

# Predicting 2D Target Velocity Cannot Help 2D Motion Integration for Smooth Pursuit Initiation

Anna Montagnini,<sup>1</sup> Miriam Spering,<sup>2</sup> and Guillaume S. Masson<sup>1</sup>

<sup>1</sup>Team Dynamic de la Perception Visuelle et de l'Action (DyVA), Institut de Neurosciences Cognitives de la Méditerranée, Centre National de la Recherche Scientifique, Aix-Marseille Université, Marseille, France; and <sup>2</sup>Department of Psychology, Justus-Liebig-University, Giessen, Germany

Submitted 26 May 2006; accepted in final form 18 August 2006

**Montagnini, Anna, Miriam Spering, and Guillaume S. Masson.** Predicting 2D target velocity cannot help 2D motion integration for smooth pursuit initiation. *J Neurophysiol* 96: 3545–3550, 2006. First published August 23, 2006; doi:10.1152/jn.00563.2006. Smooth pursuit eye movements reflect the temporal dynamics of bidimensional (2D) visual motion integration. When tracking a single, tilted line, initial pursuit direction is biased toward unidimensional (1D) edge motion signals, which are orthogonal to the line orientation. Over 200 ms, tracking direction is slowly corrected to finally match the 2D object motion during steady-state pursuit. We now show that repetition of line orientation and/or motion direction does not eliminate the transient tracking direction error nor change the time course of pursuit correction. Nonetheless, multiple successive presentations of a single orientation/direction condition elicit robust anticipatory pursuit eye movements that always go in the 2D object motion direction not the 1D edge motion direction. These results demonstrate that predictive signals about target motion cannot be used for an efficient integration of ambiguous velocity signals at pursuit initiation.

## INTRODUCTION

Motion signals from elongated unidimensional (1D) edges are ambiguous and therefore must be integrated with other sources of information to reconstruct the actual two-dimensional (2D) trajectory of the object. Psychophysical (Lorenceanu and Shiffrar 1992) and physiological (Pack and Born 2001) studies have demonstrated that local 2D feature cues (e.g., line endings) provide reliable motion signals that can be used to solve the aperture problem. The dynamics of such neural computation is reflected in the time course of smooth pursuit eye movements. Both humans and monkeys can track simple line-drawing objects like tilted lines or diamonds. The initial pursuit direction is biased toward the direction of 1D motion signals (or their average), orthogonal to the edge(s), eventually resulting in a direction error with respect to the global, 2D direction of motion. In the latter case, the tracking direction starts to be slowly corrected before the closing of the visuo-oculomotor loop, i.e., before any negative feedback signal becomes available (Lisberger and Westbrook 1985), so that ~150 ms after pursuit onset, pursuit matches the actual 2D object trajectory (Born et al. 2006; Masson and Stone 2002; Wallace et al. 2005).

A striking aspect of the initial bias for pursuit is that it is highly reproducible and seems to be immune to cognitive

influence such as shape cueing (Wallace et al. 2005). However, when the object is transiently blanked during steady-state tracking, its reappearance does not elicit the transient error observed after first target appearance (Masson and Stone 2002). The prominence of a 2D predictive signal in driving smooth pursuit after target reappearance could explain the lack of a significant tracking error because of a lower internal gain of the visuo-motor transmission (Churchland and Lisberger 2002). An alternative explanation is that 2D predictive signals are used to solve the aperture problem. Velocity and direction predictability has proven to powerfully drive anticipatory smooth pursuit (Boman and Hotson 1988; Heinen et al. 2005; Kowler and Steinman 1979). Herein, we measured tracking direction during the early phase of smooth pursuit of a single oriented line while varying motion predictability. We first probed the ability of the visual system to predict and efficiently process incoming motion signals by using predictive information about target orientation alone, while target motion direction was randomized along the horizontal axis to avoid anticipatory pursuit. Second, by using fully predictable target orientation and motion direction, we investigated the interactions between anticipatory and visually driven pursuit to measure the relative role of visual and predictive signals related to the 2D target velocity for pursuit initiation. We reasoned that if predictive information was efficiently integrated with visual processing of local and global motion signals, the resulting tracking error should be reduced or even eliminated.

## METHODS

Eye movements were recorded from three observers (1 naïve) using methods described in detail elsewhere (Wallace et al. 2005). All procedures followed the Centre National de la Recherche Scientifique (CNRS) guidelines for the use of human subjects. Briefly, a PC running the REX package controlled stimulus presentation and data acquisition. Stimuli were generated with a Sgi Fuel workstation and back-projected onto a large translucent screen (80 × 60°) using a BARCO 908s video-projector (1,280 × 1,024 pixels, 76 Hz). The position of the right eye was sampled at 1 kHz using the search-coil technique (Collewijn et al. 1975), low-pass filtered (DC–130Hz) and digitized with 16-bit resolution. Eye-position data were linearized off-line and smoothed using a spline algorithm (Busetini et al. 1991) before differentiation to obtain eye velocity profiles.

Stimuli were always a single line, either vertical or tilted ±45° relative to horizontal, (luminance: 60 cd/m<sup>2</sup>, length: 17°, tilted line, or 12°, vertical line), and moving rightward or leftward at 10°/s (5 or

Address for reprint requests and other correspondence: G. S. Masson, Team DyVA, Institut de Neurosciences Cognitives de la Méditerranée, UMR6193 CNRS, 31 Chemin Joseph Aiguier, 13402 Marseille, France (E-mail Guillaume.Masson@incm.cnrs-mrs.fr).

The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

20°/s in the speed-control experiment) over a black ( $<0.1 \text{ cd/m}^2$ ) background for 500 ms. With a single line, two types of motion signals are generated: a velocity vector normal to the 1D edge orientation (1D signal) and two velocity vectors at the line ends (2D signals). With vertical lines, all vectors describe the actual 2D trajectory of the line target. However, with tilted lines, 2D line-ends motion vectors still correspond to the line motion direction but 1D motion signals are tilted  $\pm 45^\circ$  relative to the actual 2D trajectory (Fig. 1A, top).

Observers had their head stabilized by chin and forehead rests. Each trial started with presentation of a small fixation point (laser light-emitting diode,  $0.1^\circ$ ). Subjects were required to fixate it for  $300 \pm 150$  ms, within a  $1 \times 1^\circ$  window. The fixation point was then extinguished and, after a 300-ms gap, the moving line was presented. Observers were instructed to track its center and trials were aborted if eye position did not stay within  $2^\circ$  of the object center. The gap duration was chosen such as to maximize anticipatory pursuit (Boman and Hotson 1988) when motion direction was fully predictable. We define anticipatory pursuit as a nonzero mean eye velocity computed over a 40-ms time window centered at the time of target motion onset (Missal and Heinen 2004). Visually driven pursuit responses followed target onset with an average latency of  $\sim 100\text{--}120$  ms. Early open-loop pursuit responses were estimated by computing the average eye velocity over a second 40-ms time window, centered at 160 ms after target onset. The late open-loop response was also estimated over a 40-ms window centered at 200 ms after target onset (Wallace et al. 2005). Moreover, horizontal and vertical eye accelerations were computed during the open-loop phases by differentiating eye velocities. Such analyses were performed for both horizontal and vertical eye movements.

We used a velocity threshold (20°/s for a target speed of 10°/s) criterion to detect saccades. To avoid saccade-related effects in our pursuit analysis, we cut out eye-position data during the whole duration of the detected saccade. To be conservative, we also excluded from analysis the 25 ms before and after saccade onset and offset, respectively. In addition we visually inspected individual position and velocity traces to check the saccade detection routine. We

then used the desaccaded eye-movement data of all clean trials to compute mean position and velocity profiles.

We collected 150 trials per stimulus condition (line orientation and motion direction) and observer over several days. In the first experiment, target orientation and motion direction were fully randomized to measure direction biases in the initial pursuit of single bars. Then, in experiments 2 and 3, either line orientation ( $+45^\circ$  or  $-45^\circ$ ) alone or both orientation and line motion direction (fully predictable condition) were kept constant across experimental blocks when testing the effect of target motion/orientation predictability. The order of presentation of the blocks was pseudorandomized across subjects.

RESULTS

We ran three experiments where predictability of either line orientation or motion direction or both were manipulated to see how they influence the dynamics of 2D motion integration for pursuit initiation.

Smooth pursuit initiation of a single line: effects of line orientation

When fully randomizing both line orientation (vertical,  $\pm 45^\circ$ ) and motion direction (L/R), an initial tracking direction error was consistently found with tilted lines when compared with vertical lines: A nonzero vertical component was present between 100 and 300 ms after motion onset, the direction of which was consistent with edge motion (Fig. 1A). This finding replicates and generalizes our results previously obtained in human subjects (Masson and Stone 2002; Wallace et al. 2005) with diamond-shaped line-drawings. Small transient tracking drifts, not related to stimulus orientation/direction and subject-specific, were observed in two subjects during the gap period, either on the vertical component (*subject AM*) or on both horizontal and vertical velocities (*subject AR*, see Fig. 1A, bottom). To minimize spurious effects on our measures of the

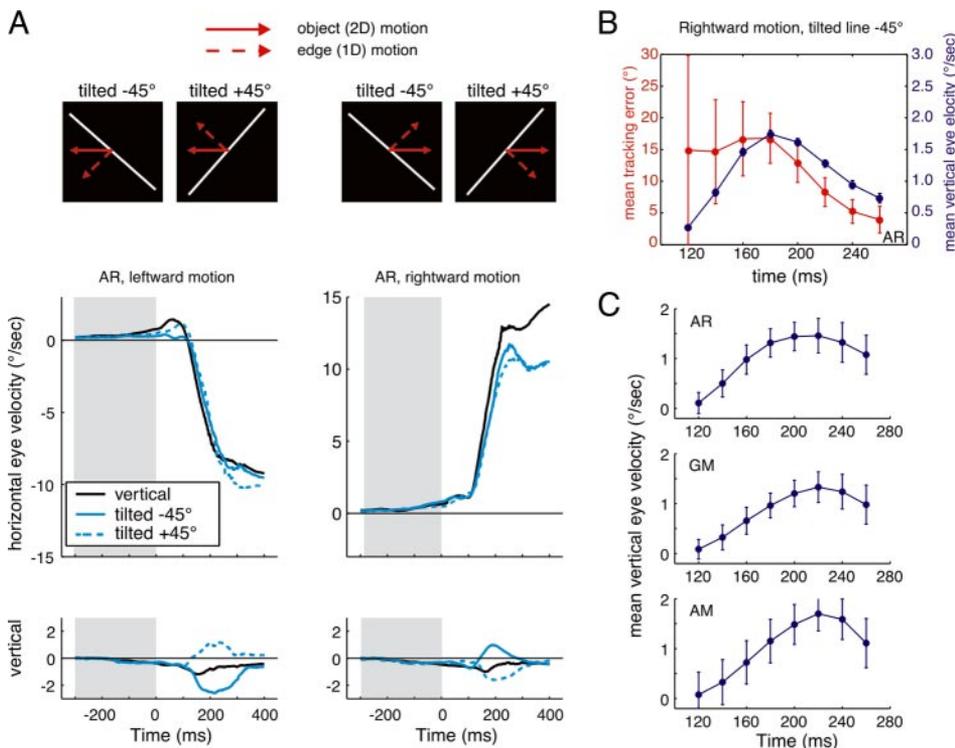


FIG. 1. Pursuit initiation of a nonpredictable line motion. A, top: cartoon of stimuli. Tilted lines elicited a transient component in the direction orthogonal to the line orientation (dotted arrows). Bottom: raw (noncorrected for individual drifts) horizontal and vertical velocity profiles of smooth pursuit responses to either vertical or tilted ( $\pm 45^\circ$ ) lines (*subject AR*). The shaded region corresponds to the gap between fixation offset and motion onset. B: angle between pursuit and bidimensional (2D) object motion directions (tracking error) and the vertical velocity are displayed against time. The mean  $\pm$  SE (circular mean and circular SE for the tracking error) across trials (40-ms time bins), are plotted for 1 representative subject and stimulus condition. C: condition-averaged vertical velocity (with standard errors) during the transient vertical excursion for all 3 subjects.

vertical bias, we therefore subtracted vertical eye-velocity measurements obtained with vertical lines from those obtained with oblique lines. Thus for all subsequent analyses, vertical eye velocity reflects the initial tracking bias related to target orientation only. To quantify this initial bias, we also measured the tracking error, i.e., the angular difference between eye tracking and object motion directions. In Fig. 1*B*, time course of tracking error and vertical eye velocity are plotted, in 40-ms bins, from 120–260 ms after motion onset. The two measures are substantially equivalent for the purpose of quantifying the initial bias in ocular pursuit. The main interest of using vertical eye velocity as a direction error index is that such measure is independent of the horizontal eye velocity that will be largely affected by 2D motion predictability. In addition, estimates of the tracking error dispersion (based on circular statistics) give rise to very large error bars for the first data-points (see Fig. 1*B*) due to the fact that both horizontal and vertical eye-velocity components are close to zero, making direction angle computations very noisy. These effects are avoided when using vertical eye velocity only. Across subjects and conditions, the transient vertical component peaked  $\sim 200$  ms after target motion onset, on average at  $1.4 \pm 0.8^\circ/\text{s}$  (Fig. 1*C*), whereas maximum average deviation of eye tracking direction was  $17 \pm 2.5^\circ$ .

Both with vertical and with tilted moving lines, frequent catch-up saccades were observed. To analyze saccades on a large sample we compiled data from both *experiments 1* and *2*, using conditions with randomized motion direction but fixed line orientation. On average across subjects, a saccade was detected in 91% of trials for vertical lines and 72% for tilted lines (80 and 50% of the saccades starting within 220 ms from motion onset for the 2 types of stimulus, respectively). Mean latency was of  $166 \pm 11$  ms for vertical lines and  $210 \pm 8$  ms for tilted lines, a highly significant difference [1-tailed *t*-test,  $t(1,16) = -3.1, P < 0.005$ ]. Mean saccadic amplitude was not statistically different [ $t(1,16) = -0.5, P = 0.6$ ] depending on stimulus type ( $2.7 \pm 0.1$  and  $2.8 \pm 0.1^\circ$  for vertical and tilted lines, respectively).

Saccadic direction was prominently horizontal, but a vertical component was not negligible. The mean absolute deviation (in degrees) from the horizontal direction was significantly lower

[1-tailed *t*-test,  $t(1,16) = -3.1, P < 0.005$ ] for the vertical line ( $3.0 \pm 0.4^\circ$ ) than for the tilted ones ( $7.6 \pm 1.4^\circ$ ). Figure 2*A* shows the histograms of saccadic direction with respect to the horizontal direction, separately for the vertical and the two tilted lines and for one representative subject. A clustering of saccadic direction data is apparent depending on the line type. The peaks of the distributions corresponding to the  $\pm 45^\circ$  tilted lines is lower ( $\sim 10^\circ$ ) but qualitatively consistent with the maximum pursuit tracking error ( $\sim 15^\circ$ ). This suggests that catch-up saccades were at least partly programmed using a biased velocity information. To verify that the saccade cut-off procedure was not affecting our measures of pursuit direction, we compared, for the tilted stimuli only, the mean open-loop peak vertical velocity for trials with ( $1.38 \pm 0.17^\circ/\text{s}$ ) and without ( $1.37 \pm 0.16^\circ/\text{s}$ ) saccades. No significant difference was detected.

The vertical components of both catch-up saccades and initial pursuit produced a shift in the vertical eye-position, which remained uncorrected afterward. To analyze this shift in gaze relative to target position, Fig. 2*B* plots, for one representative subject and separately for trials with and without saccades, the mean eye-position at four different moments during tracking: motion onset, 200, 300, and 400 ms after motion onset. Notice that the 300- and 400-ms time bins corresponded to time immediately after the initial saccade and during steady-state pursuit, respectively. Initial vertical shift while tracking a tilted versus a vertical line were roughly similar between trials with or without saccades. A two-sample *t*-test confirmed that, across subjects, the mean global vertical displacement (i.e., the difference of vertical position between steady state and motion onset) was not different [ $t(1,16) = 0.8, P = 0.4$ ] when saccades were either made or not during pursuit initiation.

#### Repeated line orientation presentation: absence of visual motion prediction

Next, we blocked stimulus presentation so that bar orientation was the same across trials, whereas motion direction was still randomized. Thus 2D motion integration became highly predictable because only two horizontal motion directions

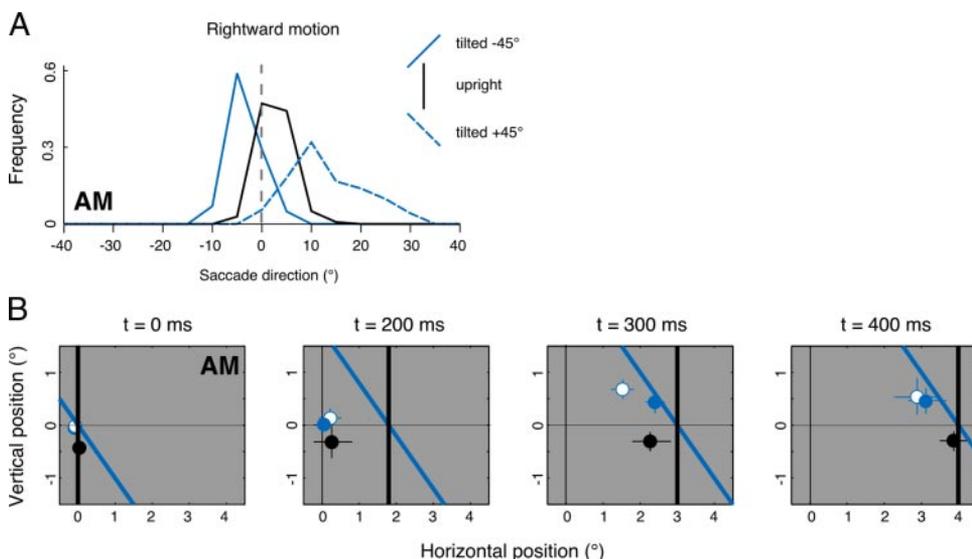


FIG. 2. Saccades and eye-position displacement during line tracking. *A*: saccade direction histograms are plotted, for a representative subject (*AM*) for rightward target motion and 3 stimulus types (upright or  $\pm 45^\circ$  lines). The direction is expressed as angle with respect to the horizontal meridian and positive values correspond to an upward deviation. *B*: mean eye position and SD (in *x-y* coordinates) is plotted for the same subject at 4 epochs during a 500-ms trial. Mean data are plotted separately for trials with saccades were present (open symbols) or absent (closed symbols) in the tilted line condition (cyan). Saccade-free trials with upright lines were nearly absent and therefore are not plotted herein. The successive positions of the upright and tilted bars are also indicated.

(L/R) were possible. If such predictability was efficiently used to help the early integration of motion cues to drive pursuit, we could have expected a reduction in the initial bias over repeated stimulus presentations. Despite the fact that we tested the subjects with long experimental runs (300 trials for a given line orientation and 2 possible directions), we did not observe any learning effect: Velocity profiles looked very similar between the first and the last 40 trials of a sequence (Fig. 3A). This is further illustrated in Fig. 3B where the mean vertical velocity during late open-loop period (time bin: 180–220 ms) is plotted over five consecutive blocks of 30 trials. Clearly, there was no monotonic reduction in vertical peak velocity. We found only 2 cases of 12 (i.e., 3 subjects  $\times$  4 stimulus conditions) where absolute mean vertical velocity was significantly lower in the last than in the first 30 trials (1-tailed *t*-test,  $P < 0.05$ ).

*Interactions between anticipatory and visually driven smooth eye movements*

In the last experiment, we repeatedly presented a single bar orientation/motion direction over 150 trials so that both target orientation and motion direction became highly predictable. We refer to this condition as the 100% condition and compare it to the randomized (50%) direction condition that was described in the previous subsection. As shown in Fig. 4A, strong anticipatory smooth pursuit responses were observed in all three subjects. Anticipatory smooth pursuit started  $\sim$ 100–150 ms after fixation offset (i.e., 200–150 ms before motion onset) and was almost purely horizontal. Mean anticipatory horizontal velocity ( $\pm$ SD) was  $0.04 \pm 0.6^\circ/s$  in the 50% condition and  $1.72 \pm 0.5^\circ/s$  in the 100% condition, a highly significant difference [3-way ANOVA (subject  $\times$  stimulus-type  $\times$  probability),  $F(1,22) = 174.2$ ,  $P < 0.0001$ ]. Only very weak vertical anticipation was seen when comparing between the two probability conditions (Fig. 4B). Across subjects and motion directions, mean absolute vertical eye velocities during

the anticipatory phase were of  $0.26 \pm 0.23$  and  $0.004 \pm 0.15^\circ/s$  for 100 and 50% conditions, respectively [ $F(1,22) = 20.6$ ,  $P < 0.01$ ]. At  $\sim$ 100 ms after line-motion onset, that is at typical pursuit latency, the horizontal velocity underwent a dramatic increase. At the same time, the strong transient vertical bias typical of tilted lines motion was observed (Fig. 4A). This vertical component was almost indistinguishable between 50 and 100% conditions as shown in Fig. 4B. Mean absolute vertical eye velocity was  $1.47 \pm 0.8$  and  $1.26 \pm 0.6^\circ/s$ , respectively, and the difference between the two conditions was not significant [ $F(1,22) = 1.21$ ,  $P = 0.33$ ]. Post hoc analysis showed that only in two stimulus conditions for *subject AR* and one for *subject AM* the vertical bias was significantly reduced in the 100% with respect to the 50% condition. Figure 4B shows that mean absolute horizontal eye velocity during open-loop response was much smaller in the 50% than in the 100% condition [mean:  $4.8 \pm 2.3$  and  $7.8 \pm 1.5^\circ/s$ , respectively,  $F(1,22) = 149.2$ ,  $P < 0.0001$ ]. Moreover, like in previous experiments, no systematic effect of learning was observed along the trial sequence (Fig. 4E).

To test the robustness of the present findings, we ran a control experiment on the same three subjects, with two additional stimulus speeds, 5 and  $20^\circ/s$ . Only one type of line tilt ( $-45^\circ$ ) was presented and compared with the upright line for both 50 and 100% conditions. We found a roughly monotonic increase of tracking bias with target speed (confirming our previous results, described in Wallace et al. 2005). This was true for both 50 and 100% conditions, strengthening our initial finding of a lack of effect of repetitions. Anticipatory horizontal velocity increased with target speed, as previously reported (Heinen et al. 2005; Kao and Morrow 1994).

To further describe visually driven pursuit initiation, we plotted mean acceleration profiles for all three subjects (Fig. 4C). In the 100% condition, horizontal eye acceleration (blue curves) increased during anticipatory tracking. At pursuit la-

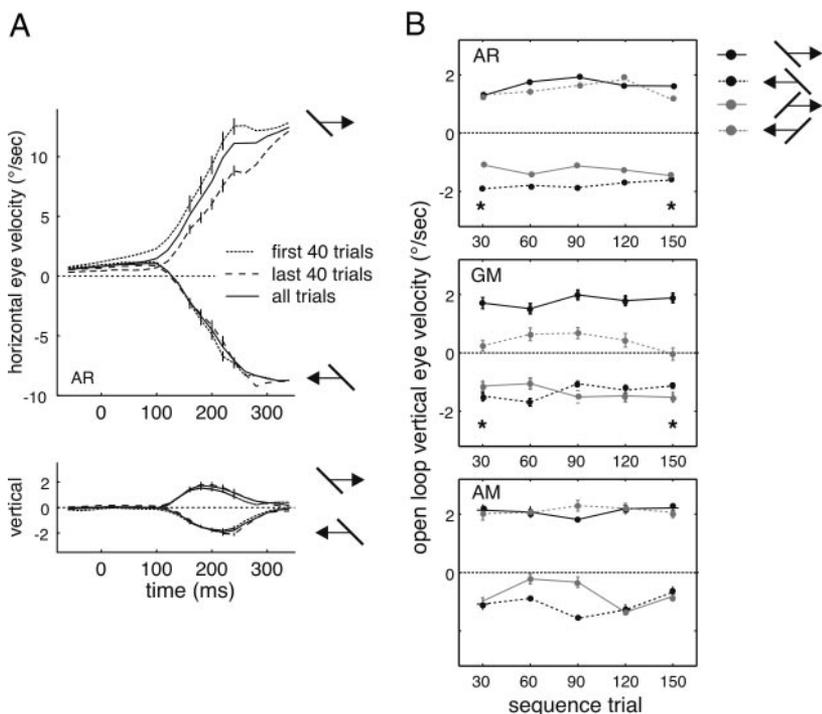


FIG. 3. Lack of visuomotor learning for pursuit of a moving bar with predictable orientation. *A*: horizontal and vertical velocity traces for 1 naïve subject. The grand average profiles are plotted together with the mean traces corresponding to the 1st and last 40 trials of a block. *B*: mean  $\pm$  SE late open-loop vertical velocity is plotted for 5 consecutive 30-trials blocks along the experimental sequence, for all subjects and conditions. Two asterisks are plotted for those conditions (2 of 12) for which the vertical velocity was significantly lower (tailed *t*-test,  $P < 0.05$ ) in the last than in the first sequence bin.

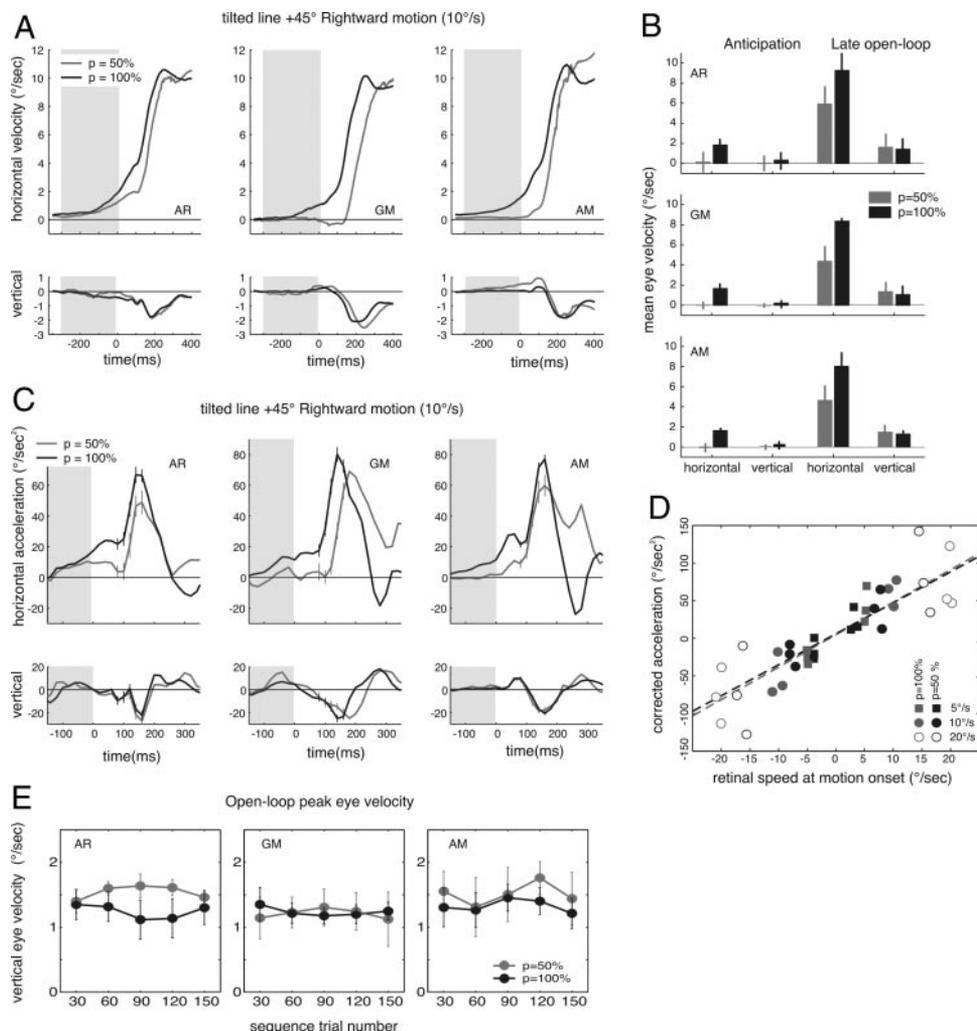


FIG. 4. Anticipatory and visually driven pursuit for a fully predictable line orientation/motion. *A*: examples of horizontal and vertical velocity traces for all 3 subjects for a +45° tilted line moving rightward. Conditions 50 and 100% are plotted as grey and black curves, respectively. Note that for *subject AR*, a remarkable horizontal anticipatory component seems to be present also in the 50% case (*top left*). The same component was present for leftward moving stimuli as well, implying that this effect was an idiosyncratic drift rather than a true anticipation. *B*: condition-averaged horizontal and vertical eye velocity ( $\pm$ SD) for both probability conditions, when measured during 2 40-ms time windows centered at *time 0* (anticipatory phase) and 100 ms after pursuit onset (late open-loop phase). *C*: horizontal and vertical acceleration profiles for all 3 subjects in the same stimulus condition as in the preceding text. *D*: individual mean peak acceleration (corrected for the anticipatory acceleration), evaluated between 140 and 180 ms after motion onset, plotted against retinal speed at target motion onset, for 1 particular orientation (−45°) and both directions. Data points corresponding to 50 and 100% conditions are plotted in grey and black, respectively, whereas different symbols are used for each target speeds. The dashed lines represent the best-fit linear regressions for the 50 and 100% conditions. *E*: mean  $\pm$  SD late open-loop absolute vertical velocity, collapsed across stimulus conditions, is plotted for 5 consecutive 30-trials blocks along the experimental sequence for each subject and each predictability level.

tency, a second brisk acceleration of the eye was seen as found previously (Kao and Morrow 1994). The amplitude of this visually driven acceleration was similar between the 2 conditions for both horizontal and vertical domains. The larger peak of horizontal acceleration in the 100% condition can be explained by the nonzero anticipatory acceleration. We computed a corrected measure of the acceleration peak by subtracting the mean anticipatory eye acceleration over the [0,100 ms] time window after motion onset. Figure 4D shows corrected acceleration against retinal speed at motion onset for all subjects, one stimulus tilt (−45°), three target speed values and the 50 versus 100% conditions. The good linear regression ( $r^2 = 0.8$ ,  $P < 0.001$ ) for the 50% condition points is consistent with the notion that eye acceleration during pursuit initiation depends roughly linearly on target retinal speed (Carl and Gellman 1987). Data points corresponding to the 100% condition fall on a linear regression line ( $r^2 = 0.7$ ,  $P < 0.001$ ) which is not statistically distinct from the 50% condition.

## DISCUSSION

In the present study, we investigated the effects of 2D target motion prediction on the visual motion integration necessary for pursuit initiation. We first showed that voluntary pursuit of a single tilted line exhibits an initial tracking bias in the

direction orthogonal to the bar orientation, as originally found with more complex objects in humans (e.g., Wallace et al. 2005) or with similar objects in monkeys (Born et al. 2006). More important, our work sheds light on three new phenomena. First, the initial tracking bias due to ambiguous local 1D motion signals remained constant across a large series of trials, when either stimulus orientation alone or orientation and motion direction were kept constant. This result suggests that the system performing the visuo-oculomotor transformation does not learn a particular solution for combining the different motion cues and that a new computation is performed at every motion onset. Second, we found that anticipatory pursuit direction was always very close to the global, 2D motion direction of the tilted lines, showing almost no sign of direction bias. This suggests that anticipatory pursuit is based on a signal fully describing object motion direction and not on a raw, low-level motion computation. Third, the visually driven pursuit was not affected by anticipatory pursuit. These two components appeared to be largely independent over a large range of target speeds.

These results have important functional significance for both visual motion integration and pursuit control. First, they suggest that learning an internal model of object motion trajectory does not help to remove the ambiguities present in retinal image motion. On the contrary, 2D motion integration is

recomputed at each stimulus presentation, irrespective of past experience. Furthermore, our results demonstrate that during pursuit initiation, extra-retinal signals driving anticipatory pursuit and low-level visual motion processing are independent. This is consistent with the scheme proposed originally by Newsome et al. (1988) where image motion and extra-retinal signals do not interact but sum together to construct the desired eye velocity. Within this framework, the retinal image motion stage is not modulated by extra-retinal signals. This would suggest that the neuronal stage of 2D motion integration is not influenced by the target velocity reconstruction stage at least during the earliest phase of object motion computation. However, we cannot rule out a role of extra-retinal signals generated during steady-state pursuit for visual motion integration. This could explain the lack of tracking error after a transient blank of the target (Masson and Stone 2002).

What is the extra-retinal signal used to drive anticipatory ocular tracking in the 2D target trajectory? A predictive signal can be based on either a visual memory of target motion or an eye-velocity memory accumulated during the previous pursuit eye movements. Barnes et al. (1997) have suggested that a pure visual-based, as opposed to eye-velocity based, memory signal would be sufficient to drive anticipatory smooth pursuit. This is consistent with our finding that anticipatory pursuit was present immediately at the beginning of a block. Moreover, anticipatory pursuit was almost purely horizontal, that is co-linear with the actual target trajectory. Because stimulus motion duration was restricted to ~500 ms, very little steady-state tracking had taken place in the preceding trials so that we can expect only a weak and noisy 2D-driven eye-velocity signal to be stored, while such stimulus duration is sufficient to accurately measure 2D line motion direction (Lorceau et al. 1993) and store this signal for predicting future target motion.

Using simple line motions, we have demonstrated that image motion integration and object motion prediction are independent signals that can be used to initiate smooth pursuit in humans. In monkeys, pursuit onset and MT neurons exhibit similar temporal dynamics for solving the aperture problem (Pack and Born 2001). The lack of learning observed in the present study would predict that the same temporal evolution of direction selectivity should be observed in MT neurons across repetitions. In monkeys, the target-related predictive signal is most probably elaborated between the lateral MST (MSTl) (Ilg 2003), the frontal eye fields (FEFs), and the supplementary eye fields (SEFs) (Fukushima et al. 2002; Missal and Heinen 2004) and not directly in the object motion integration stage (area MT). Our finding of a dissociation between retinal and target velocity computations corroborates current views of the pursuit system where these two stages correspond to two networks of cortical areas (V1-MT-MSTl and MSTl-FEF-SEF, respectively) articulated at the level of area MST in monkeys (see Thier and Ilg 2005).

#### ACKNOWLEDGMENTS

We thank Drs. R. J. Krauzlis, L. Goffart, and P. Lefèvre for a critical reading of the manuscript. We thank QNX Software Systems for supporting the use of

QNX Momentics OS for the ReX package developed at the Laboratory of Sensorimotor Research, National Eye Institute, National Institutes of Health.

#### GRANTS

A. Montagnini was supported by a fellowship from the Perception for Recognition and Action European Research and Training Network (HPRN-CT-2002-001126). M. Spering was supported by the Deutsche Forschungsgemeinschaft Graduate Program "Neuroact" (DFG 885/1). The research is supported by the Centre National de la Recherche Scientifique (CTI-2002) and by the Ministère de la Recherche (ACI-2002-0052).

#### REFERENCES

- Barnes G, Grealy M, and Collins S.** Volitional control of anticipatory ocular smooth pursuit after viewing, but not pursuing, a moving target: evidence for a re-afferent velocity store. *Exp Brain Res* 116: 445–455, 1997.
- Boman DK and Hotson JR.** Stimulus conditions that enhance anticipatory slow eye movements. *Vision Res* 28: 1157–65, 1988.
- Born RT, Pack CC, Ponce CR, and Yi S.** Temporal evolution of 2-dimensional direction signals used to guide eye movements *J Neurophysiol* 95: 284–300, 2006.
- Buseffini C, Miles FA, and Schwarz U.** Ocular responses to translation and their dependence on viewing distance. II. Motion of the scene. *J Neurophysiol* 66: 865–878, 1991.
- Carl JR and Gellman RS.** Human Smooth Pursuit: Stimulus-dependent responses *J Neurophysiol* 57: 1446–1463, 1987.
- Churchland AK and Lisberger SG.** Gain control in human smooth-pursuit eye movements. *J Neurophysiol* 87: 2936–2945, 2002.
- Collewijn H, van der Mark F, and Jansen TC.** Precise recordings of human eye movements. *Vision Res* 15: 447–450, 1975.
- Fukushima K, Yamanobe T, Shinmei Y, and Fukushima J.** Predictive responses of periarculate pursuit neurons to visual target motion. *Exp Brain Res* 145: 104–120, 2002.
- Heinen SJ, Badler JB, and Ting W.** Timing and velocity randomization similarly affect anticipatory pursuit. *J Vision* 5: 493–503, 2005.
- Ilg UJ.** Visual-tracking neurons in area MST are activated during anticipatory pursuit eye movements. *Neuroreport* 14: 2219–2223, 2003.
- Kao GW and Morrow MJ.** The Relationship of anticipatory smooth eye movement to smooth pursuit initiation. *Vision Res* 34: 3027–3036, 1994.
- Kowler E and Steinman RM.** The effect of expectations on slow oculomotor control II. Single target displacements. *Vision Res* 19: 633–646, 1979.
- Lisberger SG and Westbrook LE.** Properties of visual inputs that initiate horizontal smooth pursuit eye movements in monkeys. *J Neurosci* 5: 1662–1673, 1985.
- Lorceau J and Shiffrar M.** The influence of terminators on motion integration across space. *Vision Res* 32: 263–273, 1992.
- Lorceau J, Shiffrar M, Wells N, and Castet E.** Different motion sensitive units are involved in recovering the direction of moving lines. *Vision Res* 33: 1207–1217, 1993.
- Masson GS and Stone LS.** From following edges to pursuing object. *J Neurophysiol* 88: 2869–2873, 2002.
- Missal M and Heinen SJ.** Supplementary eye fields stimulation facilitates anticipatory pursuit. *J Neurophysiol* 92: 1257–1262, 2004.
- Newsome WT, Wurtz RH, and Komatsu H.** Relation of cortical areas MT and MST to pursuit eye movements. II. Differentiation of retinal from extraretinal inputs. *J Neurophysiol* 60: 604–620, 1988.
- Pack CC and Born RT.** Temporal dynamics of a neural solution to the aperture problem in visual area MT of macaque brain. *Nature* 409: 1040–1042, 2001.
- Thier P and Ilg UJ.** The neural basis of smooth-pursuit eye movements. *Curr Opin Neurobiol* 15: 645–652, 2005.
- Wallace JM, Stone LS, and Masson GS.** Object motion computation for the initiation of smooth pursuit eye movements in humans. *J Neurophysiol* 93: 2279–2293, 2005.