

Movement prediction and movement production

Mark Wexler and François Klam

Laboratoire de Physiologie de la Perception et de l'Action
Collège de France, 11 pl. Marcelin Berthelot, 75005 Paris, France

Abstract

The prediction of future positions of moving objects occurs in cases of actively produced and passively observed movement. Additionally, the moving object may or may not be tracked with the eyes. We studied the difference between active and passive movement prediction by asking observers to estimate displacements of an occluded moving target, where the movement was driven by the observer's manual action, or passively observed. In the absence of eye tracking, we found that in the active condition estimates are more anticipatory than in the passive conditions. Decreasing the congruence between motor action and visual feedback diminished but did not eliminate the anticipatory effect of action. When the target was tracked with the eyes, on the other hand, the effect of manual action disappeared. Our results indicate distinct contributions of hand and eye movement signals to the prediction of trajectories of moving objects.

Introduction

How do we predict the future trajectories of moving objects? Formally, the problem is ill-defined and does not admit a unique solution; but in practice, people constantly engage in this type of inductive process: witness one's surprise at a fast-moving object that goes behind a small occluder and fails to re-emerge after the expected delay.

From the point of view of a particular observer, object movement may be categorized into two broad types: actively caused and passively observed. Categorizing more finely, actively caused object movement may be direct—movement of a manipulandum that is spatially and temporally similar to the movement of the manipulating limb—or indirect—an object that, due to some mediating mechanism, follows a different path than the manipulator. Additionally, an observed moving object may or may not be tracked with the eyes. Here, we examine the consequences of these forms of object movement on the prediction of future positions of a moving target.

The prediction of movement has been studied separately in the case of motor action (mainly in the case of manual and ocular movement), and in the case of visually observed motion. Before introducing our experiments, we briefly review some of these results. We then present two experiments, whose goal is to compare the dynamics of the prediction process in the actively produced and passively observed movement.

Sensorimotor prediction

Although efferent-copy theories of motor control have existed for at least a century (Helmholtz, 1867; Holst &

Mittelstaedt, 1950; Sperry, 1950), it is only recently that we have come to appreciate the importance of the prediction of sensory results of motor actions—to be called *sensorimotor prediction*—in normal human motor planning and execution. Indeed, any motor system making use of sensory feedback data and where feedback delays are sizeable compared to output delays must supplement actual sensory feedback with predicted feedback, based on an estimate of current state and the motor command simultaneously being planned or executed. Lack of prediction would lead to instabilities and grossly inaccurate actions. Such a predictor, based on current state information and motor commands, is called a *forward model*.

As Wolpert, Ghahramani and Jordan (1995) point out, sensorimotor anticipation could have the following uses: compensation for delayed sensory feedback; cancellation of sensory effects due to self-produced movement; and the covert trying out of possible actions, to be used, for example, in motor planning. The past decade has seen an accumulation of direct neurophysiological evidence of neurons or neural ensembles in mammalian brains that are linked to the prediction of the sensory consequences of the animal's action. In the case of locomotion, O'Keefe and Recce (1993) found that the activation packet of place cells in the hippocampus of rats, believed to represent the animal's current position on a 'mental map', underwent oscillations during which it periodically anticipated the current position and transiently represented future positions on the animal's path. In the case of manipulation, Eskandar and Assad (1999) have found cells in the posterior parietal cortex of macaques that seemed to encode the predicted visual trajectories of occluded targets whose movement was under the animal's control.

In a task similar to one of the conditions in the experiments reported here, Wolpert et al. (1995) found that subjects overestimated the extent of unseen arm movements, and that this systematic bias had a very specific temporal dynamics: it initially increased, peaked at about one second of movement duration, and then decayed. The growth phase is interpreted as being due to the application of a forward model (with a gain that is greater than one, although that is a free parameter), followed by a correction toward zero bias

* We are grateful to Jacques Droulez for his encouragement and support. We would like to thank Isabelle Israël and Isabelle Siegler for lending us their eye tracker, and for patiently explaining its use.

Correspondence concerning this article should be addressed to: Mark Wexler, e-mail: wexler@ccr.jussieu.fr

due to proprioceptive feedback. Wolpert et al. postulated a model composed of a predictive mechanism that accepts as input an estimate of current state as well as the efferent copy of current motor commands; this predictor is coupled to a system that stores the current state estimate. Recent neurophysiological evidence points to the cerebellum as a possible site of this predictive mechanism (Blakemore, Wolpert, & Frith, 1998). Neuropsychological evidence suggests that a representation of the current state estimate may be stored in posterior parietal cortex (Wolpert, Goodbody, & Husain, 1998), while the results of Eskandar and Assad (1999) indicate that, at least in macaques, posterior parietal cortex may already encode predictions.

Sensorimotor prediction has been posited as a mechanism driving higher-level, cognitive functions as well. Rieser, Guth and Hill (1986) found that locomotion even in the absence of vision aided in the egocentric re-representation of spatial layout. Such visuomotor updating during locomotion could rely on the neural mechanisms documented by O'Keefe and Recce (1993). In a two-task interference study, Wexler, Kosslyn and Berthoz (1998) found that a manual rotation made a concurrent mental rotation of a visual image faster and more accurate if the two rotations were in the same direction, slower and more error-prone if they were in opposite directions; moreover, when the two rotations were in the same direction, faster motor rotation tended to speed up the mental rotation, while slower motor rotation tended to slow it down. Based on these and other correlations, Wexler et al. (1998) concluded that mental rotation must make use of some mechanisms of the motor system, most likely visuomotor prediction (for similar results, see Wohlschläger and Wohlschläger, 1998).

Eye movements and the prediction of motion

Eye movements and their underlying neural mechanisms exhibit a variety of predictive effects. Particularly clear evidence is provided by the study of Duhamel, Colby and Goldberg (1992), which documented cells in the monkey parietal cortex that shift their receptive fields in the anticipation of eye saccades. This mechanism could help the animal distinguish visual motion due to gaze shifts from that due to external object movement, and would contribute to stabilizing the visual world in the presence of an unstable retinal image during eye movements.

The dynamics of eye movements in mammals demonstrates their predictive nature. In the smooth pursuit of a visual target that suddenly changes position or speed, for instance, Barnes and Asselman (1992) found that tracking at the target's old speed continued for a short time after the trajectory change. This phenomenon can be regarded as a prediction by the oculomotor system of the target's trajectory, based on past data. Saccadic mechanisms also seem to feature predictive properties, as demonstrated by the results of Duhamel et al. (1992) in monkeys.

Eye movements, especially the smooth pursuit system, seem to share mechanisms with conscious speed perception, as demonstrated by numerous details of precision and systematic bias that the two have in common (Post & Leibowitz, 1985; Kowler & McKee, 1987; Beutter & Stone, 1998; Watamaniuk & Heinen, 1999). Haarmeier, Thier, Repnow and Petersen (1997) have described a patient who, apparently lacking efferent copy of eye movement commands, perceives motion opposite to his eye

movements. Even in the absence of any neurological disorder, anticipatory motion compensation during saccades induces brief misjudgments of position (Cai, Pouget, Schlag-Rey, & Schlag, 1997).

Eye movements have also been found to modulate visual trajectory extrapolation. Nijhawan (1994; 1997) found that the perceived position of a target moving with respect to the retina was extrapolated along its trajectory. If the target was tracked with the eyes, on the other hand, the effect disappeared (Nijhawan, 1997).

Information about manual movements seems to drive anticipatory eye movements. For instance, Steinbach and Held (1968) found that the tracking an object that is actively displaced by the observer was more accurate and smooth than tracking a passively observed moving object. Even when no active manipulation of the visual target is involved, eye movements may be especially attuned to biologically produced motion, as compared to more general dynamics. de'Sperati and Viviani (1997) found that tracking a visual target moving around an ellipse was more efficient if the speed profile followed the so-called 2/3 power law, which is actually the profile produced by human subjects making elliptical hand movements when asked to do so at a constant speed.

Eye movements are thus involved in the perception and prediction of movement. Because of their interaction with manual movement (Steinbach & Held, 1968), the presence or absence of eye movements could have a different effect on actively produced than on passively observed motion.

Passive movement prediction

In a separate and widely dispersed body of work, the prediction of the outcome of passively observed movement has also been studied. The typical protocol that has been used is a target moving in a straight line at a constant speed from point *A* to point *B*, and then disappearing behind an occluder. The subject's task is to press a button when the target is extrapolated to pass behind a marked point, *C*.

Slater-Hammel (1955) found that subjects typically overestimated t_{BC} , the time to travel between points *B* and *C*, by 10 – 20%. In a fixed-speed paradigm, it was found that the overestimation of t_{BC} increased with increasing distance *BC*, but that the subjective speed in the occluded region (i.e., BC/t_{BC}) increased, approaching its veridical value as *BC* increased. The visible distance *AB*, however, had no effect on the predictions, in the range of parameters studied by Slater-Hammel. Ellingstad (1967) varied the target speed and found a similar underestimation of speed for the faster-moving stimuli (7.26 and 1.46°/sec in terms of visual angle), but an overestimation of speed for slower-moving stimuli (0.36°/sec). Bonnet and Kolehmainen (1970) also found that relative speed in the occlusion phase was underestimated in fast-moving stimuli as compared to slow-moving ones; these authors also found an effect of the visible phase, namely that for longer distances *AB*, the relative speed was underestimated as compared to shorter visible distances. Rosenbaum (1975) studied the prediction of both constant-speed and constant-acceleration trajectories, and presented his results in terms of correlations between objective and subjective speeds and accelerations, and the other kinematics parameters; he found that subjective speeds and accelerations were highly correlated with their objective equivalents, but not with time and distance intervals taken

separately. Peterken, Brown and Bowman (1991) varied the time and space variables systematically and independently; they found that the important variable was the time interval t_{BC} over which the prediction is made, with longer prediction intervals leading to predictions that underestimated the target's displacement. Additionally, Peterken et al. studied the effect of eye movement during the prediction task, introducing a stationary fixation as well as a visual pursuit condition; no significant effect of this manipulation was found.

Prediction of observed movement is not only possible, but in some cases is unconscious, effortless and mandatory, as shown by the so-called 'representational momentum' phenomenon (Freyd, 1987). When an observer watches an object undergoing apparent motion, the memory for the final seen position is contaminated by an extrapolation along the object's apparent trajectory. This involuntary extrapolation shares some characteristics of physical motion: it advances farther for higher initial speeds and for longer time intervals, and appears to slow down and come to rest after a short interval (under 1 sec). This type of involuntary extrapolation is not confined to apparent motion, but can be observed in a variety of illusions in which a moving object appears to be farther advanced than a stationary one (e.g., Müsseler & Aschersleben, 1998; Nijhawan, 1994, 1997).

Visual extrapolation, motor prediction and our experiments

As we have seen, visual motion extrapolation has predominantly been studied in passive viewing conditions. Correspondingly, explanations for these phenomena have been sought in purely visual mechanisms. For instance, Nijhawan attributed extrapolation to an "early visual operation," and added that "the retinotopic site in the cortex maximally activated by a moving object at any given instant is the same as would be activated by a stationary object located where the moving object is at that instant" (Nijhawan, 1997). Representational momentum, another form of motion extrapolation, has been assumed to be a property of higher-level visual representations (Freyd, 1997). On the other hand, we also know that motor and visuomotor mechanisms seem to be endowed with predictive properties (Wolpert, Ghahramani, & Jordan, 1995; Blakemore, Goodbody, & Wolpert, 1998; O'Keefe & Recce, 1993; Eskandar & Assad, 1999). Indeed, an important use for visual extrapolation would be in planning motor actions towards rapidly moving objects (Nijhawan, 1994).

The goal of our work is to search for a connection between visual extrapolation and motor prediction. Concretely, we ask whether the prediction of the trajectory of a moving object depends on whether the object is actively being displaced by the observer, as opposed to being passively observed. In our experiments, active displacement was via manual rotation of a knob that displaced a temporarily occluded visual target on a computer screen; the visual movement was congruent (rotation-rotation, Experiment 1) or incongruent (translation-rotation, Experiment 2) to the motor movement. In our principal passive control condition, the visual target followed a spatio-temporal trajectory identical to one in a preceding active trial, with the only difference that the observer did not actively generate the target's movement. A difference

between the properties of the predictions made in the active and passive conditions would signify a motor contribution to visual extrapolation, whereas similar predictions in the two conditions would signify that visual extrapolation is a low-level visual process, impermeable to outside signals, such as those coming from the motor system.

Even in the passive condition, the observer was not wholly passive, as he or she could engage in eye movements such as pursuit. In our studies we also investigated the effect of eye movements on prediction by introducing separate fixation and pursuit conditions in Experiment 2, and by measuring eye movements in both experiments.

General methods

In both experiments, trials were of two types, active and passive. In the active, 'motor' condition (called MOT), the participant turned a knob, which caused the visual displacement of an arrow on the computer monitor. In Experiment 1, the arrow rotated about its center, 1 degree for every degree of motor rotation. In Experiment 2, the arrow underwent a translation from right to left as the knob was rotated. In the passive conditions, the participant watched the visual displacement without turning the knob. In the principal, 'replay' passive condition (REP), the arrow followed a spatio-temporal trajectory identical to that of a previous MOT trial. In the 'linear' passive condition (LIN), the arrow followed a constant-speed trajectory that is a linear approximation to a previous MOT trial. The reason for introducing the LIN condition was to evaluate whether any differences between the active MOT and passive REP conditions were due to the lack of motor action in the REP case, or simply to the possibly unpredictable variations in speed in the passive conditions.

All trials consisted of three phases. In the initial, visible phase, the moving arrow could be seen. In the second, occlusion phase, the arrow disappeared and remained invisible. The participants were instructed to nevertheless estimate the arrow's trajectory during the occlusion phase. In the final phase, the target was briefly flashed on the screen; its angular or linear position was shifted relative to the position it would have had had it remained visible throughout the occlusion phase. The participants' 2-alternative forced choice (2AFC) 'trajectory-prediction' task was to determine whether the shift direction was forward or backward with respect to the target's displacement direction (i.e., whether the flashed position was shifted ahead or behind the target's estimated orientation or position at the time of the flash). The sequence of phases is represented graphically in Figures 1 and 5. The amount of transport during the occlusion phase was unpredictable until the flash (i.e., there was no visible occluder).

The reason for using the 2AFC paradigm, rather than a more direct time-based response method of the type discussed in the Introduction, was to avoid interference between two motor tasks in which timing is crucial (e.g., displacing the target with one hand and pressing a button with the other when the occluded target is thought to pass a marker).

Eye movements of several participants were recorded while they were performing the tasks of Experiments 1 and 2. These eye movement recordings were performed in separate blocks.

Stimuli

The visual stimulus consisted of an arrow 4.5 cm long and 1 cm wide drawn on a computer monitor. The arrow was drawn as a white, 1 mm-wide antialiased outline on a black background.

In the MOT condition, the movement of the arrow was controlled by the participant's rotation of a knob (the details of the movement are given in the individual Methods sections of Experiments 1 and 2). Participants were free to rotate at any speed, and were instructed to use whatever speed was most comfortable. In the passive REP condition, the trajectories were frame-by-frame replays of previous MOT trials. Trajectories were sampled and displayed at 75 Hz. In the other passive condition, LIN, trajectories were constant-speed approximations to previous MOT trials, with the speed in the LIN trial equal the mean speed in the MOT trial. On a typical MOT trial, participants took several seconds to begin the motor rotation. In order not to 'dilute' the speed of the corresponding LIN trial by this dead time, the computation of the mean speed began only after the participant turned the manipulandum by a 3 deg 'trigger angle'. The mean speed is therefore computed as total angle starting from the 3 deg trigger, divided by total time starting from the trigger time. The LIN trajectory was composed of two constant-speed segments: the arrow was stationary up until the trigger time of the corresponding MOT trial, and thereafter was displaced at the constant speed.

In the visible phase, the target remained on the screen during the first 45 deg of the motor rotation (MOT condition), or the simulated equivalent (REP and LIN conditions).¹ In the occlusion phase the target was no longer displayed. This phase lasted while the knob was turned further by an amount which we shall call the *transport angle*, which took the values 30, 60 and 90 deg. Immediately following the occlusion phase the target briefly reappeared, displaced from the angle of disappearance by the transport angle plus the *deviation angle*, which took the values ± 10 , ± 30 , ± 50 , and ± 70 deg.² Perfect performance on the trajectory prediction task would thus have been to respond "behind" for negative values of the deviation angle, and "ahead" for positive values. The target flash lasted for one monitor frame; its actual time on the screen was therefore approximately equal to the decay time of green phosphor (as red and blue phosphor decay much faster), about 10 msec.

¹ All displacements, both motor and visual, are given in terms of motor or simulated-motor rotations. In the active MOT condition, this is just the angle by which the participant turned the knob. In the passive conditions (REP, LIN), a motor trajectory was visually simulated, either by an exact replication of a previous trajectory in a MOT trial (REP), or by a constant-speed approximation (LIN). Displacements in the passive conditions are given in terms of angles of the simulated trajectories. In Experiment 1, a motor or simulated-motor rotation of one degree yielded a visual rotation of one degree. In Experiment 2, a motor or simulated-motor rotation of one degree yielded a visual translation of 0.09 cm.

² Positive angles signify clockwise, i.e., the direction of rotation.

Active (MOT) trials were preceded by a verbal instruction to "turn," while passive trials (REP, LIN) were preceded by an instruction to "watch."

Apparatus

Visual display

Stimuli were displayed on a Nokia 447X monitor, set at a resolution of 0.03 cm/pixel. The vertical refresh frequency was 75 Hz. The size of the display area of monitor was 31.2 x 23.5 cm. Participants sat at a comfortable distance from the screen, typically around 50 cm away.

Manipulandum

In the MOT condition, the participant moved the visual target by turning a knob with his or her right hand. The knob was located to the right of the screen and covered by an opaque barrier, so that participants could see neither the knob nor their hands during the motor rotations. The knob's face was parallel to the computer screen (so its axis of rotation was perpendicular to the screen), and approximately 5 cm in diameter. The rotation data from the knob had a resolution better than 0.1° , and was sampled at the display frequency.

The knob was always turned clockwise, with all fingers of the right hand. Participants were instructed to rotate as smoothly as possible up to the time of the flash. To this end, participants were instructed to 'wind their hands up' counter-clockwise as much as possible before beginning the motor rotation, in order to avoid have to re-grip the knob.

Participants gave their responses in the trajectory prediction task using two buttons of a computer mouse, using the left hand.

Eye movement measurements

The eye movements of two participants were monitored using a Skalar Iris infrared reflecting eye tracker. The eye position data were sampled at the same frequency as the display monitor, 75 Hz. In the eye movement blocks, participants' head movements were restrained by means of a bite board, with the eyes at approximately 50 cm from the monitor screen. The Iris was operated in binocular position mode, with both eyes set either for horizontal or for vertical readings. The voltage readings were converted into fixation positions on the monitor by means of a calibration procedure performed periodically in which a sequence of points (radius 1 mm) was shown to the participant, who fixated each one and, while fixating, clicked a computer mouse. A least-squares fit was performed separately for the reading from each eye, where the screen position was fit as a cubic polynomial in the voltage output of the eye tracker. This gave two separate estimates of screen fixation position, which were arithmetically averaged into one final estimate in order to further reduce noise. To control for drift resulting from small head movements, an additional calibration was performed immediately prior to each trial, with just one point; the difference between estimated and actual positions of the point was added to the calibration polynomials for the subsequent trial. The RMS error of this procedure was calculated following each calibration by presenting an additional series of fixation points not used for the calibration itself. By comparing predicted and actual screen

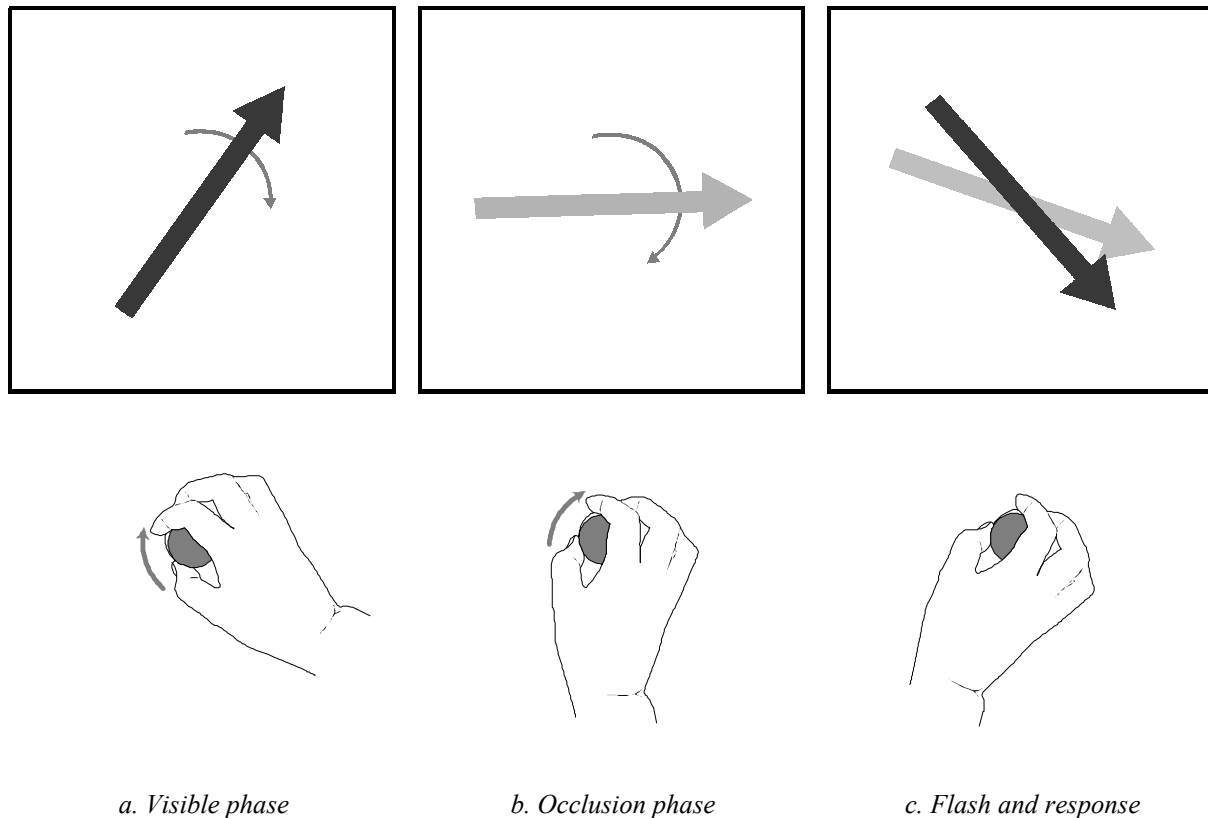


Figure 1. Illustration of the three phases of Experiment 1. The top panel shows the visual stimulus, while the bottom panel shows the simultaneous manual action in the MOT condition. Only the black arrow was visible, while the gray arrow shows a participant's possible estimate of the position.

fixation, mean error in horizontal and vertical fixation position was estimated to be between 3 and 5 mm.

Eye movement traces were scanned manually for artifacts due to blinks. In the few cases in which blinks occurred during significant phases of the trial (less than 5% of all trials), the artifacts were removed and replaced by a linear interpolation of the trace. Saccades were identified using an automated algorithm based on the following criteria. We first applied a Gaussian low-pass filter (cutoff frequency 30 Hz) in order to reduce noise in subsequent velocity and acceleration calculations. Three criteria were applied to identify saccades: 1) eye acceleration had to exceed 500 deg/sec^2 ; 2) saccade peak velocity had to be above 20 deg/sec ; and 3) saccade amplitude had to exceed 0.5 deg .³ All three criteria had to be met for saccade identification.

Design

In order to prevent learning or sequence effects, the experiments were run in blocks. Each block was composed

³ Our eye movement recordings were expressed in centimeters on the computer monitor, which is the form in which they will be analyzed below. They were converted into angular form only for the purposes of the saccade detector. The output of the saccade detector was verified by hand against actual eye movement traces, and was found to be satisfactory.

of one factorial realization of 3 transport angles (30, 60, 90 deg) x 8 deviation angles (± 10 , ± 30 , ± 50 , $\pm 70 \text{ deg}$) x 3 conditions (MOT, REP, LIN); the MOT condition was repeated twice, however, for a total of 96 trials per block. The first half of each block (48 trials) consisted of the trial sequence MOT, LIN, MOT, LIN, ..., with the speed in each LIN trial calculated from the preceding MOT trial. The second half of each block consisted of the sequence MOT, REP, MOT, REP, ..., with each REP trial being a replay of a MOT trial in the *first* half of the block. The reason for this staggered design was to prevent recognition of REP trajectories from corresponding MOT trials. Thus, half of the MOT trials (the first half of such trials in each block) had exactly matched control (REP and LIN) trials; the other half of the MOT trials did not, but they were an identical replication of the first half.

Each participant performed 6 blocks, for a total of 576 trials. The alternating active and passive trials within each block were intended to prevent any confounding of the active/passive factor with learning effects. The overall blocked design, with passive trials alternating between LIN and REP conditions, was intended to prevent confounding passive trial type with learning effects.

Experiment 1

The goal of Experiment 1 was to compare the prediction of visual motion in the case when the motion is actively produced to the case where it is passively observed. In the

Phase	Condition	Duration (sec)			Mean speed (deg/sec)		
		Transport angle			Transport angle		
		30°	60°	90°	30°	60°	90°
Visible	MOT, REP	0.63	0.60	0.61	118.5	119.8	118.4
	LIN	0.74	0.74	0.76	108.1	107.4	106.3
Occlusion	MOT, REP	0.50	1.02	1.64	127.7	117.8	106.7
	LIN	0.49	0.97	1.51	119.5	118.6	117.0

Table 1. Mean durations and speeds of the visible and occlusion phases.

active condition of this experiment (MOT), the motor action was congruent to the visual motion: both are rotations, with a visuo-motor gain of 1 (that is, for every degree of motor rotation of the manipulandum, the visual target also rotated by 1 degree).

Method

Stimuli

The sequence of each trial is illustrated schematically in Figure 1. The bottom panel shows the motor action in each of the three phases (in the MOT condition), while the top panel shows the concurrent visual stimulus. In the top panels, only the black arrow corresponds to the actual stimulus; the gray arrow is an illustration of a participant's possible estimate of the arrow's orientation during occlusion.

Each trial began with the arrow at a random orientation, with its center at the center of the computer screen. Subsequently, the arrow rotated clockwise about its center, turning 1 deg for every degree of motor (MOT condition) or simulated motor (REP, LIN) rotation.

Eye movement recordings

Participants received no specific instructions relative to eye movements. In order to compare the data of Experiment 1 with those of Experiment 2, where subjects did receive explicit eye movement instructions, we recorded the eye movements of two participants in the main experiment in separate sessions. A reduced version of the experimental design was used in the eye movement sessions, with two transport angles (30, 90 deg), six deviation angles (± 10 , ± 30 , ± 50 deg) in the three conditions (MOT x 2, REP, LIN), for a total of 48 trials. In the first 24 trials horizontal gaze position was recorded (i.e., the Iris eye tracker was in horizontal mode), while vertical position was recorded in the last 24 trials.

The horizontal and vertical recordings were preceded by calibrations, as described in the General Methods section. The calibrations consisted of 7 fixation points, positioned at 0, ± 1.2 , ± 2.4 , ± 3.6 cm, either on the horizontal axis centered at the origin in horizontal mode, or on the vertical axis in vertical mode. Each point was repeated 3 times, and points were presented in random order.

Participants

Ten unpaid volunteers (5 men and 5 women, mean age 29 years) served as participants. All had normal or corrected-to-normal vision and no known motor deficits. All participants were self-reported as right-handed, and used their right hand

in the motor task. Participants were naive as to the purpose of the experiment. After a practice block of 20 trials, each participant performed 576 trials in two sessions that lasted approximately one hour each.

Two of the above participants (1 man, 1 woman, ages 23 and 33 years, respectively) also performed separate sessions in which eye movements were recorded. The eye movement sessions were conducted several months after the main sessions.

Results

Trials in which either the duration of the occlusion phase, the combined duration of the visible and occlusion phases, or the response time exceeded 10 sec were eliminated from further data analysis; 0.9% of all trials were thus eliminated.

Trajectories and timing

Before giving the results of the main prediction task, we shall briefly present the timing and trajectory details. In the active MOT trials participants were free to perform the motor rotation at any speed, which resulted in variation in the durations of the different phases of the trial. The passive trials followed the MOT trials in mean angular speed (LIN) or trajectory (REP), so the variations in the active condition had an effect on the passive trials. Table 1 lists the mean durations and speeds of the initial visible and occlusion phases for the MOT and LIN trials (the REP trials are of course identical to MOT).

The trajectories in the MOT trials (and therefore in REP) typically consisted of an acceleration followed by a deceleration, which can be seen as a higher speed in the occlusion phase than in the visible phase for the short trials (transport angle 30°), about equal speeds in the medium trials (60°), and a slowing down in the longest trials (90°).⁴

⁴ It may seem surprising that durations in the LIN condition are somewhat longer in the visible phase than in the other two conditions, and somewhat shorter in the occlusion phase. This is due to the fact that, in MOT and REP trials, there was on the average an acceleration in the visible phase, and either no net acceleration or a deceleration in the occlusion phase.

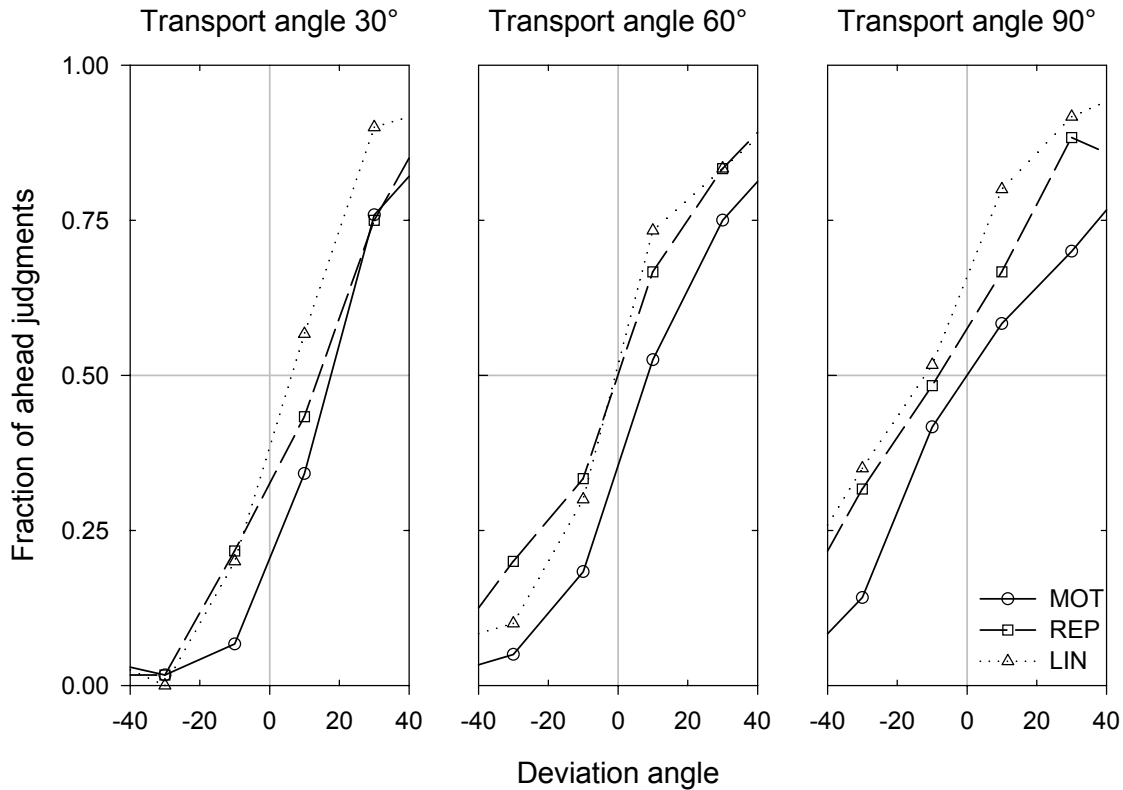


Figure 2. Mean response (fraction of responses that the probe was too far advanced) as a function of deviation angle from its true position, for the three transport angles and three conditions. Data are averaged over all participants. All angles are in degrees, with positive angles in the direction of rotation (clockwise).

Effect of movement condition and transport angle

We now turn to results of the prediction task. We can recover the participant's estimate or prediction bias by analyzing the response as a function of deviation angle. We define the response in a given condition as a fraction of trials for that condition in which the participant responded that the probe was "too far advanced." Thus, for all the transport angles, the ideal result would be a response of 0 for negative deviation angles (for which the probe was shifted backwards from its true orientation), and 1 for positive ones (for which the probe was shifted forwards).

The mean response of the ten participants for the three transport angles and in the three conditions is shown in Fig. 2. We note several features of these data. First, for all three transport angles, the MOT curve is almost everywhere to the right of the REP and LIN curves. This means that the participants' estimates of the position of the probe were farthest advanced in the active, MOT condition, and relatively retarded in the two passive conditions, REP and LIN.⁵ Second, in all three conditions the estimates became

more retarded (i.e., the bias decreased) as the transport angle increased. Finally, and not unexpectedly, the width of the curves (i.e., the span of their transition regions) increased at larger transport angles; in other words, as the estimation duration increased, the responses became more variable.⁶

To quantitatively determine individual participants' biases, we performed a logit fit of the response as a function of deviation angle, separately for each combination of participant, motor and transport angle factors, and then averaged over participants. The bias is defined as the deviation angle at which the fitted logit function crosses 0.5, while the width is the difference between the deviation angles at 0.75 and 0.25. Cases where either the absolute

⁵ A note on terminology. A "displacement bias" or just "bias" refers to the error of the displacement estimate with respect to the actual displacement; thus, if the target turned by 60° during the occlusion phase, but the subject's mean

estimate of its displacement is 70°, we shall say that the bias in this condition is +10°. We employ the terms "advanced" and "retarded" to describe estimates of target displacement that are superior and inferior, respectively, to the actual displacement during the occlusion phase (i.e., mean biases that are positive and negative, respectively). We also use the terms in a relative sense: a bias or estimate that is "more advanced" is one that is more positive, for example.

⁶ Recall that half of the MOT trials had exactly matched LIN and REP controls, while the other half did not; otherwise, the two halves were the same. As expected (since the two groups differed in no way for the subject), there was no significant effect of the control factor. We therefore included both groups in the MOT data.

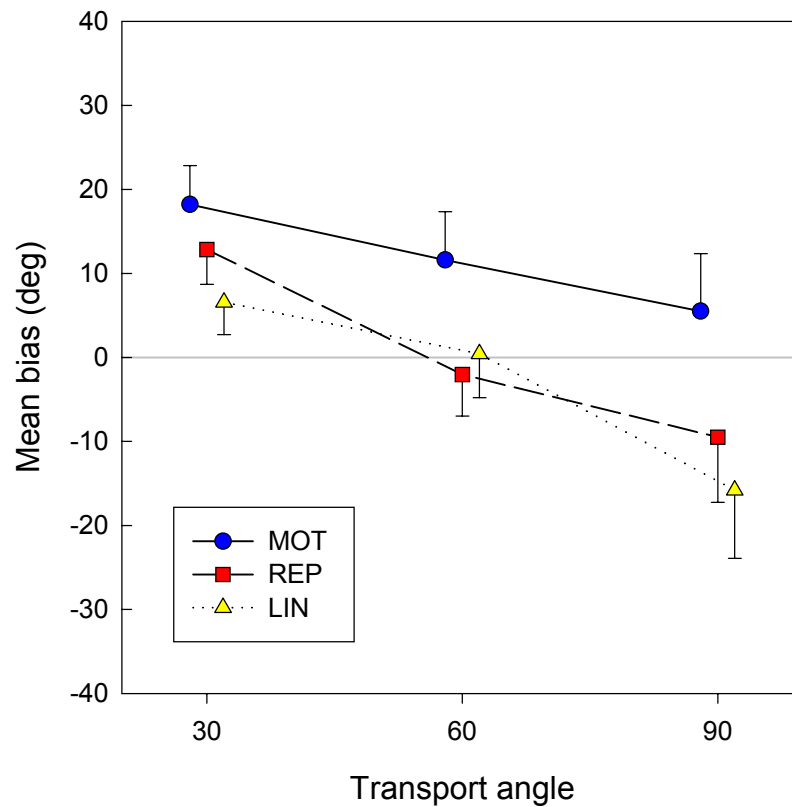


Figure 3. Estimation biases (in degrees), averaged over participants, in the three conditions and at the three transport angles. Error bars show between-participant standard errors.

value of the bias or the width of the logit curve was greater than 100° were not used in subsequent analysis; in these cases, the logit parameters were presumably not reliable. Figure 3 shows the resulting mean displacement biases. Figure 3 clearly confirms the above-mentioned trends: the MOT displacement estimates were farther advanced than those in the REP and LIN conditions, and all three decreased as transport angle increased.⁷

The positive difference in bias between the active and passive conditions was quite robust, in that it was present in individual data. The difference in bias between the MOT and REP conditions, averaged over the three transport angles, was positive in all 10 out of 10 participants. The MOT – LIN difference was positive in 9 out of 10 participants.

To further test the difference between active and passive conditions, we performed a movement condition (i.e., MOT, REP, LIN) \times transport angle ANOVA on the above bias data. The two main effects were significant: $F_{2,18} = 17.3$, $p < 0.01$ for condition and $F_{2,18} = 8.46$, $p < 0.01$ for transport angle. The interaction between the condition and transport angle factors did not reach significance ($F_{4,36} = 2.26$, $p = 0.08$). However, the difference between the active and passive conditions, compared at the extreme values of 30° and 90° of the transport angle, did show significant effects: $F_{1,9} = 5.00$, $p = 0.05$ for MOT and REP, $F_{1,9} = 8.51$, $p = 0.02$ for MOT and LIN. In other words, the difference between

the active MOT condition and the passive REP and LIN conditions increased with longer estimation time.

Comparing the conditions in pairs, there was a significant difference between the MOT and REP conditions ($F_{1,9} = 13.7$, $p < 0.01$) and between MOT and LIN ($F_{1,9} = 48.7$, $p < 0.01$). On the other hand, the difference between the two passive conditions REP and LIN was not significant ($F_{1,9} = 1.66$, $p = 0.23$). Furthermore, the main effect of movement condition was separately significant for each transport angle, including the smallest angle of 30° ($F_{2,18} = 7.17$, $p < 0.01$). Analyzing the three movement conditions separately, we found that the decrease in bias as a function of the transport angle was significant in every condition ($p < 0.01$).

In addition to analyzing the relative effects of movement condition and transport angle on the biases, we also compared the biases directly with their ideal value, namely zero. Of the nine mean biases (three movement conditions by three transport angles: see Fig. 3), a t test corrected for multiplicity (where a probability threshold of 0.006 corresponds to a single test with threshold 0.05) showed that only one is statistically significant from zero: at transport angle 30° , the bias in the MOT condition is significantly positive ($t_9 = 3.95$, $p = 0.003$, 2-tailed).

We also calculated the widths of the fitted response curves. The width is a measure of the variability of the participants' responses; sharp transitions between the two forced choices yield low widths, and vice versa. Performing an ANOVA on the widths similar to the one for biases, the only significant effect we found is of the transport angle: $F_{2,18} = 17.2$, $p < 0.01$. This effect can be seen from a careful inspection of Fig. 2, as a widening of the curves for larger

⁷ The biases in Fig. 3 are almost identical to the angles in Fig. 2 at which the curves cross the value 0.5; the differences are due to the logit fit performed on single-subject data.

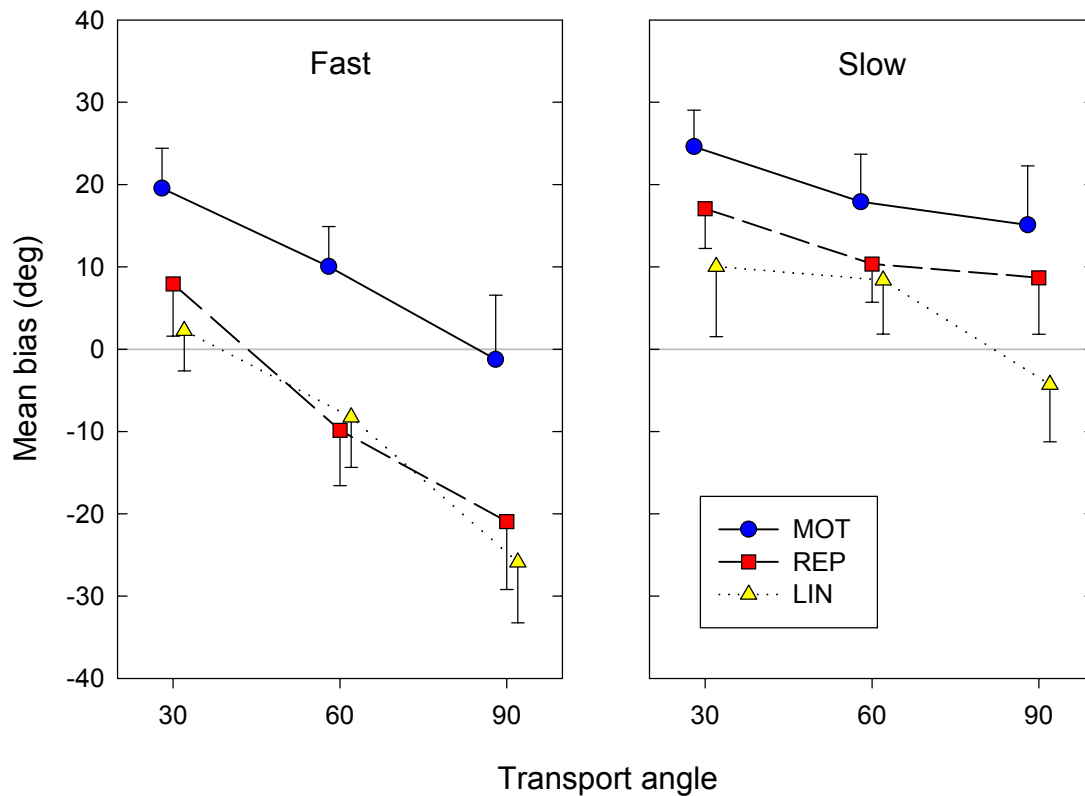


Figure 4. Mean bias averaged over participants as a function of condition and transport angle (as in Fig. 4), separately for the fast and slow trials.

transport angles. The mean width over all participants and conditions was 11.1° at transport angle 30° , 13.2° at 60° , and 15.5° at 90° . This increase in width was rather mild; comparing transport angles 30° and 90° , we have an increase of only 39%, which is small given the fact that the estimation interval (and presumably the task difficulty) increased by 200%. None of the other effects or interactions for the widths approached statistical significance.

Effect of speed

In our protocol, participants were free to rotate the knob at any speed they wished. We found, not surprisingly, that participants often showed large variations in speed between trials. We checked the effects of these spontaneous speed variations on the prediction task; in particular, we were interested in the effects of speed during the occlusion phase of the trial. To do so, in each condition (i.e., the trials for a given participant, movement condition and transport angle) we calculated the median of the mean motor speeds in the occlusion phase. We then subdivided the trials into two groups, depending on whether their mean speed fell above or below the median in their condition, thus introducing an additional categorical factor of speed. The mean angular motor speed during the occlusion phase was $72.4^\circ/\text{sec}$ for the slow trials, $165.0^\circ/\text{sec}$ for the fast trials. We then performed the analysis precisely as before (i.e., separate logit fits of mean response vs. deviation angle in each condition for each participant), but with the additional speed factor.

Figure 4 shows the mean biases calculated for the fast and slow trials. A speed \times movement condition \times transport

angle ANOVA on these biases revealed a significant main effect of speed ($F_{1,9} = 64.7, p < 0.01$): participants' estimates of probe displacement were farther advanced in the slow trials than in the fast trials. In other words, when the occlusion phase lasted longer but the actual displacement during that phase remained the same, estimates were more advanced. Furthermore, there was a significant interaction between the speed and transport angle factors ($F_{2,18} = 13.3, p < 0.01$), showing that the bias in the slow trials was significantly flatter as a function of transport angle than in the fast trials. The main effects of movement condition and transport angle remained significant.

In the fast trials, the difference between MOT and REP conditions was still statistically significant ($F_{1,9} = 5.47, p < 0.05$), while in the slow trials the difference was numerically reduced and approached, though did not reach, significance ($F_{1,9} = 4.13, p = 0.07$). The MOT – LIN difference was significant in both fast ($F_{1,9} = 27.3, p < 0.01$) and slow ($F_{1,9} = 10.7, p < 0.01$) trials, while the REP – LIN difference was significant in neither ($F_{1,9} = 0.93, p = 0.36$ and $F_{1,9} = 2.70, p = 0.13$, respectively).

The effect of speed was quite robust, and was found in individual data. In the MOT condition, the difference in biases between the slow and fast conditions, averaged over the three transport angles, was positive in all 10 out of 10 participants. In the passive REP and LIN conditions, this difference was positive in 9/10 participants.

Performing a speed \times movement condition \times transport angle ANOVA on the widths, we found two significant effects, both involving the speed factor. First, there was a significant main effect of speed: for fast trials the mean width was 9.1° , for slow trials, 12.8° ($F_{1,9} = 6.44, p = 0.03$).

Second, there was a significant interaction between the speed and the transport angle. For the fast trials, the width as a function of transport angle was flat (9.5° for transport angle 30° , 8.7° for transport angle 90°), whereas in the slow trials the width rose sharply with transport angle (9.0° for 30° , 16.5° for 90°) ($F_{2,18} = 6.46, p < 0.01$).

Eye movements

We monitored the eye movements of two participants in separate sessions of 48 trials each. During the first 24 trials for each participant, vertical gaze position was measured, while horizontal gaze was measured during the last 24 trials. As in the other sessions, participants were given no specific instructions concerning eye movements. If participants had pursued the arrowhead, horizontal eye positions would have been perfectly correlated with its horizontal position, and similarly for vertical positions. On the other hand, if participants had pursued the *tail* of the arrow, horizontal and vertical eye positions would have been *anti*-correlated with horizontal and vertical positions of the arrowhead (since the center of the arrow is at the origin of our coordinate system). Therefore, r^2 provides a good measure of pursuit in both cases: r^2 close to 1 indicates pursuit of either the head or the tail of the arrow, whereas r^2 close to 0 indicates a lack of any systematic pursuit.

Since we found no significant differences in r^2 values between vertical and horizontal movements, Table 2 presents data for both types of movement. The values given are Pearson product-moment correlations, calculated individually in each trial, and then averaged over all horizontal or vertical trials in each subject. As can be seen from these results, tracking was rather poor in the visible phase. Interestingly, ‘tracking’ was better in the occlusion phase, when the target was invisible: this was the case in all 3 conditions for both participants, but the effect was largest in the REP condition in both participants.

Participant	Condition	R^2 between eye & target	
		Visible	Occlusion
PS	MOT	0.403	0.436
	REP	0.224	0.674
	LIN	0.268	0.497
MPB	MOT	0.280	0.398
	REP	0.180	0.640
	LIN	0.306	0.406

Table 2. R^2 between eye and target positions for 2 participants in Experiment 1 whose eye movements were measured.

Discussion

There were three main results in this experiment: estimates of unseen target displacement were more advanced in the active condition than in the passive conditions; all estimates became more retarded as the occlusion distance increased, but estimates in the passive condition decayed faster; and slower rotations, i.e., longer occlusion periods, yielded more advanced displacement estimates.

The main effect was the difference between the active MOT and passive REP conditions. Despite the fact that trajectories of the visual target were identical in the two conditions, the fact of acting on the target—rather than observing it passively—had a significant effect on the prediction of its trajectory. Namely, in otherwise identical conditions, the target was predicted to be farther advanced in the active condition than in the passive condition. This effect was not only significant in aggregate data, but was present in the individual data of all ten of our participants.

At the smallest transport angle (30°), when the target’s trajectory had to be predicted over a period of about 500 msec on the average, predictions in all conditions were advanced (see Fig. 3). In other words, participants were anticipating the true orientation of the target.⁸ But even here the bias in the active MOT condition (18.5° on the average) was ahead of the bias in the passive REP condition (12.8°). At the largest transport angle (90°), where the occlusion phase lasted 1.5 sec on the average, the mean MOT bias (5.5°) was still positive, though no longer significantly different from zero. The REP bias, on the other hand, was now negative (-9.5°): participants were no longer anticipating the actual trajectory, but lagging behind. Biases in both the MOT and REP conditions decreased as the transport angle increased, i.e., displacement estimates lagged further and further behind their initial anticipatory values. However, this decrease was less steep in the MOT than in the REP condition. Thus, an actual 60° difference in target displacement during the occlusion phase translated into a 47.0° advance of the mean displacement estimate in the active MOT condition, but only a 37.7° advance of the mean estimate in the passive REP condition. The transformation of the estimated target position was therefore more faithful to actual target motion in the active than in the passive condition.

The data in the MOT condition can be compared to the results of Wolpert, Ghahramani and Jordan (1995), who studied the visual estimation of displacements of the hand. The main difference between their protocol and ours is the lack in Wolpert et al.’s protocol of an initial phase in which the displacement of the target was visible (though the subject saw the initial position before the onset of movement). Wolpert et al. found that subjects overestimated the unseen displacements, much as our participants do in the MOT condition. Furthermore, these authors also found that the absolute amount of this overestimation declined with increase of the prediction time interval, which is compatible with our result that bias in the MOT condition decreased with larger transport angles, which were highly correlated with occlusion time.

The target speed during MOT and REP trials was not constant, due to the self-generated nature of the movements. The trajectory typically underwent an acceleration followed by a deceleration that began around the transition between the visible and occlusion phases (see Table 1). In order to test whether any of the effects that we found were due to the complex nature of the trajectories involved, we introduced a second passive condition, LIN, in which the mean speed of the target was the same as in the other conditions, but in

⁸ Throughout this paper, we use ‘anticipate’ to mean ‘predict a configuration that will only be attained in the future,’ i.e., overestimate current displacement.

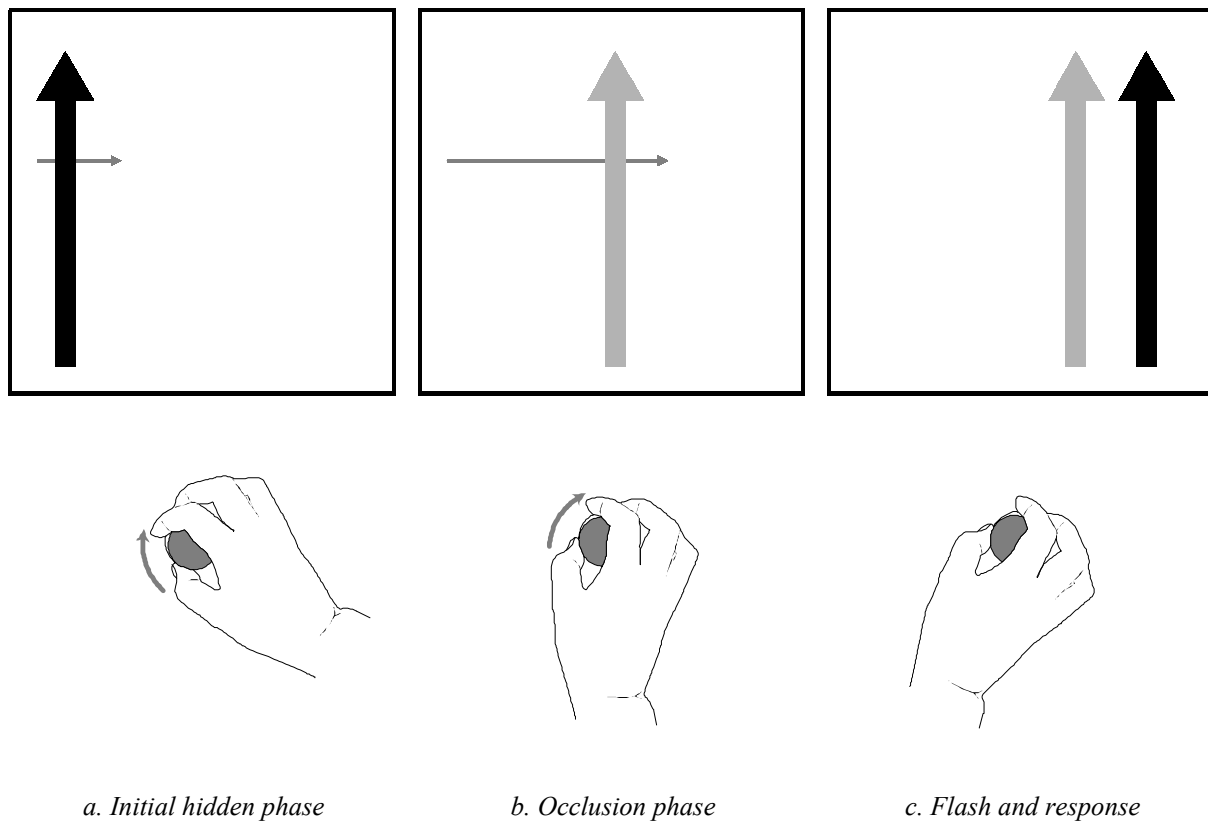


Figure 5. Illustration of the three phases of Experiment 2. The top panel shows the visual stimulus, while the bottom panel shows the simultaneous manual action in the MOT condition. The black arrow represents the actual visual stimulus, while the gray arrow shows the participant's possible estimate for the target position.

which the target moved at a constant angular speed. From a formal point of view, at least, this should be the easiest type of trajectory to predict. We found no significant difference between the two passive conditions. It does not seem, therefore, that the complexity of the trajectories in the MOT and REP conditions was responsible for the effects that we have found. Furthermore, participants were just as good at predicting the complex acceleration-deceleration trajectories in the REP condition as they were at predicting motion that is, mathematically, simplest of all: constant speed.

Another effect that we have uncovered is that of speed. All other conditions being equal, *faster* rotations resulted in predictions of target position that were more *retarded*. In other words, when participants had more time to predict, over the same prediction distance, the estimate was farther advanced. Moreover, the bias curves as a function of transport angle were significantly flatter for the slower trials than for faster the trials, implying that the rate of predicted advance of the target slowed down less for the slower than for the faster trials. Less surprisingly, the speed also had an important effect on the variance, or width, of the participants' replies: in the fast trials (i.e., ones where the target was hidden briefly), the width remained flat as a function of transport angle; in slow trials, it rose sharply. From this we may conclude that uncertainty rose rapidly with the time duration of the prediction to be made.

The effect of speed in the passive conditions REP and LIN is comparable to the findings of Ellingstad (1967) and

of Bonnet and Kolehmainen (1970) for passively observed linear motion. On the other hand, our results disagree with those of Peterken, Brown and Bowman (1991), who found that longer prediction times over fixed prediction distances led to predictions that were more retarded.

Finally, although there was a small correlation between participants' eye movements and target motion (especially in the occlusion phase), ocular tracking was rather poor.

Overall, it is clear that *generating* a movement (the MOT condition) effects the prediction of the movement's outcome, as compared to passively observing a movement (the REP and LIN conditions): in the active case the prediction is more anticipatory than in the passive case.

Experiment 2

In Experiment 1, the motor action in the MOT condition was a rotation, and so was the visual motion to be predicted. We now ask to what extent is this action-prediction effect dependent on specific movement details. Does a motor rotation advance predictions only of congruent visual motion, namely visual rotation, or is the interaction more general and thus higher-level, so that the performance of a motor action in general advances the prediction of the action's visual outcome, regardless of the specific forms of the action and visual feedback?

Experiment 2 addressed this question. The major modification with respect to Experiment 1 was that visual

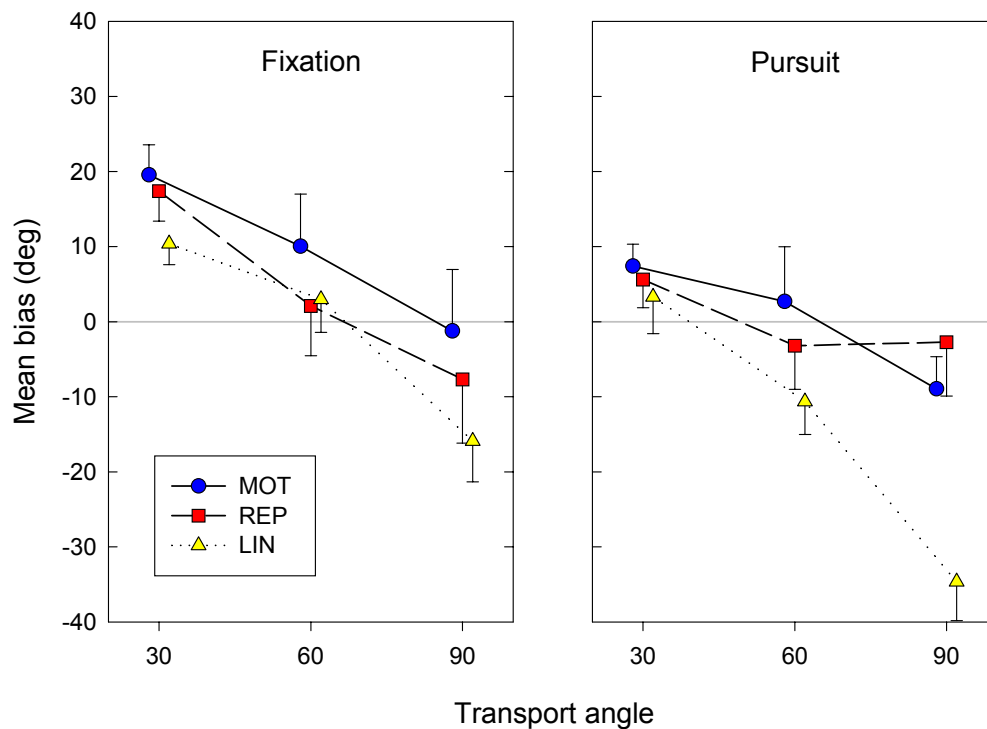


Figure 6. Mean biases in Experiment 2, as a function of eye movement, movement condition and transport angle.

feedback was no longer a rotation of an arrow on the screen, but a translation. The motor action, in the active condition, did not change: it was still a rotation.

With translational target motion, eye movements—which were poorly correlated with the rotational target motion in Experiment 1—potentially become more important. As discussed in the Introduction, eye movements themselves have predictive properties; this predictive capacity could be affected by the manual task (or lack thereof), and it could in turn affect the participant’s performance of the predictive task. To probe this interaction, we therefore introduced two eye movement conditions: in *pursuit* trials participants were instructed to follow the moving arrow with their eyes and to continue the ocular pursuit as much as possible even in the occlusion phase, after the target disappears; in *fixation* trials participants were to fixate a cross on the screen at all times. In separate sessions after the main experiment, we monitored the eye movements of two of the participants.

Method

Stimuli

The participant’s manual movement in the MOT trials consisted in a rotation of a knob, as in Experiment 1. The visual feedback, however, was no longer a rotation but a translation. A vertical, upward-pointing arrow (otherwise identical to the arrow in Experiment 1) always began near the left edge of the screen on each trial. The arrow’s subsequent movement was a translation to the right. On the MOT trials, the visuomotor gain was $10.8^\circ/\text{cm}$; in other words, for every 10.8° the participant rotated the knob, the arrow moved to the right by 1 cm. The sequence of phases in each trial is shown in Figure 5.

Design

In contrast to Experiment 1, participants had explicit eye movement instructions. On half of the trials (“pursuit”), participants were told follow the arrow with their eyes as it moved to the right, and to continue the visual pursuit as best as possible after the arrow disappeared. On the other half of the trials (“fixation”), a red fixation cross was drawn on the screen throughout the trial (1.2 cm long, centered at 3.5 cm above the tip of the arrow, 9.7 cm to the right of its initial position, corresponding to the horizontal position of the arrow following a motor rotation of 105° , or 60° after the onset of the occlusion phase), and the participant was instructed to fixate the cross throughout the trial. The experiment was run in two sessions of 288 trials each. One session had pursuit and the other had fixation trials; otherwise, the two sessions were identical. The order of the pursuit and fixation sessions was counterbalanced across participants.

Eye movement recordings

A reduced version of the experimental design was used in the eye movement sessions, with two transport angles (30, 90 deg), six deviation angles (± 10 , ± 30 , ± 50 deg) in the three conditions (MOT x 2, REP, LIN), and three repetitions, for a total of 144 trials. The eye tracker was operated in horizontal position mode. Following this main block, each participant performed a short block of 12 fixation trials, in order to verify that participants indeed fixated as they were instructed.

The horizontal eye movement recordings were preceded by calibrations, as described in the General Methods section. The calibrations consisted of 7 fixation points, positioned at 0, ± 3.75 , ± 7.5 , ± 11.25 cm on the horizontal axis centered at

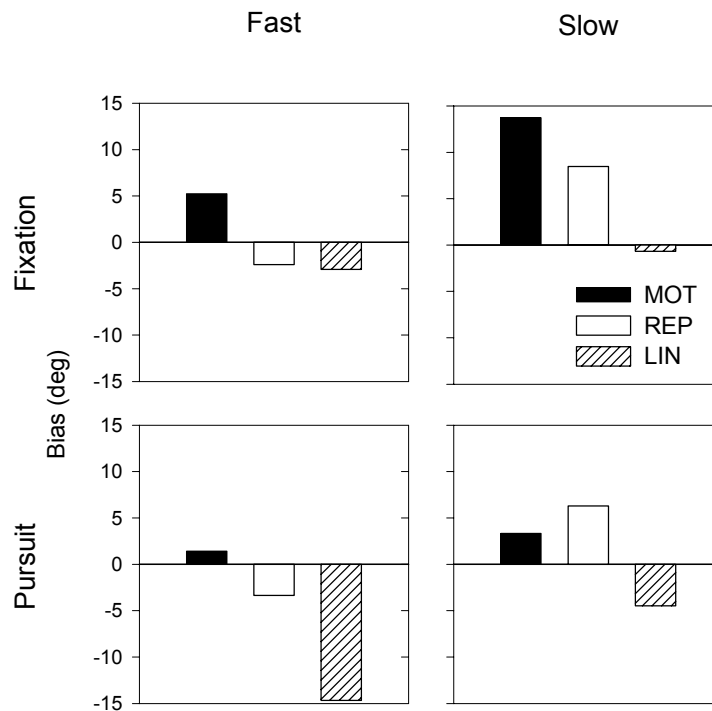


Figure 7. Mean bias (over participants and transport angles) for the three conditions, categorized by speed and by eye movement condition.

the origin. Each point was repeated 3 times, and points were presented in random order.

Participants

Eight unpaid volunteers served as participants. Group 1 (2 men, 2 women, mean age 29 years) performed fixation trials in the first session, followed by pursuit trials in the second session. Group 2 (3 men, 1 woman, mean age 24 years) performed pursuit trials in the first session, followed by fixation trials. In addition, two of these participants each performed two separate blocks with an eye tracker. All participants were self-reported as right-handed, and used their right hand in the motor task. Participants were naive as to the purpose of the experiment.

Results

Trials in which either the duration of the occlusion phase, the combined duration of the visible and occlusion phases, or the response time exceeded 10 sec were eliminated from further data analysis; 2.3% of all trials were thus eliminated.

In order to facilitate the comparison with Experiment 1, results will be presented in terms of motor rotations. Thus, a 'deviation angle' of 30°, for example, corresponds to a deviation distance of 2.8 cm to the right.

Effect of eye tracking and movement condition

The analysis that we performed was similar to that for Experiment 1. Briefly, data were categorized by participant, fixation condition, movement condition and transport angle. In each cell, mean response as a function of deviation was fitted to a logit curve. The resulting mean biases are shown

in Fig. 6, the counterpart of the data in Fig. 3, but additionally categorized by eye movement condition. Although the visual motion here is a translation, to facilitate comparison with Experiment 1 displacements are given in degrees (recall that the visuomotor gain was 10.8°/cm).

The results in the fixation condition in this experiment closely resembled those of Experiment 1 (see Fig. 3). There was a significant effect of transport angle ($F_{2,14} = 18.3, p < 0.01$), and a difference between the active MOT and passive REP and LIN conditions that approached significance ($F_{2,14} = 3.02, p = 0.08$). The latter difference is similar to the one in Experiment 1, but smaller in magnitude.

In the pursuit condition, on the other hand, any difference between the MOT and REP conditions disappeared ($F_{1,6} = 0.19, p = 0.67$). There was, however, a significant difference between these two conditions and the LIN condition ($F_{1,6} = 11.1, p = 0.02$), as well as a strong interaction between movement condition and transport angle ($F_{4,24} = 4.30, p < 0.01$), due to the much faster decrease of LIN bias as a function of transport angle than in the MOT and REP conditions.

Comparing active and passive conditions for individual participants, we found that in the fixation condition, MOT estimates were more advanced (anticipatory) than REP in 7 out of 8 participants; MOT estimates were more advanced than LIN in 6/8 participants. In the pursuit condition, MOT estimates were more advanced than REP in half the participants, while estimates are more advanced than LIN in all 8/8 participants.

Comparing the fixation and the pursuit conditions, we found that the mean effect of tracking was to retard displacement estimates. The mean bias in the fixation condition was 2.7°, while in the pursuit condition it was -7.2°; this effect approached significance ($F_{1,6} = 4.97, p =$

Participant	Condition	R^2 between eye & target Phase		Eye-target gain Phase	
		Visible	Occlusion	Visible	Occlusion
RB	MOT	0.938	0.850	0.838	1.146
	REP	0.951	0.856	0.908	0.886
	LIN	0.950	0.830	0.855	0.889
MZ	MOT	0.951	0.895	0.994	1.432
	REP	0.927	0.915	0.843	1.601
	LIN	0.947	0.900	1.024	1.134

Table 3. R^2 and gain between eye and target positions for 2 participants in the pursuit condition of Experiment 2.

0.07). An alternative measure of the robustness of the effect of eye movement was afforded by individual data. In the MOT condition, the biases for 7 out of 8 participants (averaged over transport angle) were more advanced in the fixation than in the pursuit condition. In the passive conditions, the corresponding figure was 5/8 for REP and 6/8 for LIN.

Effect of speed

To check the effect of movement speed, we categorized trials into fast and slow groups, as in Experiment 1 (based on mean speed during the occlusion phase). Figure 7 shows the mean biases for the MOT, REP and LIN conditions, categorized by speed and eye movement condition; the data were averaged over participant and over transport angle. The effect of speed was similar to that in Experiment 1: in every condition, the estimates in slow trials were farther advanced, more anticipatory than in fast trials. Performing a four-way ANOVA by eye tracking condition, movement condition, transport angle and speed, we found a significant main effect of speed: for the fast trials the mean bias was -5.6° , for the slow trials it was 3.4° ($F_{1,6} = 12.0$, $p = 0.01$). The effect of fixation was in the opposite direction as that of speed: in every case, the mean estimate for fixation trials was farther advanced than for pursuit trials.

Eye movements

During a typical trial in the pursuit condition, participants were able to smoothly track the target during the visible phase, with only occasional corrective saccades. Following the target's disappearance, the smooth pursuit persisted for 360 msec on the average, and was followed by a 'staircase' of saccades that roughly approximated the hidden target's trajectory. On the average, there were 0.66 saccades per second during the visible phase, and 2.04 saccades per second in the occlusion phase.

The mean correlation coefficients and gains between eye and target positions are shown in Table 3 for the visible and occlusion phases in the three conditions. As in Experiment 1, we calculated a Pearson product-moment correlation individually in each phase of each trial, and then averaged over trials. A gain greater than one means that the eye advanced over a greater distance than the target. In all conditions in both participants, in both the visible and occlusion phases, the correlations were very high, indicating that participants were following the instruction to pursue the target. In the visible phase, at least, gain is also close to

unity, which means that participants' eye movements were not only proportional to target movements, but were also approximately equal to them in extent. In five out of six cases, gain in the visible phase was slightly below one, meaning that the eyes moved somewhat less than the target. In the occlusion phase, gain was greater than one in both participants in the MOT condition.

In the fixation condition, on the other hand, participants made very few eye movements, as they were instructed. The standard deviation of horizontal eye position was only 0.13 cm.⁹ These small movements were uncorrelated with target motion, with the average gain 0.01. These data show that participants indeed followed the eye movement instructions, either to pursue the target, or to fixate the cross.

In the pursuit condition, there was a strong correlation between response and gaze position. Namely, when, by the time of the flash, the participant's gaze was farther advanced than the flashed position (i.e., to the right of the flash), the response tended to be that the flashed target was "too far behind," and vice versa: when the gaze was behind the flash, the response tended to be "too far ahead." Correlation coefficients between responses and flash position relative to gaze position were typically on the order of 0.7 – 0.8. We have to be careful, though, since flash position relative to gaze position was also strongly correlated with deviation angle or deviation distance. In other words, if the flashed position of the target was far to the right of its 'real' position, for example, (i.e., if the deviation angle was large and positive) the flash position also tended to be far to the right of the gaze position.

In order to disentangle these two factors, we performed a linear regression analysis with the response as the dependent variable. The two variables of interest were

1. $D(\text{flash} - \text{real})$, the deviation 'angle' or distance: the distance between the flashed position of the target and its 'real' position at the time of the flash; and

⁹ By comparison, the standard deviation in the pursuit condition was 3.03 cm. In order to attach significance to these standard deviations, consider the fact that if the eye had followed a linear trajectory, the linear extent of the movement would have been $\sqrt{12} \approx 3.5$ times the standard deviation. Thus in the fixation condition the range of eye movement was about 0.5 cm, approximately half the size of the fixation cross.

2. $D(\text{flash} - \text{gaze})$, the horizontal gaze position relative to the flash position, at the time of the flash.

These two variables together accounted for a large part of the variance of the response. Computed values of regression coefficients and R^2 are given in Table 4. Not surprisingly, response always depended significantly on $D(\text{flash} - \text{real})$. The regression coefficient of $D(\text{flash} - \text{gaze})$ was significantly different from zero in the MOT and REP conditions, and approached significance ($p = 0.08$) in the LIN condition. The regression coefficient of the gaze variable was also about twice as large in the REP as in the MOT condition, and numerically surpassed the coefficient of the $D(\text{flash} - \text{real})$ variable. This effect was observed in both participants in the eye recording sessions: the regression coefficient is 0.178 (MOT), 0.341 (REP) in one participant, $\beta = 0.236$ (MOT), 0.559 (REP) in the other. We thus conclude that the position of gaze played an important role in participants' response criteria in the MOT and REP conditions, and especially in REP, where it was as large as the deviation. In the LIN condition, on the other hand, the gaze variable played a much smaller role than in REP.

Condition	R^2	Regression coefficients	
		Flash – Real	Flash – Gaze
MOT	0.619	0.609 **	0.216 *
REP	0.668	0.428 **	0.462 **
LIN	0.694	0.688 **	0.183

Table 4. Multiple regression of response in $D(\text{flash} - \text{real})$ and $D(\text{flash} - \text{gaze})$. Significant differences from 0: * ($p < 0.05$), ** ($p < 0.01$).

Comparison of Experiments 1 and 2

In Experiment 1 both the motor action and the visual feedback were rotations; in Experiment 2 the motor action was still a rotation, but the visual feedback was a translation. To what extent did the mismatch between motor action and feedback affect the prediction task?

It is clear from a comparison of Fig. 3 and Fig. 6 that Experiment 1 and the fixation condition of Experiment 2 closely resembled one another, whereas the pursuit condition of Experiment 2 yielded estimates that are generally more retarded than the two others. Indeed, when we performed an ANOVA with experiment as a between-groups factor (three levels: Experiment 1, Experiment 2 fixation, Experiment 3 pursuit), and movement condition (MOT, REP, LIN) and transport angle as within-subject factors, we found no significant differences whatsoever between Experiment 1 and Experiment 2 fixation. On the other hand, there was a significant difference between these two and Experiment 2 pursuit, but only in the LIN condition ($F_{1,22} = 5.14$, $p < 0.05$), while the same difference in the MOT condition approached significance ($F_{1,22} = 3.42$, $p = 0.08$).

The effect of motor action is quantified by the difference in bias between the active and the two passive conditions (MOT – REP and MOT – LIN). Did the congruence of motor and visual movement (Experiment 1 vs. 2) or the eye movement condition modulate this effect? Figure 8 shows these two bias differences for Experiment 1 and Experiment 2, fixation and pursuit. For the MOT – REP, the pattern is

clear: the bias difference was greatest for Experiment 1, smaller for Experiment 2 fixation, and smaller still (even negative at large transport angles) for Experiment 2 pursuit. Moreover, these effects seem to increase with increasing transport angle. The difference between Experiment 1 and Experiment 2 fixation failed to achieve significance, though ($F_{1,22} = 1.89$, $p = 0.18$). On the other hand, the difference between Experiment 1 and Experiment 2 pursuit was significant ($F_{1,22} = 5.10$, $p < 0.05$), and its interaction with transport angle was significant as well ($F_{1,22} = 6.51$, $p < 0.05$).

Discussion

In Experiment 2 we modified the congruence of motor action and visual feedback: the action was a rotation while the feedback was a translation. We also controlled eye movement by introducing ocular pursuit and fixation conditions.

We have found that the results of the fixation condition of Experiment 2 closely resembled those of Experiment 1. The principal effect of movement condition from Experiment 1—the fact that displacement estimates in the MOT condition were more advanced or anticipatory than in the passive REP condition—was reduced in magnitude relative to Experiment 1, but not eliminated. The resemblance of the results of the fixation conditions to those of Experiment 1 is not surprising: in Experiment 1, the visual stimulus underwent a rotation. Participants were not required to track the target, and did so in an unsystematic or sporadic manner, as shown by eye movement data from Experiment 1 (see Table 2). Therefore, with respect to eye movements, the fixation condition of Experiment 2 was closer to Experiment 1. There was a trend for the MOT – REP difference in Experiment 2 fixation to be smaller than that in Experiment 1, though this difference was not statistically significant. We conclude, therefore, that the partial motor-visual mismatch introduced in Experiment 2 did not eliminate the action effect (but did possibly reduce it), given comparable eye movement conditions.

It is interesting to compare this result to the neurophysiological data of Eskandar and Assad (1999), who have found a population of cells in the posterior parietal cortex of macaques that predictively encode the unseen visual trajectories of targets that are being moved by the animal, including when the motor action and visual feedback motion are partly incongruent. Moreover, these cells only showed such a directional response when the animal performed a visuomotor prediction task quite similar to our own.

The effect of ocular pursuit on the responses in the trajectory estimation task, as compared to the fixation condition, was triple: to retard displacement estimates; to nullify the difference between the active MOT and passive REP conditions; and to retard the estimates in the LIN condition, creating a significant difference between the two passive conditions, REP and LIN. From the eye trajectories recorded from two participants, we learn that participants followed the pursuit instruction, giving smooth pursuit with corrective saccades in the visible phase, a brief period of decaying smooth pursuit in the occlusion phase followed by a staircase of saccades.

More interestingly, we have also seen that in the pursuit condition, responses in the trajectory estimation task

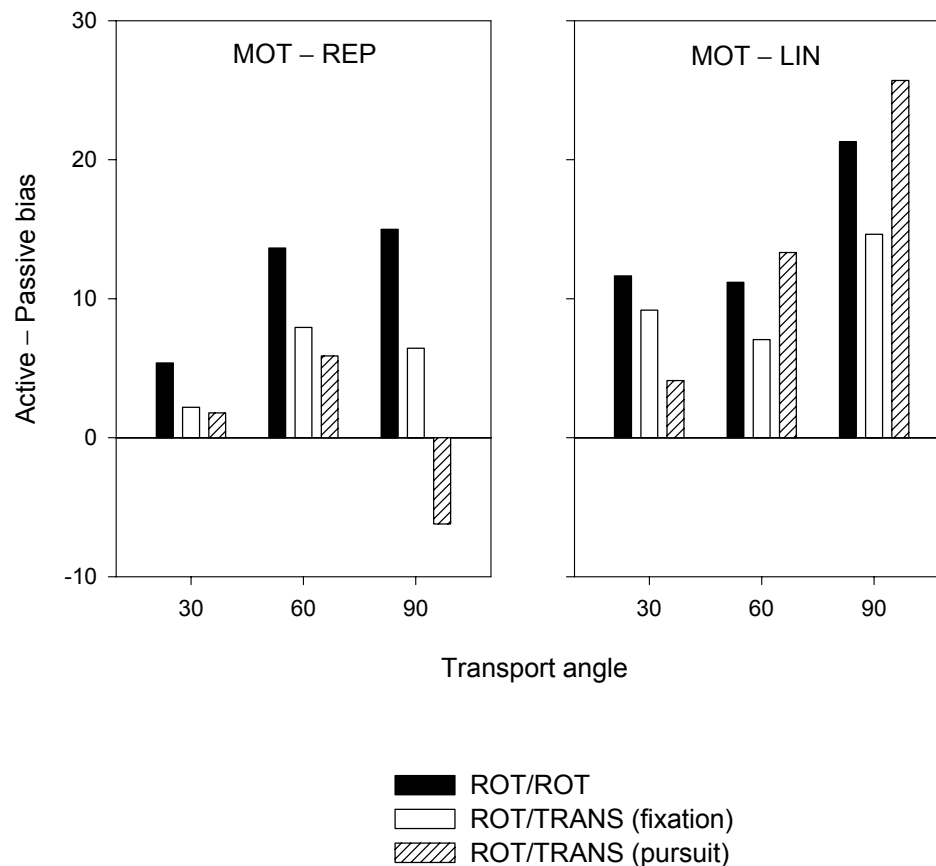


Figure 8. Differences between the active and the two passive conditions, viz. between MOT and REP and between MOT and LIN. Data are shown for Experiment 1 (motor rotation – visual rotation) and the ocular pursuit and fixation conditions of Experiment 2 (motor rotation – visual translation).

depended to some degree on gaze position relative to the flash, independently of displacement of flash position relative to the actual trajectory. This was the case in all conditions, but was most strikingly observed in the REP condition, where the mean linear regression coefficient of the gaze variable surpassed that of the deviation variable. This state of affairs is surprising, considering that the task depended only on the deviation variable (i.e., ideally the response should have always been “behind” when deviation was negative, “ahead” when deviation was positive), and that the gaze variable should have been totally irrelevant. We shall return to this point in the General Discussion.

The LIN condition, on the other hand, had extremely retarded displacement estimates, especially for large transport angles; this should be contrasted with data from Experiment 1, and those from the pursuit condition of Experiment 2, where there was no difference between the two passive conditions. The other peculiarity of the LIN condition was the low utilization of the gaze variable in the decision, seen in both participants in the eye recording trials. The gap between REP and LIN in the pursuit condition agrees with the fact that ocular pursuit soon slows down and tapers off in the absence of a visible target (Barnes & Asselman, 1992) Trajectories in the REP condition already had a deceleration during the occlusion phase, due to their ‘biological’ nature, and this is possibly why the REP predictions were less delayed than those for the constant-

speed LIN trajectories. Consistent with this interpretation is the fact that, for both of our participants in the eye recording sessions, the eye-target gain was lower in the LIN condition than in MOT or REP, at 90° transport angle. It is also worth comparing this with the finding of de’Sperati and Viviani (1997) that passively observed ‘biological’ trajectories, such as those in the REP condition, are easier to track than trajectories following other velocity profiles, such as the constant-speed LIN trajectories. The general effect of ocular tracking that we have found should be compared to the results of Nijhawan (1997), who likewise found that eye tracking impedes visual trajectory anticipation.

Finally, we have reproduced the effect of speed that had been found in Experiment 1. Targets taking longer to traverse a given distance, and therefore moving slower, yielded predictions that were farther advanced than the faster-moving, shorter-duration targets. This was true in all three conditions (MOT, REP, LIN).

General Discussion

Hand movement

The chief effect that we have demonstrated is the difference in trajectory predictions between the active (MOT) and passive (REP, LIN) conditions. Most importantly, when the observer actively caused the target to move by a manual

rotation of a knob, predictions were farther advanced—more anticipatory—than in passive trials, even when the visual stimuli were rigorously identical, as they are in MOT and REP conditions. This effect was stronger when motor action and visual motion were congruent (as they were in Experiment 1, where they were both rotations, versus Experiment 2, where the action was a rotation but the visual motion a translation), and stronger for fast trials than for slow trials. All of these effects were quite robust, and found on the level of individual data. Further, there was some evidence of an interaction between movement condition and prediction distance: the slowing down of the predicted position as a function of prediction distance appears to have been less steep in the active than in the passive case.

Along with the differences in prediction between the active and passive conditions, we have also found at least two interesting similarities. First, as the prediction distance (the displacement over which the target is occluded) increased, predicted displacements lagged farther and farther behind. This was true of both active and passive tasks, although there was evidence, especially from Experiment 1, that this slowing down was steeper in passive than in active trials. Second, for a given prediction distance, *slower* movements resulted in predictions that were *farther advanced* than do faster movements. This is also true of both active and passive conditions; here, the magnitude of the effect seemed to be roughly the same for passive as for active conditions. These two effects were found in both Experiments 1 and 2, and are individually present either in a vast majority or in all participants.

The fact that active prediction remained more anticipatory than passive, even when visual feedback was less congruent to the motor action (as in Experiment 2, relative to Experiment 1), shows that the effect of motor action on prediction is not tied to the low-level details of the produced movement and the visual stimulus, but suggests the intervention of more general, high-level mechanisms that adaptively predict the outcome of motor action, mechanisms that continue to operate even when visual motion and motor action are geometrically dissimilar.

One obvious difference between the active MOT condition, and the passive REP condition was, despite the identical trajectories, the presence in the MOT condition of information such as efferent copy of movement commands, proprioception, etc.—about the movement of the target in the occlusion phase, and the lack of such information in the REP condition. If, as far as prediction was concerned, this had been the only difference between the two conditions, we would not have expected any systematic difference in the mean estimates, but rather for the passive responses to have been less precise than the active ones. This was, in fact, not the case: REP widths (a measure of precision) were no greater than MOT widths, and there *was* a systematic difference in mean estimates, namely that MOT estimates were more advanced. We conclude, therefore, that our effects cannot be explained by the lack of movement or proprioceptive information in the passive conditions.

Eye movement

In addition to signals related to manual movement, there was an effect of eye movements on the prediction task. In the presence of ocular pursuit, the difference between the active MOT condition and the passive REP condition

(where the trajectories are identical) disappeared. Moreover, ocular pursuit retarded prediction in both active and passive conditions.

As we have seen from eye movement data in Experiment 2, in the pursuit condition observers made trajectory predictions based not only on the relative distance between the flashed target and its actual position—the only variable that should be relevant to the task—but also based the position of the flash relative to gaze. This effect was especially strong in the REP condition, where the β score of the gaze variable surpassed that of the deviation variable.

We have evidence, therefore, that in the case of ocular pursuit, the trajectory prediction task is, at least in part, *shunted* onto the oculomotor system. In other words, instead of a purely mental process of extrapolation that presumably takes place in the fixation condition, trajectory prediction is partly *externalized* in the pursuit condition. According to this version, the eyes track the invisible target based on an internal predictive signal that may or may not be consciously accessible. The conscious decision process would then use the gaze position relative to the flash as a decision criterion for the trajectory extrapolation task. The fact that the gaze position variable had more weight in the passive REP than in the active MOT condition could be interpreted to signify that the gaze information was used as a replacement in REP for the motor signals that were present in MOT.

To summarize the experimental results, our data support distinct roles for manual and eye movement in trajectory prediction. In the absence of consistent eye tracking, motor signals from manual movement serve to advance predicted target position. In the presence of eye tracking, the prediction task is partly shunted onto the oculomotor system, reducing or eliminating the effect of manipulatory movement. In what follows, we discuss possible neural mechanisms that could account for these prediction phenomena.

Possible mechanisms

What can we conclude about the neural mechanisms underlying active and passive prediction? Given the parallels that we have found between the dynamics in the active and passive cases (similar decay of subjective speed with occlusion interval, similar effect of target speed), the most parsimonious assumption will be that at least some of the mechanisms responsible for active and passive prediction are the same.

What sort of a model could parsimoniously account for both the similarities and the differences in the two cases? We shall need a representation of current target configuration (i.e., the significant degree(s) of freedom, such as the angle in Experiment 1 or linear position in Experiment 2), that we shall call the *store*. The same store could represent both observed target configuration, when the target is visible, or estimated target configuration during periods of occlusion. An attractive medium for such a store would be a population of neurons such as the one in monkey motor cortex studied by Georgopoulos et al. (Georgopoulos, Kalaska, Caminiti, & Massey, 1983), where each cell is tuned to a particular direction of arm movement and where the average direction over the population, weighted by the cells' activations, is a 'population vector' that represents the actual direction of movement. The population vector is not

merely a static representation but can rotate from one direction to another in response to task demands (Georgopoulos, Lurito, Petrides, Schwartz, & Massey, 1989). The results of Georgopoulos and Massey (1987) and Pellizzer and Georgopoulos (1993) suggest that a population vector code may be employed in neural visuomotor representations in humans, and that an overlapping representational mechanism may underlie 'purely visual' tasks, i.e., ones without an overt motor component. There is no reason to suppose that such population-based representations be confined to motor or visual rotation; they could equally well represent translation, or other types of movement.

The crucial feature of a predictive store is *updating*: based either on efferent copy of the motor command or proprioceptive information or on past visual trajectory (in the active case) or on past visual information alone (in the passive case), the store must be continually updated to reflect the estimate of the current configuration. In the active case, the store could be updated by means of a forward model, such as the Kalman filter models of Wolpert and co-workers (e.g., Wolpert, Ghahramani & Jordan, 1995), or the ANN model of Droulez (Droulez & Berthoz, 1991), that predict future state based on efferent copy of motor commands. In our experiments, for instance, during the initial visible phase, the store's time evolution reflects the movement of the perceived visual target. During the occlusion phase, the store's evolution is an integration of the estimated effects of current motor commands.

As we have already discussed, several recent results point to posterior parietal cortex as a likely site for such an updating mechanism (Duhamel, Colby, & Goldberg, 1992; Wolpert, Goodbody, & Husain, 1998; Eskandar & Assad, 1999). Other evidence indicates that a similar mechanism may exist in the cerebellum (Blakemore, Wolpert, & Frith, 1998).

In the passive case, where movement-command or proprioceptive information is not available, we can imagine two scenarios for updating. First, the store could have intrinsic dynamic properties. Having undergone a time evolution during the visible phase that simply reflects the target's seen motion, the store's dynamics may feature an effective 'momentum' (cf. Freyd, 1987), so that it continues to evolve after the target is occluded. The speed at which the store evolves during occlusion may not match the visible target speed, and may change over the occlusion period. In light of our results, the transfer function between the visible speed and the predicted speed may be a low-pass filter, which would account for the finding that predictions of high-speed trajectories were delayed as compared to low-speed trajectories. Thus, the initial speed of evolution during the predictive phase may already be some non-trivial function of the speed during the visible phase. Furthermore, this initial speed subsequently decreases, as demonstrated by our finding that predictions became more retarded for longer prediction distances.

An alternative mechanism in the case of passive prediction could be termed 'motor simulation'. During the visible phase, the observer could somehow evolve a simulated motor command that, if applied to the target, would reproduce the observed motion. Since no overt movement is produced, this motor activation would have to be inhibited from descending to the spinal chord and the periphery, much as in the case of motor imagery (e.g.,

Jeannerod, (1997)). The construction of such a 'reproductive motor simulation' is rendered more plausible by analogous properties of 'mirror neurons' in monkey frontal cortex (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992), which reproduce the motor commands necessary to execute movements observed in another animal. Similar mechanisms probably exist in humans (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). When the target disappears and its trajectory is predicted, the simulated motor command could lead to the time evolution of the predicted target position through the same forward-model mechanisms that are used in the active case. The effect of the simulated motor command on the representation of target configuration may be weaker than the effect of the re-afferent copy of an actual motor command, which would account for the constant bias difference between the active and passive conditions that we have found. In the absence of overt motor action or of visual information, this simulated motor command would decay, explaining the steeper decrease of the bias as a function of prediction distance in the passive case than in the active case.

These two candidate mechanisms for passive prediction are not mutually exclusive. It could very well be that the first—representational momentum—acts only over short periods (cf. Freyd, 1987), while the second mechanism—motor simulation—would act over longer periods. Now, representational momentum has been found to decay rather quickly. Therefore, a combination of a short-term representational momentum process and a longer-term motor simulation process could explain the speed effect, in which brief occlusions lead to predictions that are farther delayed than longer occlusions.

The mechanisms responsible for passive prediction could also play a role in the active case, of course. Yet the consistent differences that we find between predictions in the two cases lead us to suppose that the additional information present in the active case—most likely an efferent copy of the motor command—gives rise to more anticipatory predictions of the target, as compared to the processes in passive prediction. The active/passive differences that we have found are in line with theories of the predictive aspects of motor action and with the neurological evidence for anticipatory properties of neural mechanisms of movement.

References

- Barnes, G.R., & Asselman, P.T. (1992). Pursuit of intermittently illuminated moving targets in the human. *Journal of Physiology (London)*, *445*, 617-637.
- Beutter, B.R., & Stone, L.S. (1998). Human motion perception and smooth eye movements show similar directional biases for elongated apertures. *Vision Research*, *38*, 1273-1286.
- Blakemore, S.J., Goodbody, S.J., & Wolpert, D.M. (1998). Predicting the consequences of our own actions: the role of sensorimotor context estimation. *Journal of Neuroscience*, *18*, 7511-7518.
- Blakemore, S.J., Wolpert, D.M., & Frith, C.D. (1998). Central cancellation of self-produced tickle sensation. *Nature Neuroscience*, *1*, 635-640.

- Bonnet, C., & Kolehmainen, K. (1970). Le rôle de la vitesse dans l'anticipation d'un mouvement visuel. *Année Psychol*, 70, 357-367.
- Cai, R.H., Pouget, A., Schlag-Rey, M., & Schlag, J. (1997). Perceived geometrical relationships affected by eye-movement signals. *Nature*, 386, 601-604.
- de'Sperati, C., & Viviani, P. (1997). The relationship between curvature and velocity in two-dimensional smooth pursuit eye movements. *Journal of Neuroscience*, 17, 3932-3945.
- di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: a neurophysiological study. *Experimental Brain Research*, 91, 176-180.
- Droulez, J., & Berthoz, A. (1991). A neural network model of sensoritopic maps with predictive short-term memory properties. *Proceedings of the National Academy of Sciences, USA*, 88, 9653-9657.
- Duhamel, J.R., Colby, C.L., & Goldberg, M.E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science*, 255, 90-92.
- Ellingstad, V.S. (1967). Velocity estimation for briefly displayed targets. *Perception and Motor Skills*, 24, 943-947.
- Eskandar, E.N., & Assad, J.A. (1999). Dissociation of visual, motor and predictive signals in parietal cortex during visual guidance. *Nature Neuroscience*, 2, 88-93.
- Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: a magnetic stimulation study. *Journal of Neurophysiology*, 73, 2608-2611.
- Freyd, J.J. (1987). Dynamic mental representations. *Psychological Review*, 94, 427-438.
- Georgopoulos, A.P., Kalaska, J.F., Caminiti, R., & Massey, J.T. (1983). Interruption of motor cortical discharge subserving aimed arm movements. *Experimental Brain Research*, 49, 327-340.
- Georgopoulos, A.P., Lurito, J.T., Petrides, M., Schwartz, A.B., & Massey, J.T. (1989). Mental rotation of the neuronal population vector. *Science*, 243, 234-236.
- Georgopoulos, A.P., & Massey, J.T. (1987). Cognitive spatial-motor processes. 1. The making of movements at various angles from a stimulus direction. *Experimental Brain Research*, 65, 361-370.
- Haarmeier, T., Thier, P., Reppow, M., & Petersen, D. (1997). False perception of motion in a patient who cannot compensate for eye movements. *Nature*, 389, 849-852.
- Helmholtz, H.v. (1867). *Handbuch der Physiologischen Optik*. Hamburg: Voss.
- Holst, E.v., & Mittelstaedt, H. (1950). Das Reafferenzprinzip. *Naturwissenschaften*, 37, 464-476.
- Jeannerod, M. (1997). *The cognitive neuroscience of action*. Oxford: Blackwell.
- Kowler, E., & McKee, S.P. (1987). Sensitivity of smooth eye movement to small differences in target velocity. *Vision Research*, 27, 993-1015.
- Müsseler, J., & Aschersleben, G. (1998). Localizing the first position of a moving stimulus: the Fröhlich effect and an attention-shifting explanation. *Perception and Psychophysics*, 60, 683-695.
- Nijhawan, R. (1994). Motion extrapolation in catching. *Nature*, 370, 256-257.
- Nijhawan, R. (1997). Visual decomposition of colour through motion extrapolation. *Nature*, 386, 66-69.
- O'Keefe, J., & Recce, M.L. (1993). Phase relationship between hippocampal place units and the EEG theta rhythm. *Hippocampus*, 3, 317-330.
- Pellizzer, G., & Georgopoulos, A.P. (1993). Common processing constraints for visuomotor and visual mental rotations. *Experimental Brain Research*, 93, 165-172.
- Peterken, C., Brown, B., & Bowman, K. (1991). Predicting the future position of a moving target. *Perception*, 20, 5-16.
- Post, R.B., & Leibowitz, H.W. (1985). A revised analysis of the role of efference in motion perception. *Perception*, 14, 631-643.
- Rieser, J.J., Guth, D.A., & Hill, E.W. (1986). Sensitivity to perspective structure while walking without vision. *Perception*, 15, 173-188.
- Rosenbaum, D.A. (1975). Perception and extrapolation of velocity and acceleration. *Journal of Experimental Psychology: Human Perception and Performance*, 1, 395-403.
- Slater-Hammel, A.T. (1955). Estimation of movement as a function of the distance of movement perception and target distance. *Perceptual and Motor Skills*, 5, 201-204.
- Sperry, R.W. (1950). Neural basis of the spontaneous optokinetic response produced by visual inversion. *Journal of Comparative and Physiological Psychology*, 43, 482-489.
- Steinbach, M.J., & Held, R. (1968). Eye tracking of observer-generated target movements. *Science*, 161, 187-188.
- Watamaniuk, S.N., & Heinen, S.J. (1999). Human smooth pursuit direction discrimination. *Vision Research*, 39, 59-70.
- Wexler, M., Kosslyn, S.M., & Berthoz, A. (1998). Motor processes in mental rotation. *Cognition*, 68, 77-94.
- Wohlschläger A. & Wohlschläger A. (1998). Mental and manual rotation. *Journal of Experimental Psychology: Human Perception and Performance*, 24, 397-412.
- Wolpert, D.M., Ghahramani, Z., & Jordan, M.I. (1995). An internal model for sensorimotor integration. *Science*, 269, 1880-1882.
- Wolpert, D.M., Goodbody, S.J., & Husain, M. (1998). Maintaining internal representations: the role of the human superior parietal lobe. *Nature Neuroscience*, 1, 529-533.