

Accounting for direction and speed of eye motion in planning visually guided manual tracking

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¹*Institute of Information and Communication Technologies, Electronics and Applied Mathematics (ICTEAM), Université catholique de Louvain, Louvain-la-Neuve, Belgium;* ²*Institute of Neuroscience (IoNS), Université catholique de Louvain, Brussels, Belgium;* ³*Centre for Neuroscience Studies, Queen's University, Kingston, Ontario, Canada;* and ⁴*Canadian Action and Perception Network (CAPnet), Toronto, Ontario, Canada*

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Leclercq G, Blohm G, Lefèvre P. Accounting for direction and speed of eye motion in planning visually guided manual tracking. *J Neurophysiol* 110: 1945–1957, 2013. First published August 7, 2013; doi:10.1152/jn.00130.2013.—Accurate motor planning in a dynamic environment is a critical skill for humans because we are often required to react quickly and adequately to the visual motion of objects. Moreover, we are often in motion ourselves, and this complicates motor planning. Indeed, the retinal and spatial motions of an object are different because of the retinal motion component induced by self-motion. Many studies have investigated motion perception during smooth pursuit and concluded that eye velocity is partially taken into account by the brain. Here we investigate whether the eye velocity during ongoing smooth pursuit is taken into account for the planning of visually guided manual tracking. We had 10 human participants manually track a target while in steady-state smooth pursuit toward another target such that the difference between the retinal and spatial target motion directions could be large, depending on both the direction and the speed of the eye. We used a measure of initial arm movement direction to quantify whether motor planning occurred in retinal coordinates (not accounting for eye motion) or was spatially correct (incorporating eye velocity). Results showed that the eye velocity was nearly fully taken into account by the neuronal areas involved in the visuomotor velocity transformation (between 75% and 102%). In particular, these neuronal pathways accounted for the nonlinear effects due to the relative velocity between the target and the eye. In conclusion, the brain network transforming visual motion into a motor plan for manual tracking adequately uses extraretinal signals about eye velocity.

eye movement; visual motion; sensory-motor transformation; reference frame; smooth pursuit

HUMANS FACE MOVING OBJECTS in their visual environment on a daily basis (e.g., motion of cars on the roads, motion of a ball in a sports game, a kid running in the street) and often successfully interact with these objects (e.g., a handball player has to catch the ball, a car driver has to decide whether another car is far enough away to change lanes or has to estimate whether a child will or will not cross his/her way). These examples show that the human brain has developed good abilities in terms of visual motion perception and in terms of sensorimotor velocity transformation for motor planning. However, humans also move relative to the world (self-motion due to walking, driving a car) or simply reorienting their gaze with an eye movement or a combined eye-head movement (e.g.,

through saccades or smooth pursuit), generating additional visual motion that complicates motion processing for perception and action since the retinal and spatial motion of an object are different in this case (Crawford et al. 2011; Furman and Gur 2012). In particular, there is a discrepancy between the spatial and retinal motion of a moving object during smooth pursuit eye movement (Fig. 1). The goal of this study was to determine whether eye velocity during steady-state smooth pursuit is taken into account by the brain to plan a manual tracking movement (Fig. 1, blue arrow) or whether only retinal motion is used to initiate the arm movement (Fig. 1, orange arrow).

Many studies have investigated motion perception during smooth pursuit and its neural mechanisms (for review, see Furman and Gur 2012 and also Spering and Montagnini 2011). Many of these studies suggest that eye velocity is taken into account, but only partially; this incomplete compensation for eye velocity results in the well-known Filehne and Aubert-Fleischl illusions. In the Filehne illusion, a stationary object (in space) is perceived as moving in the opposite direction to the eye movement (Filehne 1922; Freeman 1999). In the Aubert-Fleischl illusion, a moving object is perceived as moving slower when it is pursued than during fixation (Aubert 1886; Fleischl 1882; Freeman 1999). In the field of heading (direction of self-motion) perception, the effects due to the eye velocity during smooth pursuit are compensated for (Bradley et al. 1996; Britten 2008; Royden et al. 1992). Motor planning during smooth pursuit has been studied for saccadic eye movements toward flashed targets (Blohm et al. 2005) and for reaching movements (Hansen 1979), showing that, under certain circumstances, current eye motion is taken into account for the motor planning. Transforming retinal signals into a spatially accurate motor plan (for the eyes or the arm) requires the brain to take the three-dimensional (3D) eye-head-shoulder geometry into account (for review, see Crawford et al. 2011). Indeed, visually guided saccade planning has been shown to account for 3D eye orientation (Crawford and Guitton 1997; Klier and Crawford 1998), and visually guided reach planning takes the 3D eye and head orientations into account (Blohm and Crawford 2007). Movements driven by the visual motion (instead of the retinal position) also account for these extraretinal orientation signals, as shown for smooth pursuit (Blohm and Lefèvre 2010) and for manual tracking (Leclercq et al. 2012). However, none of these studies has investigated whether the eye velocity during ongoing smooth pursuit was also taken into account in motor planning.

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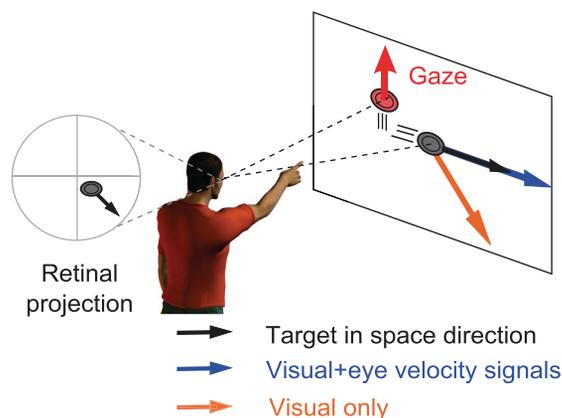


Fig. 1. Effect of eye velocity during smooth pursuit for the motor planning of manual tracking. Assume that the eyes are in steady-state smooth pursuit toward one target (red, directed upward) but another target (gray) appears in the field of view and moves to the right (black arrow). Because of the eye velocity during ongoing smooth pursuit, the retinal motion of the gray target (the new target) is significantly tilted clockwise onto the retina. Therefore, if the person decides to track the new target (gray) and if the brain only takes the retinal motion into account, this would lead to a significant directional error in the initiation of the arm tracking movement (orange arrow). Alternatively, if the brain has an internal model of the eye kinematics and uses it to combine the retinal motion and eye velocity signals, then the tracking movement would be spatially accurate (blue arrow).

In this context, we consider the case of visually guided manual tracking movements, similar to Leclercq et al. (2012). Here we investigate whether planning a manual tracking movement takes the eye velocity during smooth pursuit into account, whereas Leclercq et al. (2012) studied the effect of 3D eye and head orientations during fixation for the planning of manual tracking. In other words, does the brain use an internal signal about the eye velocity (direction and speed) and accurately combine it with the visual motion signals to generate a spatially accurate motor plan for the arm? In this study, we develop a model of the 3D eye kinematics to estimate the retinal target motion based on the spatial target motion and on the 3D eye orientation and rotational velocity. Using this model, we show that this can lead to complex effects when tracking visual targets moving in two dimensions (2D). Indeed, if the eye and target move spatially in different directions with different speeds, a linear combination of the eye velocity direction and the retinal target motion direction is not sufficient to reconstruct the spatial target motion. Note that throughout this article, velocity (of the eye or target) refers to the velocity vector, speed refers specifically to the norm of the velocity vector, and velocity (motion) direction refers to the direction of the velocity vector. We devised an experimental paradigm to test 1) whether 2D eye velocity during smooth pursuit was taken into account by the brain for planning manual tracking and in particular 2) whether the motor planning depended on the difference between the spatial target and eye speeds or whether participants only relied on a linear estimator based on the retinal and eye velocity directions.

We asked participants to initiate and maintain a tracking movement with their arm toward a point-like visual target while their eyes were in steady-state smooth pursuit. To assess whether the motor plan was spatially accurate (and therefore took the eye velocity into account) or whether the motor plan was only based on visual motion, we measured the initial direction of the arm. Indeed, the initial direction of the arm

movement reflects the direction of the motor plan (the feed-forward component of the arm movement control), because of the physiological delays that prevent the brain from using feedback signals during the first 100 ms of the movement (Desmurget and Grafton 2000). Then we compared the initial direction of the arm to the spatial and retinal directions of the tracking target (see Fig. 1). Results showed that the 2D eye velocity (the horizontal and vertical components) was taken into account by the brain when planning arm movements toward a moving target. The observed compensation for the eye movement-induced visual motion was partial, i.e., on average the initial arm trajectories were slightly biased from the target spatial motion toward its retinal motion, which was similar to (or smaller than) the biases observed in the visual motion perception literature (Furman and Gur 2005; Morvan and Wexler 2009; Suman et al. 2005a; Swanston and Wade 1988). Moreover, the difference between the smooth pursuit speed and the spatial target motion speed was taken into account in the motor planning, which indicates that the CNS does not simply use a linear estimation of spatial target motion as a motor plan for manual tracking.

MATERIALS AND METHODS

We consider two theoretical and extreme hypotheses about how the brain could plan a manual tracking movement when the eye is itself in motion. The spatial hypothesis assumes that the brain is able to perfectly combine the retinal motion information with an internal 3D eye velocity signal to compute a spatially accurate motor plan for the arm, using an accurate internal model of the 3D kinematics. This model differs from (extends) that described in Leclercq et al. (2012), since it incorporates the effect of the 3D eye rotational velocity. As can be shown (see APPENDIX), the kinematics model that transforms the manual tracking target velocity vector from retinal to spatial coordinates (and vice versa) is nonlinear and is not simply a matter of subtractions or additions of the ocular and retinal signals. In contrast, the retinal hypothesis assumes that the brain network responsible for planning manual tracking movements can only process the retinal velocity and has no access to the eye kinematics. In this case, the motor plan for the arm is simply the retinal velocity vector. Considering these two extreme cases allowed us to quantify the extent to which 3D eye velocity was taken into account. Note that the retinal hypothesis is not unlikely, since it concerns the initial arm direction and not the entire arm movement. Indeed, using delayed visual feedback (around 100 ms), the brain could correct for the errors due to the crude biased (retinal) motor plan and bring the arm to the right place.

In the following experiment, the manual tracking target (denoted TT) trajectory is specified by the experimenter in spatial coordinates. However, we cannot directly measure the TT retinal trajectory, and therefore we need to estimate it, using a 3D model of ocular kinematics. In the APPENDIX, we describe the kinematic model that computes the TT retinal trajectory as a function of the TT spatial trajectory, the 3D eye orientation, and the 3D eye rotational velocity. The 3D eye orientation and 3D eye rotational velocity are computed based on measurements.

Experimental setup. Ten right-handed healthy human participants (aged 22–29 yr; 9 naive) participated in the experiments after giving informed consent. All participants had normal or corrected-to-normal vision and were without any known sensory or motor anomalies. All procedures were conducted with approval of the Université catholique de Louvain Ethics Committee.

The experimental setup was similar to that described previously (Leclercq et al. 2012). All experiments were performed in complete

darkness. Participants were seated in front of a fronto-parallel translucent screen located at a distance of 1 m. The visual field covered by the screen was about $\pm 40^\circ$ horizontally and vertically. Two targets [a green and a red 0.2°-diameter laser spot (BFI Optilas)] were back-projected onto the screen with two pairs of mirror galvanometers (M2 and M3ST, GSI Lumonics, Billerica, MA). A dedicated real-time computer running LabVIEW RT (National Instruments, Austin, TX) controlled the illumination and position of these targets at a refresh frequency of 1,000 Hz, using custom-written code. A green LED was attached to the participant's right index finger above the nail and was directed toward the participant such that it was visible when the LED was illuminated (the real-time computer also controlled the illumination of this LED). This LED was used to provide subjects with initial hand position feedback (see below). Each participant's left eye was patched such that participants only had a monocular view of the stimuli. We did this to prevent subjects from using binocular visual cues that could be informative about 3D eye orientation or velocity. Participants' heads were upright and rested on a chin rest during a block of trials. The 3D orientation of the right eye was recorded (200 Hz) with a head-mounted 3D infrared video recording device (Chronos Vision, Berlin, Germany). The arm-in-space position was measured (200 Hz) with an active infrared marker tracking device (CodaMotion, Charnwood Dynamics, Leicester, UK) [the spatial resolution of this device is 0.3 mm for the distance from the camera and 0.05 mm for the lateral position resolution (for a 3-m distance)]. To do so, infrared markers were positioned on the right index finger (with tape), next to the LED (on the side of the finger), and on the hand, elbow, and shoulder. The head position was monitored by positioning three LEDs on the helmet.

Paradigm. We designed a manual tracking task to assess whether participants took eye velocity into account in the visuomotor transformation of visual target motion. To test for the effects of eye velocity, we had participants performing manual tracking movements toward a tracking target (TT) that started to move while the eye was in steady-state smooth pursuit (see Fig. 2). Specifically, we tested the combined effect of a difference in direction and speed between smooth pursuit eye movements and the spatial tracking target movement. We used a manual tracking task as in Leclercq et al. (2012), but the paradigm differed significantly, since at the time of the TT motion onset the head was upright and the eyes were in steady-state smooth pursuit, as opposed to a fixation condition in various 3D eye or head configurations as in Leclercq et al. (2012).

During a trial (see Fig. 2), participants first had to align the fingertip LED with TT (green dot), which was always located at the center of the screen. Participants were instructed to align their fingertip LED slightly below TT such that TT was still visible and not occluded by the finger. The finger LED was then switched off in order to prevent the use of any visual feedback of the arm. At the same time, the gaze target (GT, red dot) appeared on the screen and participants had to fixate GT. Afterwards, GT started to move at a constant velocity along a straight line and participants had to pursue it with their eyes. Finally, after a period chosen randomly between 500 and 1,000 ms (see below), TT started to move at a constant velocity (20°/s) along a straight line. Participants were instructed to manually track TT with their extended right arm while continuing to pursue GT with their eyes. Three hundred milliseconds after TT motion onset, GT and TT were extinguished for 500 ms (see Fig. 2) so that the initial part of the tracking arm movement generally occurred in the absence of the target (because of the delay in the arm movement). The occlusion period was introduced in the paradigm to minimize the visual feedback available during the initiation of the arm movement.

TT speed was always 20°/s, but TT direction, denoted α_T , varied randomly across trials between 0° and 270°, in steps of 30°. We did not test the 300° and 330° directions since TT would sometimes be hidden by the unseen extended arm. However, there were no such problems for the other directions. For each trial, GT speed was randomly chosen between 10°/s, 20°/s, and 30°/s. Thus there were 30

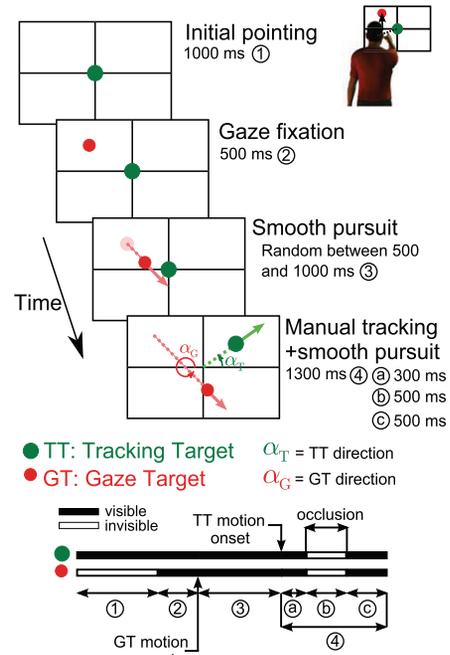


Fig. 2. Experimental paradigm. Participants first (1) aligned the extended right arm and index finger toward the tracking target (TT, green dot). They then fixated the gaze target (GT, red dot) for 500 ms (2). Then GT started to move at constant velocity along a straight line, and participants were required to pursue GT with their eyes (3). After a random period between 500 and 1,000 ms, TT started to move at constant velocity along a straight path (4). Participants were required to manually track TT while pursuing GT with their eyes. In this phase, TT and GT were visible for 300 ms (4a), and then both targets were extinguished for 500 ms (4b), followed by another visible period of 500 ms (4c).

conditions (3 GT speeds \times 10 TT directions). For each condition, there were 10 repetitions on average. The initial fixation location was randomly chosen on a circle with the lower right quadrant removed. GT motion direction, denoted α_G , was always directed toward the center of the screen, and therefore GT never started from the lower right quadrant, to guarantee that GT was visible until manual tracking started. The radius of the circle for the initial fixation location depended on GT speed: 7.5° (resp. 15° and 22.5°) for a GT speed of 10°/s (resp. 20°/s and 30°/s). To avoid predictability in space and consequently to avoid any anticipatory arm movement, GT direction was directed toward the center \pm a random component between 0° and 15° in each direction away from the center direction. Moreover, the time between GT onset and TT onset was randomly chosen between 500 and 1,000 ms, in steps of 50 ms.

Each subject performed one experimental session in 1 day. One session lasted a maximum of ~ 50 min. The experimental session started with a gaze calibration block in which participants fixated different known positions without moving the head. A pointing calibration block followed, in which participants had to look at and point their arm toward different known positions. Then 10 blocks of 30 trials were presented, interrupted after 3 or 4 blocks to repeat the calibration procedure. Thus each participant performed 300 trials. Arm fatigue was not an issue, since participants were allowed to rest their arm on the table (on which the bite bar was attached) between trials. Moreover, none of the 10 participants complained about fatigue.

Data analysis. Collected data (eye images, target positions, and arm infrared marker positions) were stored on a hard disk for further off-line analysis with MATLAB (The MathWorks, Natick, MA). 3D eye orientation (horizontal, vertical, and torsional) was extracted (in Fick coordinates) with IRIS software (Chronos Vision). Details of the extraction of eye torsion can be found in Leclercq et al. (2012). Before further processing, 3D Fick eye orientation was converted into an

angular vector representing the 3D eye orientation (Haslwanter 1995). Position and orientation signals were low-pass filtered with a zero-phase digital filter (autoregressive forward-backward filter, cutoff frequency: 50 Hz). Velocity and acceleration signals were estimated from position signals by using a central difference algorithm. The eye velocity traces were “desaccaded.” To do this, we first detected saccades, using a $500^\circ/s^2$ acceleration threshold (Blohm et al. 2005; de Brouwer et al. 2001). The eye velocity was then linearly interpolated between the eye velocity values before and after the saccade (Blohm et al. 2005; de Brouwer et al. 2001).

The location of the eyeball with respect to space was measured before each session. To this end, we temporarily put an infrared marker on the eyelid when the eye was closed and recorded the marker’s position for 10 s. This recorded position was used to compute the eye-fingertip vector during the blocks of trials. We computed the eye-fingertip vector at each time step. The 2D tracking orientation was defined by the rotation of the eye-fingertip vector (at the current time step) compared with a reference eye-fingertip vector. The reference vector was computed during the pointing calibration block (see Leclercq et al. 2012 for details).

Onset of the arm movement was automatically detected with the same procedure as in Leclercq et al. (2012): the algorithm searched for the first 200-ms window (after TT onset) where the eye-fingertip vectorial velocity (the norm of the velocity vector) was above a threshold of $3^\circ/s$ for each element within that time window. Then the algorithm selected this first window and fitted a linear regression between vectorial velocity and time. The onset of the arm movement was defined as the time when the fitted regression line crossed the zero-velocity line (Badler and Heinen 2006; Carl and Gellman 1987). All trials were visually inspected. Latency was computed for each trial, and trials with an arm movement latency shorter than 100 ms were discarded from further analysis to ensure that the arm movement was triggered by the visual input and was not anticipatory. For each trial, the initial arm movement direction was estimated over the first 100 ms after arm movement onset.

We carried out our analysis with 1,382 of 3,000 trials (46% valid trials). We first removed 1,301 trials (43.4%) because of 1) failures of the CODAmotion system (270 trials, 9%, markers not seen by the camera) or 2) failures of the Chronos eye measurement system (214 trials, 7%, eye blinks, bad eye signals), 3) because they contained saccadic eye movements in the 300-ms period after TT motion onset (725 trials, 24%, period when participants receive the visual information for motor planning, prior to the TT blanking period), or 4) because they were anticipatory trials (92 trials, 3%, i.e., those trials for which arm movement latency was shorter than 100 ms and which were discarded to avoid any potential confound with anticipation in the results). Second, we removed the trials in which the 2D eye trajectory during the 300-ms period after TT motion onset was clearly curved (317 trials, 10.6%), because it was not clear how to compute the eye motion direction in this case. These curved eye trajectories were detected by visually inspecting each trial. Importantly, the results described below are similar if those trials are included in the analysis. The task in our experiment was not easy, and eye movements of participants were sometimes attracted by TT motion, which resulted in a saccade and/or an abrupt change in smooth pursuit direction toward TT.

We used a transformation metric similar to that in Leclercq et al. (2012) to quantify the amount to which the eye velocity was taken into account in the planning of the arm movement.

observed transformation = $k_0 + \text{slope} \times \text{predicted transformation}$ (1)

where

observed transformation = retinal direction – initial arm direction (2)

predicted transformation = retinal direction – spatial direction (3)

where initial arm direction was the measured initial arm movement direction in spatial coordinates (see above), spatial direction was the

TT direction in space, and retinal direction was the retinal TT direction estimated with the measured 3D eye kinematics and using the model described in the APPENDIX. The predicted transformation was the difference between the retinal and spatial directions and corresponds to the amount that the brain has to compensate for (using extraretinal information about eye motion) such that the manual tracking plan is spatially accurate. Note that the predicted transformation is exactly equal to the predicted error (see Fig. 3) that the brain has to compensate for the motor plan to be spatially accurate. The observed transformation was the difference between the retinal direction and the initial arm direction and indicates the extent to which the brain has compensated for the eye velocity in a particular trial. The slope represents the amount of transformation; if slope = 1, the arm motor plan is spatially accurate (spatial hypothesis), but if slope = 0, the initial arm direction is exactly the retinal direction (retinal hypothesis). Therefore the slope parameter was an indicator of the amount of transformation. We estimated the slope parameter by fitting a linear regression (Eq. 1) to our data.

For each trial, the retinal direction was estimated with the average 3D eye orientation and average 3D eye rotational velocity measured during the period starting 300 ms before the arm onset (or at TT onset if the arm latency was below 300 ms) and ending 50 ms before the arm onset.

An alternative hypothesis to the retinal and spatial hypotheses is the direction hypothesis: it assumes that the brain computes the motor plan as a linear combination of the retinal direction and the eye direction and does not take the retinal target and eye speeds into account. However, in the particular case when the spatial target and smooth pursuit eye speeds are the same, it can be shown that

$$\text{retinal direction } [^\circ] = \frac{\text{eye direction} + \text{spatial direction}}{2} - 90 \quad (4)$$

For example, Fig. 3B shows an eye direction equal to 180° and a spatial direction equal to 90° . If the speeds are equal, then the retinal direction is equal to 45° (see arrow 2 in Fig. 3B). However, the retinal motion direction is different from 45° if the eye and target speeds differ (see Fig. 3B, arrows 1 and 3), even though the eye direction and spatial direction are identical to condition 2. Therefore, based on Eq. 4, the motor plan direction computed according to the direction hypothesis is

$$\text{linear direction } [^\circ] = 2 \cdot \text{retinal direction} - \text{eye direction} + 180 \quad (5)$$

To summarize, the motor plan computed under the direction hypothesis is spatially accurate (linear direction equals spatial direction) if and only if the eye and spatial target speeds are equal. But this is no longer the case if the eye and spatial target speeds differ.

To test which hypothesis the brain has implemented, we propose the following analyses. The predicted transformation can be decomposed into two components, one component (direction effect) representing the effect of taking into account the linear combination of eye and retinal directions and the other component (speed effect) representing the effect of taking into account the difference between the spatial target and eye speeds.

$$\begin{aligned} \text{predicted transformation} &= \text{retinal direction} - \text{spatial direction} \\ &= \text{direction effect} + \text{speed effect} \end{aligned}$$

where

$$\text{direction effect} = \text{retinal direction} - \text{linear direction}$$

and

$$\text{speed effect} = \text{linear direction} - \text{spatial direction}$$

To investigate whether both effects are taken into account, we run a multiple linear regression analysis:

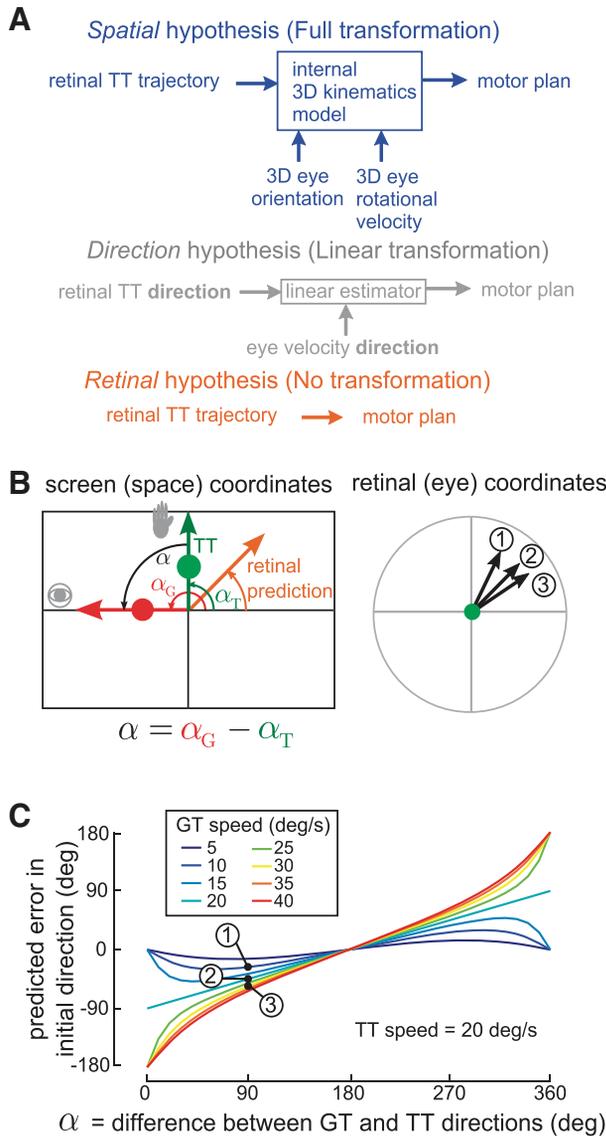


Fig. 3. Hypotheses for the planning of the arm tracking movement and model predictions. A: the spatial, direction, and retinal hypotheses are presented. In the spatial hypothesis, TT retinal velocity and extraretinal signals (3D eye orientation and rotational velocity) are combined using an internal model of the 3D eye-head-shoulder kinematics to generate a spatially accurate motor plan. In the direction hypothesis, the TT retinal motion direction and the eye velocity direction are linearly combined to generate the motor plan. In the retinal hypothesis, the planning of the arm is based on the visual motion only. B: example of discrepancy between spatial and retinal motion when the eye is in motion: here, the eye follows the red dot and moves to the left, while the TT (green dot) moves spatially upward. When the eye and TT move at the same speed, TT retinal motion is tilted by 45° (arrow 2, right). When the eye moves faster (respectively slower) than TT, TT retinal direction is further (respectively less) tilted [arrow 3 (respectively arrow 1)]. The orange arrow represents the motor plan direction predicted according to the retinal hypothesis (for case 2). C: the predicted error (difference between retinal and spatial directions) is represented as a function of the difference between GT and TT directions, for several GT speeds (TT speed is kept constant). In our experiment, we only tested 3 GT speeds (10, 20, and 30°/s).

$$\text{observed transformation} = k_0 + k_{\text{dir}} \cdot \text{direction effect} + k_{\text{speed}} \cdot \text{speed effect} \quad (6)$$

When carrying out multiple regression analyses, we performed a best regression subset analysis (using STATISTICA, StatSoft, Tulsa,

OK), which runs several multiple regressions with subsets of the dependent variables and returns the set of variables that result in significant additional information compared with variables that do not. To do this, we compare the Mallows C_p coefficient, which is an adequate measure for such comparisons (see Dowdy et al. 2004, p. 460). Briefly, the regression model with the smallest Mallows C_p coefficient must be chosen. This coefficient increases linearly with the number of regression variables, but if the additional variables improve the regression significantly, then another term decreases and C_p decreases if the improvement is sufficient enough. For example, this test was used to detect whether the variable speed effect improved the correlation coefficient or not, and therefore whether the difference between the TT and eye speeds had an influence on the amount of compensation.

RESULTS

Model predictions. How does the brain plan a manual tracking movement when the eyes are in smooth pursuit motion? The spatial hypothesis supposes that the brain adequately combines the TT retinal motion with the extraretinal signals about the eye motion (the 3D eye rotational velocity and 3D eye orientation) to compute a spatially accurate motor plan (Fig. 3A, top). In contrast, the retinal hypothesis consists in using the TT retinal motion directly as a motor plan (Fig. 3A, bottom). We also consider a third hypothesis, the direction hypothesis, which assumes that the brain combines linearly the TT retinal motion direction and the eye velocity direction (Fig. 3A, middle).

When the eye is in motion, TT retinal and spatial velocity vectors are not aligned (see APPENDIX for how to compute the retinal velocity vectors). Indeed, Fig. 3B illustrates this situation: TT moves upward (green) and the eye moves to the left (red). If the eye and the TT move at the same speed, the TT retinal motion is tilted by 45° onto the retina (number 2, Fig. 3B, right). Therefore, if the motor plan is based on the retinal motion only, then the arm movement will follow the retinal direction (orange arrow, Fig. 3B, left) and will perhaps be corrected later with the delayed visual feedback. However, if the eye motion is taken into account, then the motor plan is spatially accurate and the initial arm movement should be directed upward. If the eye moves faster than the TT, then the TT retinal motion is tilted further away from the vertical (number 3, Fig. 3B, right), while if it moves slower than TT, then TT retinal motion will be less tilted (number 1, Fig. 3B, right). Therefore, the predicted error depends on the relative speeds of the eye and the TT. In the example, α , which is the difference between the eye and TT directions, is 90°. Figure 3C shows that the retinal error depends on the relative direction α . Moreover, this dependence is linear if the eye and TT move at the same speed but becomes highly nonlinear when they move at different speeds, especially when the difference between eye and TT directions is small. Indeed, when the eye and TT move at the same speed (in space), the direction hypothesis is equivalent to the spatial hypothesis and there is no error in the motor plan if the brain uses the direction hypothesis. However, when the eye and target speeds differ, the direction hypothesis leads to inaccurate motor plans. In a subsection below, we investigate whether the brain is able to take the effects of different TT and eye speeds into account (and therefore implements the spatial hypothesis) or not (and implements the direction hypothesis).

Figure 3C illustrates the range of predicted errors if the 2D (horizontal and vertical components) eye velocity is not taken

into account (the eye is in primary orientation and there is no torsional velocity). In the particular case when GT and TT move in the same direction, $\alpha = 0^\circ$ (or $\alpha = 360^\circ$), there are three cases: 1) TT moves faster than GT, and therefore the TT retinal and spatial motion direction are identical, 2) TT moves slower than GT, and thus the TT retinal motion direction is the opposite of the spatial motion direction (180° error), and 3) TT and GT move at the same speed, and thus there is no TT retinal motion and therefore the direction is undefined. In theory, the 3D eye orientation and the torsional component of the 3D rotational velocity also play a role. In practice, their effect on the predicted error is limited compared with the effect of the 2D eye velocity. Indeed, the torsional orientation of the eye in a head-upright orientation is at most a few degrees (Dieterich and Brandt 1993). In addition, the effects due to an eccentric eye orientation (Leclercq et al. 2012) or due to the torsional eye velocity are rather small (since the head is fixed and there is no large-field visual stimulus, the torsional eye velocity is around $0^\circ/\text{s}$). However, for completeness our model takes the full 3D eye orientation and 3D eye rotational velocity into account.

From the retinal and spatial model predictions, we conclude that the motor plans can be largely different in the spatial or retinal hypothesis, depending on the relative directions and speeds between TT and the eye. The differences between the direction hypothesis and the retinal and spatial hypotheses are emphasized and detailed in *Compensation for direction and speed of eye motion*. In the following, we probe how sophisticated the motor plan computed by the brain is by measuring the initial arm tracking direction during the first 100 ms after the arm tracking onset and comparing it to the TT retinal and spatial trajectories. We chose this 100-ms time period because

it reflects the initial motor plan and is not yet influenced by the delayed sensory (visual, proprioceptive) feedback (Desmurget and Grafton 2000).

Typical trial. Figure 4 shows a typical trial of our experiment. For this particular trial, GT fixation (red disk, Fig 4A) was on the right and then GT moved to the left. TT started to move upward on the screen when GT was close to the screen center. The eye and arm tracking trajectories are represented in black. The lines are dashed during the blanking period (GT and TT were not visible), during which no visual feedback was available. The eye trajectory during the 300-ms time period between TT motion onset and the blanking start is colored in gray. The eye approximately follows a horizontal trajectory (pursuing GT) and does not change its direction toward TT. Based on the mean 3D rotational eye velocity and 3D eye orientations (time course represented in Fig. 4, right) during this 300 ms period, we estimated TT retinal velocity (see MATERIALS AND METHODS). The motor plan direction predicted by the retinal hypothesis is exactly the estimated retinal velocity and is represented in orange (Fig. 4A); the initial part of the tracking movement is emphasized in cyan (first 200 ms of the movement). For this particular trial, the initial direction of the arm is clearly not in the retinal direction, but is rather close to the TT spatial direction. This means that for that particular trial, the eye velocity was partially taken into account.

Figure 4, right, represents the time course of 3D eye orientation and rotational velocity as well as 2D manual tracking orientation and velocity during the trial. At TT motion onset (second vertical black line), the eye was indeed in steady-state smooth pursuit. The arm movement onset occurred just before the blanking of the targets (see Fig. 4E, thick black line).

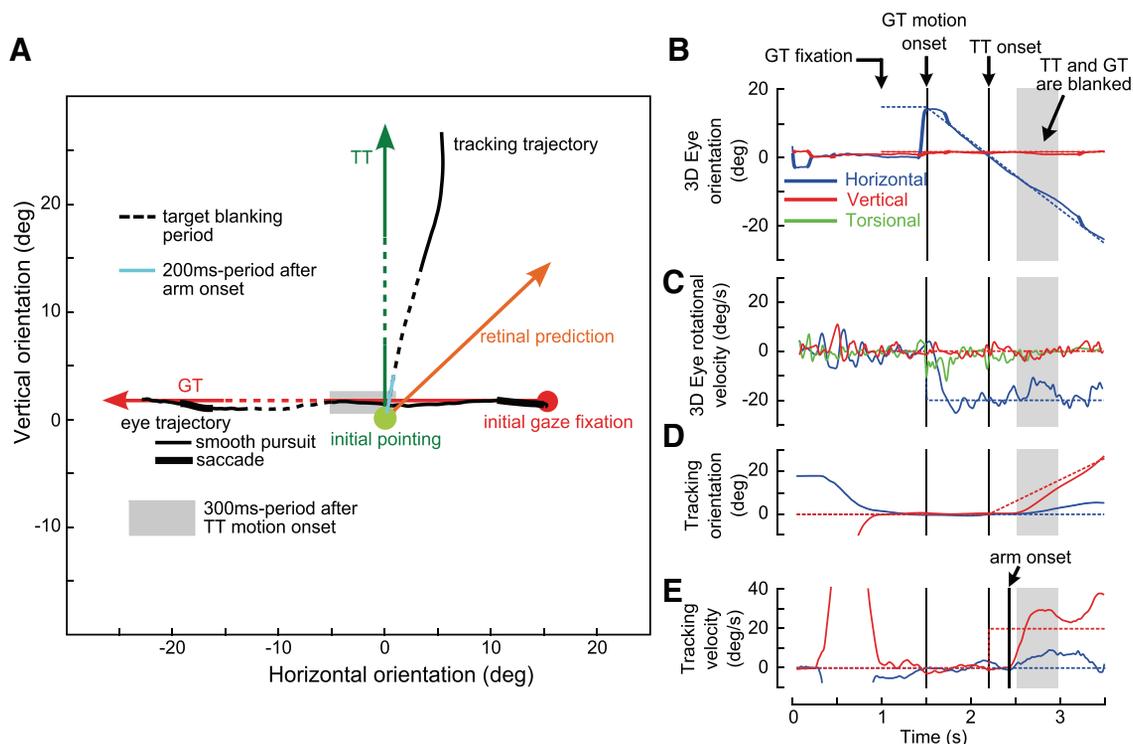


Fig. 4. Typical trial. A: 2D trajectories (on the screen, vertical vs. horizontal orientation) of GT (red disk and line) and TT (green disk and line) are represented. The 2D eye trajectory is also represented (black curve along the horizontal axis), as well as the 2D arm tracking trajectory (black curve moving upward). The cyan curve shows the arm trajectory during the first 200 ms after the arm movement onset. The orange arrow shows the direction predicted by the retinal hypothesis. B–E: for this trial, time courses of 3D eye orientation (B) and 3D eye rotational velocity (C), 2D arm tracking orientation (D) and velocity (E).

Across all valid trials and all participants, the mean arm movement onset latency was 325 ms (SD 147 ms). The mean arm latency varied from 240 to 420 ms across participants (SDs varied between 50 and 250 ms). For 7 of 10 participants, the arm started to move on average during the occlusion period (with a mean latency > 300 ms). For the trial shown in Fig. 4, the ratio between the observed transformation (about -36° , see MATERIALS AND METHODS) and the predicted transformation (about -45° , see MATERIALS AND METHODS) is roughly 80%. In the following section, we conduct analyses on all trials to estimate the amount of transformation, i.e., the slope of the linear regression between the observed transformation and the predicted transformation.

Compensation for eye velocity. The observed transformation and predicted transformation were estimated for each trial. Figure 5A represents the observed transformation as a function of the predicted transformation. Data across all participants (gray dots) and the associated linear regression line (black dashed line) are represented.

The retinal hypothesis prediction is a zero-slope line (orange in Fig. 5) since the initial arm direction is the retinal direction. Therefore, under the retinal hypothesis the observed transformation equals zero, whatever the predicted transformation. The spatial hypothesis prediction is a unity slope line (blue) since the observed transformation would be equal to the predicted transformation. Across participants, the regression slope was 0.88 (± 0.03 , 95% confidence interval, $R = 0.84$). This indicates that participants took eye velocity into account when planning their arm movement. However, the compensation for the eye velocity effect was not perfect, since the slope was significantly lower than 1 (2-sided t -test: $t[1,380] = -8.08$, $P < 0.001$).

The compensation was also computed for each participant individually. Figure 5B shows the regression slopes (and their associated 95% confidence interval) for all 10 participants. The regression slopes ranged from 0.77 (S1) to 1.02 (S10). Thus all participants took an extraretinal signal about eye velocity into account in planning the arm's tracking movement. Most of the participants had a slope lower than 1, and therefore the motor plan of the arm was on average slightly biased away from the

spatial direction toward the retinal direction, as represented in the typical trial (see Fig. 4).

As different participants have different average movement onset latencies, we investigated whether the latency of the arm movement had an impact on the amount of transformation, i.e., the regression slope. We fitted a linear regression of the transformation slope as a function of the average latency. The fitted equation was transformation slope = $0.66 + 0.69 \times$ latency [ms], suggesting a better compensation for larger latencies. However, the regression was not significantly different from 0 [$F(1,8) = 2.30$, $P = 0.17$]. We also ran the following multiple regression analysis (across all participants):

$$\text{obs transf} = k_0 + (k_1 + k_2 \times \text{latency}) \times \text{pred transf}$$

where the amount of compensation was represented by the quantity $k_1 + k_2 \times$ latency. k_1 is the regression coefficient that is independent from latency, and k_2 is the regression coefficient that quantifies the influence of the latency on the amount of compensation. The fitted parameters were 0.76 (95% confidence interval: [0.67 0.85]) for k_1 and 0.36 (95% confidence interval: [0.10 0.61]) for k_2 . Both k_1 [$F(1, 1,379) = 271$, $P < 0.001$] and k_2 [$F(1, 1,379) = 7.7$, $P = 0.006$] were significantly different from 0. This means that if the latency was 150 ms then the regression slope is 0.81, while if the latency is 350 ms the regression slope is 0.88, which indicates that the compensation is better for larger latencies. However, the latency had no effect (k_2 is not significantly different from 0) when we ran this analysis on individual participants. One possible reason to explain these differences is that the latency range was much smaller at the individual participant level compared with the latency range obtained by pooling all participants together. Regardless of the significance of the arm movement latency influence on the compensation, this effect was very small compared with the main compensation amplitude.

Compensation for direction and speed of eye motion. As described in MATERIALS AND METHODS, the direction hypothesis is an alternative to the retinal and spatial hypotheses. The direction hypothesis assumes that the brain computes a motor plan for the arm as a linear combination of the retinal TT

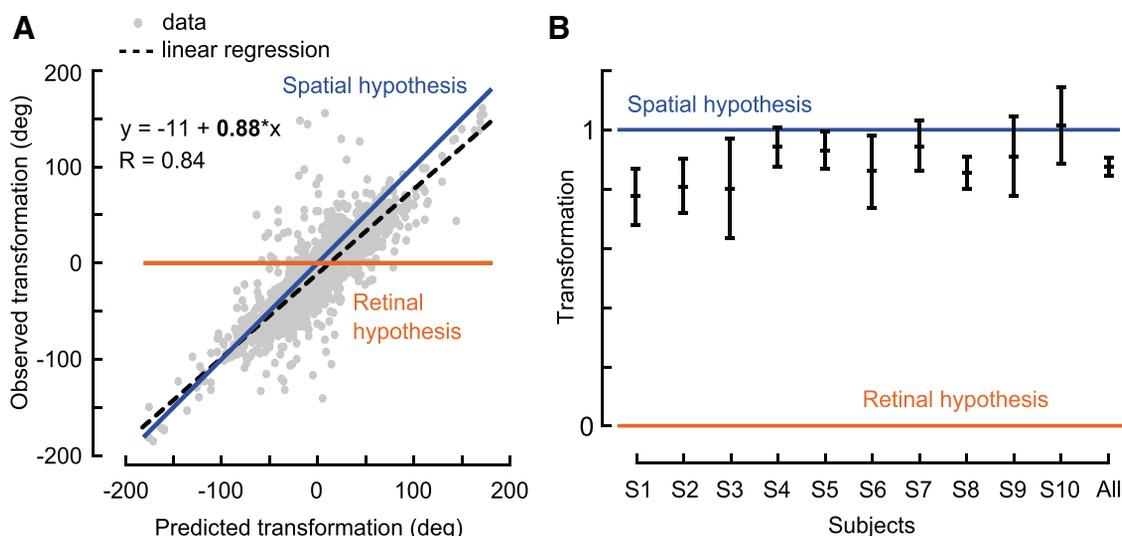


Fig. 5. Quantitative results: observed transformation vs. predicted transformation. A: data (1,382 data points) from all participants are pooled. Individual trials are in gray. A simple linear regression (black dashed line) was fitted. Predictions for the ideal retinal (orange) and spatial (blue) hypotheses are represented. B: transformation slopes (and their 95% confidence interval) are represented for each participant.

direction and the eye velocity direction and that the brain does not use (or does not have access to) the retinal TT and eye speed signals. The direction hypothesis generates a spatially accurate motor plan when the eye and spatial TT speeds are the same (see Fig. 6A, dotted lines). However, when the eye and spatial TT speeds differ, the linear direction is not spatially accurate [see Fig. 6A, dashed (eye speed = 10°/s) and solid (eye speed = 30°/s) gray lines] and thus the predictions for the spatial and direction hypotheses differ. In that case, the predicted transformation can be decomposed into two components (see MATERIALS AND METHODS for more details):

$$\text{predicted transformation} = \text{direction effect} + \text{speed effect}$$

where direction effect is the difference between the retinal direction and the linear direction (see Fig. 6A, vertical green line) and speed effect is the difference between the linear direction and the spatial direction (see Fig. 6A, vertical red line).

In this section, we investigated whether the brain only implemented a linear combination of retinal TT and eye directions or whether it also took the relative speed between eye and retinal TT into account. To investigate whether both effects

were accounted for during manual tracking, we ran a multiple linear regression analysis:

$$\begin{aligned} \text{observed transformation} = & k_0 + k_{\text{dir}} \cdot \text{direction effect} \\ & + k_{\text{speed}} \cdot \text{speed effect} \end{aligned}$$

If both k_{dir} and k_{speed} were equal to zero, this would mean that the retinal hypothesis was implemented (but we showed in the previous section that this is not the case). If $k_{\text{dir}} = 1$ and $k_{\text{speed}} = 0$, this would indicate that retinal TT and eye speeds are not taken into account by the brain (direction hypothesis), while if $k_{\text{dir}} = 1$ and $k_{\text{speed}} = 1$, then the spatial hypothesis would be implemented by the CNS. Across the 10 participants, k_{dir} ranged from 0.77 (S1) to 1.00 (S10) and k_{speed} ranged from 0.76 (S9) to 0.96 (S7) (see Fig. 6B). Both k_{dir} and k_{speed} were significantly different from 0 for each participant [in the worst case, $F(1,119) > 52, P < 0.001$]. For 6 of 10 participants (S1, 2, 3, 5, 6, 8) k_{dir} was significantly smaller than 1 ($P < 0.05$), while k_{speed} was significantly smaller than 1 for 6 participants (S2, 3, 5, 6, 8, 9). These results show that the speeds of the eye and the retinal motion are also taken into account (although not fully) for the planning of manual tracking.

Initial trials and learning. We wondered whether participants had an accurate internal model of the eye kinematics before the experimental session or whether they learned this internal model throughout the session. In the latter case, we would expect that the transformation slope, which measures how much participants compensate for the difference between retinal and spatial directions of TT, was not different from 0 in the early trials of the experimental session. Therefore, for each of 10 participants, we computed the regression slope for the valid trials of the first block. The regression slope varied between 0.71 and 1.02 (the regression was significant, P values were < 0.01) for each participant, indicating that the eye velocity was already taken into account in the first block.

Moreover, we also computed the regression slope for the valid trials of the last experimental block and compared it to the results obtained for the first block. For the last block, the regression slope varied between 0.76 and 1.25 depending on the participant (P values were < 0.01). The regression slope was significantly larger in the last block compared with the first block [repeated-measures ANOVA, $F(1,8) = 9.31, P = 0.016$]. Across subjects, the mean observed compensation was 0.87 during the first block and 0.99 during the last block. This suggests that participants slightly refined their visuomotor transformation internal model such that the compensation was better at the end of the experiment. Moreover, this improvement was observed despite the lack of feedback about the performance of participants at each trial.

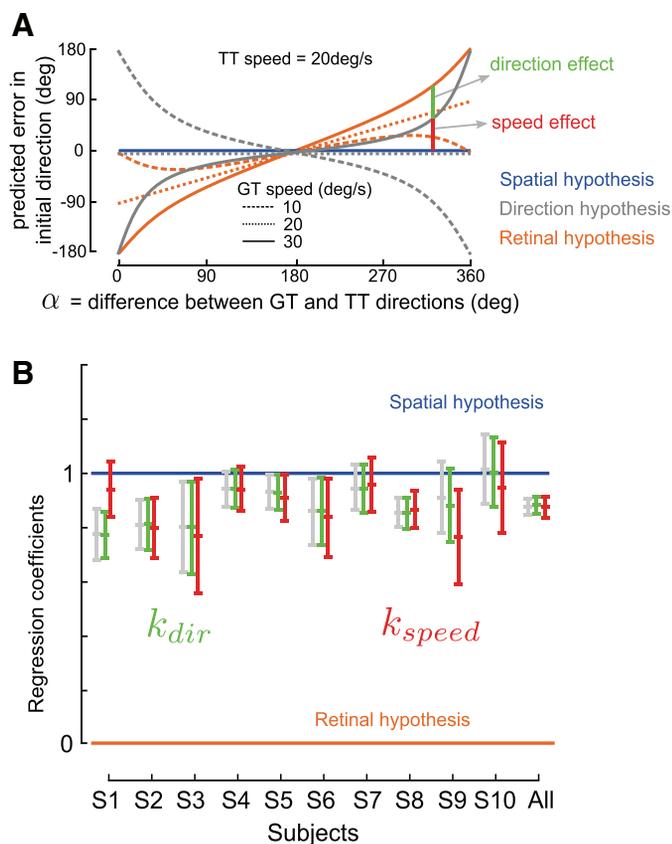


Fig. 6. Compensation for the direction hypothesis effect and the speed effect. A: the retinal hypothesis error (orange curves, see also Fig. 3) and the direction hypothesis error (gray curves) are represented for 3 levels of GT speed: 10°/s (dashed lines), 20°/s (dotted lines), and 30°/s (solid lines). The tracking target speed is 20°/s. The retinal error can be decomposed into 2 components: the direction effect (the part of the error that is taken into account if the brain implements the direction hypothesis) and the speed effect (which is the effect due to different speeds of GT and TT). B: for each participant, regression coefficients (and 95% confidence interval) of the multiple linear regression observed transf = $k_0 + k_{\text{dir}} \cdot \text{direction effect} + k_{\text{speed}} \cdot \text{speed effect}$ are shown. The gray error bars are the transformation slopes from Fig. 5B.

DISCUSSION

The goal of this study was to determine whether an extraretinal signal about eye velocity is taken into account by the brain to plan a manual tracking movement. Indeed, there is a discrepancy between the spatial and retinal motion of the tracking target due to the eye motion. Using a model of the 3D eye kinematics, we computed the direction of the retinal motion as a function of a given spatial motion and eye orientation and velocity (see Fig. 3), showing that this discrepancy can be very large. To compute the motor plan for the arm tracking movement, one strategy for the brain could be to use only the retinal

motion as driving signal (retinal hypothesis), which would lead to large errors in the initiation of the tracking movement. Alternatively, the brain could adequately combine the visual motion (direction and speed) and an eye velocity signal (direction and speed), using an internal model of the eye kinematics in order to generate a spatially accurate motor plan. The brain could also linearly combine the target visual motion direction and the eye direction to compute the motor plan (direction hypothesis). In the latter case, the motor plan would be spatially accurate if the target and eye speeds are the same, but it would lead to large errors if these speeds differ.

We designed a behavioral paradigm in which 10 participants had to manually track a point-like target while they were in steady-state smooth pursuit (tracking another point-like target with their eyes), in otherwise complete darkness. We measured the average direction of the arm movement during the first 100 ms after the arm movement onset (period short enough to ensure that the delayed sensory feedback had not intervened yet; see Desmurget and Grafton 2000) and compared it to the spatial target motion (which was known by experiment design) and the retinal target motion (estimated with the 3D kinematics model outlined in APPENDIX and the measured extraretinal signals about 3D eye orientation and 3D rotational eye velocity). Results showed that all participants compensated for the eye velocity, with a slight undercompensation (transformation slopes comprised between 0.75 and 1.02). In other words, 75–100% of the eye kinematics was taken into account. Therefore this indicates that the neural pathways responsible for the planning of manual tracking integrate retinal motion and an extraretinal eye velocity signal such that they reconstruct a nearly accurate spatial motor plan. Furthermore, we showed that participants compensated for the speed effect (the difference between the eye and target speeds), showing that the brain does not use a simple linear combination of the eye and target motion directions and that it does not neglect the speeds of the target and eye motions.

Visuomotor transformations for motor planning. Several studies have investigated the influence of the complex (nonlinear) 3D eye-head-shoulder geometry on motor planning tasks and whether related 3D extraretinal signals are taken into account (for a recent review, see Crawford et al. 2011). Crawford and Guitton (1997) showed that the brain should take the 3D eye-in-head orientation into account for saccades to be spatially accurate and obey Listing's law. This was experimentally confirmed by Klier and Crawford (1998). The planning of reaching movements toward a static target was also shown to take the 3D eye orientation into account, as well as the 3D head-on-shoulder orientation (Blohm and Crawford 2007), while Henriques and Crawford (2002) and Blohm and Crawford (2007) showed that the offset between the eye and head rotation centers was also accounted for in the planning of pointing movements. These studies investigated the visuomotor transformation for the position pathway. However, it is well established that the visual position and visual motion pathways differ in the brain (Krauzlis 2005), which implies that the visuomotor transformation for motion is perhaps differently processed by the brain. Blohm and Lefèvre (2010) showed that the visual motion is adequately transformed by the brain for the planning of spatially accurate smooth pursuit, using the 3D eye orientation. Later, we showed that visual motion is also combined with extraretinal signals about the 3D eye orientation and

3D head orientation to generate a spatially accurate motor plan for manual tracking (Leclercq et al. 2012). Other studies have investigated the visuomotor transformation for motor planning as a function of the 2D eye velocity (induced by smooth pursuit). Hansen (1979) assessed and found that the 2D eye motion was taken into account in a spatial localization task. Indeed, he recorded spatially accurate pointing movements toward the nonfoveated moving target while the eyes pursued another target. In another study, Blohm et al. (2005) showed that the 2D eye velocity was taken into account by the saccadic system in a spatial localization task toward a flashed stimulus during smooth pursuit, provided that the saccadic latency was large enough (>175 ms), giving time to the brain to integrate the eye velocity information. Saijo et al. (2005) showed that there is a direct involuntary manual reflex response generated by a large-field visual motion stimulus, named the manual following response (MFR). They revealed that this MFR is driven by retinal slip. Here we used a point-like target to drive a manual tracking movement. It is unlikely that point-like visual motion induces a MFR, as to our knowledge this has never been reported in the past. Moreover, our task allowed us to dissociate the retinal and spatial motion of the tracking target, and results showed that the initiation of the arm movement was nearly spatially accurate. Thus it shows that the arm movement that we observe is unlikely to be a MFR but results from the motor plan of a manual tracking movement.

Motion perception during smooth pursuit. In the motion perception literature, many studies have investigated motion perception during smooth pursuit. Studies tend to show that the eye velocity signal is underestimated compared with the retinal motion because the reference frame transformation is not completely performed by the neural network underlying motion perception, which leads to visual illusions like the Filehne and Aubert-Fleischl illusions (see, for example, Freeman et al. 2010; Furman and Gur 2012). But the effect of smooth pursuit on motion perception depends on the observer's task: some experiments reveal an impairment of visual motion perception during smooth pursuit, while other studies show an improvement of the perception performance during smooth pursuit (Bennett et al. 2010; Spering et al. 2011). Perception of visual motion is biased toward the retinal motion of a target (moving in a different direction from the eye), and therefore the compensation for the smooth pursuit eye movement is not complete (Souman et al. 2006; Swanston and Wade 1988). Also, compensation for the eye velocity increases with presentation duration of the target stimulus (Souman et al. 2005b). Perception of complex trajectories is also biased toward retinal motion of the target, and a neural model based on a biased eye velocity signal (80% of its real value) nicely predicts experimental results (Furman and Gur 2005). This is consistent with the degree of compensation that we observe in our motor planning task, with compensation slopes ranging between 0.75 and 1. Some authors argue that the amount of compensation for eye velocity in motion perception is dependent on the retinal direction (Morvan and Wexler 2009), while others claim that the compensation does not depend on the retinal direction (Souman et al. 2005a). In Hansen (1979), the author simultaneously assessed motor planning and motion perception: he found that the arm movement was spatially accurate while motion perception of the "not pursued target" was biased toward the retinal motion. This seems to suggest that motion

perception and motor planning differ at some stage from one another, at least in the way in which the eye velocity is taken into account.

Potential mechanisms explaining observed undercompensation. What are the possible reasons for the consistent undercompensation of the retinal motion induced by the eye movement? The traditional view and first idea that comes to mind is that the brain has access to an inaccurate eye velocity signal (or at least the ratio between eye velocity and retinal velocity is inaccurate). Indeed, if the efference copy of the eye velocity was slightly biased toward a smaller value, this would nicely explain our results. This has also been widely speculated in the motion perception literature (see, for example, Freeman et al. 2010; Furman and Gur 2005, 2012).

Recently, a Bayesian framework has been used to explain the partial compensation for the eye velocity observed in the motion perception literature and that can lead to several visual illusions (Freeman et al. 2010). The key idea is that the undercompensation is due to a difference in precision (in other words, the variability) between the retinal and eye velocities rather than a difference in accuracy. In other words, the results can be explained with sensory estimates that are both unbiased but differently affected by noise. Before being combined, the retinal motion and the eye motion are first separately estimated with a Bayes estimator that combines the likelihood and the prior distribution by assuming that the likelihood is unbiased but with an uncertainty growing with the velocity (see Freeman et al. 2010) and by assuming a Gaussian prior with a mean of 0°/s (preference for slow motion, see Weiss et al. 2002). The prior distribution has, for example, been estimated in Stocker and Simoncelli (2006). The key idea to explain the undercompensation is that the variability of the likelihood for the eye velocity is larger than that for the retinal motion (for a given speed), which leads to estimates of the eye velocity that are more biased by the prior than retinal motion estimates. This framework might also explain our results by slightly adapting it to include the motor noise.

With our paradigm, we cannot decide between these alternatives (or a combination of both), but it would be interesting to investigate this problem by designing an experiment with careful attention paid to the variability measures.

Neuronal correlates. Here we discuss some potential neural areas that could be involved in the visuomotor transformation for manual tracking movements, specifically accounting for eye movements. Two candidates for the implementation of this visuomotor transformation are the lateral and dorsal part of the medial superior temporal area, denoted MSTl (also called MSTv) and MSTd, respectively, which are a well-known stage of visual motion processing. Indeed, MST cell activity (both in MSTl and MSTd) has been shown to be driven by extraretinal eye motion signals even after removal of any visual stimulus (Newsome et al. 1988). Experiments involving a single point-like target tracked along one spatial dimension showed that the neurons of the lateral part of MSTl were modulated by eye and head motion (Thier and Erickson 1992), reflecting that target motion was encoded in spatial coordinates (Ilg et al. 2004). Moreover, using microstimulation and transient inactivation of neurons, Ilg and Schumann (2007) showed that MSTl neurons were involved in the generation of visually guided arm movements toward moving targets. This was confirmed in humans in MT+ (Schenk et al. 2005; Whitney et al. 2007), the putative

human homolog of MT/MST, which is also thought to be subdivided in two regions, similar to MSTl and MSTd (Dukelow et al. 2001). Many studies, for example, in the heading perception literature, have shown that MSTd neurons are modulated by smooth pursuit eye movements (Bradley et al. 1996; Chukoskie and Movshon 2009; Inaba et al. 2007, 2011; Lee et al. 2011; Shenoy et al. 2002) by shifting their receptive field and/or modifying their amplitude. Haarmeier and Kammer (2010) suggested that motion perception during smooth pursuit is supported by a distributed network of brain areas, since TMS applied to individual areas did not affect the motion perception results. This network is located in the parieto-occipital region, as suggested by the motion perception impairments reported in a patient with bilateral lesions in this region (Haarmeier et al. 1997). A similar distributed process is perhaps also involved in visuomotor transformations. Imaging studies also revealed that MT+ is modulated by eye velocity (Dunkley et al. 2011; Goltz et al. 2003).

The transformation could also be carried out at a later stage, in other parts of the posterior parietal cortex (PPC) that receive direct input from areas MT, MSTl, and MSTd. Indeed, in monkeys, several subareas of the PPC are modulated by visual motion: VIP (Colby et al. 1993), LIP (Bremmer et al. 1997b; Eskandar and Assad 2002), 7a (Bremmer et al. 1997b; Merchant et al. 2001), and MIP (Eskandar and Assad 2002). Also, in humans, parietal areas are modulated by visual motion (Konen and Kastner 2008). Moreover, some of these areas (LIP, MIP) receive signals about eye orientation and eye velocity through the thalamus (Prevosto et al. 2009). A portion of the neurons in area 7a and LIP could also be tuned to the direction of smooth pursuit, and their activity might be modulated by 2D eye orientation (Bremmer et al. 1997a; but see O'Leary and Lisberger 2012 for an alternative interpretation). It would be of interest to specifically search for 2D velocity transformations in these brain areas.

Origin of eye velocity signal. In the previous subsection, we discussed potential neuronal areas involved in this visuomotor velocity transformation. One condition is that these regions are modulated by visual motion and eye velocity. However, what is the origin of the 2D eye velocity signal? One possibility is that the internal eye velocity signals stem from a forward model predicting the eye velocity from an efference copy of the motor commands sent to the extraocular muscles, originating from the superior colliculus (Sommer and Wurtz 2002, 2008) or from the brain stem (Prevosto et al. 2009). Another possibility is that the 2D eye velocity signal is derived from proprioceptive eye information (Wang et al. 2007). However, this second alternative is less likely since the proprioceptive signal lags the eye movement itself by a significant delay (Xu et al. 2011) (however, this cannot be ruled out, since in our experiment the eye velocity is known before TT starts moving, because TT moves during the steady-state smooth pursuit phase). Balslev et al. (2012) suggested that the eye proprioceptive signal is more likely used for calibration (when a difference is detected between the efference copy and the actual proprioceptive feedback).

In conclusion, the brain uses a signal about the 2D eye velocity to plan spatially (almost) accurate manual tracking movements. The CNS integrates the retinal motion direction and speed with the eye velocity direction and speed, thus adequately combining them to generate the motor plan.

APPENDIX

We built a mathematical model to compute the tracking target velocity in retinal coordinates from the knowledge of TT velocity in spatial coordinates and the 3D eye orientation and rotational velocity measurements. We needed to estimate TT retinal velocity since we were not able to directly measure it. We also expressed the inverse model, which computes the tracking target velocity in spatial coordinates from the knowledge of the extraretinal inputs and TT retinal velocity. This allows us to simulate the transformation that the brain should implement were it to be spatially accurate.

Formalism. The kinematic model is implemented with the dual quaternion approach as described extensively in Leclercq et al. (2013). This formalism has been used previously in sensorimotor neuroscience articles (Blohm and Crawford 2007; Leclercq et al. 2012). In short, dual quaternions can easily represent 3D rotations, translations, or screw motions and their derivatives and provide a compact way to express the 3D kinematics of points or lines. For example, we construct a rotation dual quaternion from the rotation angle and the rotation axis.

The position of a point P in a retinal reference frame, P^{ret} , is represented by the dual quaternion

$$P^{ret} = 1 + \epsilon P^{ret}$$

where P^{ret} is the 3D vector representing the position of P in a reference frame centered on the eye and fixed with respect to the eyeball. ϵ is the dual operator for dual quaternions; it has the property that $\epsilon^2 = 0$. The velocity of point P , expressed in a retinal reference frame, is encoded as a dual quaternion as

$$\dot{P}^{ret} = 0 + \epsilon \dot{P}^{ret}$$

Moreover, the point conjugate of a dual quaternion $DQ = Q_0 + \epsilon Q_1$ is denoted DQ^* and is equal to $DQ^* = Q_0^* - \epsilon Q_1^*$, where Q_0^* is the classical quaternion conjugate: for a quaternion $Q = q_0 + \mathbf{q}$, the quaternion conjugate is $Q^* = q_0 - \mathbf{q}$, where q_0 is the scalar component of the quaternion and \mathbf{q} is the bivector component of the quaternion. More details (like the dual quaternion multiplication) on the dual quaternion formalism and its advantages can be found in Leclercq et al. (2013).

Retinal velocity model. With this dual quaternion formalism, retinal TT velocity, denoted $\dot{T}T^{ret}$, may be computed with the following model equation:

$$\dot{T}T^{ret} = R_{EH} \dot{T}T^{spat} R_{EH}^* + \frac{1}{2} R_{EH} (\Omega_{EH} \dot{T}T^{spat} - \dot{T}T^{spat} \Omega_{EH}) R_{EH}^* \quad (A1)$$

where R_{EH} is a rotation dual quaternion that represents the 3D eye-in-head rotation, Ω_{EH} is a dual quaternion representing the 3D eye-in-head rotational velocity, $\dot{T}T^{spat}$ is the tracking target location in spatial coordinates (the reference frame origin is the center of the eye), and $\dot{T}T^{spat}$ is the tracking target velocity in spatial coordinates. The first term of Eq. A1 depends on TT velocity in spatial coordinates and the current 3D eye orientation, while the second term depends on the 3D eye rotational velocity and also on TT position in spatial coordinates. We can also easily compute the retinal TT position with

$$T T^{ret} = R_{EH} T T^{spat} R_{EH}^* \quad (A2)$$

This expression will be of importance in the following. In practice, the 3D eye-in-head rotation dual quaternion, R_{EH} , is determined by the 3D eye measurements. The video-based eye-tracker system provides for the 3D eye-in-head rotation in Fick coordinates (horizontal, vertical,

and torsional components). Then we compute the single rotation angle and rotation axis, from the Fick coordinates (see Haslwanter 1995; Leclercq et al. 2013), and finally the rotation dual quaternion. For the eye-in-head rotational velocity dual quaternion, Ω_{EH} , we apply the formula (Hestenes 1994; Leclercq et al. 2013)

$$\dot{R}_{EH} = \frac{1}{2} R_{EH} \Omega_{EH} \quad (A3)$$

In practice, we first compute R_{EH} from the measurements, as described above. Then we numerically differentiate it to obtain \dot{R}_{EH} , and we then compute Ω_{EH} with formula A3.

Spatial velocity model. The inverse model computes TT spatial velocity, $\dot{T}T^{spat}$, from the knowledge of TT retinal position and velocity, as well as the 3D eye-in-head rotation R_{EH} and rotational velocity Ω_{EH} .

$$\dot{T}T^{spat} = R_{EH}^* \dot{T}T^{ret} R_{EH} + \frac{1}{2} (\dot{T}T^{spat} \Omega_{EH} - \Omega_{EH} \dot{T}T^{spat}) \quad (A4)$$

where

$$T T^{spat} = R_{EH}^* T T^{ret} R_{EH} \quad (A5)$$

This model mimics the visuomotor transformation that the brain has to carry out for the motor plan to be spatially accurate, transforming the retinal input into a spatial motor plan. Therefore, using this mathematical model, we can test various assumptions about the extraretinal signals. For example, what would be the motor plan computed by the brain if the internal 2D eye velocity signal was biased (e.g., $0.8 \times$ real 2D eye velocity)? This is easy to test by scaling Ω_{EH} by a factor of 0.8.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: G.L., G.B., and P.L. conception and design of research; G.L. performed experiments; G.L. analyzed data; G.L., G.B., and P.L. interpreted results of experiments; G.L., G.B., and P.L. prepared figures; G.L., G.B., and P.L. drafted manuscript; G.L., G.B., and P.L. edited and revised manuscript; G.L., G.B., and P.L. approved final version of manuscript.

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