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## RESEARCH ARTICLE

# Local motion inside an object affects pointing less than smooth pursuit

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**Abstract** During smooth pursuit eye movements, briefly presented objects are mislocalized in the direction of motion. It has been proposed that the localization error is the sum of the pursuit signal and the retinal motion signal in a ~200 ms interval after flash onset. To evaluate contributions of retinal motion signals produced by the entire object (global motion) and elements within the object (local motion), we asked observers to reach to flashed Gabor patches (Gaussian-windowed sine-wave gratings). Global motion was manipulated by varying the duration of a stationary flash, and local motion was manipulated by varying the motion of the sine-wave. Our results confirm that global retinal motion reduces the localization error. The effect of local retinal motion on object localization was far smaller, even though local and global motion had equal effects on eye velocity. Thus, local retinal motion has differential access to manual and oculomotor control circuits. Further, we observed moderate correlations between smooth pursuit gain and localization error.

**Keywords** Smooth pursuit · Localization · Sensory-motor integration

## Introduction

During smooth pursuit eye movements, a briefly flashed stimulus is mislocalized in the direction of motion (Hazelhoff and Wiersma 1924; Mita et al. 1959). This forward error

was found to be larger ahead of the pursuit target than behind (Mitrani and Dimitrov 1982; van Beers et al. 2001), and depends on the trajectory after the flash (Rotman et al. 2004), spatial context (Noguchi et al. 2007), and velocity (Kerzel et al. 2006). Similar localization errors were observed during involuntary slow eye movements (optokinetic nystagmus, Kaminiarz et al. 2007). The initial interpretation of the error was that the time necessary to perceive an object is not corrected for when retinal and extraretinal information is integrated. In other words, a delayed cortical signal about the flash's position is matched to the current position of the eye (Hazelhoff and Wiersma 1924). Consequently, the distance travelled by the eye during signal transmission divided by object velocity indicates the latency of perception (review in Schlag and Schlag-Rey 2002).

An alternative to latency-based explanations was put forth by Rotman et al. (2005). Rotman et al. noted the apparent discrepancy between accurate combination of retinal and extraretinal signals in everyday life, and the blatant errors observed in the lab. According to these authors, the key to understanding erroneous localization of flashes is the lack of retinal motion. Because the duration of a flash is very short, it does not travel a substantial distance across the retina and fails to create retinal motion. Therefore, the flash is perceived as an object moving at the same speed as the smooth pursuit target, and visible persistence may well contribute to the error (see Kerzel 2000). In support of this idea, the forward error for targets moving with the pursuit target (i.e., no retinal motion) was of the same magnitude as for flashed targets. Further, the error decreased as the presentation time of static stimuli was increased from 1 to 193 ms. Rotman et al. (2005) state that “the perceived position depends on the sum of the pursuit signal and the retinal motion, integrated over some time.” (p. 361). Their

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estimate of the integration period was 200 ms. If a target that is stationary in space remains visible throughout the entire integration period of about 200 ms, the retinal motion signal cancels the pursuit signal and no forward error occurs. With presentation times smaller than 200 ms, the retinal motion signal is smaller than the pursuit signal, and a localization error in the direction of pursuit results. A strong prediction of this account is that for conditions with equal pursuit, the localization error should follow the retinal motion signal in the integration window.

### Local versus global object motion and object localization

The first goal of this paper was to investigate whether motion on the surface of a to-be-localized object affects its localization. For goal-directed actions, only the global shape and global motion of the object is relevant. For instance, the local motion of a football's internal pattern (i.e., stripes, diamonds, etc.) that results from object rotation is not informative about the position of the ball itself. Therefore, it should be ignored to accurately hit the ball. To date, it is unclear whether the sensory-motor system distinguishes between global and local object motion during smooth pursuit eye movements. It may well be that it uses both sources of retinal motion to estimate target position, which would modulate the forward error observed in judgments of global object position. That is, if any object-related source of motion is considered to localize the global object position during smooth pursuit, the forward error may change when local and global motion signals are in conflict. In terms of Rotman et al.'s (2005) model, one may wonder whether local motion signals are also subtracted from the smooth pursuit signal.

During eye fixation, it has already been shown that the global position of an object with ill-defined edges (kinetic or blurred) is displaced in the direction of internal object motion (De Valois and De Valois 1991; Ramachandran and Anstis 1990). The illusory displacement of kinetic objects shows that global position and local motion are not processed independently. In studies using Gabor patches (i.e., a Gaussian-windowed sine-wave grating), a position shift was confirmed with presentation times as low as 50 ms (Chung et al. 2007), and the illusory displacement was found to decrease with increasing eccentricity (De Valois and De Valois 1991). Presumably, motion of the sine-wave shifts the perceived centroid of the grating in the direction of motion. Consequently, the leading edge seems to have a larger extent and higher contrast (Tsui et al. 2007). Overall, the size of the motion-induced localization error is small ( $\sim 0.05^\circ$ – $0.3^\circ$ ). However, it is a very robust illusion that is easily observed with vastly different methods such as per-

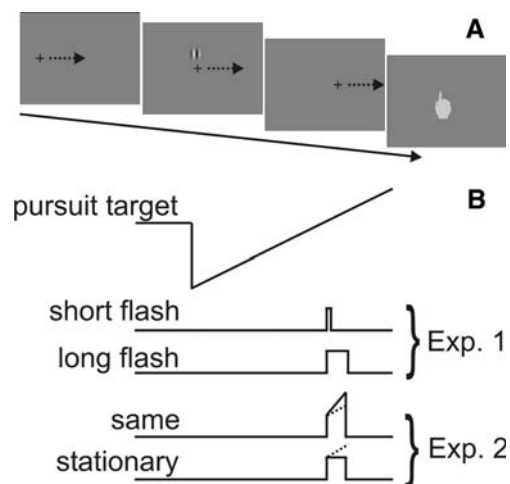
ceptual comparisons, manual pointing, or saccadic eye movements (Kerzel and Gegenfurtner 2005).

### Overview of experiments

In the present experiments, observers pursued a small red cross and localized a briefly presented Gabor patch by touching it with their index finger (see Fig. 1a). The flash appeared either in the fovea or at eccentricities of  $2^\circ$  and  $5^\circ$ . As stationary backgrounds reduce pursuit gain more strongly when close to the fovea (Kimmig et al. 1992), we expect foveal flashes to reduce pursuit gain more than peripheral flashes. Because pursuit velocity decreases only after flash presentation, the retinal velocity of the flashed stimulus will not vary between fovea and periphery.

In Experiment 1, retinal motion of the entire object opposite to pursuit, referred to as *global motion*, was manipulated by changing the presentation time of the flash (see Fig. 1b). Long flashes produce more retinal motion opposite to pursuit than short flashes. According to Rotman et al. (2005), retinal motion signals opposite to pursuit cancel out extra-retinal eye movement signals. Therefore, the localization error should be reduced with long flashes.

In Experiment 2, retinal motion produced by the local features inside the object, referred to as *local motion*, was



**Fig. 1** Illustration of experimental stimuli and task. **a** Subjects followed a fixation cross with their eyes (smooth pursuit task). The flash was a Gaussian-windowed sine-wave (Gabor patch). The Gaussian was always stationary in space. After flash presentation, the fixation cross continued to move for 500 ms before it disappeared. Participants were required to point to the flash position. The movement endpoints were recorded by a touch-sensitive monitor. **b** In Experiment 1, a short or a long flash (10 vs. 90 ms) was presented and the sine-wave was always stationary in space. In Experiment 2, the sine-wave drifted either in the same direction as the smooth pursuit target, but at twice its speed, or it remained stationary. Motion of the sine-wave is shown in the graph, and motion of the pursuit target is indicated by a dotted line for comparison

manipulated by changing the velocity of the sine-wave grating. The Gaussian envelope was always stationary in space. When the sine-wave drifted in the same direction as the pursuit target, but at twice its velocity, there was local motion in the same direction as the smooth pursuit eye movement. When the sine-wave was stationary, retinal motion of the grating was opposite to pursuit. The two conditions are approximately balanced in terms of unsigned retinal velocity: a sine-wave drifting twice faster in the same direction produced retinal velocity of  $+11^\circ/s$  in the direction of pursuit, while a spatially immobile grating produced retinal velocity of  $-11^\circ/s$  opposite to pursuit. Thus, motion smear is similar in both conditions.

The difficulty in the present research is to disentangle effects of retinal motion on object localization from effects of retinal motion on smooth pursuit. Remember that both retinal motion and eye velocity are supposed to affect object localization. Thus, if retinal motion reduces eye velocity and the localization error at the same time, it is unclear whether eye velocity, retinal motion, or both contribute to the localization error. Luckily, our experimental manipulation of motion type resulted in identical effects on smooth pursuit, and we will therefore be in a position to evaluate effects of motion type independently of eye velocity.

Another approach to disentangle retinal and eye velocity is to measure the correlation between eye velocity and localization error at different intervals relative to flash presentation. Variations in eye velocity during flash presentation (referred to as early interval) will produce variations in the retinal velocity of the flash. Of course, it is important to calculate these correlations for the same physical stimulus to assure that retinal motion is only determined by eye velocity. Therefore, correlations were calculated separately for each presentation time and direction of sine-wave motion. Variations in eye velocity after flash presentation (referred to as late interval) determine the strength of the eye signal during the integration period (Rotman et al. 2005). The relative size of the correlations in the early and late intervals will indicate whether smooth pursuit after the flash has an effect independently of retinal motion.

## Experiments 1 and 2

### Methods

#### *Participants*

Twenty naïve participants with normal or corrected-to-normal vision participated and were randomly assigned to Experiments 1 or 2 ( $N = 10$  for each experiment). The experimental procedures were in accordance with the ethical standards of the 1964 Declaration of Helsinki.

### *Apparatus and Stimuli*

The stimuli were presented on a 21 inch (diagonal) CRT with a resolution of  $1,280$  (H)  $\times$   $1,024$  (V) pixels at a refresh rate of 100 Hz. Participants' head position was stabilized with a chin rest at 47 cm from the screen center. Eye movements were recorded by an EyeLink 2 system (SR-Research, Osgoode, Canada). An ELO Touchsystems (Fremont, California, USA) interface recorded the touched position on the monitor surface. Response times were recorded by means of a gamepad 20 cm in front of the touch screen. The experiment was run in a dimly lit room.

The main stimulus was a Gaussian-windowed sine-wave (Gabor patch). The sine-wave had a spatial frequency of 0.6 cycles/ $^\circ$  and the Gaussian had a space constant of  $0.9^\circ$ . In Experiment 1, a stationary Gabor patch was presented for 10 ms (one refresh) at 100% contrast or for 90 ms at 55% contrast (see Fig. 1b). The different contrast values were selected to approximately match the apparent contrast for the two presentation times. In Experiment 2, the Gabor patch was either stationary or drifted at a velocity of  $22^\circ/s$  in the same direction as the pursuit target. To improve the quality of perceived motion, the contrast was modulated in time. It followed a Gaussian with a standard deviation of 20 ms and a peak of 100% contrast. Total presentation time of the Gabor patch was 70 ms (i.e., seven frames) and peak contrast was reached after 40 ms.

The flash appeared randomly at one of three different eccentricities: in the fovea, at  $2^\circ$ , and at  $5^\circ$ . When the flash appeared at an eccentricity of  $2^\circ$  or  $5^\circ$ , it could appear at eight different angles around the smooth pursuit target (from 22.5 to 337.5 degrees of rotation in steps of 45). The three o'clock position was considered the  $0^\circ$  orientation. In a control experiment with two observers (BU and DK), we found that the direction of motion of the sine-wave could be discriminated with almost perfect accuracy (95–100% accurate responses) at all eccentricities during fixation.

The smooth pursuit target was a red  $0.4^\circ \times 0.4^\circ$  cross composed of  $0.11^\circ$  wide lines moving at  $11^\circ/s$ . At the start of a trial, it appeared at  $11^\circ$  either to the left or right of the screen, and it always moved toward the opposite side.

### *Task and procedure*

Before data collection, the touch screen and the eye tracker were calibrated. To this end, participants were asked to touch or look at known positions on the screen. A linear transformation of touch interface to screen coordinates was used.

At the beginning of each trial, the pursuit target was shown in its eccentric position. To initiate target motion, participants pressed a designated button of the gamepad with their right index finger. Participants were asked to

maintain the button depressed until the flash appeared. Participants' task was to follow the pursuit target with their eyes and to hit the flash when it appeared (see Fig. 1a). The flash appeared between 300 ms before and 300 ms after the pursuit target passed the center of the screen. The smooth pursuit target disappeared 500 ms after flash onset.

Reaction times longer than 100 ms and shorter than 800 ms were considered acceptable. The time constraint assured that responses measured rapid, presumably dorsally guided pointing movements, and not a more cognitive memory image. Previously, it has been shown that fast responses are more strongly affected by motion-induced illusions than delayed responses (Yamagishi et al. 2001). Pursuit gain had to be within  $1 \pm 0.3$  during flash presentation. Visual and auditory feedback was provided after non-acceptable trials. Trials that did not meet the criteria for inclusion were repeated in the remainder of the experiment. About one-third of the trials had to be repeated.

### Design

Participants worked through 384 trials: two motion conditions (exposure of 10 vs. 90 ms in Experiment 1; same direction vs. stationary in Experiment 2)  $\times$  two smooth pursuit directions (leftward, rightward)  $\times$  three eccentricities ( $0^\circ$ ,  $2^\circ$ ,  $5^\circ$ )  $\times$  eight angles  $\times$  four repetitions.

### Results

The localization error was the difference between the endpoint of the manual movement and the true flash position. A positive localization error corresponds to a localization error in the direction of smooth pursuit.

Trials in which a saccade occurred during the interval from 36 ms before flash onset to 36 ms after flash onset were removed ( $\sim 5\%$  in all experiments). An acceleration criterion was used to detect saccades ( $>5,000^\circ/s^2$ ). Velocity traces were low-pass filtered (Butterworth filter, 40 Hz). Pursuit gain was averaged in bins of 36 ms. If more than two-thirds of the samples in a bin were missing due to saccades, the bin was discarded. Before averaging across bins, bins that were more than three standard deviations from the respective mean were excluded. Bins are referred to by the mean sample time. That is, the bin from 0 to 36 ms is referred to as 18 ms bin and that from 36 to 72 ms as 54 ms bin, etc.

The differences between conditions with and without retinal motion are shown in Table 1. We present the means, standard deviations, and a measure of the effect size. We chose the quotient of the mean difference over the standard deviation of this difference (Faul et al. 2007),  $d_z$ , because it seems most appropriate for a within-subjects design. Cohen (1992) classified effect sizes of 0.2, 0.4, and 0.8 as small,

**Table 1** Differences between conditions with little retinal motion opposite to pursuit and conditions with strong retinal motion opposite to pursuit

	Localization			Smooth pursuit		
	Mean	SD	$d_z$	Mean	SD	$d_z$
Experiment 1						
$0^\circ$	0.70	0.34	2.07	0.058	0.021	2.70
$2^\circ$	0.48	0.26	1.85	0.036	0.023	1.52
$5^\circ$	0.33	0.17	1.91	0.018	0.027	0.66
Experiment 2						
$0^\circ$	0.23	0.19	1.20	0.068	0.026	2.66
$2^\circ$	0.01*	0.18	0.08	0.051	0.028	1.83
$5^\circ$	0.12*	0.19	0.67	0.034	0.023	1.47

Means, standard deviations, and  $d_z$ , a measure of effect size, are shown for localization error and smooth pursuit gain. Means that are *not* significantly different from zero are indicated by an asterisk

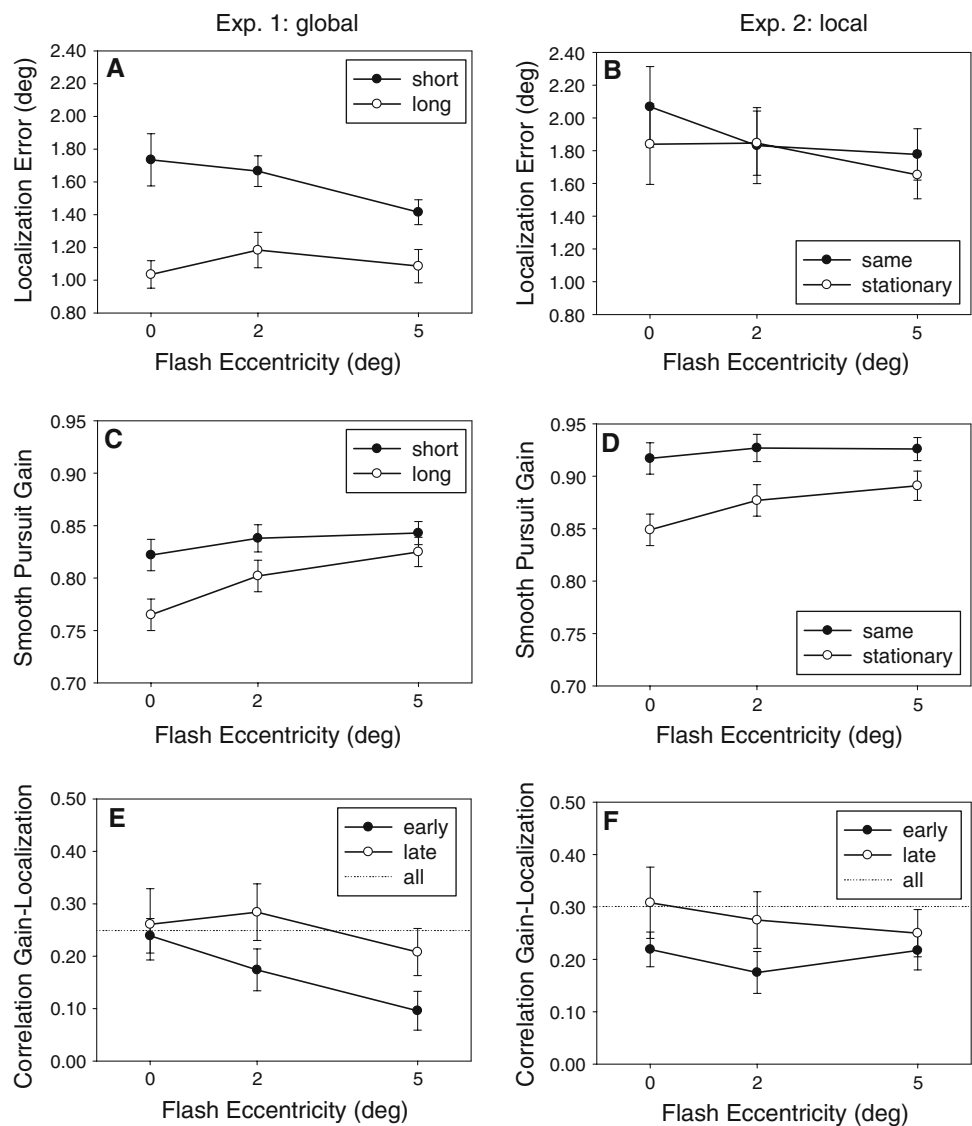
medium, and large, respectively. As can be seen in the table, most effect sizes are very large, except for the localization error with local motion.

### Localization error

Mean localization error is graphed in Fig. 2a, b. A three-way ANOVA with motion type (global, local; i.e. Experiment 1 vs. Experiment 2) as a between-subject factor, and eccentricity ( $0^\circ$ ,  $2^\circ$ ,  $5^\circ$ ) and retinal motion as within-subject factors was conducted. The factor "retinal motion" refers to the strength of the retinal motion signal opposite to the direction of the pursuit eye movement: A short flash produced less retinal motion opposite to pursuit than a long flash (Experiment 1), and a sine-wave drifting in the same direction as the pursuit target produced less retinal motion opposite to pursuit than a stationary sine-wave (Experiment 2).

There was a main effect of motion type,  $F(1,18) = 4.84$ ,  $P < 0.041$ , showing that the localization error was larger with local than with global motion ( $1.8^\circ$  vs.  $1.4^\circ$ ). The localization error decreased with increasing eccentricity ( $1.7^\circ$ ,  $1.6^\circ$ ,  $1.5^\circ$ ),  $F(2,36) = 6.22$ ,  $P < 0.01$ , and was greater with weak retinal motion signals opposite to pursuit ( $1.8^\circ$  vs.  $1.4^\circ$ ),  $F(1,18) = 62.69$ ,  $P < 0.001$ . Importantly, the effect of retinal motion was modulated by motion type,  $F(1,18) = 23.20$ ,  $P < 0.001$ , showing that retinal motion opposite to pursuit affected the localization error far more when it was global ( $1.1^\circ$  vs.  $1.6^\circ$ ) than when it was local ( $1.8^\circ$  vs.  $1.9^\circ$ ). Further, retinal motion and eccentricity interacted, showing that the effect of retinal motion decreased with increasing eccentricity (differences of  $0.5^\circ$ ,  $0.3^\circ$ ,  $0.2^\circ$  for the three eccentricities). Finally, the three-way interaction,  $F(2,36) = 3.70$ ,  $P < 0.05$ , showed that the effect of retinal motion decreased steadily toward the

**Fig. 2** Results of Experiment 1 (a, c, e) and Experiment 2 (b, d, f). The mean localization error as a function of eccentricity and flash duration (Experiment 1) or motion of the sine wave (Experiment 2) is shown in the *top row*. A positive error indicates a localization error in the direction of motion. Mean smooth pursuit gain (averaged from bin 18 to 236 ms, see Fig. 3) is shown in the *middle row*. Mean correlations between gain and localization error are shown in the *bottom row*. The correlation was calculated for early bins (18–54 ms), late bins (162 and 198 ms), and all relevant bins (18–198 ms). Correlations were calculated separately for each retinal motion condition. *Error bars* indicate the between-subjects standard error



periphery with global motion (differences of 0.7°, 0.5°, 0.2°), while it initially decreased and then increased again with local motion (differences of 0.2°, 0°, and 0.1°). For all combinations of experiment, retinal motion, and eccentricity, the forward error was significantly different from zero,  $t_s(9) > 7.4$ ,  $P_s < 0.001$ .

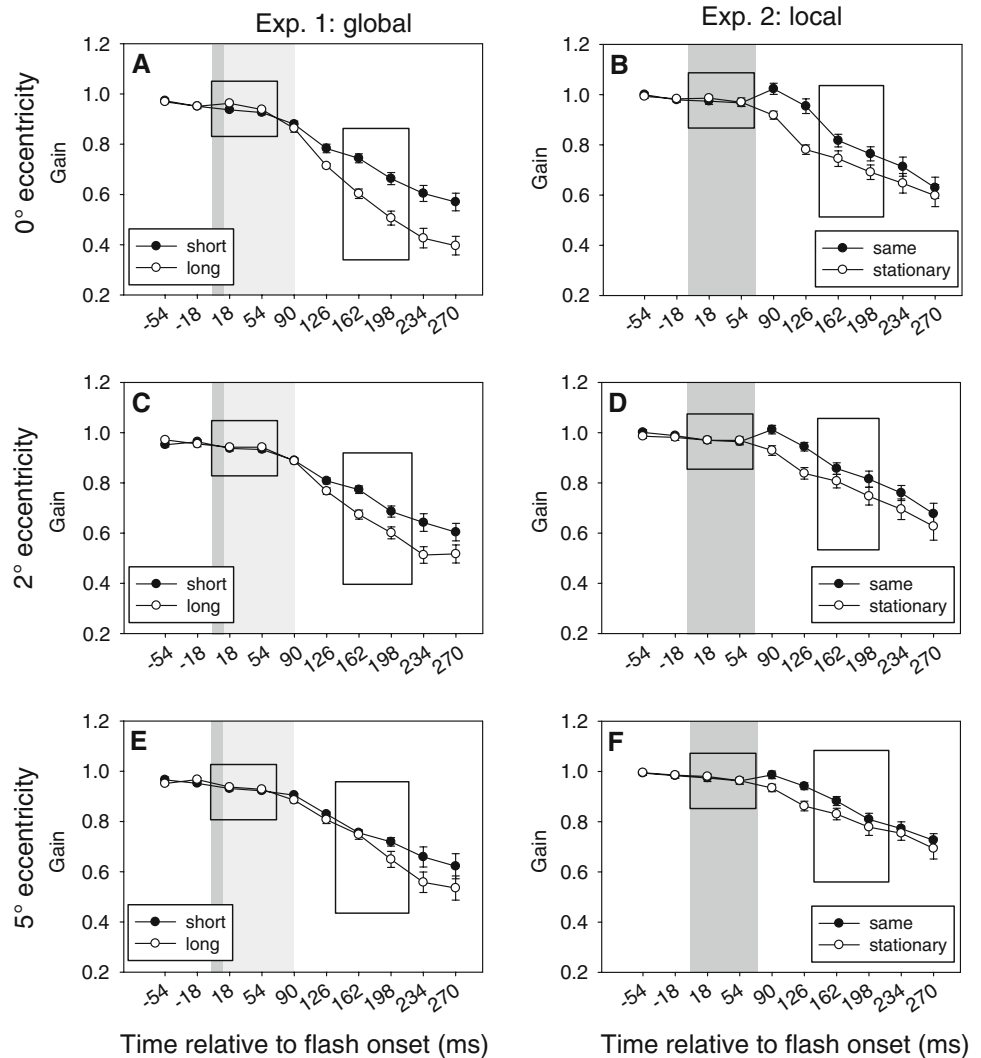
### Smooth pursuit gain

Mean smooth pursuit gain is graphed in Figs. 2c, d and 3. Figure 3 shows that pursuit gain decreased about 100 ms after target onset. This is highly consistent with previous reports (Mitrani et al. 1979; Rotman et al. 2004, 2005). Because the pursuit target continued to move for another 500 ms, the decrease shows that observers voluntarily stopped pursuing the target. When the pursuit target disappears, the pursuit response was shown to last for another ~0.3–0.6 s (Mitrani and Dimitrov 1978), which seems to

match the present results. The most likely reason for the disruption is that observers prepared a saccade toward the perceived flash location (Mitrani et al. 1979; Rotman et al. 2004, 2005). In other words, observers do not keep their gaze directed at the endpoint of the smooth pursuit response, but correct for some of the “overtracking” when making a saccade to the stimulus location. However, whether or not observers make such a saccade does not influence the size of the localization error (Rotman et al. 2005)

In the analysis of pursuit gain, we averaged pursuit gain from 18 to 198 ms after flash onset, because the subsequent analyses of eye–hand correlations show that both early and late intervals are important. The same three-way, mixed-factors ANOVA (motion type  $\times$  eccentricity  $\times$  retinal motion) as on localization error was carried out. Pursuit gain was higher with local than with global motion (0.90 vs. 0.82),  $F(1,18) = 19.64$ ,  $P < 0.001$ . Pursuit gain increased

**Fig. 3** Mean smooth pursuit gain as a function of eccentricity ( $0^\circ$ ,  $2^\circ$ ,  $5^\circ$  from top to bottom row), time after flash onset, and experimental condition in Experiment 1 (a, c, e) and Experiment 2 (b, d, f). The gain was averaged across 36-ms intervals that were centered on the indicated time. The shaded area indicates the presentation time of the flash. The outline rectangles indicate the early and late intervals. Error bars indicate the between-subjects standard error



with increasing eccentricity of the flash (0.84, 0.86, 0.87),  $F(2,36) = 30.24$ ,  $P < 0.001$ . Retinal motion opposite to the direction of pursuit reduced pursuit gain (0.84 vs. 0.88),  $F(1,18) = 137.25$ ,  $P < 0.001$ . However, the effect of retinal motion was not further qualified by motion type,  $F(1,18) = 3.43$ ,  $P = 0.081$ , showing that retinal motion opposite to pursuit had similar effects with global and local motion. If anything, the effect of retinal motion tended to be larger with local (0.92 vs. 0.87) than with global motion (0.83 vs. 0.80), which is opposite to the pattern we saw in the localization data. The interaction between eccentricity and retinal motion was significant,  $F(2,36) = 13.22$ ,  $P < 0.001$ , indicating that the decrease of pursuit gain due to retinal motion was stronger in the fovea (differences of 0.06, 0.04, 0.03 for the three eccentricities).

Correlations between pursuit gain and localization error

Correlations were calculated for each observer separately and mean correlations across observers are shown in

Fig. 2e, f. Individual correlation coefficients were subjected to inferential testing to assure the independence of observations (e.g., Cumming et al. 2007). Because Fisher's Z values were basically identical to the original values, we chose to use uncorrected correlations. First, we correlated localization error and mean gain (averaged across bins 18–198 ms) using all trials of each subject. Nine out of ten observers in each experiment showed a significant positive correlation. The mean correlation (averaged across subjects) was 0.25 with global motion and 0.30 with local motion. By  $t$  test, both means were significantly different from zero,  $t_s(9) > 5.26$ ,  $P_s < 0.001$ .

We then calculated correlations for each combination of retinal motion and eccentricity, again averaging across bins from 18 to 198 ms. The same mixed-factors ANOVA (motion type  $\times$  eccentricity  $\times$  retinal motion) as above was run. A significant effect of eccentricity was confirmed,  $F(2,36) = 5.37$ ,  $P < 0.009$ . Correlations between localization error and gain decreased toward the periphery (0.32, 0.29, 0.23). No other effects were significant.

Next, we calculated correlations for different intervals relative to flash presentation. The early interval from 18 to 54 ms<sup>1</sup> comprises bins in which no effects of flash presentation were evident (cf. Fig. 3). The late bins were chosen at the end of the presumed integration interval of 200 ms (162 and 198 ms bins). We ran a three-way, mixed-factors ANOVAs with motion type (global, local) as between-subject factor, and time interval (early, late), eccentricity (0°, 2°, 5°), and retinal motion as within-subject factors. Correlations were larger in the late than in the early interval (0.26 vs. 0.19),  $F(1,18) = 9.45$ ,  $P < 0.007$ , and decreased with increasing eccentricity (0.26, 0.23, 0.19),  $F(2,36) = 3.45$ ,  $P < 0.043$ . No other effects were significant.

## Discussion

The most important result is that local retinal motion had a far smaller effect on the localization error than on global retinal motion. At the same time, the effect of local retinal motion on smooth pursuit gain was similar to the effect of global retinal motion. Thus, we are in a position to conclude that object localization during smooth pursuit largely disregards local retinal motion. At least, local motion is far less important in the integration of eye movement and retinal motion than global motion.

While the effect of local retinal motion on object localization was small, it was nonetheless significant (difference of 0.12°),  $t(9) = 2.80$ ,  $P < 0.021$ . It may be that motion-induced displacement (De Valois and De Valois 1991) accounts for this effect. It is known that motion-induced displacement increases in the periphery, and we see a similar tendency in the data of Experiment 2. Despite the significant localization error, it is still safe to conclude that local motion has a far smaller effect on object localization than on global motion, while having an equal influence on pursuit gain. Thus, it is not the case that local motion was altogether ineffective.

To some extent, this conclusion is inconsistent with research on the manual following response (Brenner and Smeets 1997; Gomi et al. 2006; Mohrmann-Lendla and Fleischer 1991; Saijo et al. 2005; Whitney et al. 2003). In these experiments, hand trajectories followed the motion of a large structured background. Gomi et al. (2006) found

that the spatiotemporal tuning functions of the manual following response were highly similar to those of reflexive oculomotor following. Therefore, the authors concluded that manual and ocular responses shared computation of visual motion. In Experiment 2, we observed an ocular following response, because changes in eye velocity occurred as early as ~90 ms after flash presentation. Compared to the 54 ms bin, both increases and decreases of pursuit gain in the 90 ms bin were significant (cf. Fig. 3b, d, f),  $t_s(9) > 2.7$ ,  $P_s < 0.022$ , suggesting that the onset of the ocular following response occurred somewhere between 54 and 90 ms. Despite the effect on smooth pursuit, hand movements were not always influenced by local retinal motion. For instance, there was a highly significant effect of retinal motion on smooth pursuit at 2° of eccentricity (difference of 0.05),  $t(9) = 5.78$ ,  $P < 0.001$ , while no such effect was evident in the localization data (cf. Fig. 2b, d). The obvious reason for the absence of a manual following response in our experiment is that the size of our Gabor patches was smaller than the size of the backgrounds used in previous studies. The latter typically covered the whole screen, while our stimuli were only ~2° large. A possible conclusion is that retinal motion influences smooth pursuit more easily (with smaller stimulus dimensions) than pointing movements.

Differences between global and local motion show that retinal motion and eye velocity have (at least partially) independent effects on the localization error. Independent contributions are further corroborated by correlations between smooth pursuit and localization error. While smooth pursuit gain in the early and late intervals was correlated with the localization error, the post-flash correlation was stronger. This shows that the eye velocity during the presumed integration interval of ~200 ms contributes independently to the localization error. In other words, the correlation between eye and hand is not a mere reflection of differences in retinal motion that are caused by variations in eye velocity during flash presentation. In separate analyses not reported here, we confirmed this result by correlating the late interval with the localization error and partialled out the pursuit gain in the early interval. A significant correlation remained.

Further, the correlation between smooth pursuit and pointing explains why the effect of retinal motion on object localization was larger in the fovea than elsewhere: consistent with previous research (Kimmig et al. 1992), conflicting motion signals reduced pursuit gain more strongly when presented in the fovea than when presented in the periphery. Because postflash eye velocity partially determines the localization error, effects of eccentricity on pursuit gain were mirrored in the localization data: Retinal motion reduced pursuit gain and the localization error more strongly in the fovea than in the periphery.

<sup>1</sup> Collapsing across the 18 and 54 ms bins does not perfectly represent the different presentation times of 10 and 90 ms. However, reducing the number of bins to just one leads to a much noisier estimation of pursuit gain, given that for each trial, only a 36 ms epoch is considered. Because interval size and variability are not independent, our analysis would be compromised. Therefore, we used the same early interval in all conditions. Restricting the analysis to the data of Experiment 2 (local motion), which does not suffer from these problems, produced similar results.

Interestingly, the correlation between pursuit gain and localization error was stronger in the (para-) fovea than in the periphery. Remember that correlations were calculated separately for each retinal motion condition. Thus, the stronger correlation between eye and hand cannot be attributed to the stronger effects of retinal motion with foveal flashes. It may be that the increased correlation is due to the natural coalignment of gaze and pointing targets. Typically, we point to where we look (e.g., Gielen et al. 1984; Neggers and Bekkering 2000). Therefore, observers may have a tendency to point to their current gaze direction when the target has been presented in the fovea.

The decreasing correlation between gain and localization error may also explain some puzzling effects of eccentricity: the decrease of the localization error toward the periphery was accompanied by an increase of pursuit velocity. This is opposite to what is expected on the basis of the positive trial-by-trial correlation between pursuit gain and localization: if pursuit gain increases, the localization error should also increase. We believe that the effect of eccentricity is an exception to this rule, because the influence of eye velocity on the localization error decreases toward the periphery. For foveal targets, the strong coupling between gaze and pointing increases the localization error: Smooth pursuit continues after flash presentation and gaze will therefore be displaced in the direction of motion. Because observers typically point to their current gaze direction and the foveal location of the flash reinforced this tendency, a large error resulted. Decoupling gaze and pointing is easier for peripheral targets, because we point at targets in the periphery less often. This reduces the correlation between pursuit gain and localization and brings down the localization error in the periphery.

Overall, the present results support Rotman et al.'s (2005) model. We confirmed that retinal motion reduces the localization error, but that local motion does not have a strong effect as global motion. Despite the far smaller influence of local retinal motion on localization, the effect on pursuit gain was large as that with global motion. Further, there always was a correlation between pursuit gain and localization error, suggesting that pursuit gain contributes independently to the localization error. While the present results certainly support Rotman et al.'s model, there are alternative accounts.

In a related study, Whitney and Goodale (2005) asked subjects to reach to the remembered position of a target during smooth pursuit. They observed that a stationary background presented during pursuit reduced the pointing error compared to a background that moved along with the pursuit target. Among other things, they suggested that visual motion may help update the target's representation in eye-centered coordinates. It is known that eye-centered as well as head-centered representations exist (e.g., Duhamel

et al. 1997). When an object is coded in an eye-centered reference frame, its coordinates have to be updated each time the eye moves. Whitney and Goodale suggested that due to the underestimation of the distance during smooth pursuit (Mack and Herman 1972), a forward localization error occurs. Their results suggest that retinal motion produced by large background objects may help correct this underestimation. Retinal motion of an object presented during smooth pursuit may have a similar function: for stationary objects, the retinal motion vector during smooth pursuit directly indicates how far the eye has moved. After target offset, the visuo-motor system may use this vector to more accurately estimate the amplitude of the eye movement. For flashed targets, no such vector is available, which necessitate reliance on the notoriously imprecise extraretinal signal. Future research will have to disentangle these two accounts.

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