Inhibition of Steady-State Smooth Pursuit and Catch-Up Saccades by Abrupt Visual and Auditory Onsets

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Kerzel D, Born S, Souto D. Inhibition of steady-state smooth pursuit and catch-up saccades by abrupt visual and auditory onsets. *J Neurophysiol* 104: 2573–2585, 2010. First published September 15, 2010; doi:10.1152/jn.00193.2010. It is known that visual transients prolong saccadic latency and reduce saccadic frequency. The latter effect was attributed to subcortical structures because it occurred only 60–70 ms after stimulus onset. We examined the effects of large task-irrelevant transients on steady-state pursuit and the generation of catch-up saccades. Two screen-wide stripes of equal contrast (4, 20, or 100%) were briefly flashed at equal eccentricities (3, 6, or 12°) from the pursuit target. About 100 ms after flash onset, we observed that pursuit gain dropped by 6–12% and catch-up saccades were entirely suppressed. The relatively long latency of the inhibition suggests that it results from cortical mechanisms that may act by promoting fixation or the deployment of attention over the visual field. In addition, we show that a loud irrelevant sound is able to generate the same inhibition of saccades as visual transients, whereas it only induces a weak modulation of pursuit gain, indicating a privileged access of acoustic information to the saccadic system. Finally, irrelevant changes in motion direction orthogonal to pursuit had a smaller and later inhibitory effect.

INTRODUCTION

Pursuit eye movements serve to stabilize the image of a moving target on the fovea. Target selection for smooth pursuit is under voluntary control and involves visual selective attention (Kerzel et al. 2008; Khurana and Kowler 1987; Lovejoy et al. 2009; Madelain et al. 2005). Target selection is essential for the maintenance of smooth pursuit because reflexive following of self-induced background motion has to be suppressed (Kowler et al. 1984; Lindner et al. 2001; Schwarz and Ilg 1999; Suehiro et al. 1999). There is evidence that target selection during steady-state smooth pursuit is close to perfect. Kowler et al. (1984) reported that trained subjects were able to track a dot field without loss in precision when a physically identical dot field was superimposed and moved into the opposite direction. However, brief and unexpected changes in background motion do affect smooth pursuit (Schwarz and Ilg 1999; Suehiro et al. 1999). Compared with fixation, background motion during smooth pursuit elicits a larger tracking response, showing that the sensitivity to motion is enhanced during smooth pursuit. In contrast to motion stimuli, brief and unexpected luminance changes have a much weaker impact. Luminance transients in peripheral objects or small flashes do not perturb ongoing pursuit when the stimuli can be ignored (Blohm et al. 2005; Kerzel et al. 2008).

To some degree, the apparent resistance of steady-state pursuit to perturbation by visual onsets is different from the known susceptibility of pursuit initiation to visual perturbation. Knox and Bekkour (2004) showed that the onset of a small irrelevant stimulus at motion onset increased pursuit latency. The effect of the distractor decreased with increasing eccentricity and was absent if the distractor appeared in the same direction as the target. Because a slowing of pursuit onset was only observed when the distractor was distant from the target, the perturbation was named "remote distractor effect."

A similar pattern of results was observed for saccades. Saccades were more strongly delayed with distractors close to the fovea, and no delay occurred when the distractor was close to the target (Walker et al. 1997). Models of saccade generation often consider the intermediate and deep layers of the superior colliculus (SC) as a neural correlate of the remote distractor effect (Findlay and Walker 1999; Godijn and Theeuwes 2002; Kopecz 1995; Munoz and Fecteau 2002; Trappenberg et al. 2001). The SC is a retinotopically organized structure that receives input from the retina and the cortex, including sensory, motor, and associative areas (Moschovakis et al. 1996; Sparks and Hartwich-Young 1989). Visual stimuli elicit peaks of activity in the SC. Additionally, stimulation of the intermediate and deep layers triggers saccades. Models of saccade generation assume that a saccade is triggered once the activity passes a threshold. If a distractor stimulus occurs at the same time as the target, two peaks of activity arise. Because the target- and distractor-related activities inhibit each other, the rise to threshold of target-related activity is delayed. Thus competition in a race to threshold may account for the distractor effect.

Recently, it has been shown that the SC is not only important for saccade generation but also plays a role in target selection for smooth pursuit (Carello and Krauzlis 2004; Krauzlis and Dill 2002). To generate a smooth pursuit response, however, motion processing in medial temporal (MT) and medial superior temporal (MST) cortex is necessary (for reviews, see Ilg 2008; Krauzlis 2004), and stimulation of the SC in the absence of motion input does not result in smooth pursuit, but in a saccade (Robinson 1972; Stryker and Schiller 1975). Furthermore, catch-up saccades that realign the eye when smooth pursuit falls behind the target are in some regard different from regular saccades (review in Orban de Xivry and Lefevre 2007). Catch-up saccades are not simply directed at the position of the target at a given moment but take into account its current retinal motion to predict its future position (Gellman and Carl

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1991; Keller and Johnson 1990; Kim et al. 1997). Catch-up saccades depend on intact cortical motion processing (May et al. 1988) and the trigger mechanism depends not only on the position error, but uses a prediction of the time at which the eye trajectory will cross the target, which also depends on retinal velocity error (de Brouwer et al. 2002). The partially different inputs into the saccade and smooth pursuit system may explain why flashed distractors appear to have a larger effect on saccade generation than on steady-state pursuit.

An alternative hypothesis is that steady-state pursuit and saccades are similarly affected by abrupt onsets but that thresholds for perturbing smooth pursuit are higher. Previous studies presenting irrelevant flashes during steady-state smooth pursuit used small stimuli of 0.2 (Blohm et al. 2005) or ~2° (Kerzel et al. 2008) and found no effects when the stimuli could be ignored, but deviations toward the flash or reductions of pursuit gain when the stimuli were task relevant. For pursuit onset, Knox and Bekkour (2004) found a slowing of latencies with small distractors of 0.3°, which is quite similar to the stimuli used in studies on steady-state pursuit.

In this study, we tested whether steady-state pursuit would be perturbed if larger stimuli are used. In a study on saccadic responses, Reingold and Stampe (2002) presented large distractors (30° wide × 8° high) at 4° above and below fixation. They observed that saccadic frequency decreased as shortly as 60–70 ms after flash onset, which pointed to a subcortical origin, possibly in the SC. Furthermore, Edelman and Xu (2009) reported that the inhibition of saccades was stronger with large (4 × 4°) than with small (0.25 × 0.25°) distractors. Therefore we examined whether inhibition may be observed during steady-state pursuit when large stimuli are used. Our results show, for the first time, that smooth pursuit and catch-up saccades are inhibited by irrelevant visual onsets. We examined effects of flash predictability, eccentricity, stimulus contrast, acoustic stimulation, and motion reversals on the distractor effect. We estimated the latency and magnitude of the decrease to evaluate the possibility that the SC underlies the inhibitory effects.

METHODS

Participants

Undergraduate psychology students at the University of Geneva participated in the experiments. All subjects reported normal or corrected to normal vision. There were 12 subjects in *experiment 1*, 7 in *experiment 2*, 12 in *experiment 3*, 11 in *experiment 4*, and 9 in *experiment 5*.

Apparatus and stimuli

The stimuli were presented on a 21-in (diagonal) CRT with a resolution of 1,280 (H) × 1,024 (V) pixels at a refresh rate of 100 Hz. Participants' head position was stabilized with a chin rest at 46 cm from the screen center. Eye movements were recorded with a head-mounted, video-based eye tracker (EyeLink II, SR-Research, Osgoode, Ontario, Canada) at a sample frequency of 250 Hz. The experiment was run in a dimly lit room.

A 0.4 × 0.4° cross made of 0.11° lines was used as pursuit target. The target moved at 10.8°/s for 2 s. The trajectory was centered on the midpoint of the screen. The flash was presented randomly between 0.5 and 1.5 s after motion onset. The flash consisted of two one-dimensional Gabors that extended from the left to the right side of the monitor (Fig. 1). The Gabor consisted of a sine-wave grating with a
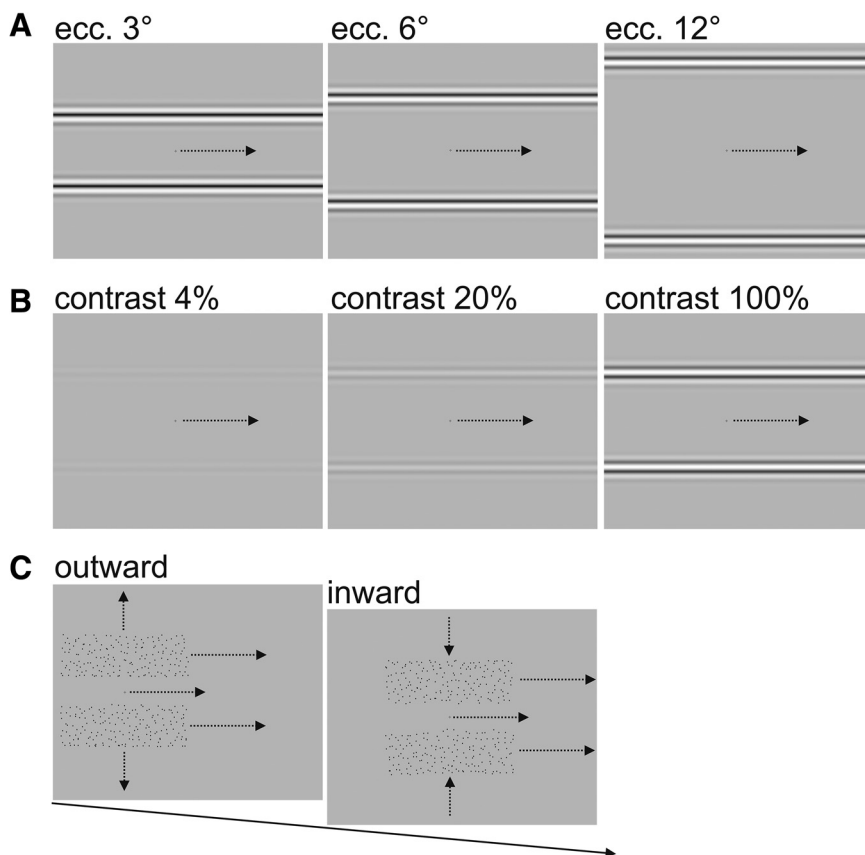

FIG. 1. Examples of experimental stimuli in *experiments 2*, *3*, and *5* (*A, B,* and *C,* respectively). The stimuli are drawn to scale, and each image corresponds to the complete screen surface (46 × 37°). Arrows were added for illustration.

spatial frequency of 0.6 cycles per degree multiplied by a Gaussian luminance envelope with an SD of 1.5°. The extent of the stimulus was 46° horizontally and ~6° vertically. As contrast approached zero gradually along the vertical dimension because of the Gaussian, the vertical extent is a matter of criterion. We chose four times the space constant of the Gaussian as an approximation of the vertical extent (cut-off at ~5% contrast). The eccentricity of the stimuli is given with respect to the thus defined edge. One Gabor was presented above, the other below fixation. The presentation time of the flashes was 30 ms. In Reingold and Stampe (2002), the upper and lower part of the screen (beyond 4° of eccentricity) turned from gray to white for 33 ms. We opted for a sine-wave modulation of luminance (i.e., mean luminance was equal to background luminance) because we were worried that the change in pupil size accompanying mean luminance changes may reduce the reliability of our eye movement recordings, which were based on tracking the pupil centroid. In *experiments 1–3*, the flashed Gabor was shown at various times, eccentricities, and contrast.

In *experiment 4*, we additionally included a condition in which a click sound of 10 ms duration (22 kHz, broadband noise) was presented. Clicks were presented via loudspeakers to the left and right of the screen at a distance of ~75 cm from the subject. The sound level at the subject's head was ~83 db(A). We felt that the clicks were as loud as possible without being uncomfortably loud.

In *experiment 5*, we did not present the flashed Gabors, but dynamic dot fields above and below fixation. The dot fields were horizontally centered on the pursuit target (see Fig. 1C). The horizontal velocity of the dots matched the pursuit target. Additionally, the dots moved toward or away from fixation (i.e., inward or outward motion) at a velocity of 14.4°/s. Each trial started randomly with inward or outward flow. At 0.5–1.5 s after onset of target motion, the direction of motion changed. In the single change condition, it simply changed to the opposite direction (from inward to outward, or from outward to inward). In the double change condition, it changed to the opposite direction for 50 ms and reverted to its original direction (e.g., inward, outward for 50 ms, then inward again). Each dot field was a 22 × 8° (horizontal × vertical) grid with one dot placed in each 1 × 1° cell. The dot positions were jittered randomly by ±0.5° vertically and horizontally. Dot lifetime was 50 ms, and on- and offsets were asynchronous across the dot field. Care was taken to avoid changes in the overall position or size of the grid when the direction was changed.

Task and procedure

Before collecting data, the apparatus was calibrated by showing nine points on a 3 × 3 grid and recalibrated after ~108 trials. At the beginning of each trial, the pursuit target was shown at 10.8° to the left or right. To perform a drift correction, participants pressed a designated button on a game pad. If the drift correction was successful, the target started to move toward the opposite side of the screen. To assure a gain close to 1, trials in which pursuit gain was outside 1 ± 0.3 in the interval 100 ms before flash presentation were aborted in some experiments and repeated in the remainder of the experiment. In experiments with on-line gain check, between 6 and 14% (mean = 7%) of the trials had to be repeated. The on-line pursuit check was used in *experiments 3* and *5* and for five of seven subjects in *experiment 2*. In experiments without on-line gain check, we verified off-line by visual inspection that the subject was adequately following the target (without formal criteria). About 2% of the data were excluded after visual inspection (because of poor preflash pursuit, as defined by low gain and frequent and large saccades, anticipatory slowing before flash presentation, etc.).

Data analysis

To identify saccades, the output of the EyeLink II eye movement parser was used. The criterion used to detect saccade onset was acceleration larger than 4,000°/s^2 and velocity larger than 22°/s. Velocity traces were filtered with a 40-Hz low-pass, zero-phase-shift Butterworth filter. Saccades and four samples (16 ms) before and after each saccade were removed from the velocity traces. Additionally, we removed episodes with eye gain outside the range from −0.2 to 2.2 that reflect slowing or acceleration of the eye that were not detected as saccades (see Fig. 2, *A* and *B,* for an example). The discarded episodes were replaced by linear interpolation between the last sample before the gap and the first sample after the gap. Furthermore, we calculated the percentage of trials in which a saccade occurred for each sample (saccade frequency). We did not calculate saccade rates because this requires averaging in a moving window. To not smear the time course of the effects, we only analyzed the sample-by-sample frequencies.

Data were averaged across repetitions for each condition and participant to assure independence of the observations in statistical
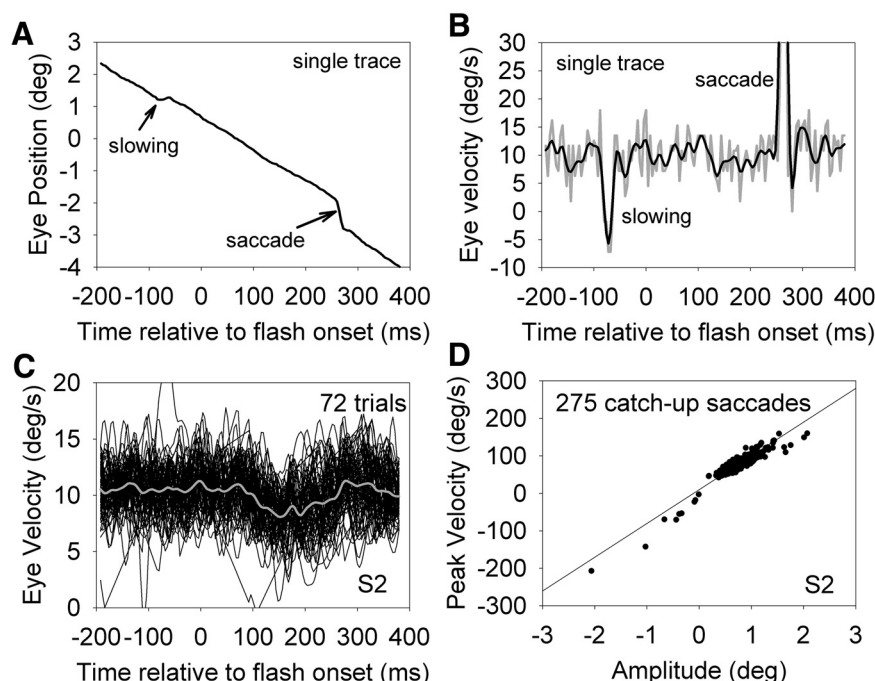
FIG. 2. *A*: eye position in a single trial. The algorithm to detect saccades sometimes missed changes in eye velocity that cannot be classified as smooth pursuit (here: slowing). These episodes were removed based on a velocity criterion after low-pass filtering. *B*: eye velocity for the same trace as in *A* (gray: unfiltered, black: filtered at 40 Hz, low-pass). The slowing and catch-up saccade are easily visible. *C*: 72 traces of eye velocity from a single observer. The gray line represents the mean trace. Target velocity was 10.8°/s. *D*: the main sequence relationship between peak velocity and amplitude for the same observer (unfiltered velocity).

tests (Cumming et al. 2007). In other words, only one trace was retained per condition and participant for statistical testing. An example of individual trials and an individual mean trace is shown in Fig. 2C. Individual mean traces from the unpredictable flash condition of *experiment 1* are shown in Fig. 3. All observers showed a decrease of pursuit gain ∼100 ms after flash onset (the decrease was very subtle for S3, but nonetheless significant). It is also clear that there is considerable variability between subjects and within each individual trace. Because of this, it was difficult to find an algorithm that reliably detected the onset of the decrease in all subjects. Although S7 shows a nice single-dipped decrease, other subjects show only small dips that are immediately followed by upward deflections (e.g., S6). Also, the decrease was mostly abrupt, but gradual decreases did also occur (S11, S4). As can be seen in Fig. 4A, the signal-to-noise ratio in the grand average was poor and even poorer in individual averages (see Figs. 2C and 3). In the 576-ms episode around flash onset that we were interested in, eye velocity gain had a mean SD of 0.24 (range, 0.17–0.37; averages of individual subjects in the unpredictable condition of *experiment 1*). However, we were looking for a decrease of ∼10% (i.e., a decrease in gain of ∼0.1; see Table 1) that would not be visible in individual trials. We therefore searched for a method of onset detection that could deal with low signal-to-noise ratios and that additionally allowed us to compare the latencies across conditions. Finally, we resorted to a method used in research on event-related potentials to detect the onset of the lateralized readiness potential: the jackknife method (Miller et al. 1998; Ulrich and Miller 2001).

First, the onset of a deflection is defined either by an absolute or a relative criterion. Here, we used the midpoint between baseline and minimum gain as a relative criterion. The baseline was the average gain in a time window from −200 to −4 ms before flash onset, and the minimum gain was determined in a 200-ms time window following flash onset. The midpoint between baseline and minimal gain was

defined as criterion. The first sample that was equal or smaller than the criterion was considered as the onset of the flash-induced decrease. Second, the onset was not detected in individual mean traces but in grand averages that are calculated for various subsamples. We entered one trace for each condition and observer into the analysis. For each condition, n jackknife subsample scores were calculated by temporarily removing subject i (i = 1 . . . n) from the grand average. That is, after removing subject i (i = 1 . . . n), the traces of the remaining n − 1 subjects were averaged. Thus each subject was removed from the grand average once. For each subsample trace, the onset was calculated, resulting in n subsample scores. When comparing onsets of different condition by means of ANOVA, the F statistic used in ANOVAs has to be corrected by the formula $F_{corrected} = F/(n − 1)^2$ to correct for the much smaller variability of the subsample scores (Ulrich and Miller 2001). Thus inferential statistics are much more conservative to compensate for the reduced variability.

Next, we applied the same jackknife-based analysis to the frequency of catch-up saccades (Fig. 4, C and D), but with a different criterion value. Because the variability in the frequency of catch-up saccades was even larger than in the smooth pursuit traces (Fig. 4C) and the baseline values were reduced because of the on-line exclusion of trials in some experiments, the criterion value was lowered to 30% of the difference between minimal frequency and baseline (instead of 50%).

The main objective of the jackknife method was to compare the latency of the decrease in smooth pursuit gain between the different experimental conditions. Note that other methods of onset detection, such as searching for a series of significant t-test between consecutive samples, do not allow for such a comparison. Nonetheless, we carried out t-tests and display the results along with the jackknife analysis (Figs. 5 and 6). Although we are confident that the differences between conditions and the time windows are reliably defined, the
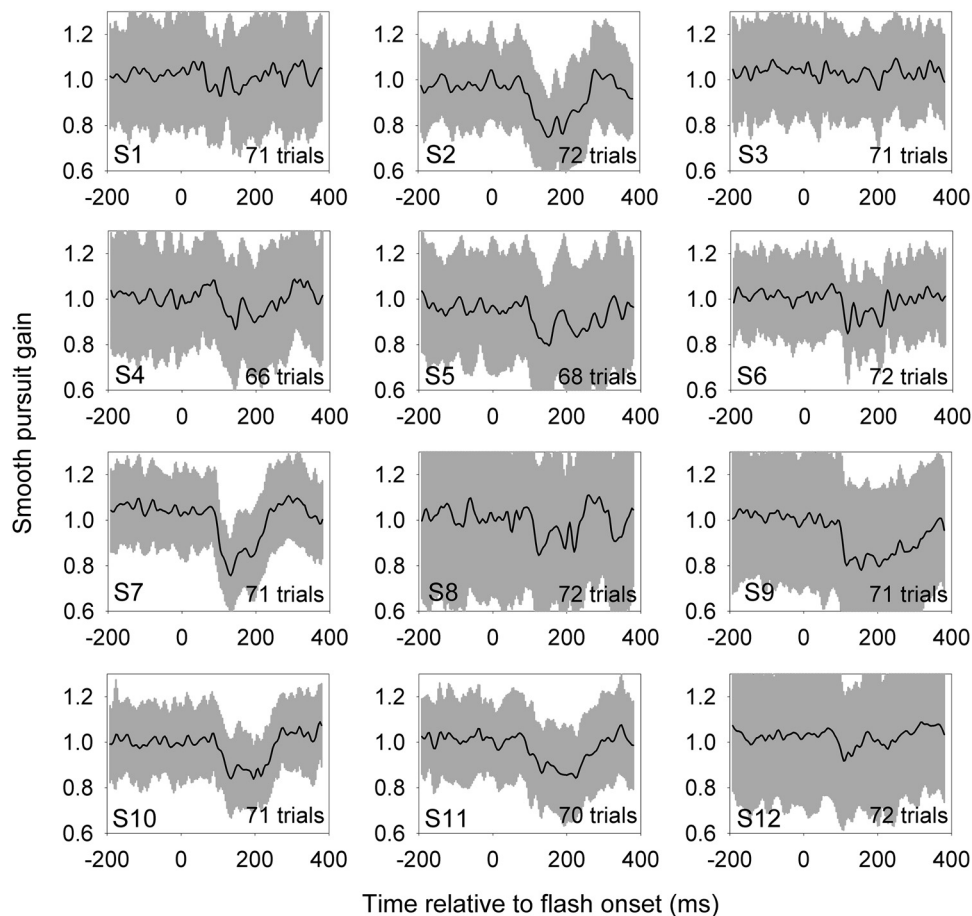

FIG. 3. Mean individual traces from 12 observers in *experiment 1*, condition with unpredictable flashes. The mean traces were obtained by averaging across ∼71 trials. The gray regions indicate the SD across those trials.
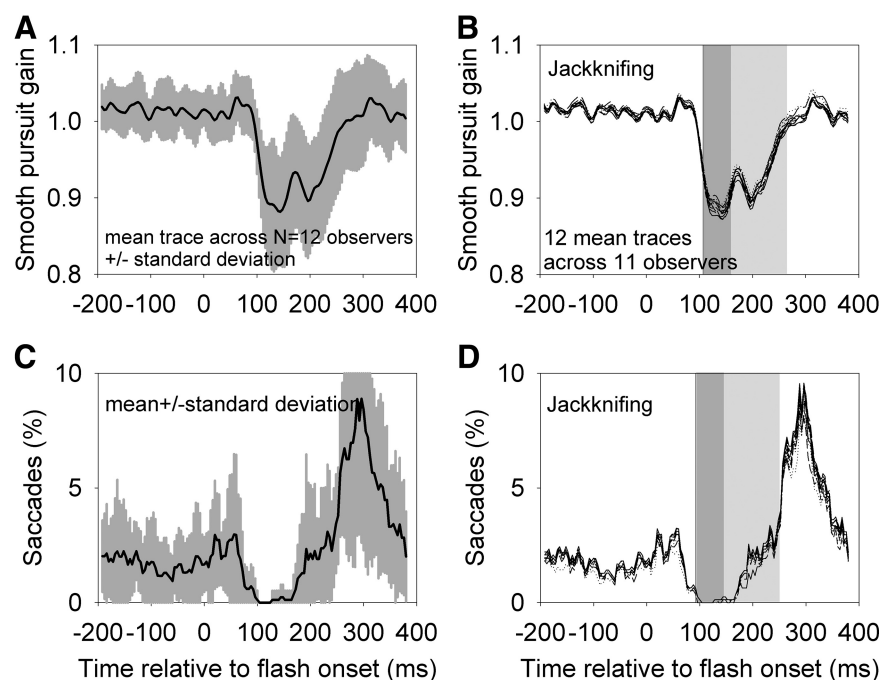
FIG. 4. Illustration of the Jackknife procedure. The data are taken from *experiment 1*, unpredictable flash condition ($n = 12$). *A* and *C*: the smooth pursuit gain and mean percentage of saccades, respectively. The trace represents the average across the 12 observers and the error bar show the between-subjects SD of the mean trace. *B* and *D*: the 12 average traces that result when each participant is excluded once from averaging (i.e., from the grand average). The vertical gray and light gray areas indicate the early and late decrease in pursuit gain or saccade rate, respectively.

absolute values are only approximations. Averaging across trials and subjects is bound to smear the onsets of changes in smooth pursuit or saccade frequency. However, the onset of the change in pursuit velocity turned out to be rather abrupt, which may attenuate this weakness.

We examined whether smooth pursuit gain or saccade frequency would change after the flash. After visual inspection of the data, we defined an early time window from 0–52 ms after the onset of the decrease in pursuit gain to measure the initial decrease. A later time interval from 56 to 160 ms includes the recovery phase after the initial drop. To test whether differences between baseline (200-4 ms before onset) and early or late intervals were significant, we used *t*-test and adjusted the level of significance according to the Bonferroni criterion (5% divided by the number of tests). The results of these tests are reported in Tables 1 and 2. Differences between conditions were

tested by repeated-measures ANOVAs when there were more than two conditions and by *t*-test otherwise.

RESULTS

Experiment 1: Predictable versus unpredictable flashes

Previous studies showed that attention modulates the effect of peripheral stimuli on smooth pursuit. In particular, it was found that flashes or onsets do not affect pursuit if the subject is instructed to ignore them (Blohm et al. 2005; Kerzel et al. 2008). In this experiment, observers were always instructed to ignore the flash, but the flash was either predictable or unpredictable. In principle, predictable flashes allow for

TABLE 1. *Results for smooth pursuit gain in experiments 1–5*

	Onset of Decrease, ms	Baseline Gain	Change	
			Early (0–52 ms)	Late (56–160 ms)
Experiment 1				
Unpredict	107 (2)	1.015 (0.024)	−12% (6)*	−8% (6)*
Predict	110 (2)	1.022 (0.029)	−12% (4)*	−4% (3)*
No flash	—	1.016 (0.027)	−1% (2)	−2% (1)*
Experiment 2				
3°	100 (0)	1.008 (0.036)	−9% (4)*	−6% (6)
6°	103 (2)	1.007 (0.034)	−7% (3)*	−5% (5)
12°	107 (2)	1.007 (0.031)	−6% (3)*	−4% (5)
Experiment 3				
4%	124 (1)	1.016 (0.023)	−11% (9)*	−5% (6)*
20%	116 (0)	1.015 (0.018)	−11% (9)*	−7% (6)*
100%	105 (2)	1.016 (0.028)	−11% (7)*	−11% (8)*
Experiment 4				
Flash	110 (2)	0.969 (0.047)	−11% (7)*	−12% (7)*
Click	114 (2)	0.969 (0.046)	−5% (2)*	−5% (3)*
Experiment 5				
Reversal	127 (2)	1.018 (0.011)	−6% (2)*	−2% (2)

Means are presented in the format mean (SD). Mean onset of inhibition of pursuit gain relative to flash onset and mean smooth pursuit gain in the baseline interval (− 200 to −4 ms) are shown. To characterize the change of pursuit gain in the interval after the onset of the decrease, we show the differences in percent between pursuit gain in the baseline and the early and late intervals after inhibition started. *Changes (in percent) that were significantly different from zero. The *P* level was corrected for the number of comparisons (i.e., the number of conditions) by Bonferroni correction.
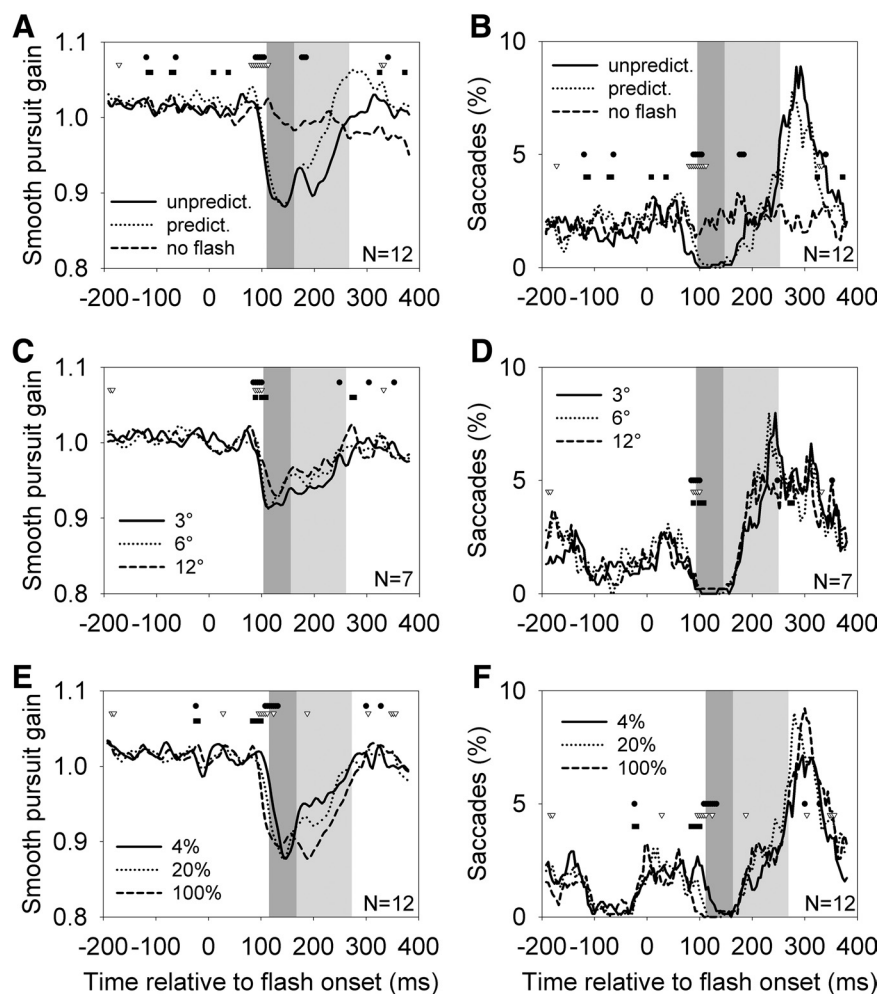
FIG. 5. Results from *experiments 1–3* (corresponding to rows 1–3). *Left*: smooth pursuit gain as a function of experiment and condition. *Right*: the percentage of trials with a catch-up saccade for each sample. The symbols in the *top* and *middle* of the figures indicate significant *t*-test between consecutive samples. The *t*-tests were run on averaged traces from individual observers (*n* = 12, 7, or 12). The *top row* (circles) corresponds to the 1st entry in the legend (i.e., unpredictable), the *2nd row* (triangles) to the 2nd (i.e., predictable), and the *3rd row* (squares) to the 3rd entry (i.e., no flash). The dark gray area is the early postflash interval from 0 to 52 ms after onset of the decrease. The onsets were determined separately for each condition, but in the graph, only the average onset across conditions is shown. The light gray area is the late postflash interval from 56 to 160 ms after the average onset of the decrease. Mean onsets for each condition are reported in Table 1.

advance focusing of attention to reduce perturbations by the flash.

A flash with 100% contrast was presented for 30 ms at an eccentricity of 5° (edge-to-edge). In one block of 72 trials, the flash always appeared when the target had reached the screen center, 1 s after motion onset (predictable flash). In another block of 144 trials, no flash was presented in 50% of the trials. In the remaining 50%, the flash was presented unpredictably between 0.5 and 1.5 s after motion onset. The order of predictable and unpredictable blocks was counterbalanced across participants (*n* = 12). In no-flash trials of the unpredictable condition, we used flash onset times from the same distribution as in the flash condition to generate a no-flash baseline over similar time windows. Inspection of Fig. 5*A* shows that smooth pursuit gain was close to 1 and even slightly greater than 1. The high gain may be attributed to the very predictable and repetitive target motion that allowed subjects to anticipate the trajectory. Predictable and unpredictable flashes produced a decrease of pursuit compared with the baseline that was virtually identical initially, but diverged ~50–100 ms after onset of the decrease. For both predictable and unpredictable flashes, inhibition occurred with a latency of ~110 ms after flash onset (jackknife analysis; Table 1). Visual inspection of Fig. 5*A* shows that the interval from 0 to 52 ms after onset of inhibition (early interval) and from 56 to 160 ms after the onset (late

interval) captures the initial decrease and the (differential) recovery of pursuit gain quite well.

Table 1 reports the results of *t*-test comparing the mean change of pursuit gain in the early and late interval to zero. The decrease of pursuit gain after flash presentation was significantly different from zero in the early and late intervals (−12% in both cases). Also, the early inhibition with predictable and unpredictable flashes was significantly larger than in control trials [−12 vs. −1%, *t*(11) > 5.22, *P* < 0.001], showing that it is distinct from the anticipatory slowing seen in control trials. The late inhibition with unpredictable flashes was significantly larger compared with control trials [−8 vs. −2%, *t*(11) = 3.46, *P* = 0.005], but this difference did not quite reach significance with predictable flashes [−4 vs. −2%, *t*(11) = 2.32, *P* = 0.041; Bonferroni corrected critical, *P* = 0.025]. Although the inhibition observed with unpredictable flashes did not differ from the inhibition observed with predictable flashes in the early interval (−12% in both cases), there was a tendency for larger inhibition with unpredictable than with predictable flashes in the late interval [−8 vs. −4%, *t*(11) = 2.61, *P* = 0.029]. The different time course suggests that expectations regarding the occurrence of the flash did not eliminate the initial perturbation caused by the flash but allowed for a faster recovery. Thus the initial oculomotor response does not seem to be affected by high-level, cognitive factors.

TABLE 2. *Results for catch-up saccades in experiments 1–5*

			Change	
	Onset of Decrease, ms	Baseline Frequency, %	Early (0–52 ms)	Late (56–160 ms)
Experiment 1				
Unpredict	92 (7)	1.7% (1.0)	−94% (13)*	36% (172)
Predict	103 (2)	1.9% (1.3)	−86% (28)*	21% (111)
No flash	—	1.7% (0.9)	15% (63)	38% (47)
Experiment 2				
3°	94 (5)	1.3% (0.6)	−91% (25)*	109% (83)*
6°	94 (6)	1.6% (0.8)	−96% (6)*	169% (141)
12°	91 (6)	1.6% (0.7)	−78% (31)*	75% (81)
Experiment 3				
4%	132 (0)	1.2% (0.7)	−66% (57)*	232% (199)*
20%	112 (0)	1.1% (0.4)	−88% (28)*	178% (215)*
100%	93 (2)	1.0% (0.4)	−90% (16)*	196% (615)
Experiment 4				
Flash	89 (4)	3.1% (1.3)	−87% (19)*	29% (105)
Click	96 (0)	2.9% (1.0)	−81% (27)*	7% (48)
Experiment 5				
Reversal	128 (0)	1.3% (0.6)	−55% (21)*	86% (59)*

Means are presented in the format mean (SD). Mean onset of the inhibition of catch-up saccades relative to flash onset and mean saccadic frequency in the baseline interval (−200 to −4 ms) are shown. To characterize the change of saccadic frequency in the interval after the onset of the decrease, we show the differences in percent between the baseline and the early and late intervals after the decrease started. *Changes (in percent) that are significantly different from zero. The Bonferroni correction was applied.

Furthermore, the mean latency of inhibition in flash trials was used to determine early and late intervals in the no-flash control condition. Table 1 and Fig. 5*A* show that there was also a significant decrease of smooth pursuit gain in the late interval of control trials. The traces in Fig. 5*A* show that pursuit gain tended to slowly decrease across time in control trials. This slowing in pursuit is likely to reflect an anticipation of the end of the trial and therefore the end of the requirement to pursue. Nevertheless, the much larger amplitude of the early decrease clearly shows that flash-induced inhibition is distinct from anticipatory slowing.

Analysis of catch-up saccades showed that there was an abrupt decrease of the frequency of catch-up saccades at about the same time as the decrease in smooth pursuit gain. In the baseline interval, the frequency of a catch-up saccade was ~1.8% (Fig. 5*B* and Table 2). That is, a catch-up saccade occurred on average on 1.8% of the trials for each sample point. In the early interval after the onset of inhibition (from 0 to 52 ms after onset of the decrease), the frequency decreased to almost zero. The initial inhibition with unpredictable and predictable flashes (−94 and −86%, respectively) was significantly different from zero (Table 1) and from the no-flash control condition [15%, $t(11) > 6.09$, $P < 0.001$]. In the late interval (56–160 ms), the saccadic frequency in flash trials neither differed from the baseline interval nor from no-flash trials (nonsignificant increases ranging from 21 to 38%), suggesting that catch-up saccades recovered rapidly. There was no difference between predictable and unpredictable flashes in the early or late intervals.

Of note, there was a sharp increase in the saccade rate above the baseline after the analysis interval. This effect can most likely be attributed to the lag accumulated by the absence of saccades during the "saccade suppression" period and the decrease in pursuit gain around the same time and is not analyzed further.

Finally, we aimed at confirming the robustness of the effects by running a *t*-test on the repetitions of each condition for each

subject individually. Table 3 reports the number of subjects that showed a significant decrease ($P < 0.05$), separately for each condition and late interval (early/late). All 12 subjects showed a significant *t*-test for the unpredictable and predictable flash conditions in the early interval, but only 1 subject showed a significant effect when there was no flash. In line with the

TABLE 3. *Results of within-observer t-tests on smooth pursuit gain and catch-up saccade rate in experiments 1–5*

			Significant *t*-Tests (Early/Late)	
	No. Trials	No. Subjects	Pursuit	Saccade
Experiment 1				
Unpredict	71	12	12/8	11/4
Predict	71	12	12/7	9/2
No flash	70	12	1/3	1/0
Experiment 2				
3°	67	7	7/4	6/0
6°	68	7	6/5	7/0
12°	67	7	6/4	4/0
Experiment 3				
4%	63	12	12/8	7/0
20%	64	12	12/8	10/0
100%	65	12	11/12	6/1
Experiment 4				
Flash	91	11	9/10	10/1
Click	91	11	7/8	10/0
Experiment 5				
Reversal	203	9	9/3	5/0

For each observer, we subtracted the gain and saccade rate in the early (0–52 ms) and late (56–160 ms) intervals from the baseline interval (−200 to −4 ms). Differences were calculated for each trial using the onsets obtained by jackknife method. For each subject, a *t*-test against zero was run on the difference values from trials repeating a single condition. The mean number of trials is shown for each condition. The number of participants with a significant individual *t*-test ($P < 0.05$, uncorrected) is shown for the early and late intervals (format: #early/#late). Only significant decreases are reported. Some subjects did not make any or very few catch-up saccades. Therefore, the number of significant *t*-tests for catch-up saccade tends to be lower than for smooth pursuit gain.

recovery of smooth pursuit gain in the late interval, the number of significant *t*-tests was smaller in the late interval. For saccade frequency, the pattern was similar. It has to be noted that our results on saccade frequency, although showing a massive effect, do not mean that inhibition could be detected on every single trial. There were many trials with no saccades in the respective intervals such that it is more appropriate to look at the individual frequencies and the analysis that were carried out across subjects (cf. Table 2).

Experiment 2: Variation of eccentricity

Previous research on the remote distractor effect in smooth pursuit and saccades has shown that foveal distractors slow down latencies more than peripheral distractors (Knox and Bekkour 2004; Walker et al. 1997). Unlike the (peripheral) target of a saccadic eye movement, the target for steady-state pursuit is presented in the fovea. To avoid sensory target–distractor interactions between a foveal target and a foveal distractor, we used a minimal distractor eccentricity of 3°.

The eccentricity of the flashed Gabors varied randomly between 3, 6, and 12° (edge-to-edge).The flash appeared unpredictably between 0.5 and 1.5 s after target motion onset on each trial (as in all the remaining experiments). The contrast of the Gabor stimuli was fixed at 100%. Seven naïve students participated, but the on-line gain check was applied to only five subjects because of a programming error. The jackknife analysis showed that inhibition of pursuit gain occurred at 100, 103, and 107 ms after flash onset for eccentricities of 3, 6, and 12°, respectively. An ANOVA showed that these differences were not significant. The magnitude of inhibition in the early interval (from 0 to 52 ms after onset of the decrease) was significantly different from zero in all conditions (Fig. 5C; Table 1) and decreased with increasing eccentricity [−9, −7, and −6%, respectively; $F(2,12) = 7.39$, $P = 0.008$]. The inhibition of pursuit gain in the late interval (from 56 to 160 ms) was smaller than in the early interval and not significantly different from zero. Nonetheless, a significant effect of eccentricity emerged, $F(2,12) = 9.97$, $P = 0.003$, showing that inhibition was smaller at high eccentricities (−6, −5, and −4%, respectively).

The latency of the decrease in catch-up saccades was 94, 94, and 91 ms for eccentricities of 3, 6, and 12°, respectively, with no significant differences (Table 2; Fig. 5D). In the early interval (0–52 ms after onset), saccadic frequency significantly decreased by −78 to −96% relative to baseline, but the inhibition was unaffected by eccentricity. In the late interval, there was a tendency for more saccades than in the baseline interval (109, 169, and 75% for 3, 6, and 12°, respectively), which reached significance in the 3° eccentricity condition. The results were further corroborated by *t*-tests on the repetitions of each condition for each subject (Table 3). For both pursuit and saccades, there were many significant *t*-tests in the early interval but far less in the late interval.

Overall, there was some evidence for stronger perturbation of pursuit gain with distractors closer to the fovea. Although these effects were statistically significant, they were surprisingly small. A flash at an eccentricity of 12° produced a decrease that was only slightly reduced relative to a flash at 3° (decrease of −6 vs. −9%). In contrast, the remote distractor effect on pursuit or saccadic latencies was abolished at eccen-tricities of 8° (Knox and Bekkour 2004; Walker et al. 1997). Furthermore, there were no effects of eccentricity on the frequency of catch-up saccades, confirming that the distractor effect did not strongly depend on eccentricity.

Experiment 3: Variation of contrast

We varied stimulus strength by varying the contrast of the Gabor stripes. Stimulus contrast has recently been shown to strongly modulate the remote distractor effect with regular saccades (Born and Kerzel 2008). The Michelson contrast of the distractor grating was varied between 4, 20, and 100%, whereas the target was unchanged. The eccentricity of the distractor was fixed at 5°. Figure 4E and Table 1 show that the latency of inhibition shortened with higher flash contrast (124, 116, and 105 ms, respectively), which was confirmed by a significant main effect of contrast on latencies, $F_{corrected}(2,22) = 4.74$, $P = 0.019$. This result is consistent with longer neural processing times for low-contrast stimuli (Bell et al. 2006; Roufs 1963; White et al. 2006). The magnitude of the decrease did not differ between the three conditions in the early interval from 0 to 52 ms after onset of the decrease (−11% for all conditions; $F < 1$), but the magnitude of inhibition was stronger with high-contrast stimuli in the late interval from 56 to 160 ms after onset of inhibition]−11, −7, and −5% for high, medium, and low contrast, respectively; $F(2,22) = 18.01$, $P < 0.001$], suggesting that the recovery of smooth pursuit was delayed with high-contrast flashes.

Analysis of the frequency of catch-up saccades yielded similar results. The latency of inhibition was shorter with high-contrast flashes [93, 112, and 132 ms for high, medium, and low contrast, respectively; $F_{corrected}(2,22) = 21.58$, $P < 0.001$]. There was a significant decrease of −66 to −90% in the early interval that did not differ between conditions. In the late interval, there was a significant increase in saccadic frequency with 4 and 20% stimulus contrast (232 and 178%, respectively) but not with 100%, suggesting that the inhibition of catch-up saccades lasted longer with 100% contrast (cf. Table 2). Furthermore, inspection of Fig. 5F shows that the on-line pursuit criterion eliminated most of the trials with a saccade occurring in the interval from 100 to 10 ms before flash onset. This dip is purely technical and only reflects our criteria for trial inclusion.

The principal effect of contrast on the initial decrease was a delay of 20 ms with low-contrast stimuli. Surprisingly, the initial amplitude of inhibition did not vary as a function of contrast. In the late interval, however, there was a modulation by contrast. Because *experiment 1* has shown that expectations affect behavior in the late interval, it is likely that contrast-induced changes in the late interval also reflect higher-level processes. For instance, it may be that the salient high-contrast gratings attracted attention despite being irrelevant to the task (Jonides 1981; Posner and Cohen 1984).

Experiment 4: Click versus flash

Presentation of a tone affects saccadic responses in different ways. If the tone is presented during the exploration of a visual scene, fixation duration increases, which suggests that the irrelevant tone inhibits saccades (Graupner et al. 2007; Pannasch et al. 2001). In contrast, the presentation of an irrelevant
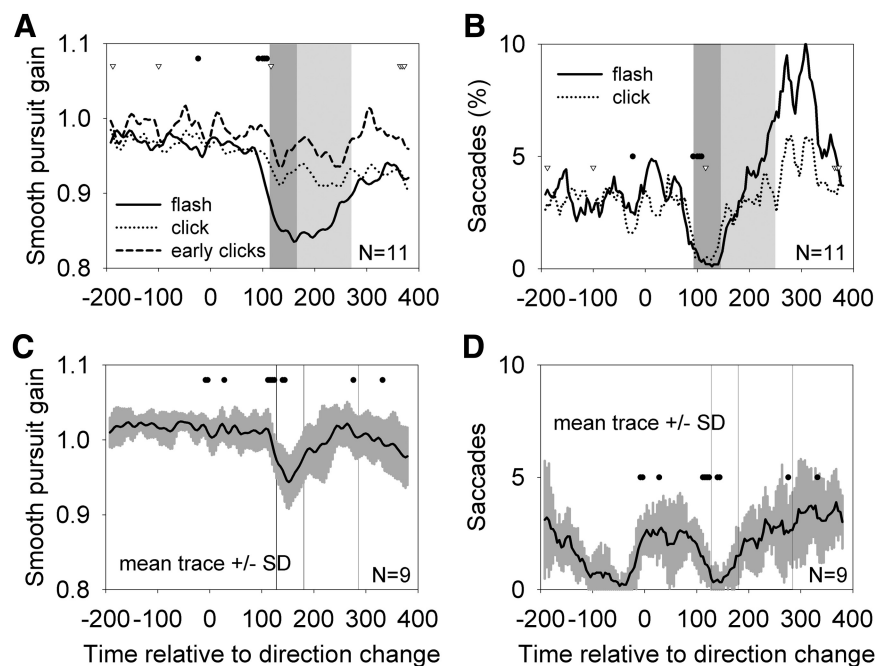
FIG. 6. Results from *experiments 4* and *5* (corresponding to rows 1–2). Early clicks are those that were presented before the target crossed the center of the screen. *Left*: smooth pursuit gain as a function of experiment and condition. *Right*: the percentage of trials with a catch-up saccade. The dark gray area is the early postflash interval from 0 to 52 ms after the average onset of the decrease. Onsets for each condition are shown in Table 1. The light gray area is the late postflash interval from 56 to 160 ms after the average onset of the decrease. The symbols indicate significant *t*-test between consecutive samples. In *C* and *D*, the gray area shows ±SD.

tone simultaneous to target onset reduces saccadic latencies, suggesting facilitation rather than inhibition of saccadic eye movements (Colonius and Diederich 2004; Diederich and Colonius 2007; but see Ilg et al. 2006). The apparent contradiction may be resolved by saying that simultaneous presentation of acoustic and visual stimuli in studies results in facilitation while asynchronous presentation results in inhibition. Because the target is continuously visible during ongoing pursuit (similar to a visual scene during exploration), target and distractor are asynchronous, and therefore we expect inhibition to prevail, although firm predictions are difficult to derive because the cited studies deal with saccades to peripheral stationary targets, whereas we are measuring smooth pursuit and catch-up saccades, which are directed to moving and mostly (para-)foveal targets.

On each trial, either a flash at 100% contrast at an eccentricity of 5° (edge-to-edge) or a brief click sound of 10-ms duration and 83-dB(A) loudness was presented in random order. Because the loudspeakers to the left and right of the screen were clearly visible to the subject, the subjective impression was not that the click came from straight ahead. By jackknife analysis, the flash produced a decrease of pursuit gain at 111 ms. The flash produced a significant reduction of pursuit gain in the early and late intervals of −11 and −12%, respectively (Table 1). The click produced a decrease at 114 ms and the early and late decrease was −5 and −5%, respectively. *t*-Tests showed that inhibition by a flash was significantly larger than inhibition by a click in both intervals, *t*(10) >2.76, *P* < 0.02. When looking at the trace of the click condition (Fig. 6*A*), it is difficult to determine whether there actually was a decrease caused by the click, because the dip occurring after 114 ms seems to be part of a general decrease. As in *experiment 1*, the slow decrease may result from anticipatory slowing. To disentangle anticipatory slowing and distractor-induced decrease in the click condition, we re-ran the analysis on the trials in which the click was presented before the target crossed the screen center (i.e., when the click

occurred early in a trial and therefore no anticipatory slowing was expected yet). Figure 6*A* shows the respective trace in which no anticipatory slowing is visible. The jackknife procedure on early click trials indicated a latency of 123 ms, and a subsequent *t*-test showed that the decrease of 4% in the early interval was significant, *t*(10) = 3.72, *P* = 0.004, confirming that there was a small, but significant decrease. Also, 7 of 11 observers showed a significant decrease in the early interval (Table 3).

Furthermore, catch-up saccades showed virtually identical dips after flash and click events. The onset of the decrease in saccadic frequency (as determined by jackknifing) occurred at 92 and 96 ms in the flash and click conditions, respectively. In both conditions, there was a significant decrease in the early interval (−87 and −81% for flash and click, respectively), and the magnitude of inhibition was equal with flashes and clicks (*P* > 0.4).

Overall, this experiment showed that inhibition of saccadic eye movements may dissociate from inhibition of smooth pursuit. Whereas the effect of a click on smooth pursuit gain was much smaller than the effect of a flash, catch-up saccades were inhibited to the same degree by clicks and flashes. The inhibition of catch-up saccades is consistent with the prolongation of fixation duration during visual exploration after presentation of an acoustic distractor (Graupner et al. 2007; Pannasch et al. 2001). The (relative) resistance of smooth pursuit gain to acoustic distraction shows that visual signals are the main input into the pursuit system. For instance, pursuit of acoustic targets results in low gain (Berryhill et al. 2006) that is no better than pursuit of an imagined motion stimulus (Boucher et al. 2004). Because smooth pursuit is mainly driven by motion signals, the poor pursuit of auditory targets was taken as evidence for the absence of auditory motion signals (Boucher et al. 2004). In contrast, saccades to auditory targets can be reliably elicited (Yao and Peck 1997; Zambarbieri 2002), showing that acoustic stimuli provide position signals for the saccadic system. We suggest that catch-up saccades

were inhibited by clicks because of acoustic input into the saccadic system.

Experiment 5: Abrupt changes of irrelevant direction of motion

The previous experiments have shown that abrupt onsets perturb the execution of smooth pursuit and catch-up saccades. Others have reported similar inhibition of catch-up saccades by transient offsets of the pursuit target (Orban de Xivry et al. 2009). Here, we wanted to examine whether an abrupt change that is not an onset would also inhibit the tracking response. To this end, we presented abrupt changes of motion direction. Two dot fields moved along with the pursuit target. Additionally, the dots moved vertically away or toward fixation (Fig. 1C). The vertical direction of motion of the dot fields changed abruptly between 0.5 and 1.5 s after target motion onset. It either changed for 50 ms and returned to the original direction (double change) or remained different until target offset (single change). We expect inhibition to be less pronounced than in the previous experiments because sudden onsets are very salient and have been shown to easily capture attention (Jonides 1981; Posner and Cohen 1984). In contrast, although motion onsets are well known to automatically attract attention, motion by itself does not capture attention (Abrams and Christ 2003), which suggests that it is less salient than sudden onsets.

Data from the single and double change conditions were combined because they were essentially identical. Therefore average traces were based on ~240 trials for each subject. The jackknife analysis showed that pursuit gain decreased 127 ms after flash onset. The initial decrease of −6% was significant (Table 1; Fig. 6C), but not the late decrease of −2%. We ran a between-subject comparison with the unpredictable flash condition of *experiment 1* to evaluate differences between an abrupt visual onset and an abrupt change in motion direction. The decrease occurred later with a direction change than with a flash (127 vs. 107 ms), $F_{corrected}(1,19) = 8.04$, $P = 0.021$, and was less strong in the early (−6 vs. −12%), $F(1,19) = 7.645$, $P = 0.012$, and late intervals (−2 vs. −8%), $F(1,19) = 10.17$, $P = 0.005$.

The jackknife analysis of saccadic frequency showed that a decrease occurred at 128 ms. Table 2 and Fig. 6D show that catch-up saccades were significantly less frequent in the early interval by −55% and significantly more frequent by 86% in the late interval. However, the relative increase in the late interval relative to baseline may be caused by a reduction of baseline saccadic frequency resulting from the on-line pursuit check. In a between-subjects comparison, the latency did not differ significantly from the unpredictable flash condition in *experiment 1*, possibly because of the rather high variability of the latencies in *experiment 1*. We did not compare the magnitude of the decrease because *experiment 1* was not run with an on-line pursuit check, whereas *experiment 5* was. The resulting differences in baseline saccade frequency preclude a direction comparison.

We conclude that unexpected events, such as abrupt onsets, but also changes in motion direction, inhibit smooth pursuit and catch-up saccades. The later onset and smaller amplitude of inhibition may be explained by the lower saliency. Alternative, one may speculate that characteristics of the SC contribute to the difference between abrupt onsets and changes in motion

stimuli. Single cell recordings in the rostral part of the SC showed that neurons responded well to motion stimuli but were not selectively tuned to the direction or speed of motion (Krauzlis 2004a,b). On the assumption that changes in motion direction are invisible to the SC, we may speculate that signals that are only visible to cortical areas such as MT or MST suffice to produce a distractor effect during steady-state pursuit. The longer latency of the motion-induced distractor effect is also consistent with the longer latencies of single-cell responses in areas MT/MST (on the order of 73 ms; Schmolesky et al. 1998) compared with the SC (on the order of 35–47 ms for bright stimuli; Rizzolatti et al. 1980). Nonetheless, we rather believe that that some saliency signal generated in higher-level areas such as the lateral intraparietal area (Gottlieb 2007) generates the distractor effect with visual transients and motion stimuli. Subjectively, the visual transient was more salient than the change in motion direction and therefore the perturbation was stronger and the respective latencies shorter.

DISCUSSION

This study showed that irrelevant visual events perturb smooth pursuit and catch-up saccades. A large visual stimulus generating no retinal motion in the direction of pursuit reduced smooth pursuit gain by 6–12% and almost entirely suppressed catch-up saccades. Previous results using small stimuli have shown that irrelevant flashes do not affect smooth pursuit when they can be ignored and the stimuli are small (Blohm et al. 2005; Kerzel et al. 2008). Our data show that large visual transients inhibit smooth pursuit gain and catch-up saccades. Similarly, increasing inhibition with increasing stimulus size has been reported for regular saccades (Edelman and Xu 2009). In our experiments with a high-contrast flash, the decrease occurred at ~100 ms after flash presentation. With low contrast, the decrease occurred later, in accordance with results showing that the processing of low-contrast stimuli is delayed. The latency of the inhibition of steady-state pursuit was longer and smaller than the inhibition of saccades in a related study using similar stimuli (Reingold and Stampe 2002; Stampe and Reingold 2002). Reingold and Stampe (2002) had speculated that the short-latency inhibition occurring 60–70 ms after flash onset originated in the SC. The latencies of pursuit inhibition that we observed in this study are in the range of smooth pursuit onset latencies (Carl and Gellman 1987) and therefore do not isolate any particular neural structure. Possibly, descending projections from higher-level motion centers to the SC account for this variant of the distractor effect as well as for its longer latency. Furthermore, the inhibition of smooth pursuit gain was rather small (between 6 and 12% of pursuit gain) compared with saccadic inhibition. Previous work has shown that saccade frequency was reduced by ~80–100% after the presentation of a flash (Edelman and Xu 2009; Reingold and Stampe 2002; Stampe and Reingold 2002). Despite the rather weak effect on pursuit gain, we observed inhibition of catch-up saccades by 80–100% with high-contrast flashes that was quite similar to the inhibition observed with regular saccades. Thus despite the different latencies, trigger mechanisms, and cortical substrates, "regular" and catch-up saccades show inhibition of similar magnitude.

Another outcome of this series of experiments is that the initial decrease of pursuit gain and saccadic frequency is impervious to both low-level and high-level factors. The magnitude of the early decrease was not affected by expectations regarding the occurrence of the flash, stimulus contrast, and only slightly by eccentricity. That is, even very faint stimuli of 4% contrast and very peripheral stimuli at 12° of eccentricity inhibited the tracking response. Nonetheless, predictability and contrast had an effect on the recovery phase (i.e., the late interval). With predictable flashes, the recovery was quicker, and with high-contrast stimuli, the recovery was slower. This suggests that there are two distinct phases: an initial rapid decrease that depends very little on stimulus strength (i.e., stimulus contrast) and cognitive factors and a later recovery period that is affected by signal strength and cognitive factors.

The reduction of smooth pursuit gain was mirrored by an almost complete inhibition of catch-up saccades. The latency of the decrease in catch-up saccades was comparable to the decrease in smooth pursuit gain (~100 ms after flash). The only exception to this rule occurred with the acoustic stimulus. Surprisingly, the effect of a loud sound was as effective as a visual stimulus in decreasing the catch-up saccade frequency and showed similar latency. Integration of signals from various modalities in the SC can explain the effectiveness of auditory signals in decreasing saccade rates. The deep layers of the SC contain spatiotopically organized auditory maps (Jay and Sparks 1984). Many cells are responsive to auditory and visual stimuli (Wallace et al. 1998). A special link between auditory signals and saccadic responses has been previously tested by analyzing saccadic and manual reaction times to auditory, visual, or combined modality targets. It has been shown that using combined stimuli produces greater facilitation for saccades compared with manual responses (Hughes et al. 1994). The remarkable accuracy of saccades toward auditory targets (Zahn et al. 1978) speaks also in favor of the effectiveness of auditory signals in generating gaze and attention shifts. On the other hand, sounds only marginally affected pursuit gain in our study, raising the possibility that sounds have no access to the pursuit system (Boucher et al. 2004).

Despite this dissociation, most of the data in this study rather show that catch-up saccades and steady-state smooth pursuit are similarly affected by distractor presentation. Single cell studies have confirmed that target selection is accomplished by similar neural mechanisms at the level of the SC for smooth pursuit and saccades (Carello and Krauzlis 2004; Krauzlis and Dill 2002). Models of saccadic control describe distractor effects as the result of long-range inhibitory interactions between target and distractor signals in the SC (Findlay and Walker 1999; Godijn and Theeuwes 2002; Kopecz 1995; Munoz and Fecteau 2002; Trappenberg et al. 2001). However, the latency of the effects observed in these experiments does not exclusively point to the SC. Because of the rather long latencies, cortical centers are likely to contribute.

Besides inhibitory interaction, the distractor effect may be attributed to an involuntary spread of attention that results from the onset of a large, high-energy transient in the periphery. Cortical areas involved in attention orienting and eye movement programming largely overlap, which is true of saccadic (Corbetta et al. 1998) and pursuit eye movements (Acs and Greenlee 2008), although pursuit eye movements may be more robust to concurrent attentional demands. During pursuit, attention is focused on the target (Kerzel and Ziegler 2005; Kerzel et al. 2008, 2009; Khurana and Kowler 1987; Lovejoy et al. 2009; Madelain et al. 2005; Souto and Kerzel 2008). Pursuit gain diminishes when attention is spread over nonpursued objects (Khurana and Kowler 1987) but not necessarily when it is spread over targets moving in the same direction (Kerzel and Ziegler 2005; Kerzel et al. 2009).

A common influence on pursuit gain and saccade rate may be mediated by the reflexive deployment of attention over a wide area of the visual field that may interrupt overt orienting (eye movements) toward the target. In our study, such a global deployment of attention might be induced by the large peripheral flash. This interpretation does not exclude the SC as the origin of inhibition, because the SC is believed to be involved in the generation of the reflexive orienting of attention (Condy et al. 2004; Muller et al. 2005; Sapir et al. 1999; Sereno et al. 2006; Sparks 1986). That explanation does not suppose that the distractor arises from inhibitory interactions within the SC, possibly as in the remote distractor effect, but rather from interactions within a bottom-up attentional network comprising the SC (Shipp 2004). There is evidence that spreading attention across the visual field may promote fixation. Directing attention globally has been shown to strongly reduce the rate of saccades (Weber et al. 2000). Similarly, attending to a large ring around the pursuit target reduces pursuit gain more than attending to a small ring (Madelain et al. 2005).

We also showed that, in the absence of a visual onset, using a change in the direction of a field of moving dots as a distractor can also generate similar inhibition of smooth pursuit and catch-up saccades. This is in line with studies showing a reduction of the rate of catch-up saccades after the offset of the pursuit target (Orban de Xivry et al. 2009). Distraction of oculomotor programs is thus not confined to visual events, or to onsets, again arguing for a general inhibitory mechanism.

Finally, we may speculate about the functional purpose of the transient inhibition. In general, the visual effect of smooth pursuit is to stabilize moving objects of interest on the retina, thereby making them easier to perceive. Conversely, stationary objects in the background become less visible because of self-induced motion. The purpose of the inhibition of smooth pursuit could be to rapidly shift priorities from processing of the tracked target to processing of potentially important events in the background by inhibiting all oculomotor programs, allowing for clear vision of the background. Furthermore, inhibition of current motor plans and programs may allow for faster reaction times to new events by reducing the competition for new motor signals.

Conclusions

We showed that large, irrelevant flashes reduce pursuit gain and catch-up saccade rate. The relative long latency suggests that higher-level processes are involved. The effects of irrelevant transients may represent a mechanism promoting fixation, probably mediated by the deployment of attention over the visual field, turning the tables toward processing of global scene information. In addition, we showed that a loud irrelevant sound is able to generate the same inhibition of saccades as visual transients, while it only induces a weak modulation of

pursuit gain, indicating a privileged access for acoustic information to the saccadic system.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

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