Processing of Retinal and Extraretinal Signals for Memory-Guided Saccades During Smooth Pursuit

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[1]*Centre for Systems Engineering and Applied Mechanics, Université Catholique de Louvain, Louvain-la-Neuve, Belgium;* [2]*Laboratory of Neurophysiology, Université Catholique de Louvain, Brussels, Belgium; and* [3]*National Eye Institute, National Institutes of Health, Bethesda, Maryland*

Blohm, Gunnar, Marcus Missal, and Philippe Lefèvre. Processing of retinal and extraretinal signals for memory-guided saccades during smooth pursuit. *J Neurophysiol* 93: 1510–1522, 2005. First published October 13, 2004; doi:10.1152/jn.00543.2004. It is an essential feature for the visual system to keep track of self-motion to maintain space constancy. Therefore the saccadic system uses extraretinal information about previous saccades to update the internal representation of memorized targets, an ability that has been identified in behavioral and electrophysiological studies. However, a *smooth* eye movement induced in the latency period of a memory-guided saccade yielded contradictory results. Indeed some studies described spatially accurate saccades, whereas others reported retinal coding of saccades. Today, it is still unclear how the saccadic system keeps track of *smooth* eye movements in the absence of vision. Here, we developed an original two-dimensional behavioral paradigm to further investigate how smooth eye displacements could be compensated to ensure space constancy. Human subjects were required to pursue a moving target and to orient their eyes toward the memorized position of a briefly presented second target (flash) once it appeared. The analysis of the first orientation saccade revealed a bimodal latency distribution related to two different saccade programming strategies. Short-latency (<175 ms) saccades were coded using the only available retinal information, i.e., position error. In addition to position error, longer-latency (>175 ms) saccades used extraretinal information about the smooth eye displacement during the latency period to program spatially more accurate saccades. Sensory parameters at the moment of the flash (retinal position error and eye velocity) influenced the choice between both strategies. We hypothesize that this tradeoff between speed and accuracy of the saccadic response reveals the presence of two coupled neural pathways for saccadic programming. A fast striatal-collicular pathway might only use retinal information about the flash location to program the first saccade. The slower pathway could involve the posterior parietal cortex to update the internal representation of the flash once extraretinal smooth eye displacement information becomes available to the system.

INTRODUCTION

Space constancy is an essential feature of the visual system that allows us to perceive a stationary object as immobile during self-movement even though its image shifts across the retina (Bridgeman 1995; Deubel et al. 1998; Niemann and Hoffmann 1997; Stark and Bridgeman 1983). In the case where visual information is absent, the question arises whether space constancy of memorized targets still holds during eye movements. This issue has been extensively studied for the saccadic system using the so-called double-step and colliding saccade paradigms (Aslin and Shea 1987; Becker and Jürgens 1979; Dassonville et al. 1992; Dominey et al. 1997; Goossens and Van Opstal 1997; Hallett and Lightstone 1976a,b; Mays and Sparks 1980; Mushiake et al. 1999; Schlag and Schlag-Rey 1990; Schlag et al. 1989; Tian et al. 2000). In both experimental conditions, a saccadic eye movement is evoked either visually or by microstimulation before primates have to direct their line of sight to a previously memorized spatial location. In this situation, the retinal error of the memorized target does not correspond anymore to the required eye movement. Nevertheless, saccades are spatially accurate. The authors conclude that extra-retinal information about the first eye movement is available to the saccadic system to adapt the second saccade amplitude. The saccadic system is thus able to keep track of its own movements.

During *smooth*-pursuit movements, the question of space constancy becomes more complicated. In this case, a *smooth* eye movement is induced before the occurrence of the saccade directed toward the memorized target. Again, to align gaze with the correct spatial location of the memorized target, the retinal input has to be updated by extraretinal signals about the smooth eye displacement. Thus the saccadic system needs additional information from another motor system—the smooth-pursuit system—to compensate for smooth eye displacements. Today, it is still not clear how such memory-guided saccades are programmed during smooth eye movements. Recent studies indicate that gaze shifts to targets memorized before visually guided smooth pursuit and executed after the end of pursuit are spatially accurate (Baker et al. 2003; Herter and Guitton 1998). Also, when targets were briefly flashed during smooth pursuit but the localization was performed only after the smooth-pursuit target disappeared, memory-guided saccades seemed to be better predicted by the spatial error hypothesis (i.e., saccades directed to the actual target position in space, accounting for the retinal error and intervening movements during the latency period) than by the retinal error hypothesis (i.e., saccade directed to the retinal position of the target irrespective of intervening eye movements) (Ohtsuka 1994; Schlag et al. 1990; Zivotofsky et al. 1996). Taken together, these results suggest that the saccadic system has indeed access to information about smooth eye displacement during the memory period. However, when a target is briefly flashed at the moment of the smooth-pursuit target extinction and a targeting saccade is immediately trig-

gered, its amplitude is better predicted by the retinal error than by the spatial error (Gellman and Fletcher 1992; McKenzie and Lisberger 1986). These results are clearly contradictory with the above-mentioned hypothesis of space constancy during smooth eye movements and the question arises what can explain this apparent contradiction.

To answer this question, we propose to investigate how memory-guided saccades are programmed during smooth pursuit. In particular, because long memory periods seemed to allow space constancy during self-generated movement (Baker et al. 2003; Herter and Guitton 1998; Ohtsuka 1994; Schlag et al. 1990; Zivotofsky et al. 1996), whereas this was not the case for short memory periods (Gellman and Fletcher 1992; McKenzie and Lisberger 1986), we will investigate the role of response latency in the saccade programming process. By doing this, we will be able to make the link between the above-mentioned results of short-latency retinal and long-latency spatial saccade programming. Therefore we developed a two-dimensional (2-D) experimental paradigm in which we presented a briefly flashed target during smooth-pursuit eye movements. This 2-D arrangement of the paradigm allowed us to separate retinal and extraretinal signals and to obtain saccade programming parameters for horizontal and vertical eye-movement components separately. Furthermore, a detailed analysis of saccade latencies made it possible for the first time to link the saccadic execution time to the programming of the memory-guided eye movement. As a result, we will show that there is a transition between retinally coded short-latency saccades and spatially coded longer-latency eye saccades and that this transition is reflected in a bimodal saccadic latency distribution. We will also analyze which sensory parameters influence the system's decision to trigger short- or longer-latency saccades. These results shed light on the use of extra-retinal signals when tracking smooth eye movements in the absence of visual input and reconcile previous contradictory results concerning the programming of memory-guided saccades during smooth self-motion. Our paradigm thus allowed us to identify two coupled processes for saccade execution.

METHODS

Eight healthy human subjects aged between 23 and 38 yr and without any known oculomotor anomalies were recruited after informed consent. Three of them were completely naïve of oculomotor experiments. All procedures were conducted with approval of the Université Catholique de Louvain Ethics Committee, in compliance with the Helsinki Declaration (1996).

Experimental setup

Subjects faced a 1-m distant, tangent translucent screen that covered about ±45° horizontally and ±40° vertically of their visual field. They sat in complete darkness and their head was restrained using a chin rest. Two different targets—a green and a red spot— were back-projected onto the screen. The green spot was projected by a Tektronix (Beaverton, OR) 606A oscilloscope using custom optics and measured ~1.5°. This green spot was the smooth-pursuit target. A second target was a red laser spot that measured 0.2° and was projected onto the screen via two M3-Series mirror galvanometers (GSI Lumonics, Billerica, LA). This red spot was only briefly presented during 10 ms, and we will thus refer to it as a "flash" [flash durations between 5 and 20 ms have been used successfully (Gellman and Fletcher 1992; Schlag et al. 1990)]. A dedicated real-time com-

puter running LabViewRT (National Instruments, Austin, TX) software controlled position, velocity, and illumination of both targets. We recorded the movements of one eye using the scleral search coil technique (Skalar Medical BV, Delft, The Netherlands) (Collewijn et al. 1975; Robinson 1963).

Paradigm

All recording sessions were composed of blocks of 40 trials each. Data acquisition started with two blocks of fixation control (FIX) trials followed by a varying number of blocks of test trials, such that a total recording duration of 30 min was not exceeded. Flashes were presented during fixation (control FIX), during ongoing smooth pursuit ("flash during ramp" FDR test) or after the pursuit ramp offset ("flash after ramp" FAR control).

Fixation control (FIX) trials started with a green central fixation spot. At a random time 500–1,000 ms after the trial began, a 10-ms red flash was presented at a random position between −10° and +10° horizontally and vertically. Subjects were asked to look at the memorized target position as soon as the flash appeared and to fixate this position until the end of the trial. They had to redirect gaze to the memorized target position even though the fixation spot remained illuminated. One thousand milliseconds after the flash, the green fixation spot was extinguished for 500 ms to indicate the end of the trial.

Test trials started with a 500-ms initial fixation period (green target) at 20° eccentricity (Fig. 1A, IF) in a random direction around the straight-ahead position. The initial fixation point was thus located at a random position on a 20° circle around the straight-ahead direction (Fig. 1A, - - -). Then the green spot performed a step away from the center of the screen and a ramp movement (Fig. 1A, ramp) back toward the center of the screen. The size of the step was calculated in such a way that the target crossed the initial fixation point after 200 ms. This step was introduced to reduce the probability of occurrence of a catch-up saccade during pursuit initiation (Rashbass 1961). The ramp velocity varied randomly between 10 and 40°/s. A 10-ms red flash (Fig. 1A, flash) was presented at a random time between 500 and 1,500 ms after the ramp movement onset. The flash position was randomly chosen in a squared ±10° (horizontal and vertical) window around the actual pursuit ramp position. The ramp movement continued until the end of the trial. All trials lasted for 3 s. Subjects were instructed to follow the green pursuit target and to look at the memorized position of the flash as soon as they saw the flash.

In addition to the test trials, all subjects performed "flash after ramp" control (FAR) trials. FAR controls were similar to test trials, but the green pursuit ramp target was extinguished at a random time between 500 and 1,000 ms after the ramp movement onset and remained extinguished until the end of the trial. At a random time 0–500 ms after the pursuit ramp extinction, a red flash was presented in a ±10° window (horizontally and vertically) around the extrapolated ramp position. We chose to introduce this random extinction period to obtain different patterns of eye velocity after the flash presentation. Beside this, all stimulus parameters and subject's instructions remained the same as for test trials.

Data acquisition and analysis

Two NI-PXI-6025E data-acquisition boards (National Instruments, Austin, TX) sampled the position of one eye and both targets (horizontally and vertically) at 500 Hz. Collected data were stored on a hard disk for off-line analysis with Matlab scripts (Mathworks, Natick, MA). Position signals were low-pass filtered using a zero-phase digital filter (autoregressive forward-backward filter; cutoff frequency: 50 Hz). Velocity and acceleration were derived from position signals using a weighted central difference algorithm on a ±10-ms interval. The cutoff frequency of the derivative filter was 33 Hz.

smooth-pursuit system does not pause during saccades and thus has a significant contribution to the measured saccade amplitude (de Brouwer et al. 2001, 2002). Therefore to examine the output of the saccadic system in isolation, the measured value of the saccade amplitude (AMP) has to be corrected by an estimate of the smooth-pursuit contribution P_{Amp} (see Fig. 1B). The corrected saccade amplitude is then $S_{Amp} = AMP - P_{Amp}$. The smooth-pursuit contribution P_{Amp} is calculated by multiplying the saccade duration S_{Dur} with the mean value of the eye velocity before and after the saccade (de Brouwer et al. 2001, 2002; Keller and Johnsen 1990; Smeets and Bekkering 2000). Here, we performed the same correction of the saccade amplitude for 2-D saccades. We tested the validity of the correction for each subject individually on the main sequence relationship between saccade duration S_{Dur} and vectorial amplitude AMP. For all subjects, the corrected vectorial saccade amplitude S_{Amp} was significantly better correlated to S_{Dur} than the uncorrected amplitude AMP (t-test, $P < 0.01$). We thus validated the previously proposed method of the saccade amplitude correction for 2-D data. All analyses in this paper will thus use the corrected saccade amplitude S_{Amp}.

For our analysis, we measured different parameters as illustrated in Fig. 1B. The range of these parameters is provided in Table 1. At the moment of the flash, we measured the horizontal and vertical component of the position error PE_F (= retinal error) and eye velocity EV_F and also the smooth-pursuit gain ($gain_{SP,F}$). Following the above-described procedure, the total saccade amplitude AMP was divided into a purely saccadic component S_{Amp} and a smooth-pursuit contribution P_{Amp}. Position error $PE(t)$ and smooth eye displacement $SED(t)$ were measured continuously until 1,000 ms after the flash. For the analysis of the saccade latency, we partitioned our data into two distinct subsets, i.e., foveofugal (FF) and foveopetal (FP) flashes (see Fig. 1C). In FP (FF) trials, the flash was presented ahead (behind) the actual eye position with respect to the direction of the eye trajectory. Thus as the terms "foveofugal" and "foveopetal" intuitively suggest, the eye motion made the fovea to move either away (foveo*fugal*) or toward (foveo*petal*) the target at the moment of the flash presentation. It should be noted that a FP flash could evoke both onward and backward saccades (with respect to the smooth eye movement direction, see typical trials in Fig. 2). We also calculated the angle β_R between EV_F and the position error PE_F at the moment of the flash.
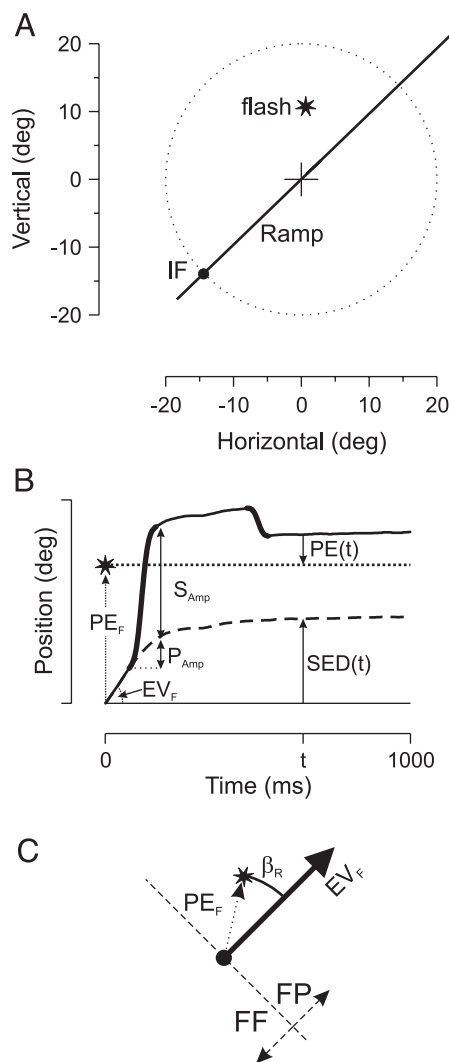
FIG. 1. Experimental paradigm and data analysis. *A*: test trials paradigm. The initial fixation point (○, IF), the pursuit ramp and the flash (*) are represented. - - -, the possible positions of the initial fixation point. *B*: extracted parameters. At the time of the flash (*; - - -, the memorized flash position), position error (PE_F) and eye (—, saccades in bold) velocity (EV_F) were sampled. The 1st saccade amplitude was divided into the purely saccadic (S_{Amp}) and the smooth (P_{Amp}) component. Position error ($PE(t)$) and smooth eye displacement [$SED(t)$] are also represented. *C*: direction of smooth pursuit with respect to the location of the flash. β_R is the angle between position error (PE_F) and eye velocity (EV_F) at the moment of the flash. The visual field was divided into foveofugal (FF) and foveopetal (FP) hemifields. See text for more details.

All trials were aligned on flash onset. Figure 1B illustrates an example in one dimension, starting from the moment of the flash onset (time: 0 ms) until 1,000 ms after the flash. The instantaneous smooth eye displacement at time t was defined as the integral of the smooth eye velocity $EV_S(t)$ over time, starting at the moment of the flash [$SED(t) = \int_0^t EV_s(t')dt'$]. The smooth eye velocity $EV_S(t)$ was obtained by removing saccades from the velocity trace. Saccades were detected using a $500°/s^2$ acceleration threshold. We then measured the eye velocity before and after the saccades and interpolated linearly between these values to obtain an estimation of the smooth eye velocity during saccades (see METHODS section of de Brouwer et al. 2002 for more details).

To analyze the first saccade programming, the saccadic amplitude had to be corrected for the contribution of the smooth-pursuit system. It has indeed been shown for horizontal eye movements that the

TABLE 1. *Measured parameters*

| Parameter	Component	Mean ± SD	Median [25..75]%
Parameters at the moment of the flash			
$\|PE_F\|$ (°)	X	5.447 ± 3.478	5.258 [2.644..7.878]
	Y	5.531 ± 3.619	5.253 [2.584..7.997]
$\|EV_F\|$ (°/s)	X	10.819 ± 7.718	9.395 [4.687..15.231]
	Y	9.201 ± 6.459	8.077 [4.220..12.853]
$Gain_{SP,F}$ (.)		0.678 ± 0.256	0.708 [0.500..0.865]
Saccade-related parameters			
$\|S_{Amp}\|$* (°)	X	5.057 ± 3.524	4.506 [2.187..7.348]
	Y	4.573 ± 3.602	3.770 [1.670..6.716]
$gain_S$ (.)	X	0.908 ± 0.371	0.898 [0.683..1.117]
	Y	0.805 ± 0.388	0.791 [0.546..1.024]
$\|SED_{S,beg}\|$ (°)	X	1.992 ± 1.848	1.440 [0.661..2.771]
	Y	1.669 ± 1.472	1.239 [0.617..2.268]
$\|SED_{S,end}\|$ (°)	X	2.568 ± 2.166	2.010 [0.974..3.632]
	Y	2.168 ± 1.724	1.742 [0.926..2.989]
Final orientation parameters			
$\|PE_{end}\|$ (°)	X	2.319 ± 2.030	1.778 [0.816..3.311]
	Y	2.156 ± 1.889	1.684 [0.817..2.912]
$\|SED_{end}\|$ (°)	X	3.217 ± 2.640	2.595 [1.219..4.503]
	Y	2.851 ± 2.256	2.329 [1.165..4.012]

$n = 4,464$ trials.
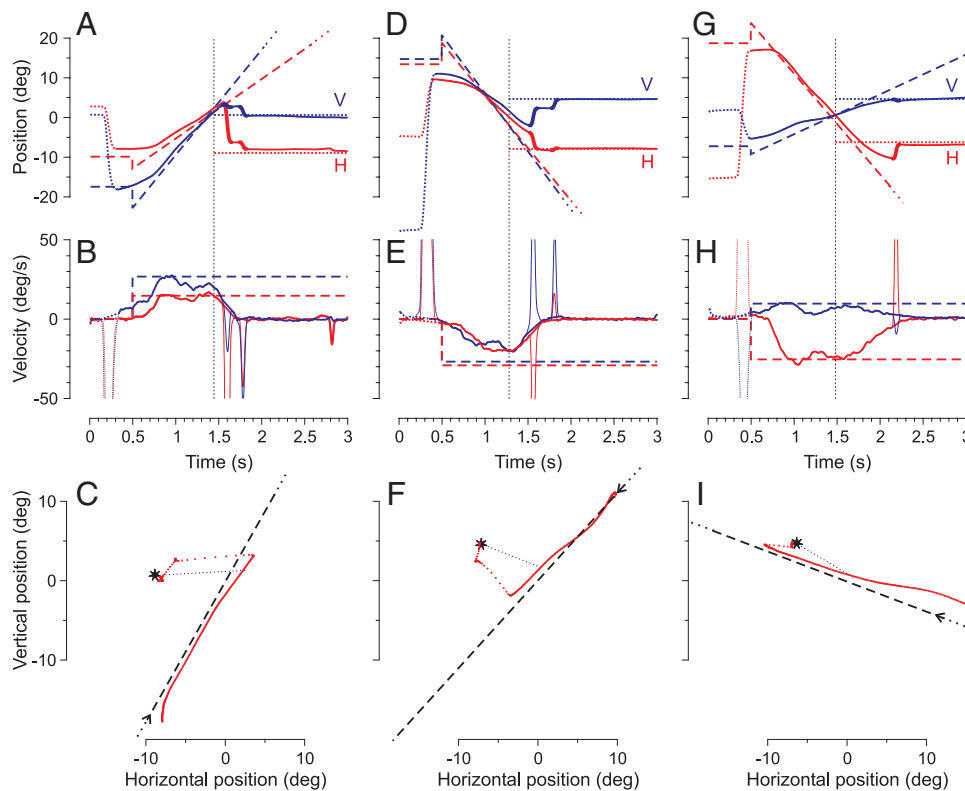
FIG. 2. Typical trials. Three typical trials are shown. *A–C*: a short-latency (104 ms) trial; *D–F*: a long-latency (238 ms) trial; and *G–H*: very-long-latency (674 ms) trial. *A, D, G*: position vs. time representation of the pursuit target (dashed lines), the flash (horizontal dotted lines stand for the memorized flash position) and the movement of 1 eye (solid lines) separately for horizontal (red, H) and vertical (blue, V) components. Relevant saccades are represented with bold lines. The vertical dotted line indicates when the flash was presented. *B, E, H*: velocity vs. time representation of the trial. Saccades are represented with thin lines; other conventions are the same as in *A, D,* and *G. C, F, I*: vertical vs. horizontal representation of the trial. The dashed line represents the pursuit ramp target and the arrow indicates the movement direction. The eye position is represented with a red dot every 6 ms. When the dots are separated, this indicates a fast (saccadic) eye movement; otherwise the movement is smooth. The flash (star) is connected to the eye trace by a thin dotted line that indicates where the eye was at the moment of the flash ($= PE_F$).

We performed our statistical analyses either using Statistica (StatSoft, Tulsa, OK) or Matlab (Mathworks) programs. For the presentation and description of our results, we used the classical expression of the regression coefficient R (and corresponding *P* values for significance) to provide an indication of the goodness-of-fit. This was the case for linear regressions as well as for nonlinear fitting.

RESULTS

We recorded a total of 5,855 test trials. All trials were visually inspected. We discarded trials with saccades occurring around the moment of the flash ≤ 65 ms after the flash onset ($n = 956$) and trials where subjects could not localize correctly the flashed target (final error $>10°$) or did not trigger any saccade ($n = 435$). The total number of valid trials we used in our analyses was thus $n = 4,464$ ($\sim 76\%$). We also recorded a total of 1,957 control FIX trials and 5,919 control FAR trials, of which 1,542 ($\sim 79\%$) and 4,402 ($\sim 74\%$), respectively, were valid. Subjects reported that they did not have any difficulties in performing the experimental tasks.

Figure 2 shows three trials with a typical short-latency (*A–C*), long-latency (*D–F*), and very-long-latency (*G–I*) first saccade, respectively. We were only interested in saccades that occurred after the onset of the flash (dotted vertical line in the six top panels of Fig. 2). The first orientation saccade in Fig. 2, *A–C,* had a latency of 104 ms with respect to the flash and was almost parallel to the position error vector at the moment of the flash PE_F ($=$ retinal error; dotted line in Fig. 2*C*). It seems that this saccade did not take into account the smooth eye movement during the latency period. However, a second saccade was triggered and compensated for the remaining error. A different behavior is shown in the second typical trial, in Fig. 2, *D–F,* where the first saccade toward the flash had a latency of 238 ms and was not parallel to PE_F vector (Fig. 2*F*). Indeed,

this saccade seemed to take into account the fact that the eye was moving during the latency period. However, a second saccade was still needed to correct for the remaining error. Figure 2, *G–I,* shows an extreme case where the first saccade was triggered very late (latency: 674 ms). This example shows an almost perfect compensation for the smooth eye displacement that took place during the latency period. Remarkably, although the horizontal retinal position error at the moment of the flash was negative, the horizontal saccade amplitude was positive. These three trials in Fig. 2 illustrate the influence of latency on the characteristics of the first saccade. The programming of short latency saccades appears to be directed to the retinal position of the flash whereas there is a bias toward the spatial location of the flash when saccade latency increases.

Programming of first saccade

Typical trials in Fig. 2 seemed to indicate that short- and long-latency saccades were not programmed in the same way. Short-latency saccades (see Fig. 2, *A–C*) appeared to be parallel to the vector of retinal position error at the moment of the flash, whereas long-latency saccades (see Fig. 2, *D–I*) indicate that extra-retinal signals about the ongoing eye movement during the latency period of the saccade could also influence its programming. Long-latency saccades would thus be spatially more accurate than the retinal short-latency saccades. Figure 3 shows a comparison of the retinal versus the spatial saccadic programming hypothesis as a function of saccade latency. Figure 3 shows scatter plots of the first saccade direction for the retinal and spatial error hypothesis, for short (<150 ms)- and long (>300 ms)-latency trials separately. This confirmed the tendency shown in our example trials (Fig. 2), i.e., short-latency saccades were better described by the retinal error
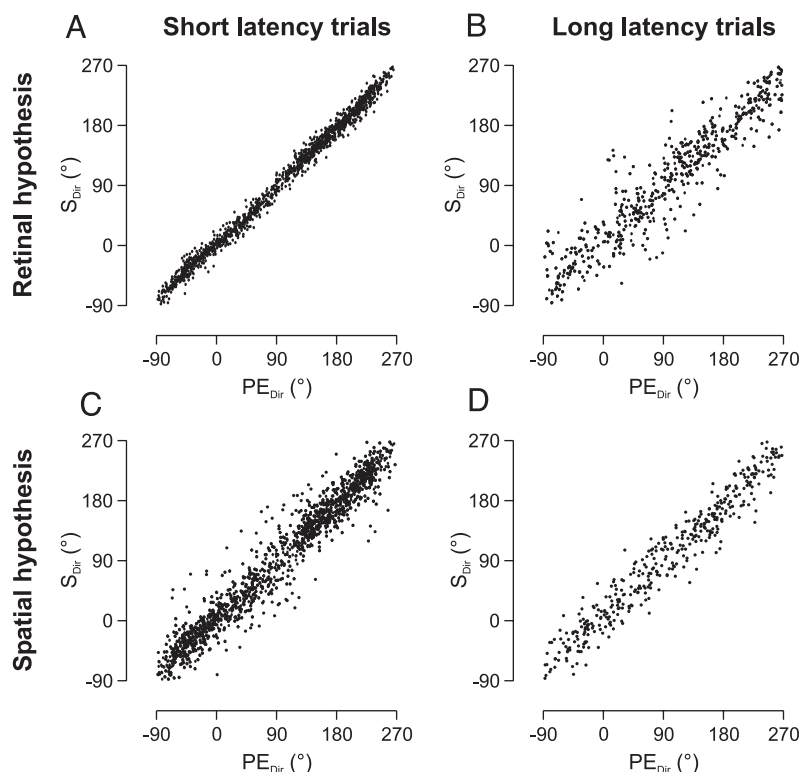
FIG. 3. Retinal vs. spatial saccade programming. Scatter plots of raw data for the 1st saccade direction (S_{Dir}) as a function of the direction of the position error (PE_{Dir}). The retinal error hypothesis (*A* and *B*) is compared with the spatial error hypothesis (*C* and *D*) separately for short-latency trials (latency $<$150 ms, *A* and *C*) and long-latency trials (latency $>$300 ms, *B* and *D*).

hypothesis, whereas long-latency saccades were spatially more accurate. A qualitatively and quantitatively very similar behavior was observed for FAR control trials (data not shown).

To analyze the transition between the retinal and spatial programming of the first orientation saccade, we developed a smooth eye displacement compensation index (CI). This index varies from zero (retinal error hypothesis) to one (spatial saccade programming) and is calculated as follows

$$CI = 1 + \frac{PE_{\parallel}}{SED} \qquad (1)$$

Position error ($PE_{\parallel}$) and smooth eye displacement (SED) were measured in the direction of (and thus parallel to) smooth pursuit. Following *Eq. 1*, if $PE_{\parallel} = -SED$, then the system did not compensate for SED and thus CI = 0 (retinal programming). If the system does compensate for SED, then $PE_{\parallel} = 0$ and thus CI = 1 (spatial programming). Values for CI between 0 and 1 indicate the percentage of SED compensation of a saccade. Figure 4 shows the results of this analysis. Figure 4*A* shows the distribution of the compensation index CI for short ($<$150 ms, ▨) and long ($>$300 ms, □) latency first saccades. In *B,* we represented the evolution of CI with saccade latency. This shows that short-latency saccades were ~85% retinal and only 15% spatial. In contrast, the programming for longer-latency saccades converges ~75% spatial coding, leaving a 25% retinal contribution to the saccadic programming. Furthermore, Fig. 4*C* shows the evolution of the compensation index over time for each subject individually. This confirms the results from Fig. 3 indicating that short-latency saccades are programmed retinally, whereas there is a transition toward the spatial error hypothesis for longer saccade latencies.

To be sure that the retinal to spatial transition we observed was not due to some side-effect of saccade programming, we measured the saccadic gain orthogonal to the pursuit ramp

movement direction in Fig. 5. Because there was no SED in this orthogonal direction, the saccadic gain was a good measure of the movement's accuracy. As a result, there was neither a significant modulation of this saccadic gain for different latencies, nor a difference between test trials and FIX control trials (see Fig. 5). It should be mentioned that the scatter in Fig. 5 was essentially due to small position errors.

Saccadic latency distribution

We plotted the first saccade latency histogram for FDR trials, FAR controls, and FIX controls in Fig. 6, *A–C,* respectively. One can easily identify two modes in the latency distribution. To further characterize the two modes of these histograms, we fitted a double-recinormal distribution to our data. The double-recinormal distribution for the latencies has the following expression

$$\frac{1}{T_{lat}} = A_1 \cdot gauss(\mu_1, \sigma_1) + A_2 \cdot gauss(\mu_2, \sigma_2) \qquad (2)$$

The inverse of the saccade latency T_{lat} was thus fitted by two independent Gaussians. This is equivalent to the hypothesis of two separate and noninteracting decision processes of the LATER type (Carpenter and Williams 1995). Indeed, the LATER model states that the inverse of saccade latency is proportional to the rate of rise of a decision signal divided by the decision threshold. The particularity of the LATER model is that the decision signal is assumed to rise linearly with a normally distributed rate of rise. We essentially chose this double-recinormal fit function because it described well our data and allowed us to quantify with very few parameters the entire latency distribution. However, to justify the use of this particular probability density function, we performed a k-fold cross-validation applying the Kolmogorov-Smirnov statistical
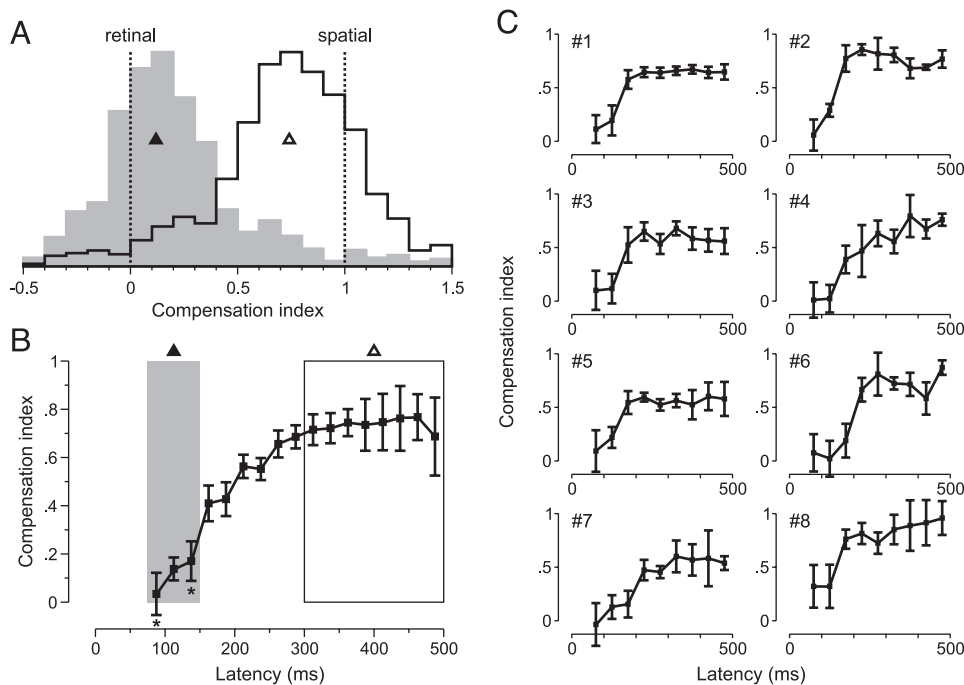
FIG. 4. First saccade compensation index for smooth eye movements. *A*: histograms for the distribution of the compensation index as calculated in *Eq. 1* for short-latency trials (latency <150 ms, ▨) and long-latency trials (latency >300 ms, □). A 0 compensation index corresponds to retinal saccade programming, whereas a unitary compensation index corresponds to spatially accurate saccades. △ and ▲ refer to *B*. Histograms are normalized in amplitude. *B*: evolution of the compensation index for different saccade latencies. ■ and whiskers indicate means ± SE (25-ms bins). *, when the means are not significantly different from 0 (*t*-test, *P* > 0.05). ▨ with ▲: corresponds to the data represented in ▨ of *A*. □ with △, the data range of □ in *A*. *C*: evolution of the compensation index for different saccade latencies individually for each of the 8 subjects (50-ms bins).

one-sample distribution test. Therefore we used a random subset of 75% of our data to estimate the fit parameters of *Eq. 2* by means of standard least-square data fitting using the Gauss-Newton method. Afterward, we performed a Kolmogorov-Smirnov analysis to test if the remaining 25% of our data were distributed identically to the previously identified distribution. This procedure was performed $k = 1,000$ times. As a result, we found an average 98.3% acceptance of the double-recinormal probability density function hypothesis (5% significance level).

To estimate the fit parameters, we applied the same least-square data fitting as used above. As a result, we obtained the means and SDs (inverse time scale) for the best fit of *Eq. 2* on the histograms. Hereafter, we will provide values for $m_i = 1/\mu_i$ (location of the maximum) and $s_i = \frac{1}{2} \cdot \left(\frac{1}{\mu_i - \sigma_i} + \frac{1}{\mu_i + \sigma_i} \right)$ (estimated scatter), which are in the real-time domain and thus intuitively easier to interpret. Maxima ± scatter were 115 ± 40 and 225 ± 41 ms, respectively, for both modes of the double-recinormal fit (dotted line) on the latency histogram of FDR trials in Fig. 6*A*, 110 ± 35 and 222 ± 25 ms for FAR trials in Fig. 6*B*, and 134 ± 36 and 220 ± 21 ms for FIX controls in Fig. 6*C*. Note, that there were also two distinct latency modes for both FAR and FIX control trials. However, in the FAR control situation, the less frequent second mode might be due to the fact that the flashed stimulus did not compete any more with the pursuit ramp target. Interestingly, the minimum between the two modes in Fig. 6*A* was located ~175 ms, which was approximately the time needed for the extraretinal smooth eye movement signal to be taken into account for the saccade programming (see CI in Fig. 4). The individual latency histograms of FDR trials for each subject in Fig. 6*D* demonstrate that both latency modes were present in each subject, although with different proportions and slightly different locations of the maxima.

Previous studies showed that there is an inhibition of saccade initiation to previously attended positions (Klein 2000)

and that there is a directional asymmetry of saccade latency during smooth-pursuit eye movements (Kanai et al. 2003; Tanaka et al. 1998), i.e., saccades executed in the same direction as pursuit have shorter latencies than saccades in the opposite direction. All these experiments describe saccade latencies to visible stationary or moving targets. Here we investigated whether a similar behavior could also be observed for memory-guided saccades to briefly flashed targets. Furthermore, previous studies that analyzed smooth-pursuit-related directional differences in saccade latency used only horizontal stimuli and eye movements. Here, our 2-D paradigm will allow us to test saccadic latencies for different positions of the flash with respect to the smooth-pursuit direction.

To address the question of a possible directional asymmetry of saccade latencies, we separated our data into foveofugal (FF) and foveopetal (FP) trials (see METHODS section, Fig. 1C). Figure 7, *A* and *C,* shows the latency distributions of FF (▨, - - -) and FP (□, ···) data separately for
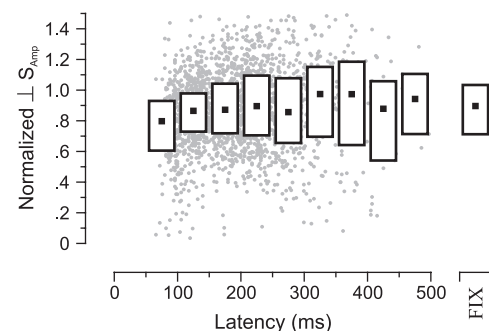

FIG. 5. Saccade accuracy. The normalized saccade amplitude perpendicular to the initial ramp movement direction was used as an indicator for the subject's saccade accuracy. The latency-dependent computations of this median saccade gains were compared with the fixation (FIX) control situation. ◎, individual saccades; ■ and □, the median and quartiles. In addition, individual tests for each subject showed no significant latency dependence of the saccade accuracy (*t*-test, *P* > 0.1).
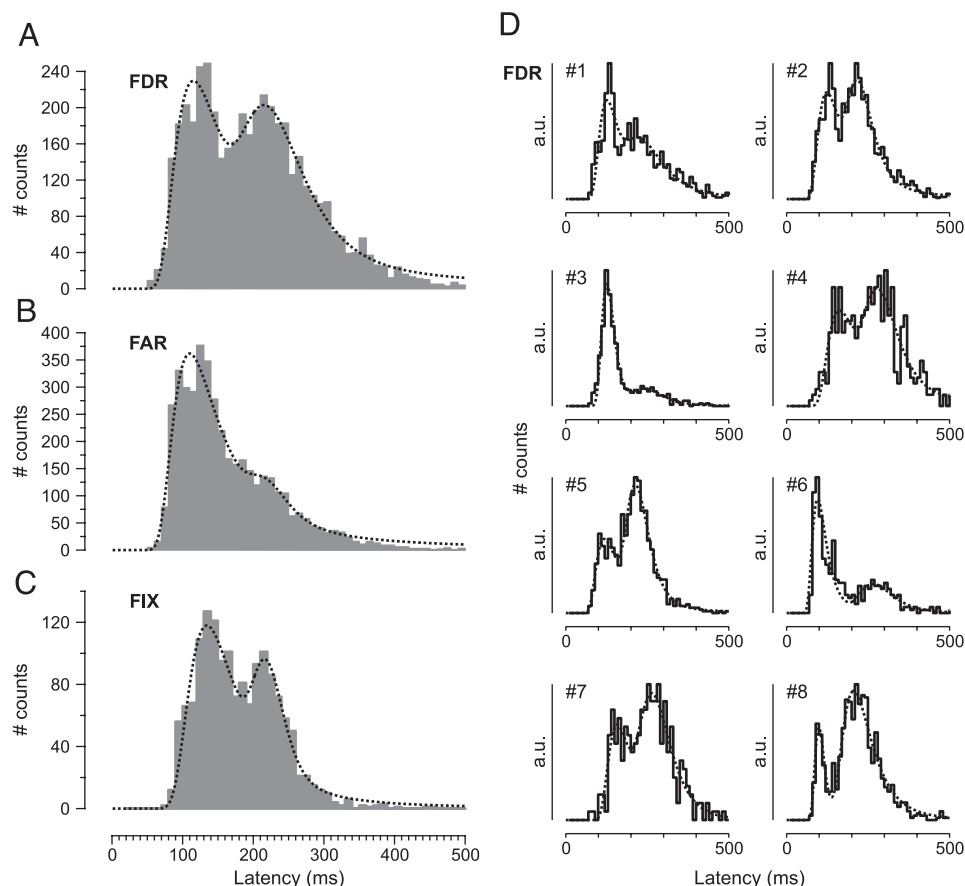
FIG. 6. First saccade latency. *A*: latency histogram for flash during ramp (FDR) trials (*n* = 4,464). The dotted line represents a double-recinormal fit function with maxima at 115 and 225 ms. *B*: latency histogram for flash after ramp (FAR) control trials (*n* = 4,402). The double-recinormal fit function has maxima at 110 and 222 ms. *C*: latency distribution for FIX control trials. Fitted distribution maxima are at 134 and 220 ms. *D*: individual histograms for the 1st saccade latency distribution of all 8 subjects in the case of FDR trials. The fitted distribution maxima varied between 96 and 163 ms for the 1st latency mode and between 207 and 286 ms for the 2nd mode.

FDR and FAR trials. Interestingly, the relative importance of the short- and long-latency modes changed between FP and FF trials, whereas their location was approximately constant. FP trials contained more short-latency than long-latency saccades, whereas the opposite was the case for FF trials. Thus the mean latencies for saccades to the FF and FP hemifield were 214 and 191 ms, respectively for FDR trials (Fig. 7*A*) and 158 and 172 ms, respectively for FAR controls (Fig. 7*C*). The difference between both means was highly significant (*t*-test, *P* < 0.0001) in both cases. Note that the FP and FF data sets were slightly different in their total number of trials; this was due to an asymmetry in the paradigm. Therefore we also tested the FP/FF hemifield difference for a subset of our data with identical properties (we used the same range and distribution of PE_F) for FP and FF and found no difference with the above-reported results. On average, the latency of FF saccades was larger, but they were spatially more accurate when compared with FP saccades.

Our 2-D paradigm allowed us to go one step further and to ask for the first time whether the asymmetry in saccade latencies reported in Fig. 7, *A* and *C,* was due to a pursuit related focus of attention or whether it might be the result of an inhibitory hemifield effect. Therefore we present in Fig. 7, *B* and *D,* polar plots of mean saccade latencies depending on the angle β_R between the flash position and the pursuit eye-movement direction at the moment of the flash (see METHODS section, Fig. 1*C*). It can be easily observed that almost all mean latencies within the same hemifield had the same values and that there was a relatively sharp transition between the FP and FF hemifields.

How did the system decide whether to rapidly trigger a short latency but inaccurate saccade or to wait longer and trigger a spatially more accurate saccade? We investigated a possible dependence of the first saccade latency on the main sensory parameters measured at the moment of the flash appearance, i.e., the position error PE_F and eye velocity EV_F at the moment of the flash. In addition, we tested other parameters, like the smooth-pursuit gain ($gain_{SP,F}$) at the moment of the flash, the target velocity or the duration of ongoing smooth-pursuit eye movement, but the overall regression results were best using the above-mentioned sensory variables. This analysis was also motivated by previous findings that showed a dependence of the mean saccade latency on the distance between the eye and the target (Bell et al. 2000; Clark 1999; Hodgson 2002; Kalesnykas and Hallett 1994).

The position error PE_F at the moment of the flash was the first sensory parameter that influenced the distribution of saccade latency. Figure 8*A* shows the dependence of the first saccade latency on the distance PE_F between the flash and the eye for FDR (black) and FAR (gray) data. Mean values and standard errors in Fig. 8A essentially indicated that for small position errors (PE_F < 5°) the latency was larger than for larger PE_F. We separated our data into three categories depending on PE_F, i.e., small (PE_F < 5°), medium (5° < PE_F < 10°) and large (10° < PE_F) values, and computed the latency histograms and double-recinormal fits in Fig. 8B. For small PE_F values, the long latency mode of the histogram was more important than for larger PE_F values. While the value of the location of the short-latency mode's maximum remained roughly constant, the
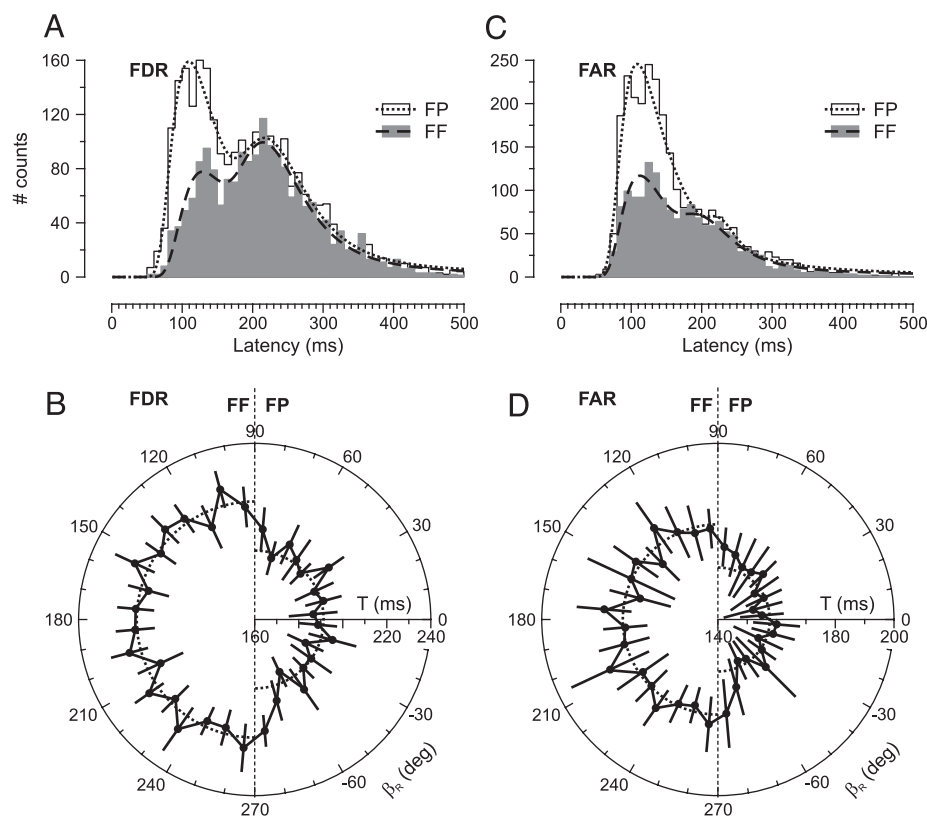
FIG. 7. Saccade latency dependence on direction. *A*: The latency histogram for FDR trials as in Fig. 6*A* but divided into 2 populations, i.e., foveofugal (FF, ▨, *n* = 1,884) and foveopetal (FP, □, *n* = 2,580) flash presentations. Maxima for the latency fit on the data were 129 and 223 ms for FF (- - -) and 110 and 228 ms for FP (· · ·) flashes. *B*: polar plot of FDR saccade latencies as a function of the angle of flash appearance β_R relative to the smooth pursuit direction. $\beta_R = 0°$ corresponds to a flash presented straight ahead in the direction of the eye movement. ○ and whiskers indicate mean ± SE for the 10°-angle bins. · · ·, mean values of the FF (214 ms) and FP (191 ms) hemifield separately. The difference between both means was highly significant (*t*-test, *P* < 0.0001). *C*: as for *A,* the FAR latency histogram was divided into foveofugal (FF, ▨, *n* = 1,768) and foveopetal (FP, □, *n* = 2,634) flash presentations. FF maxima were at 113 and 207 ms; FP maxima were at 109 and 228 ms. *D*: polar plot of saccade latencies as a function of the flash direction relative to the smooth pursuit direction. The same conventions as in *B* apply. The mean values of FF and FP hemifield saccade latencies were 172 and 158 ms, respectively. The difference between both means was highly significant (*t*-test, *P* < 0.0001).

longer latency mode of the distribution moved toward shorter latencies with increasing PE_F.

The second sensory parameter we found to influence the first saccade latency was the smooth eye velocity EV_F at the moment of the flash. Figure 8*C* shows that the saccade latency depended approximately linearly on EV_F for FDR (black) and FAR (gray) data. The regression equation on raw data of the linear fit (solid line) was $y = 158$ ms $+ 2.48$ ms* x ($R = 0.183$, $P < 0.0001$) for FDR trials and $y = 139$ ms $+ 2.80$ ms* x ($R = 0.226$, $P < 0.0001$) for FAR controls. Similar to Fig. 8*B,* we subdivided our dataset into different ranges of the sensory parameter EV_F (vertical dotted lines in Fig. 8*C*) and plotted the corresponding latency histograms and double-recinormal fits in Fig. 8*D*. Figure 8*D* clearly demonstrates that the shift in mean saccade latency with higher EV_F values was due to the increased relative importance of the long-latency mode. This effect was underlined by the fact that the location of the long-latency mode's maximum was slightly shifted toward larger values with increasing EV_F.

As a conclusion, our results concerning the influence of the sensory parameters on the first saccade latency revealed two distinct effects. First, large eye velocity (EV_F) and small position error (PE_F) increased the relative importance of the long-latency mode with respect to the shorter-latency mode. Second, we observed a shift of the long-latency mode toward larger values when eye velocity (EV_F) was high and position error (PE_F) was small. Performing the same analysis using both sensory parameters in combination increased this effect yielding to an absence of the first latency mode for combined small PE_F and large EV_F, whereas long-latency saccades disappeared for a combination of large PE_F and small EV_F (data not shown).

We would like to emphasize that the hemifield difference between FP and FF flashes (see Fig. 7) was still present in all analyses concerning the sensory parameters in Fig. 8 (data not shown) and significant (*t*-test, $P < 0.01$). We explicitly tested that our results were not an artifact of some combined parameter effect or even due to slight asymmetries of our dataset. As a result, we report here that both the FP/FF latency difference and the latency dependence on the sensory parameters at the time of the flash were consistent and unbiased effects. Furthermore, even though there were differences in the individual latency histograms when computed for each subject separately, all the above-described latency effects were present for all subjects.

Time course of orientation

After the first orientation saccade toward the memorized position of the flash, we usually observed one or more corrective saccades that brought the eye closer to the spatial position of the flash. This was the case irrespectively of whether the first saccade was triggered with short or longer latency (see typical trials in Fig. 2). The way in which the system reaches the memorized goal determined by a flash during smooth eye movements has previously been investigated for horizontal eye movements by Blohm et al. (2003), who showed that the saccadic system was able to compensate for smooth anticipatory eye movements with a certain delay. Here, we observed qualitatively the same behavior, i.e., some time was needed for the smooth eye displacement to be taken into account (see 1st saccade programming results).

As already mentioned, the purpose of secondary "catch-up" saccades was to compensate for the remaining uncorrected smooth eye displacement. Thus to analyze in more details the
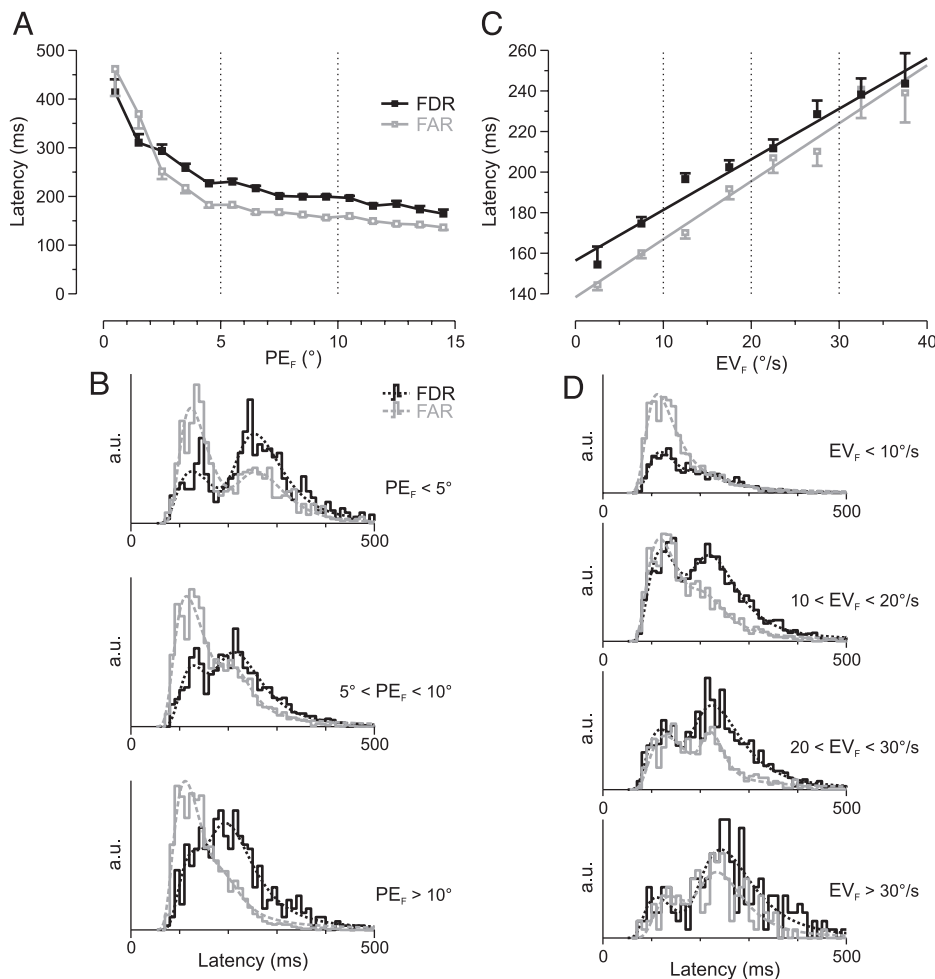
FIG. 8. Sensory parameters influence saccade latency. *A*: 1st saccade latency as a function of the distance PE_F between the flash and the eyes. black box, FDR trials; white box, FAR controls. Squares and whiskers indicate mean and SE ($n = 27–493$). Separations (vertical dotted lines) of data for values of PE_F refer to histograms in *B*. *B*: latency histograms (solid lines) and double-recinormal fits (dotted lines) for 3 subsets of data with respect to the range of PE_F values and for FDR (black) and FAR (gray) trials separately. *C*: 1st saccade latency dependence on the eye velocity EV_F at the moment of the flash. Black data are FDR trials; gray data stand for FAR controls. Squares and whiskers indicate mean and SE ($n = 49$ to 1225). The solid line represents the linear fit on raw data. Vertical separations (dotted lines) refer to panel D. *D*: latency histograms (solid lines) and double-recinormal fits (dotted lines) for different subsets of the data with respect to different ranges of EV_F values and for FDR (black) and FAR (gray) trials separately.

consequences of the secondary saccades, we computed the compensation index (CI) of *Eq. 1* for up to four saccades after the flash presentation and for different saccade latencies (measured with respect to the flash onset). The results of this analysis are shown in Fig. 9 for both FDR trials (black) and FAR controls (gray). Note that there is an initial increase of the compensation index only for the first saccade (shown in more details for FDR trials on Fig. 4). For all successive saccades, this index is approximately constant. It should also been noted that the three secondary catch-up saccades did not completely compensate for the smooth eye displacement.

Finally, we analyzed the contribution of the total smooth eye displacement SED_{end} to the final position error PE_{end}, taking into account that there might also be a residual contribution of the retinal position error PE_F (measured at the moment of the flash) to PE_{end}. Table 1 indicates the ranges of these parameters. The second-order regression for PE_{end} with the variables PE_F and SED_{end} provided the following results for the horizontal and vertical components of FDR trials

$$PE_{end,X} = (-.121 \pm .037) + (.013 \pm .006)*PE_{F,X}$$

$$- (.465 \pm .009)*SED_{end,X} \quad (R = 0.622, P < 0.001) \quad (3)$$

$$PE_{end,Y} = (-.703 \pm .035) + (.091 \pm .005)*PE_{F,Y}$$

$$- (.429 \pm .010)*SED_{end,Y} \quad (R = 0.559, P < 0.001) \quad (4)$$

As a consequence, the saccadic system compensated differently for the retinal error information (PE_F) and the extraretinal

information about the total smooth eye displacement (SED_{end}). The compensation for the retinal flash position error PE_F was 98.7% (subject variability: 80.1–121.1%) horizontally (*Eq. 3*) and 90.9% (subject variability: 71.3–106.5%) vertically (*Eq. 4*) at the end of the orientation process. Note that this was a better performance than after the first orientation saccade (see Fig. 5 and Table 1). Furthermore, the final compensation for the smooth eye displacement (extraretinal signal) was 53.4% (subject variability: 36.5–87.2%) horizontally (*Eq. 3*) and 57.1% (subject variability: 45.0–73.3%) vertically (*Eq. 4*). Thus *Eqs. 3* and *4* provided a measure of the accuracy of the orientation process that compensated almost perfectly for PE_F and accounted for ~55% of SED (see compensation index, Fig. 9, *B–D*). It is worth noting that we computed the compensation index only if a saccade took place, whereas the regression analysis of *Eqs. 3* and *4* included all trials irrespectively of the number of executed saccades. Our values were lower than the previously reported 70% overall SED compensation in the case of target localization during smooth anticipatory eye movements (Blohm et al. 2003). The regression analysis for FAR control provided results similar to the test trials (data not shown).

DISCUSSION

The programming of memory-guided saccades during smooth eye movements reflects the performance of the system in maintaining space constancy. To investigate this mecha-
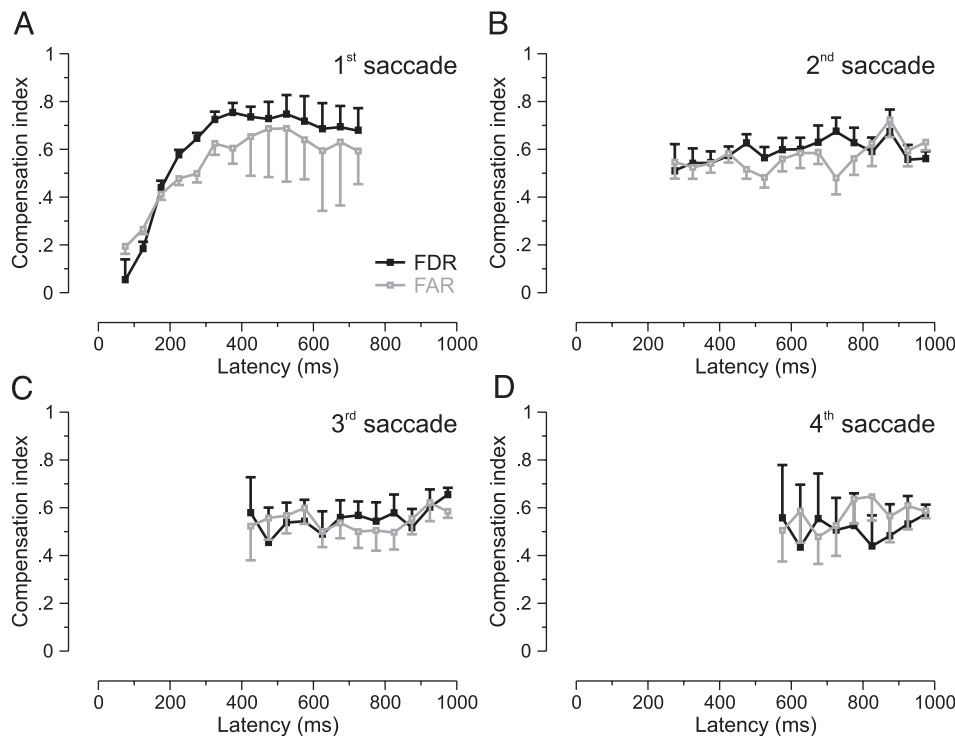
FIG. 9. Consequences of the secondary "catch-up" saccades. Compensation indices as a function of saccade latency with respect to the onset of the flash. Black data are FDR trials; gray data stand for FAR controls. Squares and whiskers indicate mean and SE. *A*: compensation index for the 1st saccade (for FDR: the same data as in Fig. 4*B* but with larger bin sizes). *B*: compensation index of the 2nd saccade ($n = 3{,}378$). *C*: effect of the 3rd saccade on the compensation index ($n = 1{,}743$). *D*: compensation index for the 4th saccade ($n = 707$).

nism, we presented a briefly flashed target during smooth-pursuit eye movements and analyzed the characteristics of the first saccade. As a result, we found that short-latency saccades were better correlated with retinal error than with spatial error, whereas the opposite was the case for longer-latency saccades. The saccadic system approximately needed 175 ms before extraretinal information about the smooth eye displacement could be used in saccade programming. This behavior was also reflected in the latency distribution, where we found two distinct modes—a short-latency and a longer-latency mode—separated at ~175 ms. We interpret our results as evidence for the existence of two different neural processes for saccade programming: one fast but inaccurate and the other slower but spatially more accurate.

Saccadic reaction times

We observed a bimodal distribution of saccade latencies in our test trials and in both control data sets. Similar distributions have been observed previously during saccadic "gap" and "overlap" paradigms (Fischer et al. 1993, 1997; Reulen 1984a,b; Saslow 1967). To quantify our bimodal first saccade latency distribution, we fitted a double-recinormal distribution to our data. We used this particular distribution because it described very well our data with only very few parameters. However, as already mentioned in RESULTS, this procedure is theoretically equivalent to the hypothesis of two distinct saccade trigger mechanisms of the LATER type (Carpenter and Williams 1995; Reddi and Carpenter 2000; Reddi et al. 2003) that work in parallel and do not interact. Although we cannot prove that such a mechanism exists, it is supported by our data because all latency distributions agree with the hypothesis of two parallel decision processes. As we demonstrated in Fig. 8, the system's decision between both processes depended on the set of sensory parameters (distance of the target from the fovea

and eye velocity) at the moment of the flash. Indeed, the effect of position error on saccade latency has previously been described (Bell et al. 2000; Clark 1999; Hodgson 2002; Kalesnykas and Hallett 1994), and it makes sense that the system needs more time for small position errors to decide whether it is necessary to trigger a saccade. We did also observe this effect for our fixation control trials (data not shown) and our "flash after ramp" (FAR) controls (Fig. 8, *A* and *B*), i.e., the longer latency mode essentially resulted from flashes presented at small position errors. The influence of eye velocity on saccade latency however was—to our knowledge—a novel finding. Because for large smooth-pursuit velocities the error after a short latency saccade (retinally programmed) would be big, the system might prefer to wait longer for extraretinal smooth eye displacement information to become available (see Fig. 4). This "waiting strategy" allowed the system to perform spatially more accurate initial saccades. Thus the relationship between saccade latency and eye velocity described the system's tradeoff between speed and accuracy.

We showed in Fig. 7 that the mean saccadic latency is shorter for flashes presented in the direction of the movement (foveopetal) than for flashed targets presented in the opposite direction (foveofugal). This is compatible with previous findings for horizontal catch-up saccades during smooth pursuit of continuously visible targets (Kanai et al. 2003; Tanaka et al. 1998). In these studies, saccades in the same direction as smooth pursuit had shorter latencies than saccades in the opposite direction. In addition, this latency asymmetry was also present in our FAR control trials where no visible target was present. Kanai et al. (2003) hypothesized that this difference in latencies is due to the inhibition of saccades to previously attended positions during smooth pursuit, a particular instantiation of the "inhibition of return" (IOR) effect (see Klein 2000 for a review). At first sight, our data seemed to be compatible with such a hypothesis. However, our 2-D para-

digm allowed us for the first time to show that this latency asymmetry is a hemifield effect and not related to a "focus of attention," as IOR would predict (Maylor and Hockey 1985; Posner et al. 1985). Nevertheless, our results would be compatible with an attentional facilitation in the direction of the movement, if this facilitation was extended to the whole foveopetal hemifield and was not restricted to a focus of attention (Maylor and Hockey 1985; Posner et al. 1985). The purpose of such a hemifield bias could simply be to facilitate movement in the direction of heading.

Saccades compensate for self-motion

The analysis of the saccade latencies revealed a bimodal distribution. The presence of these two different saccade trigger processes was also reflected in the way saccades were programmed. We showed indeed that saccades with short latencies (<175 ms) were programmed using the only available retinal information, i.e., position error at the moment of the flash. This is in accordance with previous studies (Gellman and Fletcher 1992; McKenzie and Lisberger 1986) and contrasts with the situation where continuous visual feedback is present. In the latter condition, orientation saccades to the object's spatial location are programmed using two types of retinal information, i.e., position error and the relative velocity of the eyes with respect to the target (retinal slip) (de Brouwer et al. 2001, 2002; Gellman and Carl 1991; Keller and Johnsen 1990; Ron et al. 1989). However, although retinal information about smooth self-motion was absent in our experiment, longer-latency (>175 ms) saccades used a different programming mechanism that included extraretinal information about the smooth eye displacement in addition to the retinal position error.

All previous studies support our results. McKenzie and Lisberger (1986) reported that short-latency memory-guided saccades during pursuit eye movements were retinally coded. However, one monkey showed a bias of the suggested retinally saccade coding toward a more accurate spatial amplitude programming, that the authors attributed to the monkey's participation in previous smooth tracking experiments. However, this monkey also had particularly long mean saccade reaction times compared with the two other monkeys. We believe that our results explain the third monkey's bias toward the spatial coding hypothesis simply as a consequence of longer latencies. Other studies showed that when memory-guided saccades were executed after a delay period, smooth self-motion was compensated and saccades were spatially accurate (Baker et al. 2003; Herter and Guitton 1998; Ohtsuka 1994; Schlag et al. 1990; Zivotofsky et al. 1996), which is fully compatible with our results. Thus we described here the missing piece in the puzzle of self-motion integration, i.e., the temporal transition between the retinal and spatial representation of the visual world in the oculomotor system.

Initially, McKenzie and Lisberger (1986) used a paradigm similar to our FAR controls in an attempt to differentiate between two different types of saccade models, i.e., position and displacement models. Position models (Robinson 1975; Van Gisbergen et al. 1981) assume that the signal of desired eye position is compared with a signal of the current position of the eye in the orbit to generate a motor command. In contrast, displacement models (Jürgens et al. 1981) assume that

a desired displacement—rather than a desired position—signal is used to drive the saccadic eye movement. During a saccade, this desired displacement is compared with an internal representation of the movement already executed to produce the movement command. McKenzie and Lisberger (1986) trained monkeys to make saccades to flashes memorized during smooth eye movements to test the position versus the displacement model. The monkeys made saccades to the retinal position of the flash (Gellman and Fletcher 1992; McKenzie and Lisberger 1986), which validated the displacement model because the position model would have predicted a spatially accurate eye movement. However, our data reported here as well as previous findings (Baker et al. 2003; Herter and Guitton 1998; Ohtsuka 1994; Schlag et al. 1990; Zivotofsky et al. 1996) support the idea that if more time is available to the system before the onset of the orienting eye movement, saccades can be spatially accurate. This implies that there must be an additional mechanism available to perform this retinal to spatial transformation, but apparently, such a mechanism takes some time and is not implemented at the level of the saccadic displacement integrator. Hereafter, we will propose a neural mechanism that could account for all the data.

Hypothesized underlying neural mechanisms

We believe that our results reflect the presence of two different neural mechanisms for retinal and extraretinal information processes characterized by different processing times. In this section, we will shortly lay out one hypothesis of the underlying neural pathways that might be involved in the integration of smooth-pursuit eye movements and the orientation to memorized targets.

The major forebrain and midbrain structures involved in the programming and/or control of saccades are the posterior parietal cortex (PPC), the frontal eye fields (FEFs), the dorsolateral prefrontal cortex (DLPC), the basal ganglia, the cerebellum (CB), and the superior colliculus (SC) (see for a review Krauzlis and Stone 1999; Leigh and Zee 1999). It is generally accepted that SC is essential to generate short-latency saccades (Fischer and Ramsperger 1986; Munoz and Wurtz 1992; Schiller et al. 1987). Indeed, Schiller at al. (1987) showed a lateralized absence of short-latency saccades in monkeys after unilateral SC ablation, whereas longer-latency saccades were still present. This was not the case for FEF ablation, which had no long-term effect on saccade latencies (Schiller et al. 1987). Therefore we propose that the short latency saccades we reported here were essentially mediated by a fast "striatal-collicular pathway" (Leigh and Zee 1999). This contrasts with longer-latency saccades that are known to involve most of the above-cited structures including PPC.

It has previously been suggested (Duhamel et al. 1992; Heide et al. 1995), that PPC plays a key role to account for extraretinal signals (Tobler et al. 2001) when keeping track of self-motion to ensure space constancy. Indeed, the lateral intraparietal area (LIP) and area 7a in PPC receive information about upcoming saccades to update the spatial representation of visual stimuli (Andersen et al. 1985; Bremmer et al. 1997). Therefore we propose that the memorized flash position in our experiment is stored in PPC (Barash et al. 1991; Paré and Wurtz 1997; Pierrot-Deseilligny et al. 1991) and updated by smooth eye displacement information when it becomes avail-

able. The smooth eye displacement signal could result from an integration process of the smooth motor command (Blohm et al. 2003), which might take some time. Such a process could involve parts of the cerebellum—highly involved in generating smooth pursuit (Lisberger et al. 1987; Pola and Wyatt 1991)—and smooth eye displacement information could be projected either directly or via the thalamus (Clower et al. 2001) to PPC to update the spatial representation of the flash. This would explain why in our data smooth eye displacement information took ~175 ms to become available to the saccadic system. According to this view, the classical saccade pathway would be responsible for retinally coded saccades. An additional feedback pathway for the integration of smooth-pursuit eye movements could then be added to these classical structures to ensure space constancy during smooth eye movements. Our observation that smooth eye movement integration was characterized by a delay (~175 ms) implies that the system only compensates for the smooth eye displacement that has already been integrated. This might explain why the compensation mechanism is not an all-or-none process. However, we cannot exclude a possible role of proprioception (Steinbach 2000) for the spatial orientation toward the flash, although proprioception is thought not to be a predominant source for spatial localization (Weir 2000) and the control of eye movements in general (Lewis et al. 2001).

We suggest using our original 2-D paradigm in neural recording studies to identify the neural correlates underlying the monitoring of smooth pursuit. The presence of two separate control modes for memory-guided saccades during smooth eye movements could provide a new testing bench to investigate the neural processes of smooth motion integration. More generally, our results provide a new path to investigate the interaction between smooth pursuit and saccadic systems.

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