presented a single sweep of the pursuit target and presented flashes as it passed several positions within a 10 deg part of the trajectory. Each position was sampled an equal number of times and subjects pointed with their index finger. Three different velocities were used: 3.5, 7.1 and 14.1 deg/s. The flashes were always presented at the same retinal position (centered on the fovea), but the time of target presentation and therefore the spatial position of the flash was unpredictable.

3.1. Method

3.1.1. Participants

Six naïve students meeting the same requirements as in Experiment 1 participated in this second experiment.

Stimulus, *apparatus*, *procedure*, *and design* were the same as in Experiment 1 with the following exceptions. The flash was always shown at the position of the pursuit target. It could be presented when the pursuit target was at one of seven possible positions on its trajectory (within 5 deg of the screen center). The pursuit target's starting position depended on its velocity so that the pursuit target moved for 400 ms before reaching the first possible target position (i.e. before coming within 5 deg of the screen center). This ensured that there was enough time to pursue the target for all three target velocities: 3.5, 7.1, and 14.1 deg/s. The pursuit target continued to move for 400 ms after the flash was presented.

The three luminance conditions (dark/dim flash, dark/bright flash, light/dim flash) were blocked. Each block consisted of the 42 combinations of 2 target directions (left, right), 7 flash positions, and 3 velocities, each repeated twice. In each session, each luminance condition was administered once (therefore each session consisted of 3 blocks). Observers worked through 2 sessions for a total of 540 acceptable trials. About 32% of the trials had to be repeated.

3.1.2. Statistics

Data treatment was as in Experiment 1 with the following exceptions. Because the target was always presented at the same retinal position, we did not include a stationary control condition. Constant biases to localize targets too far to the left or right will cancel out when the error is calculated with respect to the direction of motion because the same number of trials with target motion to the left and right were presented. Only the horizontal error was considered. Data were subjected to a within-subject, three-way ANOVA (3 luminance conditions, 3 target velocities, 7 trajectory lengths). The possible flash positions were coded such that 0 deg was the first possible flash position (always after 400 ms of pursuit target motion; shortest trajectory), and 10 deg was the last possible flash position (longest trajectory).

3.2. Results

Seven percent of the trials that had passed the online-control during the experiment were excluded because there were saccades within 100 ms of the flash.

3.2.1. Horizontal error

Mean horizontal errors are shown in Figs. 3A and B. A three-way ANOVA revealed a significant effect of luminance condition: $F(2,8) = 5.85$, $p < 0.05$, $\varepsilon = 0.69$. The forward error was slightly, but significantly lower with a bright target in a dark room (1.3 deg) than with a dim target in a dark room (1.6 deg) or a dim target in a light room (2.0 deg, $ps < 0.02$). The forward error in the latter two conditions (dim target in either dark or light room) was not significantly different. The forward displacement was significantly different from zero for all three luminance conditions ($ps < 0.05$). There was a significant main effect of velocity: $F(2,8) = 141.95$, $p < 0.01$, $\varepsilon = 0.53$. The error increased with increasing velocity from 0.12 deg at the slowest velocity (3.5 deg/s) to 1.3 deg at 7.1 deg/s and 3.4 deg at the fastest velocity (14.1 deg/s). There was a significant interaction between luminance condition and velocity: $F(4,16) = 9.93$, $p < 0.01$, $\varepsilon = 1.20$. The increase of the forward error with increasing velocity was stronger in the dark, and was especially strong for the dim flash. There was also an interaction between luminance condition and trajectory length (i.e. position along the trajectory): $F(12,48) = 4.95$, $p < 0.01$, $\varepsilon = 1.26$. The forward displacement decreased with increasing trajectory length in the dark (0.6–1.2 deg), but not in the light (0.2 deg). The decrease was particularly evident for the bright flash in the dark.

3.2.2. Variability

A three-way ANOVA on the standard deviation revealed a significant effect of luminance condition: $F(2,6) = 20.49$, $p < 0.01$, $\varepsilon = 0.71$. The standard deviations were larger in the dark (about 1.5 deg^2) than in the light (0.7 deg^2). The standard deviations also increased with increasing velocity: $F(2,6) = 90.62$, $p < 0.01$, $\varepsilon = 1.14$. They were 1.0, 1.3, and 1.4 deg^2 for the slow, medium, and fast velocity, respectively.

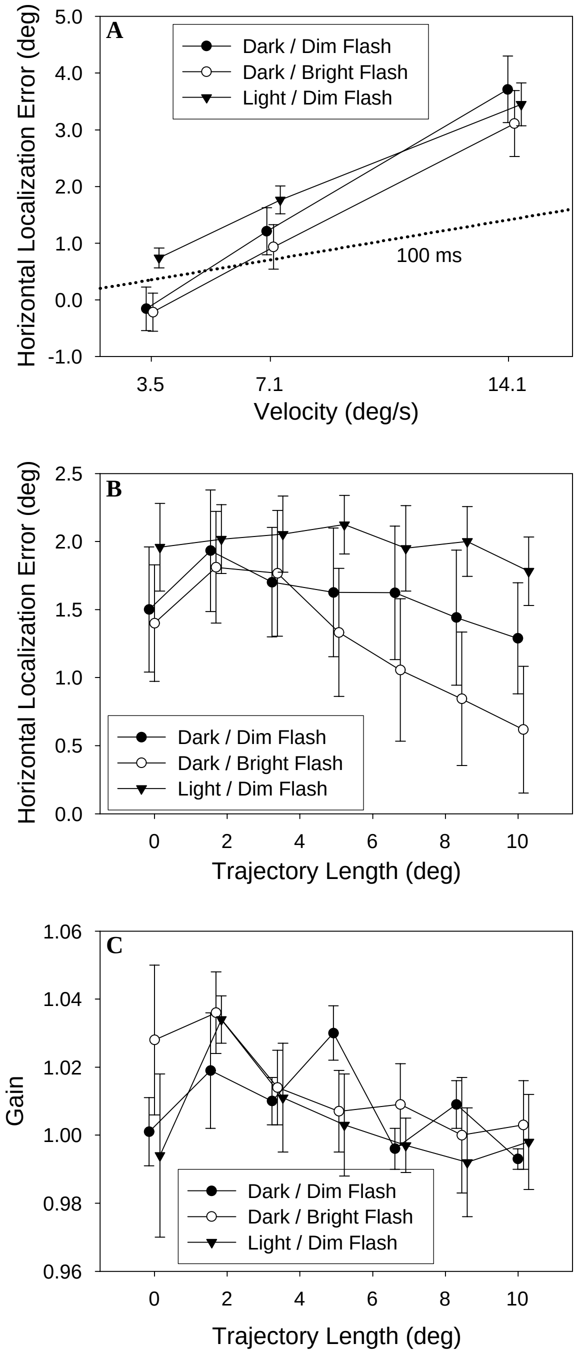

Fig. 3. Mean horizontal localization error as a function of luminance condition and velocity (A) and as a function of luminance condition and trajectory length (B). Note that the horizontal positions of the symbols were slightly set apart to allow for better readability. In fact, the same velocities and trajectory lengths were used in the three conditions (as specified in the text). The dashed line in (A) shows a timing error of 100 ms. (C) shows the pursuit gain as a function of trajectory length and luminance condition.

3.2.3. Reaction times

Mean reaction and total times are shown in Table 2. Again a three-way ANOVA revealed a significant effect of luminance condition: $F(2,8) = 9.41$, $p < 0.05$,

Table 2
Mean reaction time and total time (in ms) as a function of velocity and trajectory length

Length	Reaction time			Total time		
	3.5 deg/s	7.1 deg/s	14.1 deg/s	3.5 deg/s	3.5 deg/s	3.5 deg/s
0°	374	354	349	702	680	699
1.7°	345	331	328	685	670	684
3.4°	338	319	317	681	658	678
5.1°	329	321	314	670	661	677
6.7°	323	312	316	671	657	678
8.5°	323	319	318	671	656	680
10.1°	326	319	320	670	660	678
Mean	337	325	323	679	663	682

Between-subject standard errors ranged between 5 and 13 for the reaction times, and between 8 and 16 for the movement times.

$\varepsilon = 0.97$. Reaction times were slower in the dark with a dim target (337 ms) than in the other two conditions (both about 324 ms). Reaction times decreased with increasing velocity (341, 329, and 315 ms): $F(2,8) = 13.18$, $p < 0.05$, $\varepsilon = 0.51$. They also decreased with increasing trajectory length (from 359 to 322 ms): $F(6,24) = 20.86$, $p < 0.01$, $\varepsilon = 0.47$. The interaction between velocity and trajectory length was also significant: $F(12,48) = 2.61$, $p < 0.05$, $\varepsilon = 0.76$. The decrease of reaction time with increasing trajectory length was larger for slow than for fast velocities, suggesting that it depends on the duration from pursuit target onset rather than on the position. However, if the duration were the only factor one would expect large differences between the three velocities, which was not the case. The changes in reaction time along the trajectory were 48, 35, and 29 ms for the slow, medium, and fast velocity, respectively. A similar overall pattern of results was observed for the total times.

3.2.4. Gain

The mean gain of the pursuit eye movements is shown in Fig. 3C. A three-way ANOVA did not reveal any significant main effects or interactions. The gain was close to unity.

3.3. Discussion

Again, and in contrast to the study of Hansen (1979), we found reliable forward displacement in the dark. However, in this experiment the light conditions did have some effect. The interactions with velocity and trajectory length that emerged may cast some light on why Hansen's results were so different from those of more recent studies. However before turning to this we will discuss some of the other results.

The stronger increase of the forward shift with increasing velocity is consistent with the idea that the latency of retinal information is not compensated for. However, the increase of the spatial error was stronger than what is expected on the basis of a constant delay of retinal information. The temporal error (spatial error/velocity) was 34, 183, and 241 ms for velocities of 3.5, 7.1, and 14.1 deg/s, respectively. Brenner et al. (2001) already noted that the temporal error increased somewhat with increasing velocity, however this effect is much more prominent in the present data set than in theirs (where it changed from 100–150 ms).

In our experiment the effect of velocity depended on the luminance condition. Forward displacement was absent at the slowest velocity in the dark, but was clearly present at higher velocities. In the light, forward displacement was reliable across all velocities and the increase of the forward error with increasing velocity was smaller. The forward error was also larger if the flash was presented early: after a short trajectory had been passed. Again, this effect was larger in the dark than in the light. It should be noted that the decrease of the forward shift with increasing trajectory length cannot be attributed to a decrease in smooth pursuit gain (see Fig. 3C). Although the pursuit gain dropped slightly (but not significantly) toward the end of the trajectory, this drop did not differ between the three luminance conditions.

One possible explanation for the effects of velocity and trajectory length in the dark may be sought in the underestimation of eye velocity during smooth pursuit. A moving object that is stabilized on the fovea by smooth pursuit is perceived to move more slowly than an object moving at the same physical velocity across the retina of a stationary eye (Aubert–Fleischl-phenomenon, Aubert, 1886; Fleischl, 1882). This underestimation only occurs in the absence of other visual references that may be used to estimate target speed. The underestimation of velocity during smooth pursuit is accompanied by an underestimation of trajectory length. Mack and Herman (1972) gauged this underestimation to be about 20% and 10% for velocities of 4.5 and 10.5 deg/s, respectively. The error was larger for the lower velocity. One may speculate that the reduced gain of the extraretinal signal introduces a bias in the perceived position of the eye. That is, the perceived eye position lags behind the true eye position. This will lead to a systematic bias to mislocalize the targets opposite the direction of motion. This bias will increase with increasing trajectory length, in particular at slow velocities, giving a compression of space. Combining such a bias with a forward shift could explain the effects of velocity and trajectory in the dark in our experiment. However this cannot explain Hansen's findings because he found no effect at any velocity.

An alternative account of the effect of trajectory length was suggested in a study concerned with the localization of a smooth pursuit target that suddenly disappears (Mitrani, Dimitrov, Yakimoff, & Mateeff, 1979). Similar to the localization of a flash during pursuit in the present experiment, Mitrani et al. reported that the forward mislocalization of the smooth pursuit target decreased with increasing trajectory length. They too suggested that the larger error at the beginning of the movement was due to an inaccurate estimation of eye velocity. They proposed that as the motion continued, the precision of the extraretinal velocity estimate improved, because integration time increased which allows for more accurate localization toward the end of the trajectory. This idea can also accommodate the effects of velocity that we found, because more time passes until the trajectory is traversed at slow velocities, so the precision of the velocity estimation may be higher and the errors smaller. This could also account for the performance in Hansen's study, if people integrate the velocity estimate across the repeated oscillations, but does not explain why forward displacements were found at all velocities in another study using oscillating pursuit in the dark (Brenner et al., 2001).

4. General discussion

In contrast to studies on perisaccadic compression, spatial expansion during pursuit was not modified by the presence of visual references (such as the screen borders). Neither did the differences in target luminance (or contrast) in our study influence the spatial expansion in the way that target contrast affects perisaccadic compression. Michels and Lappe (2004) reported that high contrast stimuli give less compression than low contrast stimuli. In Experiment 1, there was no difference between the bright and the dim flashes. In Experiment 2, the forward displacement actually changed more with trajectory length for the bright flash in the dark than for the dim flash, which is in direct contrast to the results on saccadic compression. Nevertheless, the spatial compression around saccade onset and the spatial expansion during smooth pursuit do bear some similarity. For instance, the spatial compression orthogonal to the direction of the saccade is maximal for target positions beyond the saccade target (Kaiser & Lappe, 2004). Similarly, we found that the expansion orthogonal to the direction of smooth pursuit was maximal for target positions ahead of the target. Thus, it is premature to conclude that the localization errors near saccades and during smooth pursuit are fundamentally different, although our results do suggest that they may be.

Although our findings are not easily reconciled with those of Hansen (1979), we did manage to find some conditions in which there was no forward shift. We already saw that there was a tendency for the forward shift to be small for long durations of pursuit. In Fig. 3B we see that the shift is particularly small for the *bright* flash in the dark. This points to a possible reason for the discrepancy between Hansen's study and many later ones. Although Hansen does not mention the luminance of his flash, it is quite likely that he used a higher luminance than was used in this and many other studies that use CRT screens. If the tendency that we see in Fig. 3B can be extrapolated to higher flash luminance values, and the forward shift is also reduced by prolonged pursuit, Hansen's findings would be reconciled with ours, and those of many other studies. Of course we would still need to explain why the extent of the forward shift depends on the flash luminance and is only *absent* in the dark. However these questions are still premature because the smaller forward shift for bright flashes, far along the trajectory, in the dark, could also be the result of a particularly strong spatial compression for such flashes under these conditions (note that we did not find a reduced compression for the bright flashes in the dark in the first experiment). In any case our study shows that the forward shift of the perceived positions of targets flashed during smooth pursuit is found both with and without the presence of other visible structures. There appear to be conditions in which this forward shift disappears, but these conditions are exceptions rather than the general rule.

Acknowledgments

DK was supported by the Swiss National Foundation SNF 10011-107768/1, MPA by the European Commission through a Research Training Network (“Perception for Recognition and Action”: HPRN-CT-2002-00226) and NZ by the Deutsche Forschungsgemeinschaft (DFG KE 825/4-1,2 and DFG FOR 560 “Wahrnehmung und Handlung”).

References

Aubert, H. (1886). Die Bewegungsempfindung. *Pflügers Archiv, 39*, 347–370.

Brenner, E., & Cornelissen, F. W. (2000). Separate simultaneous processing of egocentric and relative positions. *Vision Research, 40*(19), 2557–2563.

Brenner, E., & Smeets, J. B. (2000). Motion extrapolation is not responsible for the flash-lag effect. *Vision Research, 40*(13), 1645–1648.

Brenner, E., Smeets, J. B., & van den Berg, A. V. (2001). Smooth eye movements and spatial localisation. *Vision Research, 41*(17), 2253–2259.

Bridgeman, B., Van der Heijden, A. H. C., & Velichkovsky, B. M. (1994). A theory of visual stabiliy across saccadic eye movements. *Behavioral and Brain Sciences, 17*(2), 247–292.

Fleischl, E. V. (1882). Physiologisch-optische Notizen. 2. *Mitteilung der Sitzung Wiener Bereich der Akademie der Wissenschaften, 3*, 7–25.

Hansen, R. M. (1979). Spatial localization during pursuit eye movements. *Vision Research, 19*(11), 1213–1221.

Hazelhoff, F. F., & Wiersma, H. (1924). Die Wahrnehmungszeit. Erster Artikel: Die Bestimmung der Schnelligkeit der Wahrnehmung von Lichtreizen nach der Lokalisationsmethode [The time to perception: first article: the determination of the speed of perception of light stimuli with the localization method]. *Zeitschrift für Psychologie, 96*, 171–188.

Kaiser, M., & Lappe, M. (2004). Perisaccadic mislocalization orthogonal to saccade direction. *Neuron, 41*(2), 293–300.

Kerzel, D. (2000). Eye movements and visible persistence explain the mislocalization of the final position of a moving target. *Vision Research, 40*(27), 3703–3715.

Lappe, M., Awater, H., & Krekelberg, B. (2000). Postsaccadic visual references generate presaccadic compression of space. *Nature, 403*(6772), 892–895.

Mack, A., & Herman, E. (1972). A new illusion: the underestimation of distance during pursuit eye movements. *Perception and Psychophysics, 12*(6), 471–473.

Mateeff, S., Yakimoff, N., & Dimitrov, G. (1981). Localization of brief visual stimuli during pursuit eye movements. *Acta Psychologica, 48*(1), 133–140.

Michels, L., & Lappe, M. (2004). Contrast dependency of saccadic compression and suppression. *Vision Research, 44*(20), 2327–2336.

Mitrani, L., & Dimitrov, G. (1978). Pursuit eye movements of a disappearing moving target. *Vision Research, 18*(5), 537–539.

Mitrani, L., & Dimitrov, G. (1982). Retinal location and visual localization during pursuit eye movement. *Vision Research, 22*(8), 1047–1051.

Mitrani, L., Dimitrov, G., Yakimoff, N., & Mateeff, S. (1979). Oculomotor and perceptual localization during smooth eye movements. *Vision Research, 19*(5), 609–612.

Müsseler, J., & Kerzel, D. (2004). The trial context determines adjusted localization of stimuli: reconciling the Fröhlich and Onset Repulsion Effects. *Vision Research, 44*(19), 2201–2206.

Ross, J., Morrone, M. C., Goldberg, M. E., & Burr, D. C. (2001). Changes in visual perception at the time of saccades. *Trends in Neurosciences, 24*(2), 113–121.

Rotman, G., Brenner, E., & Smeets, J. B. (2002). Spatial but not temporal cueing influences the mislocalisation of a target flashed during smooth pursuit. *Perception, 31*(10), 1195–1203.

Rotman, G., Brenner, E., & Smeets, J. B. (2004). Quickly tapping targets that are flashed during smooth pursuit reveals perceptual mislocalisations. *Experimental Brain Research, 156*(4), 409–414.

Schlag, J., & Schlag-Rey, M. (2002). Through the eye, slowly: delays and localization errors in the visual system. *Nature Review Neuroscience, 3*(3), 191–215.

van Beers, R. J., Wolpert, D. M., & Haggard, P. (2001). Sensorimotor integration compensates for visual localization errors during smooth pursuit eye movements. *Journal of Neurophysiology, 85*(5), 1914–1922.