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Spering M, Gegenfurtner KR. Contextual effects on smooth-pursuit eye movements. *J Neurophysiol* 97: 1353–1367, 2007. First published November 29, 2006; doi:10.1152/jn.01087.2006. Segregating a moving object from its visual context is particularly relevant for the control of smooth-pursuit eye movements. We examined the interaction between a moving object and a stationary or moving visual context to determine the role of the context motion signal in driving pursuit. Eye movements were recorded from human observers to a medium-contrast Gaussian dot that moved horizontally at constant velocity. A peripheral context consisted of two vertically oriented sinusoidal gratings, one above and one below the stimulus trajectory, that were either stationary or drifted into the same or opposite direction as that of the target at different velocities. We found that a stationary context impaired pursuit acceleration and velocity and prolonged pursuit latency. A drifting context enhanced pursuit performance, irrespective of its motion direction. This effect was modulated by context contrast and orientation. When a context was briefly perturbed to move faster or slower eye velocity changed accordingly, but only when the context was drifting along with the target. Perturbing a context into the direction orthogonal to target motion evoked a deviation of the eye opposite to the perturbation direction. We therefore provide evidence for the use of absolute and relative motion cues, or motion assimilation and motion contrast, for the control of smooth-pursuit eye movements.

INTRODUCTION

When we smoothly move our eyes in the natural environment, we usually track small moving objects set against a complex visual background. To obtain a veridical percept of object motion and to accurately track an object, the visual system must segregate the object from the background. Since early Gestalt psychology, it has been assumed that low- and high-level visual cues can be used to achieve this task without much effort (Albright and Stoner 2002; Rock and Palmer 1990; Roelfsema 2006). However, under some circumstances our visual system fails and the interaction between object and background cannot be resolved. For instance, in his report on induced motion, Duncker (1929) showed that a stationary, fixated object was perceived as moving into the opposite direction to a second moving object, either an object of the same size as the stationary target or a large object (such as a frame surrounding the stationary target). The observed perceptual effects are large and impressive (for a recent demonstration see Anstis and Casco 2006). Zivotofsky et al. (1995) introduced a variation of the illusion, in which a small target object moved horizontally across a vertically moving background. The background motion added an illusory component to the perceived direction of target motion, resulting in a perceived diagonal target trajectory. Similarly, the Duncker illusion was shown to affect saccades (Zivotofsky et al. 1998) and pointing movements (Soechting et al. 2001), but not smooth-pursuit initiation. Zivotofsky (2005) found that the early pursuit response was driven by *absolute motion* of the target or context, rather than by induced motion of the context. However, the initiation of slow-phase optokinetic nystagmus (OKN) was affected by apparent target motion. Waespe and Schwarz (1987) presented a moving optokinetic stimulus while monkeys attempted to maintain fixation and found an OKN initiation in the direction opposite to that of the optokinetic stimulus.

Born et al. (2000) found an increase in monkeys' initial pursuit acceleration into the direction opposite to that of the neurons' preferred motion direction in response to microstimulation of wide-field sites in area MT. In a behavioral study conducted by the same authors, the microstimulation period was substituted with a brief motion of the background. Again, the direction of pursuit eye movements was shifted into the direction opposite to that of background motion. Allman et al. (1985) already reported earlier that cells in owl monkeys' area MT changed their response to a moving target when the background was moving: Most cells showed an inhibition that increased with increasing background velocity. Tanaka et al. (1986) provided further physiological evidence for surround inhibition. Some MT and MST cells show both: *1*) a suppressed response to a bar stimulus presented in the center when a peripheral dot pattern was moving into the same direction at the same speed and *2*) an enhanced response to central motion for opposite motion in the periphery. Taken together, these results indicate that some cells in macaque area MT are sensitive to relative image velocity and that pursuit can be driven by *relative motion.*

A number of behavioral studies indicate that pursuit eye movements are affected by stationary or dynamic visual backgrounds in monkeys (Keller and Khan 1986; Kimmig et al. 1992; Mohrmann and Thier 1995) and humans (Collewijn and Tamminga 1984; Masson et al. 1995; Niemann and Hoffmann 1997), but results obtained with moving full-field textured backgrounds are inconsistent. Some studies provide evidence for spatial summation or averaging of absolute motion signals: A full-field textured background moving into the same direction as the pursuit target increased pursuit velocity, whereas a background moving into the opposite direction decreased eye velocity (Masson et al. 1995). Similarly, a brief background perturbation evoked a transient increase in eye velocity into the direction of the perturbation (Lindner et al. 2001; Schwarz and Ilg 1999; Suehiro et al. 1999). However, other results are consistent with the idea that motion contrast or relative motion

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signals are relevant for controlling pursuit in the presence of a moving background: Niemann and Hoffmann (1997) found an increase in initial acceleration when the background moved into the direction opposite to that of the pursuit target.

These inconsistencies might result from methodological differences between studies with respect to the choice of observers, stimuli, and studied pursuit interval (for a summary see Born et al. 2000). More important, however, the results from these studies might be affected by a number of possible caveats: An experimental paradigm with a drifting full-field textured background activates both the pursuit and the optokinetic system. Suppressive effects on pursuit velocity by full-field textured backgrounds that are stationary (Mohrmann and Thier 1995) or moving opposite to the pursuit target (Masson et al. 1995) were previously claimed to be a consequence of evoked OKN with saccades directed opposite to the ongoing pursuit eye movement (see Lindner and Ilg 2006). Furthermore, with a full-field background the local motion signal from the target is masked by the global motion signal from the background. To avoid these problems, we used a remote visual background that did not cover the target trajectory. A remote, peripheral background minimizes optokinetic influences (Van Die and Collewijn 1986) and disentangles local and global motion signals. Using such a context, we examined the visual features that determine the nature of the interaction between target and context. In a series of experiments we systematically varied visual properties of the context (horizontal and vertical motion direction, velocity, orientation, contrast) and tested the spatiotemporal sensitivity of pursuit performance to these variations.

METHODS

Observers

In all, nine observers (mean age: 28 ± 8 yr) participated in this study: three highly trained lab members (including the first author) and six undergraduate students from the University of Giessen, Germany, who were paid for their participation and who had participated in earlier eye-tracking experiments. All observers had normal visual acuity. Seven observers were naïve as to the purpose of the experiments. Unless stated otherwise, the pattern of results was the same for highly trained and less well trained and for naïve and nonnaïve observers. All experiments were in accordance with the principles of the Declaration of Helsinki for the protection of human subjects.

Eye-movement recording and visual stimuli

The position of each observer's right eye was measured with a dual-Purkinje-image infrared eyetracker (Fourward Technologies Generation VI; Crane and Steele 1985) at 500 Hz. Viewing was binocular and each eye's view was through a 45° angled glass plate with >90% transmittance. Observers were seated with their heads stabilized by a forehead rest and a bite bar made of dental medical material. Eye-position data were stored for off-line analysis. We recorded position traces for 500 ms before the onset of stimulus motion. Eye-velocity (eye-acceleration) profiles were yielded from low-pass filtered and digitalized eye-position (eye-velocity) data. Data were smoothed with a second-order Butterworth filter with a cutoff at 40 Hz (position) or 60 Hz (velocity). Observers viewed the stimuli on a gamma-corrected Sony Trinitron F-900 23-in. monitor (1,024 × 660; 100 Hz). The display was 29 × 19° at a viewing distance of 94 cm, with a mean background luminance of 40 cd/m^2. Each pixel subtended 1.7 arc min. The pursuit target was a Gaussian dot (diameter: 33 pixels, 0.93°), presented at 50% contrast, and moving horizontally at a constant velocity of 11.28°/s. We used a step–ramp paradigm (Rashbass 1961) to prevent saccades in the direction of target motion during pursuit initiation. The optimal displacement size for the step–ramp was defined individually for each observer in a preliminary experiment and was 2.6° (230 ms) on average. A visual context consisting of two horizontal sinusoidal gratings with a spatial frequency of 0.5 c/deg and 100% contrast was presented above and below the target trajectory. The context had the same mean luminance as that of the background. The two sinusoidal gratings were 1.13° apart and randomly shifted in phase by 0 to 0.5 cycles, to avoid induced or phantom grating effects (McCourt 1982; Tynan and Sekuler 1975). The context remained stationary throughout the trial, moved horizontally along with the target or into the opposite direction, or was briefly perturbed for 300 ms during the steady-state phase of the eye movement. We also tested different background contrasts and orientations.

Experimental paradigm and procedure

Each observer completed between one and five blocks of 180–240 trials for each experiment in sessions lasting no longer than 45 min. Within one block, trials for different conditions were randomly interleaved. Each block of trials started with a calibration of the horizontal and vertical eye position and the eye tracker output signal. Calibration data along the horizontal and vertical axes were fit with a regression line. The correlation coefficients between data and regression line were always at r values ≥0.98. Regression parameters were later used to rescale eye-tracker position output in the analysis of trials from that session.

Each block of trials was started by the experimenter. A single trial started with 500-ms central fixation of the target in the presence of the stationary visual context (Fig. 1). The target then stepped to the left or right of fixation and started to move back across the fovea for 1,000 ms. In experiments with a drifting context, the context started to drift into the same or opposite direction to target motion at the onset of target motion at the time of the target step. Trials with leftward and rightward horizontal target motion were equally balanced and randomized within a block of trials. Observers were instructed to smoothly track the horizontal target. The total duration of target motion (step and ramp) was about 1,200 ms. After each trial, there was a pause of 1,000 ms to give observers ample time for blinking and to make a saccade back to the center of the screen. In the perturbation experiment, we used a slightly different design to have the perturbation occur roughly in the center of the screen. After initial fixation, the target reappeared at 10.5° to the left or right of fixation and remained there for 500 ms with the visual context already present. The target then moved centripetally in a step–ramp fashion for 1,500 ms (with the ramp motion duration depending on the individual observer's step size).

Eye-movement data analysis

Eye movements were analyzed following methods described previously (Spering et al. 2005). Briefly, saccades in each trace were detected using a combined position criterion and fixed-velocity cutoff (30°/s). A period of 30 samples (60 ms) before and after saccade onset and offset was excluded to account for saccadic backshoot and overshoot arising from the lens slip artifact found in Purkinje eye-tracking records (Deubel and Bridgeman 1995). Traces were then aligned to pursuit onset. Pursuit onset was defined as the intersection of two sliding regression lines along the position trace. The intersection had to exceed a fixed-velocity criterion (25% of target velocity) to qualify as pursuit onset. If a saccade occurred within a time window of 250 ms after stimulus motion onset, no pursuit onset was determined and the trial was excluded from further analysis (roughly 10%

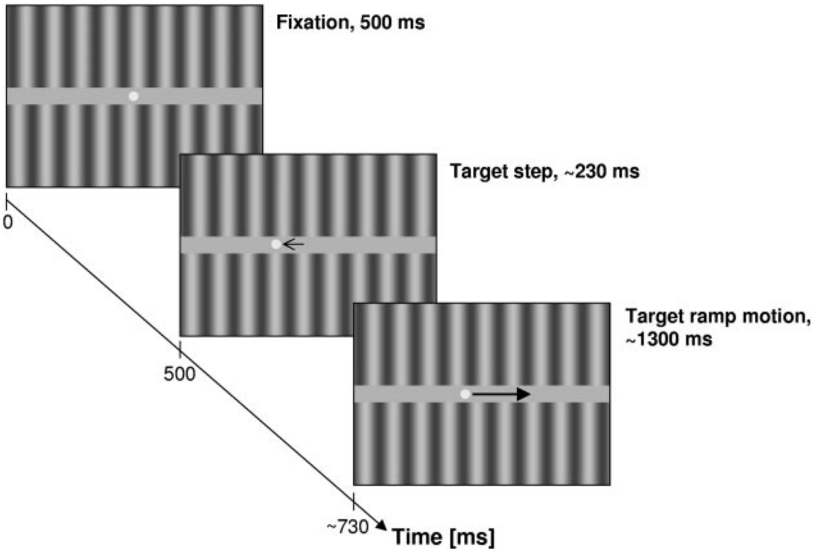

FIG. 1. Trial episode in first experiment. Each trial began with fixation of the target in the presence of the stationary context. A target step to the left or right of fixation position was followed by a foveopetal ramp movement. Observers were instructed to follow the horizontal target. In experiments with a drifting context, the context started to drift on target motion onset (i.e., at the beginning of the step).

of trials from all observers within a given experiment). During visual inspection of position and velocity traces, we also excluded trials in which the eye tracker lost the signal (roughly 5% of trials). We analyzed pursuit latency and eye acceleration during the open-loop phase (initiation, 0–140 ms after pursuit onset). This interval was chosen because it precedes the first visual feedback about the initial eye movement of pursuit (e.g., Lisberger et al. 1987). Eye velocity was analyzed during the closed-loop phase, where the eye reached a steady velocity (500–700 ms after pursuit onset). We disregarded the last 200 ms of pursuit because one observer, who participated in most of the experiments, consistently showed strong anticipatory slowing (see Robinson et al. 1986) toward the end of the trial. We also analyzed the number of horizontal saccades between pursuit onset and trial end. Acceleration, velocity, pursuit latency, and number of saccades were calculated individually in each trial and then averaged across conditions for each observer. Possible differences between conditions were tested statistically by repeated-measures ANOVA or by paired samples *t*-test. *P* values of post hoc pairwise comparisons were Bonferroni-corrected, following Holland and Copenhaver (1988). To quantify the effect of a textured context, we calculated a suppression index (SI; see Kimmig et al. 1992) for both stationary ($\mathrm{SI}_{\mathrm{stat}}$) and drifting ($\mathrm{SI}_{\mathrm{drift}}$) contexts: $\mathrm{SI}_{\mathrm{stat}} = (1 - \mathrm{R}_{\mathrm{stat}}/\mathrm{R}_{\mathrm{control}}) \times 100\%$, $\mathrm{SI}_{\mathrm{drift}} = (1 - \mathrm{R}_{\mathrm{drift}}/\mathrm{R}_{\mathrm{stat}}) \times 100\%$, where R is the initial acceleration or steady-state velocity averaged across all trials of the respective condition. A positive SI indicates a decrease in pursuit acceleration/velocity; a negative SI indicates an increase. Error bars in all plots denote SEs. Note that error bars might be small and therefore not visible.

RESULTS

We recorded eye movements from human observers who were asked to smoothly pursue a small, horizontally moving target. Above and below the target trajectory, we presented a stationary or drifting sine-wave grating with varying motion direction, contrast, or orientation.

Effect of a stationary context

First, we tested the effect of a stationary context versus a homogeneous gray background in four observers who each did a total of 360 trials. Because we did not find any systematic differences in any of the pursuit characteristics between rightward and leftward pursuit in this or any of the following experiments, we averaged across the two target directions in all experiments reported here. Error trials were excluded as described in METHODS, with an equal number of trials remaining for statistical analysis in each condition (78% on average). Figure 2 shows a mean velocity trace for one observer (*A*) and mean steady-state velocity (*B*), acceleration (*C*), pursuit onset (*D*), and saccade number (*E*) for each of the four observers and averaged across observers.

A stationary context tended to decrease steady-state eye velocity [$t(3) = 1.98$, $P = 0.06$, $\mathrm{SI}_{\mathrm{stat}}$ 5.38 ± 4.69%]. This effect was present in all observers, except in naïve observer CB. Initial eye acceleration was decreased significantly [$t(3) = 5.14$, $P = 0.007$, $\mathrm{SI}_{\mathrm{stat}}$ 9.21 ± 5.89%]. In the presence of a stationary context, pursuit latency was increased significantly by 7.4 ms on average [$t(3) = -4.15$, $P = 0.01$] and all observers showed a significantly higher number of catch-up saccades (+0.72 saccades) compared with the control condition [$t(3) = -3.03$, $P = 0.03$].

Effect of contrast and orientation of a stationary context

Keller and Khan (1986) investigated the effects of stationary visual backgrounds on pursuit in monkeys. They found a large suppressive effect on initial pursuit acceleration, which was not modulated by alterations in background luminance. More recently, it was shown that the human ocular following response to a circular, drifting, vertically oriented sinusoidal grating was tuned to contrast and orientation of a flickering surround (Barthélemy et al. 2006). Whereas latency and early phase of ocular following were largely unaffected by the surrounding grating, eye velocity during the later phase decreased. This suppression was strongest when the surround was isoorientated to the center grating and increased with increasing contrast—a finding resembling neurophysiological data obtained from macaque area MT by Pack et al. (2005). Here, we varied contrast and orientation of a stationary context in two separate experiments, to test whether the effect of a stationary context on pursuit acceleration, velocity, latency, and saccade number was tuned to contrast and orientation. We used five levels of contrast (as percentages): 0 (control condition, homogeneous background), 0.78, 1.56, 6.25, and 100. Four observers did 80

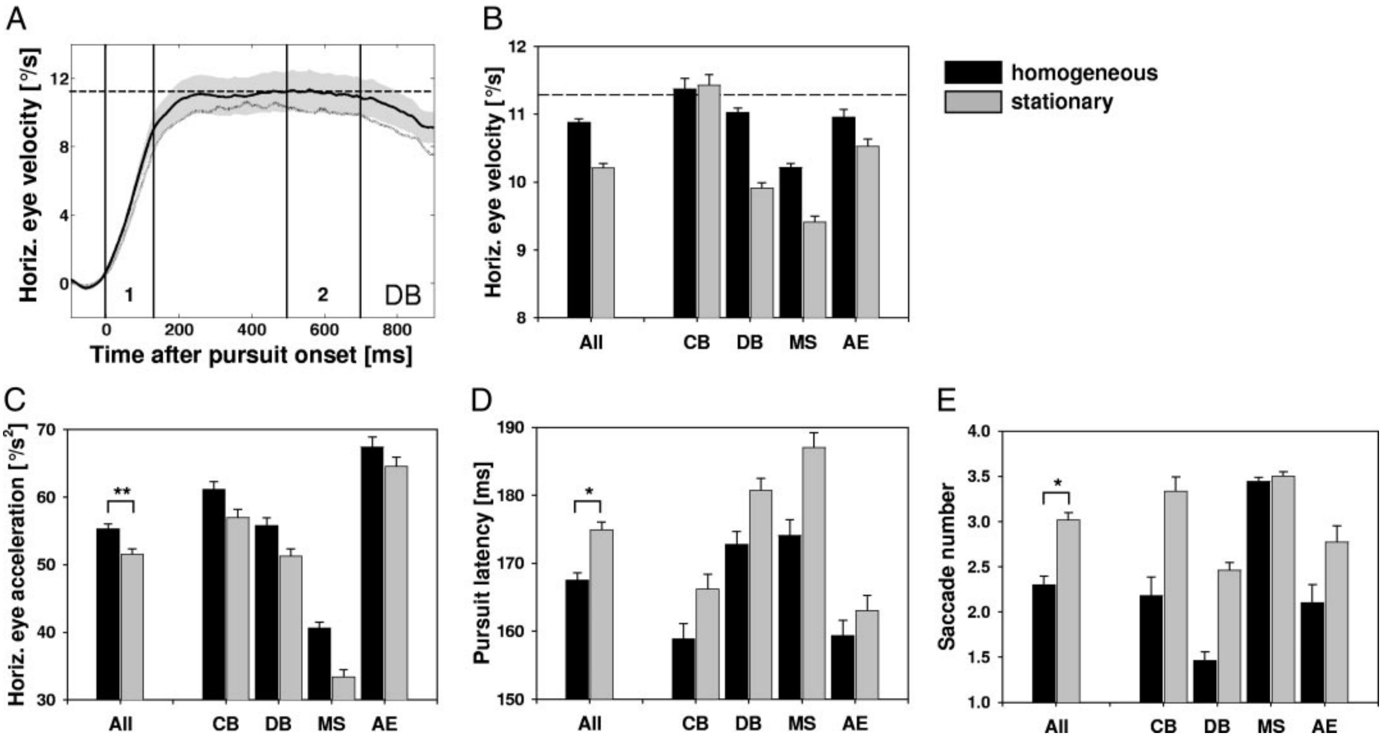

FIG. 2. *A*: exemplary desaccaded and filtered horizontal eye velocity profiles for observer DB, aligned to pursuit onset ($n = 172$ trials in each condition). A stationary context (dotted gray line) was tested against a homogeneous gray background as a control condition (solid black line). SD for eye velocity in the control condition is indicated by the shaded gray area. Horizontal dashed black line denotes target velocity at 11.28°/s. Vertical black lines depict the beginning and end of phases for analyzing *1*) initial acceleration (open-loop phase, 0–140 ms) and *2*) steady-state velocity (closed-loop phase, 500–700 ms). *B*: mean eye velocity (horizontal dashed line denotes target velocity). *C*: acceleration. *D*: pursuit latency. *E*: saccade number. Error bars denote SEs. Stars indicate significant differences between stationary context condition and homogeneous context condition in a paired-samples *t*-test: $^{\star}P < 0.05$, $^{\star\star}P < 0.01$.

trials per condition; across all conditions, 89% trials were used for analysis. As the result of a higher number of early saccades in the 100% contrast condition caused by the stronger context effect, we had to exclude more trials from that condition (71%) than from the lower-contrast conditions (94% on average).

As shown by results depicted in Fig. 3, initial acceleration and steady-state velocity decreased and pursuit latency and number of saccades increased with increasing context contrast. The size difference in SEs can be explained by the difference in trial number between the 100% contrast condition and the lower contrast conditions. A repeated-measures ANOVA showed a significant main effect of contrast on velocity [$F(4,12) = 8.77$, $P = 0.001$], acceleration [$F(4,12) = 9.62$, $P < 0.001$], pursuit latency [$F(4,12) = 4.1$, $P = 0.03$], and saccade number [$F(4,12) = 15.57$, $P < 0.001$]. Interestingly, the decrease in acceleration and velocity and the increase in latency were not linear. In comparison to the 0% contrast condition, acceleration and velocity were higher at low contrast (0.78%) and latency was slightly lower in the respective condition. However, a post hoc comparison revealed no significant difference between the low-contrast condition and the control condition for these pursuit characteristics. In contrast to earlier studies, we find that context effects on pursuit initiation and maintenance are modulated by contrast.

Next, we varied context orientation in a 100% contrast context and tested four observers (60 trials per condition each, 88% remaining trials, equally distributed across conditions). The stationary context was presented vertically (0°), horizontally (90°), or tilted 30 or 60° clockwise or counterclockwise, resulting in six different orientations, as indicated by the cartoon in Fig. 4*A*. Figure 4, *B–D* shows that pursuit was generally best when the context was oriented horizontally with respect to the pursuit target. Orientation had a significant main effect on velocity [$F(5,15) = 4.86$, $P = 0.008$] and saccade number [$F(5,15) = 3.05$, $P = 0.03$, indicated by a repeated-measures ANOVA]. However, the differences between vertical and oblique orientations were very small and not significant in a post hoc comparison and thus these data cannot be used as direct evidence for an orientation tuning of the context-suppression effect.

Effect of a drifting context

In a second series of experiments, we tested the effect of a context drifting along with the pursuit target, or into the opposite direction at either the same speed, or slower or faster than the pursuit target. The context started to drift at the onset of target motion (target step). Note that the resulting retinal image velocity is negative when the context is moving into the same direction as that of the target at a slower speed and when it is stationary (control condition). Retinal image velocity becomes increasingly negative when the context moves into the direction opposite to that of the target, even when context speed is slower than target speed. Four observers participated, doing between one session and five sessions of 200 trials each. After visual inspection, 74% trials remained on average. More trials had to be excluded from the opposite-direction conditions (60% trials remaining on average) than from the same-direction conditions (86% remaining) or the control condition

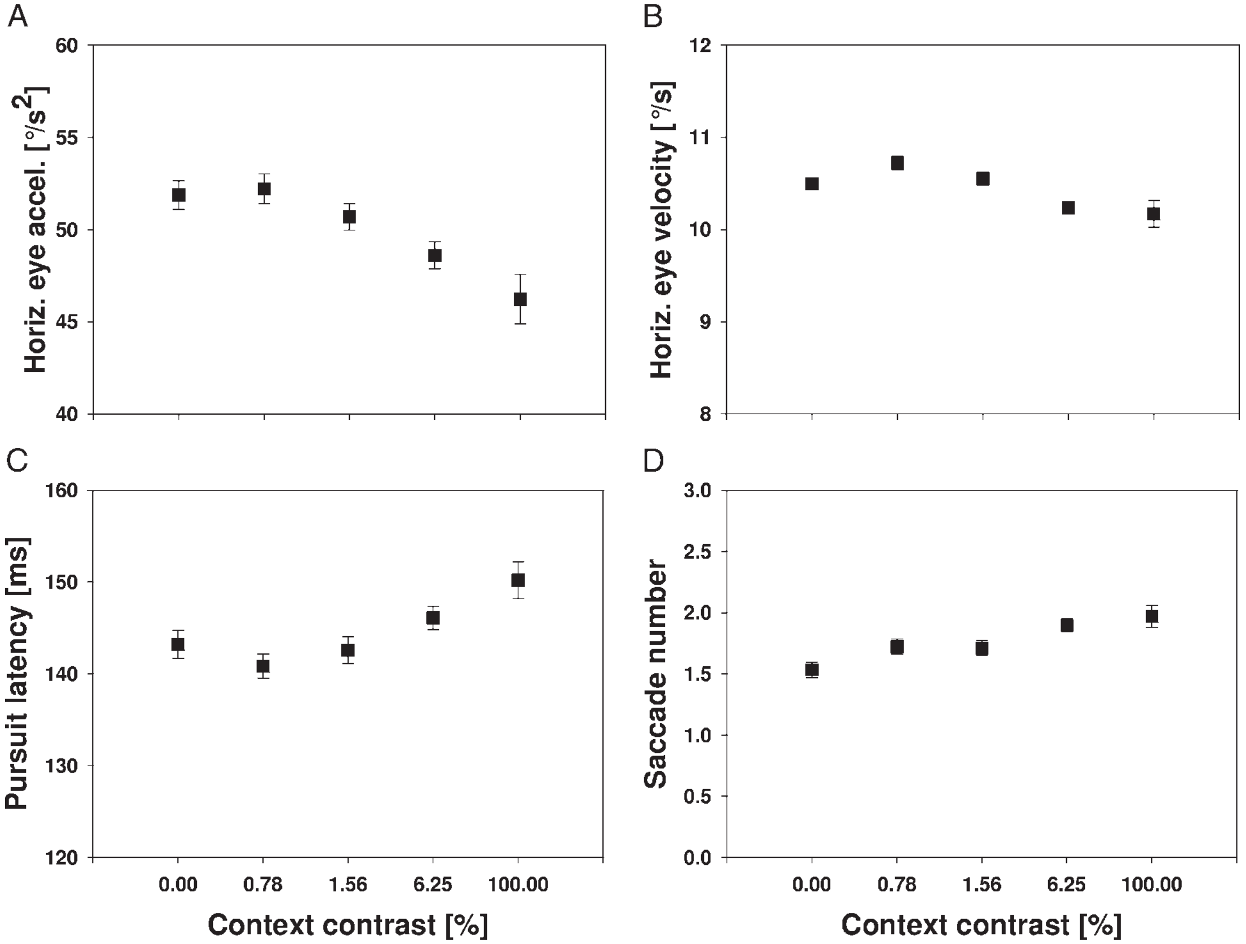

FIG. 3. Mean eye acceleration (*A*), velocity (*B*), pursuit latency (*C*), and saccade number (*D*) for 4 observers for 5 levels of context contrast. Error bars denote SEs.

(75%). When the context was drifting into the opposite direction, more saccades occurred at the time around pursuit onset.

Figure 5, *A* and *D* shows mean velocity profiles for two observers for a stationary context (black line) and a context drifting into the same (red) or opposite direction (blue) as that of the target at three different speeds. During the initiation phase, in observer CB, eye velocity in the experimental conditions (drifting context) did not differ much from eye velocity in the control condition (stationary context). In observer DB eye velocity in some experimental conditions dropped below the eye velocity in the control condition toward the end of the initiation phase, especially when the context drifted opposite to the pursuit target. In both observers eye velocity in most experimental conditions rose above the level of eye velocity in the control condition during the transition between initiation and steady-state phase. At about 150 ms into the steady-state phase, eye velocity was generally higher for the experimental conditions, irrespective of context speed. This pattern of results—no difference during the initiation phase and higher eye velocity in experimental conditions during the steady-state phase—was confirmed in all observers (Fig. 5, *B*, *C*, *E*, and *F*). Eye velocity increased when the context went into either the same or the opposite direction (Fig. 5*B*). The overall effect of context motion on eye velocity was significant in a repeated-measures ANOVA [$F(6,18) = 11.25$, $P < 0.001$]. Eye velocity was significantly increased in the high-velocity context conditions (see results of post hoc comparison in Fig. 5*B*), except when the context was drifting into the same direction as that of the target at a slower speed. The effect tended to be larger when the context drifted along with the target than when it drifted into the opposite direction. The difference between same and opposite motion directions was not significant in a post hoc comparison. We found an increase in steady-state velocity with SI_{drift} ranging between $-4.13 \pm 0.99\%$ for a context drifting slowly into the opposite direction to $-14.88 \pm 8.07\%$ for a context drifting fast into the same direction as that of the target. As mean eye-velocity profiles indicate, the overall effect of a drifting context on initial eye acceleration was not significant [$F(6,18) = 1.06$, $P = 0.42$] and post hoc comparisons were also not significant (Fig. 5*C*). A drifting context significantly affected pursuit onset [$F(6,18) = 20.62$, $P < 0.001$], although the result pattern was different from that for velocity: Latency was highest (199.4 ± 2.13 ms) when the context was drifting fast into the direction opposite to that of the target and dropped to about 144.4 ± 2.54 ms when the context was drifting fast into the same direction. Therefore latency systematically decreased from negative to positive context velocity (Fig. 5*E*). Corresponding to the increase in eye velocity with increasing context velocity, the saccade number was highest for stationary contexts or contexts drifting slowly along with the target (Fig. 5*F*).

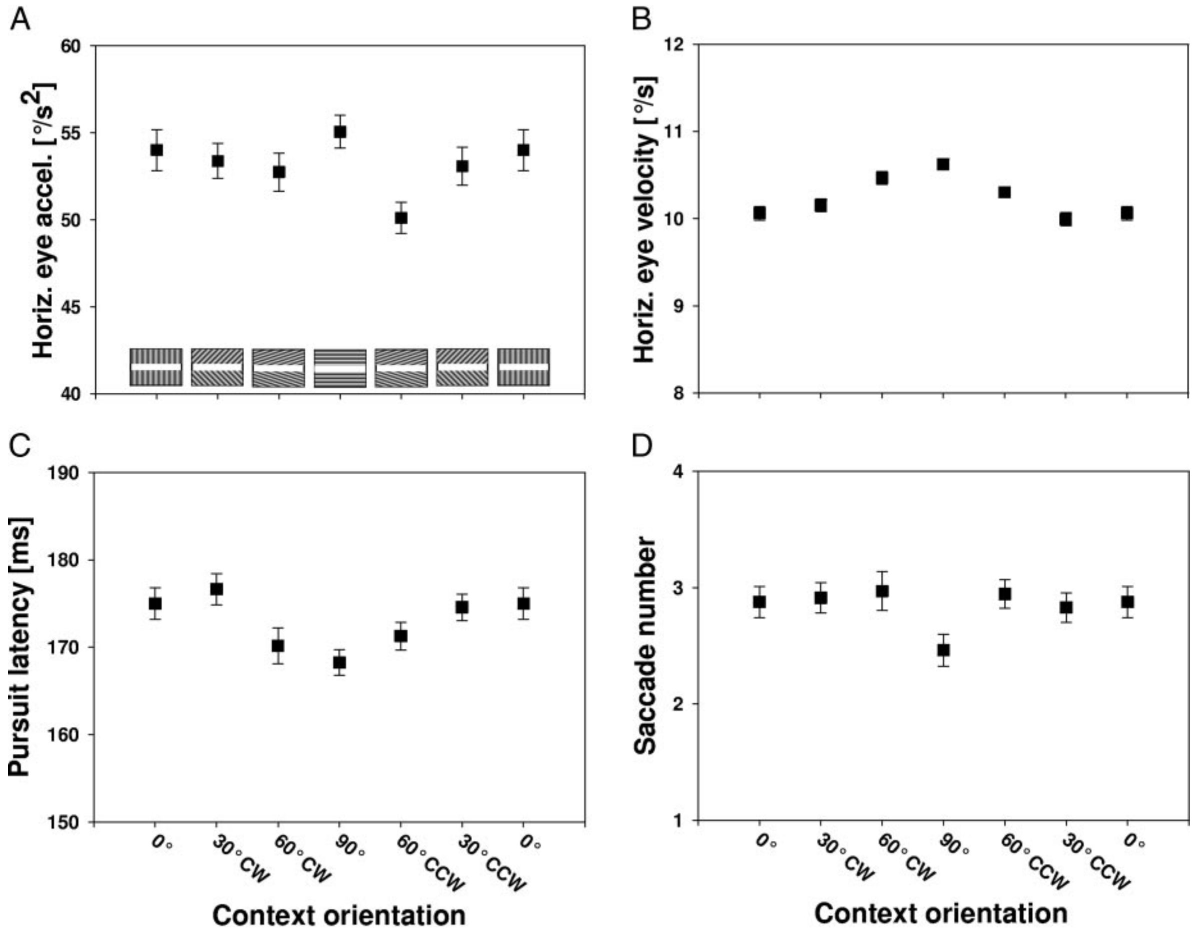

FIG. 4. Mean eye acceleration (*A*), velocity (*B*), pursuit latency (*C*), and saccade number (*D*) for 4 observers for 6 context orientations. Results for the 0° condition are repeated in each figure. Error bars denote SEs.

When the context drifted opposite to the target, pursuit onset was often preceded by a saccade into the opposite direction, as indicated by mean eye-velocity profiles (Fig. 5, *A* and *D*). Closer analysis of the direction of these initial saccades in trials with opposite context motion showed that 43.1% of the saccades were backward saccades (as opposed to 3.3% in the same context motion condition and 7.8% in the stationary context condition). Apparently, a visual setup consisting of a central moving target and a peripheral drifting context can evoke pursuit eye movements, as well as the OKN. The high number of saccades into the opposite direction points to the fact that OKN suppression was not successful during pursuit initiation.

Effect of contrast and orientation of a drifting context

Contrast and orientation of the drifting context were varied in two separate experiments, each conducted with five observers doing 40–60 trials per condition. In the contrast experiment, 85% trials remained. Similarly to the contrast variation experiment reported earlier for a stationary context, more trials had to be excluded from the 100% contrast condition (65%) as compared with all other conditions (94% on average). In the orientation experiment, 74% remained, with the amount of remaining trials ranging unsystematically from 60 to 95% between conditions. The levels of context contrast and orientation were the same as those in experiments with a stationary context. The context was drifting into the same or opposite direction to that of the target.

Results for the contrast-variation experiment are summarized in Fig. 6 and Table 1*A*. For a context drifting along with the target, initial eye acceleration first rose and then fell with increasing levels of contrast. However, the difference between the control condition (0% contrast) and the lowest contrast condition was not significant in a post hoc comparison. Steady-state velocity had a tendency to rise with increasing context contrast, when the context drifted into the same direction as that of the target, and hardly changed when the context drifted opposite to the target, as shown by a significant interaction. Both pursuit latency and saccade number decreased with increasing levels of contrast for a context drifting into the same direction and increased when the context was drifting into the direction opposite to that of the target. Context-motion direction significantly affected both onset and saccade number; interactions between direction and contrast were also significant. Overall, as shown by the significant interactions between contrast and context motion direction, the effect of context on velocity, latency, and saccade number increases with increasing contrast.

In the next experiment, orientation of a drifting context was varied. The drifting context was tilted 30 or 60° clockwise or counterclockwise. Results (Fig. 7) differed depending on the motion direction of the context, although orientation did not

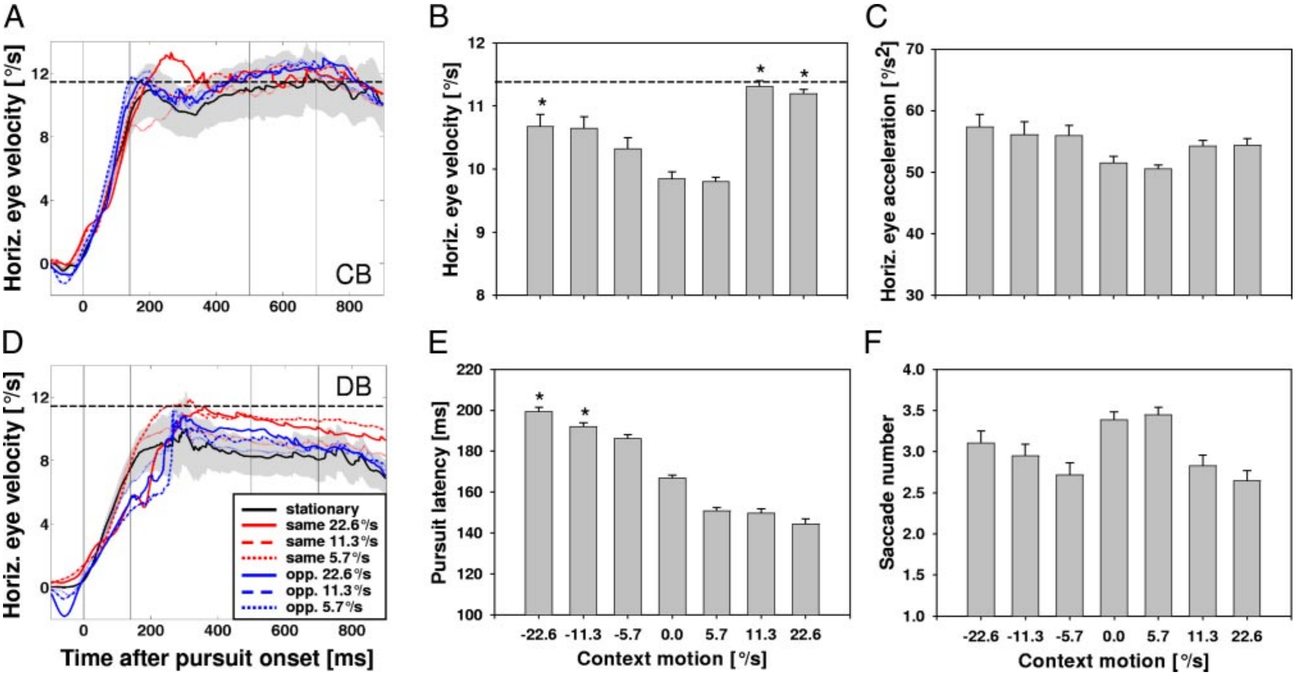

FIG. 5. *A* and *D*: exemplary filtered horizontal eye velocity profiles (with saccades) for observer CB (*A*) and DB (*D*), aligned to pursuit onset (n = 60–70 trials in each condition). A stationary context (control condition, black solid line) was tested against a context drifting into the same (red) or opposite (blue) direction to the target. SD for eye velocity in the control condition is indicated by the shaded gray area. Different line types denote different context speeds (dotted: 5.7°/s, dashed: 11.28°/s, solid: 22.56°/s). Horizontal dashed black line denotes target velocity at 11.28°/s. Vertical lines depict beginning and end of phases for analyzing acceleration and velocity. *B*: mean eye velocity (horizontal dashed line denotes target velocity) for 4 observers. *C*: acceleration. *E*: pursuit latency. *F*: saccade number. Error bars denote SEs. Stars indicate significant differences between stationary context condition (control) and moving context conditions in a post hoc comparison.

affect pursuit in a systematic way. Accordingly, a repeated-measures ANOVA with direction and orientation as factors showed significant main effects of direction on velocity, latency, and saccade number (see Table 1*B*), and significant interactions on acceleration, velocity, and latency, but no main effect of orientation. A 30° clockwise or counterclockwise tilted context drifting into the same direction as that of the target showed a tendency to increase acceleration and velocity as compared with a context being closer to the horizontal orientation (60° clockwise or counterclockwise). However, none of the post hoc comparisons calculated for individual orientation differences reached significance.

Effect of perturbing a stationary or drifting context

To test the spatiotemporal properties of stimuli that give rise to motion signals for the maintenance of pursuit, the context motion was varied during steady-state pursuit. Eye velocity was previously shown to be sensitive to brief perturbations of stationary or drifting full-field backgrounds during pursuit maintenance (Kodaka et al. 2004; Lindner and Ilg 2006; Lindner et al. 2001; Schwarz and Ilg 1999; Suehiro et al. 1999). Schwarz and Ilg (1999) report a marked asymmetry in the sensitivity for background motion perturbation: When a full-field textured background (randomly distributed vertical line elements) increased in speed in the direction of the pursuit target for 200 ms, eye velocity showed a transient perturbation time-locked to the onset of the disturbance. However, when the background was perturbed opposite to the pursuit target, the ongoing eye movement was not affected (see also Lindner et al. 2001). Similarly, Suehiro et al. (1999) perturbed a stationary background or a background drifting along with the pursuit target for 40 ms while human observers fixated or smoothly tracked a target (see Kodaka et al. 2004 for a similar study on monkeys). The perturbation effect was generally larger during pursuit than during fixation. When a *stationary* background was perturbed in the direction of the pursuit target, the effect was larger than when the perturbation occurred in the opposite direction. When perturbing a *drifting* background, eye velocity changed irrespective of the direction of perturbation.

To extend these findings to a remote context, we used a stationary or drifting context and introduced a 300-ms motion injection during the steady-state phase of the eye movement, starting 450 ms after target onset. During the perturbation the context was either moving into the same or opposite direction to that of the target at the same speed (if context was stationary on initiation), or faster (22.56°/s) or slower (5.46°/s). Note that retinal image velocity was always negative when the context was stationary or drifting into the opposite direction, irrespective of perturbation speed. We compared these conditions with a baseline of nonperturbed trials with stationary or drifting unchanged contexts. Five observers participated in this experiment, doing between one and three blocks of 200 trials. After manual inspection of the data, 86% of all trials remained, distributed equally across conditions. We calculated peak horizontal eye velocity in the time interval after perturbation onset until the end of the perturbation for each condition.

Figure 8*A* shows a horizontal velocity trace for one observer, starting from stimulus motion onset. Plotted here is the condition where the context drifts along with the target and is perturbed to drift either faster or slower. Note

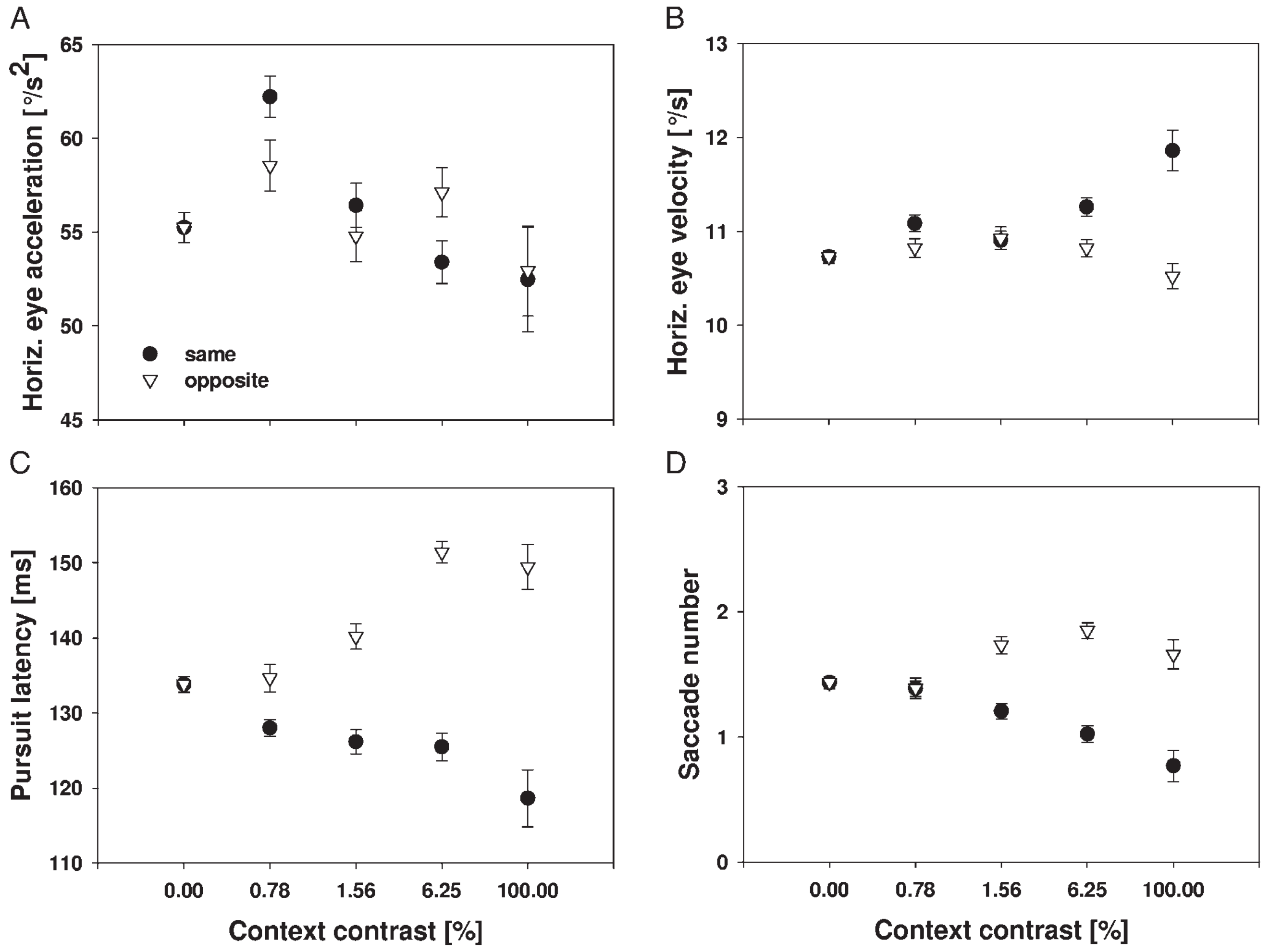

FIG. 6. *A*: mean horizontal eye acceleration averaged across open-loop phase for 5 observers for 5 levels of context contrast and 2 context motion directions (same: context drifts along with target; opposite: context drifts into opposite direction to target). *B*: horizontal eye velocity averaged across closed-loop phase. *C*: pursuit latency. *D*: saccade number. Error bars denote SEs.

that eye velocity at target onset is not zero. This is explained by the fact that in this experiment the context was already in motion while the observer was still fixating. The anticipatory pursuit eye movement was particularly strong in observer DB. Although this might be considered a problem for analyzing the initiation phase, we disregarded the problem because we focused solely on the critical time period starting after perturbation onset.

As Fig. 8 shows, there was a strong effect of context perturbation on horizontal eye velocity when the context drifted along with the target. When the context was perturbed to drift faster, the eye sped up; when the context drifted slower, the eye slowed down. The perturbation effect started at about 100 ms after the onset of the perturbation. Interestingly, the effect was not present when the context was stationary or drifted into the opposite direction to that of the pursuit target at the beginning and end

TABLE 1. *Repeated-measures ANOVA results for experiments with a drifting context that varied in contrast or orientation*

		Acceleration		Velocity		Pursuit Latency		Saccade Number	
	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
					A. Contrast				
Direction	1,4	0.91	0.40	12.23	**0.02**	48.89	**0.002**	73.06	**0.001**
Contrast	3,12	8.63	**0.003**	0.84	0.50	2.58	0.10	1.76	0.20
Dir × Cont	3,12	0.40	0.76	10.38	**0.001**	7.00	**0.006**	10.31	**0.001**
					B. Orientation				
Direction	1,4	1.20	0.33	18.30	**0.01**	60.82	**0.001**	31.08	**0.005**
Orientation	3,12	1.16	0.37	0.10	0.99	0.60	0.63	1.55	0.25
Dir × Ori	3,12	3.54	**0.05**	16.14	**0.001**	4.19	**0.03**	2.86	0.08

Significant values are highlighted in bold.

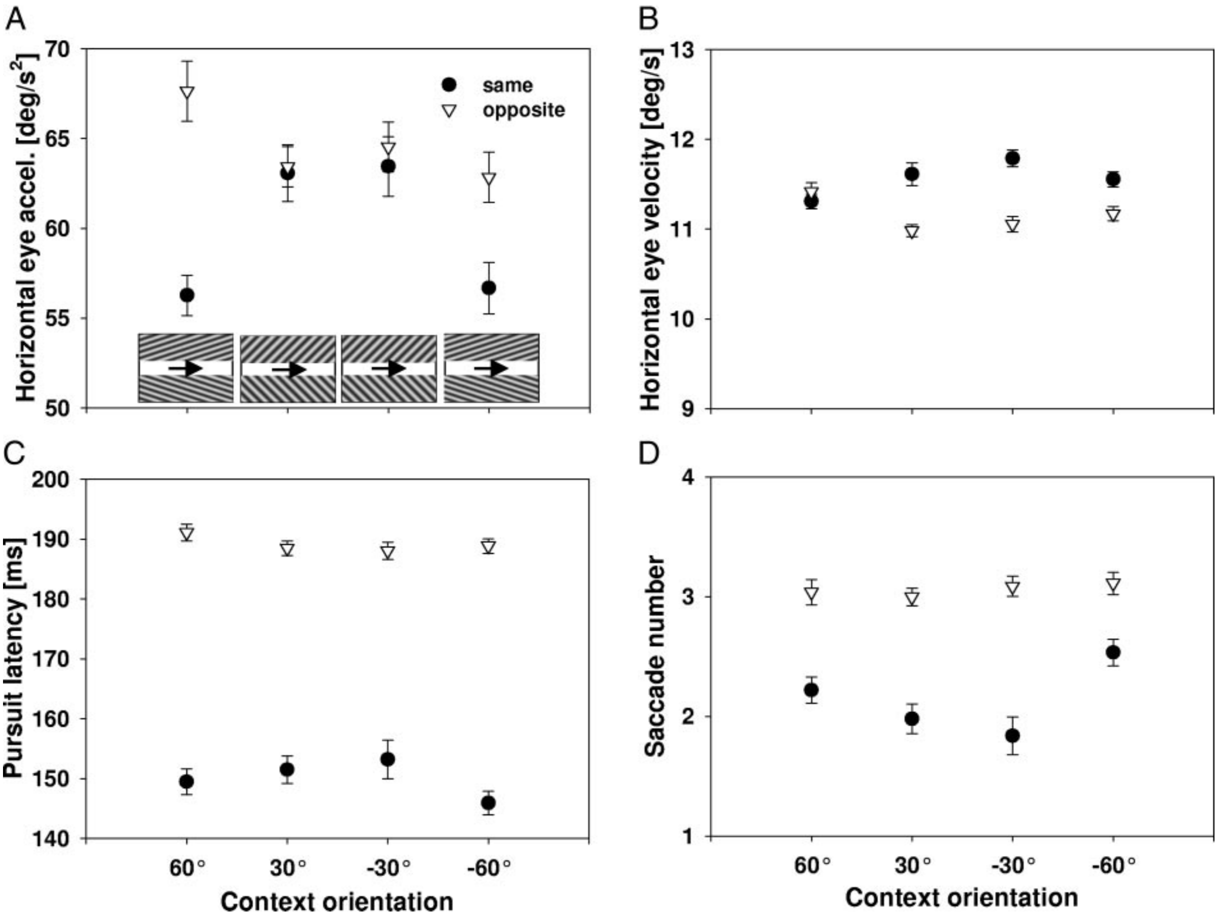

FIG. 7. *A*: mean horizontal eye acceleration averaged across open-loop phase for 5 observers for 4 levels of context orientation and 2 context motion directions (same: context drifts along with target; opposite: context drifts into opposite direction to target). *B*: horizontal eye velocity averaged across closed-loop phase. *C*: pursuit latency. *D*: saccade number. Error bars denote SEs.

of the trial (Fig. 8*B*). These results are exactly in line with the previous results reported above, showing this asymmetry in human observers with a full-field textured background.

Effect of context perturbation orthogonal to target motion

In addition to the asymmetry in horizontal eye velocity in response to a horizontal shift of a full-field background, Lindner et al. (2001) reported that horizontal eye velocity was not affected by vertical background perturbations. Further, the authors found that vertical eye velocity was modulated in the direction of the background shift. When the background briefly shifted upward/downward, vertical eye velocity was deflected in the corresponding direction by about 2°/s, with significantly larger modulations obtained by upward perturbations (see also Suehiro et al. 1999).

Here, we also tested the effect of a horizontally oriented context that was briefly perturbed to drift upward or downward into the vertical direction. The context was stationary on eye movement initiation and started to drift upward or downward at 11.28°/s during the steady-state phase, starting 450 ms after the beginning of the trial for 300 ms. Three observers participated in this experiment, each doing between one and three sessions of 180 trials. After visual inspection and exclusion of error trials following the criteria described in METHODS, 91% of all trials remained in each condition. For analysis, we chose a 150-ms time interval starting at 100 ms after perturbation onset. We analyzed mean horizontal eye velocity and peak vertical eye velocity during this interval. Our results are different from those obtained by Lindner et al. (2001) and by Suehiro et al. (1999). First, a vertical perturbation produced strong horizontal slowing (Fig. 9, *A* and *B*).

Horizontal eye velocity decreased significantly by about 1°/s for upward [$t(2) = 7.51$, $P = 0.01$] and downward [$t(2) = 3.96$, $P = 0.03$] context perturbation. Second, and more surprisingly, when the context drifted upward, the eye was deflected downward and vice versa for a downward perturbation. This effect on peak vertical eye velocity was significant for upward [$t(2) = 3.13$, $P = 0.05$] and downward perturbations [$t(2) = -5.17$, $P = 0.02$]. Again, the modulation in eye velocity started about 100 ms after perturbation onset.

In a control experiment, we tested whether the effect was maintained when the context was already in motion on initiation of the eye movement. Here, the context initially moved at 1.41 or 2.82°/s and was perturbed after 450 or 300 ms at 11.28°/s. In three observers, we confirmed the effect of vertical perturbations on vertical eye velocity, as shown by a significant main effect of perturbation direction [$F(1,2) = 26.0$, $P = 0.04$, repeated-measures ANOVA]. Figure 10 shows a mean vertical eye velocity profile for one

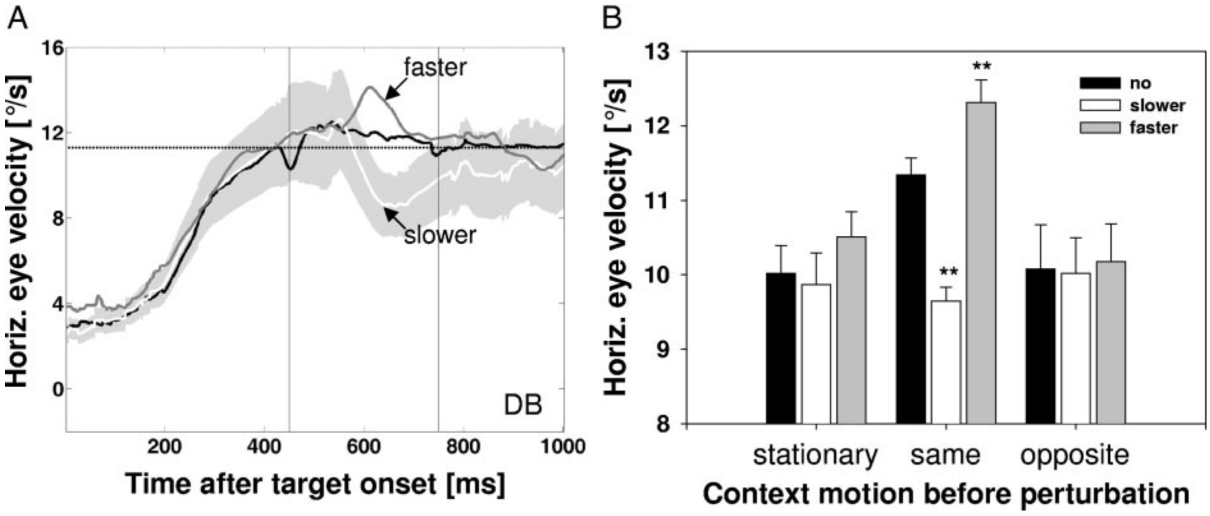

FIG. 8. *A*: horizontal eye velocity profile for one representative observer. A control condition with a stationary unchanged context (black line) was compared against 2 perturbation conditions, in which the context moved faster (gray) or slower (white) for 300 ms. SD for eye velocity in the experimental condition "slower" is indicated by the shaded gray area. Horizontal dotted black line denotes target velocity at 11.28°/s. Vertical black lines depict perturbation duration and critical time interval for analysis. *B*: horizontal peak velocity (maximum for context moving faster, minimum for slower, respectively) for 3 context motion conditions and 3 perturbation conditions for 5 observers. Error bars denote SEs. Stars denote significant results in a post hoc comparison.

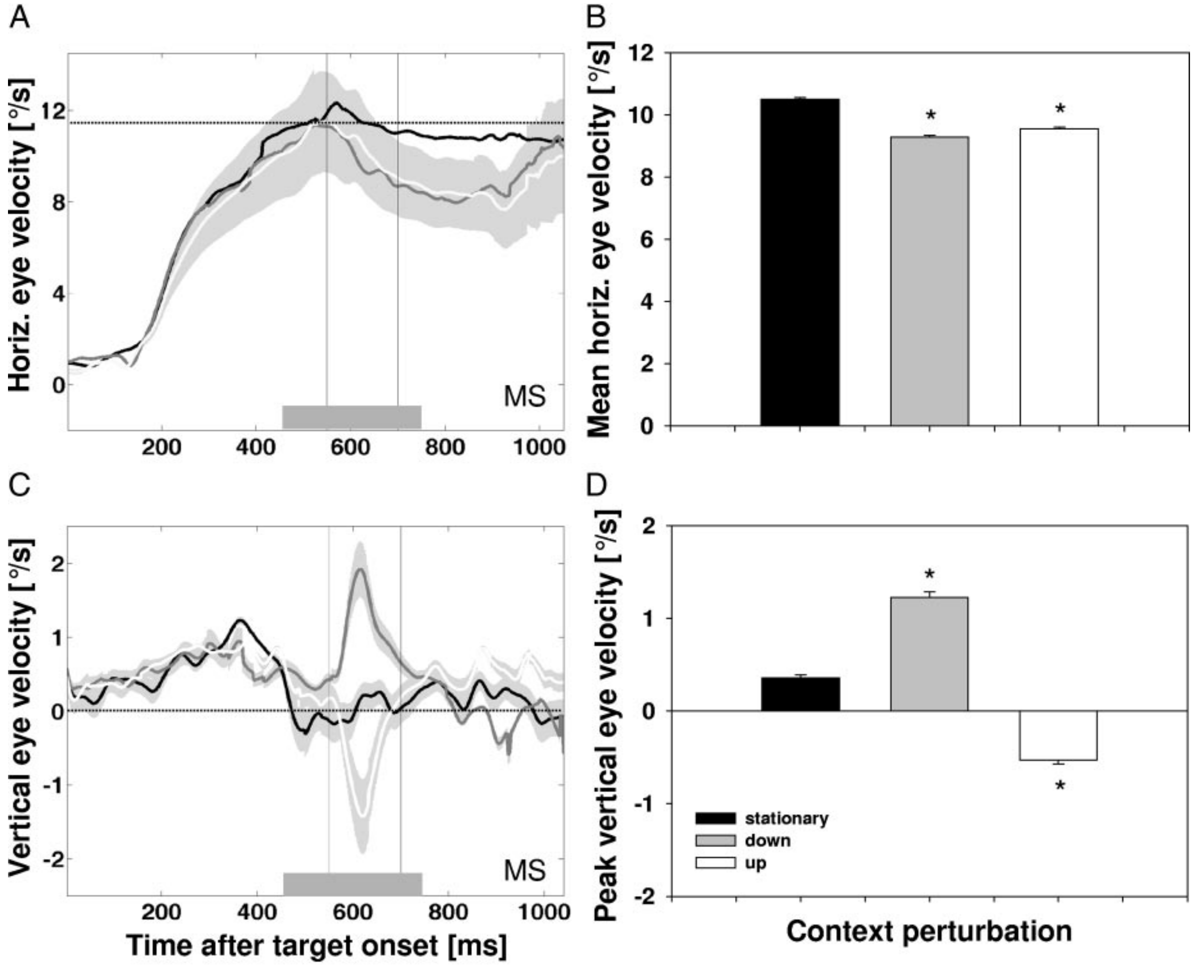

FIG. 9. *A* and *C*: horizontal and vertical eye velocity profiles for one representative observer. A control condition with a stationary context (black line) was compared with 2 perturbation conditions. Horizontally oriented context was moving downward (dark gray) or upward (white). SD for horizontal eye velocity in the experimental condition "up" and for vertical eye velocity in all conditions, respectively, is indicated by the shaded gray areas. Vertical black lines mark beginning and end of critical time interval for analysis. Horizontal gray bar denotes perturbation interval (300-ms duration). Horizontal dotted line corresponds to target velocity (11.28°/s horizontal, 0°/s vertical). *B* and *D*: corresponding mean horizontal eye velocity and peak vertical eye velocity during critical time interval for 3 observers. Error bars denote SEs. Stars illustrate significant differences between control and perturbation conditions in a paired-samples *t*-test.

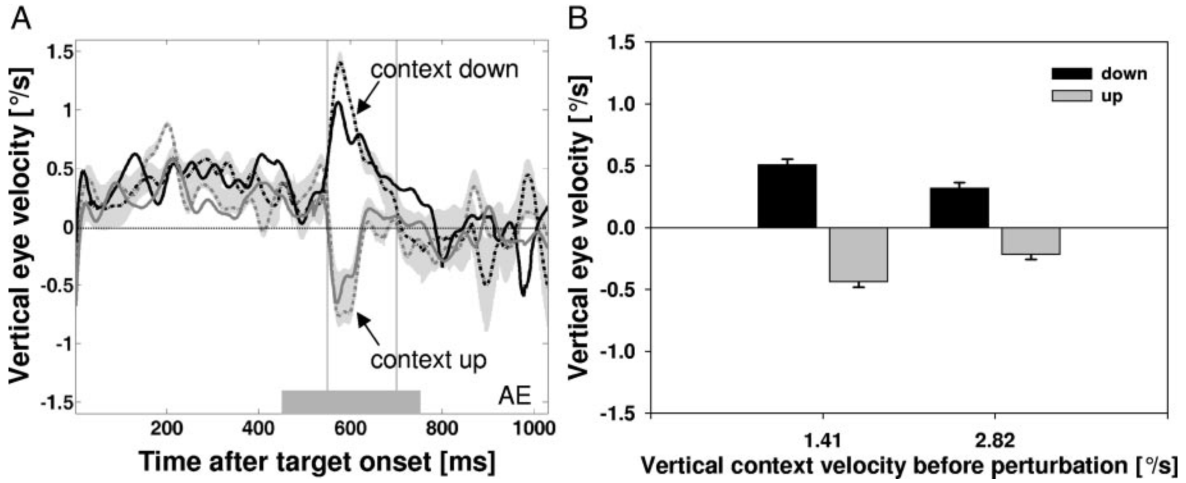

FIG. 10. *A*: vertical eye velocity profile for one representative observer. Context drifted upward or downward with 1.41 or 2.82°/s, before being perturbed (horizontal gray bar denotes perturbation duration). SD for eye velocity in the experimental condition, in which the context is initially moving at 1.41°/s is indicated by the shaded gray area. Horizontal dotted line corresponds to target velocity (0°/s vertical). *B*: corresponding peak vertical eye velocity for 3 observers during critical time interval. Error bars denote SEs.

observer (*A*) and peak vertical velocity for three observers (*B*). The vertical deviation effect was overall smaller than that in the experiment with the stationary context and decreased with increasing context velocity before the perturbation, confirmed by a significant interaction between context perturbation direction and velocity [$F(1,2) = 30.2$, $P = 0.03$]. There was no significant main effect of velocity [$F(1,2) < 1$, n.s.].

DISCUSSION

With the aim of describing the visual signal that drives smooth-pursuit eye movements in a complex environment, we examined how the spatiotemporal properties of the pursuit response were influenced by different types of visual context. We conducted experiments with a stationary or drifting visual context, which was varied in motion direction, velocity, contrast, and orientation. Here, we compare our results to those obtained in previous behavioral studies on pursuit eye movements in monkeys and humans (see Table 2).

Effect of a stationary context

For stationary contexts, we found that the context slowed down initial eye acceleration and steady-state velocity. This

TABLE 2. *Overview of results from behavioral studies on context effects on pursuit*

	No Effect	Pursuit Enhancement	Pursuit Impairment
Context stationary	No effect on velocity (6) No effect on latency (3, 4, 8)		5–20% reduction in steady-state velocity (1, **2,** 3, 7, 9, 10) 9–60% reduction in initial acceleration (2, 3, 4) or velocity (8) Longer latency (2, 9)
Context moves in pursuit direction	No effect on latency (8, 10)	Maximum 38% increase in initial velocity (8) 14–28% increase in steady-state velocity (**2**, 8, 10) Shorter latency (**2**)	
Context moves opposite	No effect on latency (8, 10)	Increase in initial acceleration (**2,** 10) 4% increase in steady-state velocity (**2**)	Maximum 7% decrease in initial velocity (8) Maximum 12% decrease in steady-state velocity (8, 10) Longer latency (**2**)
Context perturbation in pursuit direction	Small or no effect on velocity when context stationary or moving opposite before perturbation (**2**)	Transient velocity increase in perturbation direction (5, 7, 11, 12)	
Context perturbation opposite	Small or no effect on velocity (**2,** 5, 7, 11, 12)	Transient velocity change irrespective of direction for context moving in pursuit direction before perturbation (**2,** 5, 12)	
Orthogonal context perturbation		Transient velocity increase in perturbation direction (7, 12)	Transient velocity increase in direction opposite to that of perturbation (**2**)

The behavioral studies refer to results with respect to human research. Numbers correspond to references given in the following: (1) Collewijn and Tamminga (1984); (2) present study: Spering and Gegenfurtner (marked bold in table body); (3) Keller and Khan (1986); (4) Kimmig et al. (1992); (5) Kodaka et al. (2004); (6) Kowler et al. (1978); (7) Lindner et al. (2001); (8) Masson et al. (1995); (9) Mohrmann and Their (1995); (10) Niemann and Hoffmann (1997); (11) Schwarz and Ilg (1999).

result is in line with previous findings and the effect is of a magnitude similar to that of the effects observed in human observers (Masson et al. 1995). In monkeys, the effects on initial eye acceleration were considerably larger (Kimmig et al. 1992). Note that in these studies the visual texture covered the whole screen. Using a full-field visual background is potentially problematic because the local motion signal from the target is masked by the global motion signal from the background. In one of their control experiments, Kimmig et al. (1992) showed that the effect of a stationary background on initial eye acceleration was not eliminated when the background (a stationary random dot pattern) was partially occluded with a horizontal strip of card, onto which the target was projected. As the width of the central horizontal space increased from 0 to 60°, the detrimental effect of the stationary background on pursuit initiation was reduced to roughly 20% of the original effect size. From the comparison of our data with these findings we can conclude that the detrimental effect of a stationary background on pursuit acceleration and velocity is retained over a larger area of space and not restricted to the central part of the visual field that directly surrounds the target.

Concerning pursuit latency, our results differ from those of most previous studies (see Table 2), where either no effect was found on latency (Keller and Khan 1986; Kodaka et al. 2004) or the effect on latency was eliminated when the context was peripheral (Kimmig et al. 1992). Following from the result that initial acceleration and latency were differentially affected by a stationary background Kimmig et al. (1992) hypothesized that two separate mechanisms might be used for triggering and driving the decoding of target motion. These authors further proposed that the effect of a background on pursuit latency might be driven by a local mechanism and mediated by neurons with smaller receptive fields, whereas the effect on pursuit acceleration might be driven by a global mechanism and mediated by neurons with extensive receptive fields. Our results challenge the view that different mechanisms are responsible for driving pursuit initiation in the presence of a full-field background and remote visual context. We report effects of a stationary context on both initial acceleration and pursuit latency. Generally, context effects on latency can be caused by perceptual, motor, or cognitive mechanisms. Active pursuit of the target causes a retinal image shift of the stationary context into the direction opposite to that of the pursuit target. Such context image motion on the retina drives a passive pursuit or OKN response into the opposite direction. To smoothly track the target, the OKN response will have to be suppressed (Lindner and Ilg 2006; Worfolk and Barnes 1992; Wyatt and Pola 1984), possibly causing a delay in initiating pursuit. Regarding cognitive mechanisms, it has been suggested that latency effects result from the observer's inability to attend to the target in the presence of a textured context because the context renders the target less salient (Masson et al. 1995). We do not believe that the context effects reported here were modulated by attention. The target does not come on suddenly, but is presented in the presence of the stationary context for 500 ms, before it starts to move. The observer was instructed to fixate the target.

It was noted above that a stationary context did not slow down pursuit in one naïve observer. It is possible that this observer managed to completely ignore the context, whereas the other three observers showed a slowing in eye velocity and a corresponding increase in saccade number. However, the naïve observer also showed an increase in saccade number, a decrease in pursuit acceleration, and an increase in latency in the presence of a stationary context. Therefore we cannot conclude from this that there are two groups of observers—one that is affected by the context and another one that is not—as implied by Ilg and Thier (1996).

The effect of a stationary context was modulated by contrast and orientation to some extent. The impairing effect of a stationary context on pursuit increased with increasing contrast both during pursuit initiation and maintenance. The data reveal an interesting tendency in that this increase was not linear. It was previously reported that motion sensitivity can be higher at low contrast (Tadin et al. 2003) and that V1 receptive-field organization shifts from surround suppression at high contrast to spatial summation being 2.3-fold greater at low contrast (Sceniak et al. 1999). However, our effects are too weak to provide evidence for a similar effect in stationary surrounds in pursuit eye movements. Keller and Khan (1986) did not find a modulating effect of background luminance on suppressive effects. These authors varied background luminance in two monkeys and used two levels of contrast ("dim": 74%; "bright": 80%). In comparison to our work or to the study by Barthélemy et al. (2006), which show effects of contrast on surround suppression, the range of contrast levels tested by Keller and Khan (1986) does not cover the complete range of contrast levels needed to reliably demonstrate contrast effects. Barthélemy et al. (2006) did not find effects of contrast on the initiation of ocular following. This might be explained by the fact that the effect of contrast evolves only after some time. The latency for the ocular following response is much shorter than that for a pursuit eye movement and the time intervals used for analyzing latency and the open-loop phase in Barthélémy's and our study are therefore not comparable.

The effects of orientation were less systematic, except that the influence of a stationary context was largely diminished when the context was oriented horizontally and aligned to the pursuit trajectory. Therefore there is no clear indication that effects of remote stationary or drifting contexts on pursuit are tuned to orientation.

Effect of a drifting context

We observed that a drifting context generally increased pursuit acceleration and velocity. Latency decreased with increasing context velocity from negative to positive (i.e., latency was shortest when the context drifted fast into the same direction as that of the target). Our findings differ from some of the previous results (see Table 2). Masson et al. (1995) found a decrease in steady-state velocity in the presence of a drifting full-field background, which we did not observe. It is possible that the pursuit response to the target in the Masson et al. study was counteracted by an optokinetic response induced by opposite background motion, resulting in a decrease in eye velocity. In the present experiments, we attempted to control for the effects of OKN by using a remote visual context. Concerning pursuit initiation, Niemann and Hoffmann (1997) found an increase in initial acceleration in the presence of a context drifting opposite to that of the pursuit target. In accordance with this study, we observed that a drifting context increased eye velocity and acceleration irrespective of its motion direction. Taken together, these results and the neurophysiological data obtained by Born et al. (2000) provide evidence for a motion-contrast mechanism underlying pursuit control in the presence of a drifting context.

Previous studies do not report background effects on pursuit latency (Table 2). It is interesting that we consistently see effects on pursuit latency. The latency ranges we observed with a stationary (167–175 ms) or drifting context (144–200 ms) are well within the range observed in previous studies (e.g., average latency 180 ms in Masson et al. 1995) and thus cannot arise from differences in effect size. We are not the first to report context-dependent latency effects, which were also found in a study by Ferrera and Lisberger (1995). When a distractor moved into the same direction as that of a pursuit target, latency was decreased; when the distractor moved opposite to the target direction, latency increased, irrespective of whether the monkey attended to the distractor. It is therefore more likely that the effect on latency observed here is directly related to context motion rather than to cognitive factors. The effect on latency clearly scales with context direction and velocity. A context drifting fast into the same direction as that of the pursuit target seems to push the eye and boosts pursuit onset. A context drifting fast into the opposite direction seems to pull the eye back and delays pursuit onset, possibly by inducing an optokinetic motion signal. To initiate a smooth-pursuit response, the resulting OKN has to be suppressed. OKN suppression was previously shown to occur at an early stage before or during pursuit onset (Wyatt and Pola 1984) and can be stronger for a context moving into the direction opposite to that of the pursuit target (see Lindner and Ilg 2006 for a discussion on pursuit–OKN interaction). In our experiment, OKN suppression was not perfect, as indicated by the high number of saccades, in particular backward saccades during pursuit initiation in the presence of a context drifting opposite to that of the pursuit target.

Contrast boosted the effect of a drifting context on velocity, latency, and saccade number. The effect of orientation for contexts drifting into the same direction as that of the target was generally higher, although orientation did not significantly modulate the effect of a drifting context.

Effect of context perturbation

When a context that drifted along with the target was briefly perturbed during the steady-state phase, eye velocity changed in the direction of context perturbation (i.e., when the context was perturbed to drift faster, eye velocity increased). Perturbing a context that drifted opposite to the target did not have an effect on eye velocity. Our results for a perturbed stationary or drifting context were similar to data obtained with a full-field textured background (see Table 2). Interestingly, the results for a context perturbation in or against pursuit direction and a context drifting along with or opposite to the target differ in our series of experiments. In the perturbation experiment, the context was drifting along with the target at the same speed, before the context was perturbed into the same or opposite direction. In the drifting context experiment, on the contrary, the context was either drifting into the same or opposite direction at the same or different velocity as that of the target for the entire duration of the trial. Apparently, these differences lead either to assimilation of eye velocity to context velocity (perturbation experiment) or to motion-contrast effects (drifting context experiment). Possibly, it is the complexity of the figure–ground segregation task that determines which motion signal processing strategy—motion assimilation (e.g., vector averaging or vector summation) or motion contrast—is used. In the drifting context experiment, target and context velocity and direction do not change in the course of a trial. The segregation of target and context might therefore be more difficult than in the perturbation experiment. However, from our data we cannot draw conclusions about when the system uses which processing strategy.

During smooth-pursuit eye movements, eye speed is adapted to changes in target velocity in a similar way (Kowler and McKee 1987; Krauzlis and Miles 1996). The time course, latency, and size of the effect obtained from perturbing a horizontally moving context is very similar to the data yielded from target velocity perturbations (compare our Fig. 9*A* with Fig. 1*B* in Churchland and Lisberger 2005). It was previously proposed that internal gain regulation for changes in eye velocity during pursuit maintenance might be accomplished by cortical area MST. A similar mechanism might control the compensation for context-velocity perturbations and it is likely that eye-velocity modulation relies on the perception of the visual target. Therefore it seems crucial to test observers' perception of target velocity when either the context, or the target speed, or both are perturbed.

When the context was oriented horizontally and drifted vertically up or down, horizontal eye velocity was decreased time-locked to the perturbation onset and the vector of the vertical velocity component went into the direction opposite to context-motion direction. Because of the similarities in timing (e.g., duration of perturbation), our results can be directly compared with those obtained by Linder et al. (2001). These authors did not observe effects of orthogonal context perturbation on horizontal eye velocity and found that vertical eye velocity followed perturbation direction (see also Suehiro et al. 1999). Previous studies and our experiments differ only with respect to the type of background used. Whereas we used a high-contrast horizontally oriented sine-wave grating, Lindner et al.'s background consisted of random texture elements, such as vertical lines, and Suehiro and colleagues used random-dot patterns. We assume that our context stimulus produced a stronger apparent motion signal that might have caused the deviation into the direction opposite to perturbation. The vertical deflection observed in our study resembles findings that we obtained recently with two stimuli moving into different directions: the horizontal one, predefined as the target; the other one a distractor with unpredictable motion direction. In a series of experiments, we showed that the eye transiently deviated away from the distractor into the vertical direction opposite to it (Spering et al. 2006). Both sets of results are in line with the early observations made by Duncker (1929). When observers in Duncker's experiments relied on the second object or the background as a frame of reference, the target was perceived to move into the opposite direction to that of the background or to the second moving object.

In contrast to the background type used in the Lindner et al. (2001) study, the context used in the present experiment might have been more prone to be perceived as a reference frame because of the clearly visible border separating the elongated window for target motion from the upper and lower halves of the sine-wave grating. As a result, the target might have received an apparent motion component into the direction opposite to that of context motion. These results do not provide evidence either for a weighted averaging of motion vectors or for successful motion segmentation because horizontal eye velocity was also affected by the perturbation. The vertical deviation effect, instead of being considered as overcompensation or pursuit error, might provide an adaptive mechanism for controlling target selection in the presence of a drifting context, as has been indicated by comparable studies in other species, such as honeybees (Srinivasan and Zhang 2004; Srinivasan et al. 1991). Similar compensatory motor actions are reported in human walking (Warren et al. 2001). In our results, however, the vertical deflection does not result in a stable retinal image. Rather, it seems that the context is used as a reference frame, as implied earlier in studies by Duncker (1929) on induced motion. Interestingly, Zivotofsky (2005) showed that this perceptual phenomenon was not reflected in the pursuit response, which followed the actual target motion. Our findings confirm the perceptual data obtained by Duncker (1929) and the vertical deviation is also in line with neurophysiological findings showing that neurons in macaque area MT are sensitive to motion contrast (Born et al. 2000). Despite this evidence, it is not yet clear whether effects of a visual background on pursuit eye velocity can be regarded as a direct behavioral consequence of center-surround interactions in MT receptive fields.

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