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Extrapolation of Visual Motion for Manual Interception

John F. Soechting and Martha Flanders
Department of Neuroscience, University of Minnesota, Minneapolis, Minnesota

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Soechting JF, Flanders M. Extrapolation of visual motion for manual interception. *J Neurophysiol* 99: 2956–2967, 2008. First published April 24, 2008; doi:10.1152/jn.90308.2008. A frequent goal of hand movement is to touch a moving target or to make contact with a stationary object that is in motion relative to the moving head and body. This process requires a prediction of the target's motion, since the initial direction of the hand movement anticipates target motion. This experiment was designed to define the visual motion parameters that are incorporated in this prediction of target motion. On seeing a go signal (a change in target color), human subjects slid the right index finger along a touch-sensitive computer monitor to intercept a target moving along an unseen circular or oval path. The analysis focused on the initial direction of the interception movement, which was found to be influenced by the time required to intercept the target and the target's distance from the finger's starting location. Initial direction also depended on the curvature of the target's trajectory in a manner that suggested that this parameter was underestimated during the process of extrapolation. The pattern of smooth pursuit eye movements suggests that the extrapolation of visual target motion was based on local motion cues around the time of the onset of hand movement, rather than on a cognitive synthesis of the target's pattern of motion.

INTRODUCTION

Interception of a moving target involves prediction in that the hand's movement is initiated in a direction that anticipates the target's future motion. A reasonably accurate prediction of target motion should involve the target's present location (distance and direction relative to the hand), its velocity (speed and direction), and its acceleration (rate of change in speed and rate of change in direction). Furthermore, the time to interception should also be estimated. However, it is not clear whether cortical processing mechanisms are able to use all of these parameters to plan the initial direction of the hand motion. For example, the rate of change in the speed of a visual target is sensed imperfectly, if at all (Lisberger and Movshon 1999), and this parameter has only a weak influence on smooth pursuit eye movements (Krauzlis and Lisberger 1994a; Soechting et al. 2005).

Previous studies on this topic have focused on the effect of target speed. Some investigators have reported that the initial direction of the interceptive hand movement is based on the target's location at the start of the hand movement and on a default speed rather than the target's actual speed (Brouwer et al. 2002; de Lussanet et al. 2004; Smeets and Brenner 1995a). To the contrary, Eggert et al. (2005) concluded that under open-loop conditions, the amplitude of the hand movement was influenced by the target's speed. Generally, visual target motion is curved. However, in most previous experiments the target moved in a straight line, leaving unanswered the extent to which information about the target's rate of change of direction (curvature) is incorporated in the movement plan for interception.

We have recently begun to investigate the control of interceptive hand movements under more general conditions—for targets that moved quasi-unpredictably along two-dimensional curved trajectories (Mrotek and Soechting 2007b)—under which subjects were free to initiate interception at a time of their own choosing. In those experiments, the initial direction of the hand movement was well correlated with an extrapolation of the target's motion at the onset of the hand movement. Specifically, we found that the hand moved toward a point that corresponded to the location the target would occupy about 150 ms into the future if it continued to move in the same direction and at a constant speed. Since movement interception was generally initiated when the curvature of the target's motion was small, and when the target was within a small range of distances from the hand, we could not determine whether the curvature of the target motion or the hand's movement time was incorporated into the planning.

In the present series of experiments, we address the question of the extent to which curvature of target motion and the time required to intercept the target influence the planning of the hand movement. We did this by presenting subjects with circular or oval trajectories and by instructing the subjects to initiate the interception when the target was at a wider range of distances from the hand. We will show that under these conditions, the planning of the direction of the interception movement does incorporate the time to interception and the target's curvature.

METHODS

Subjects and experimental overview

Twelve human subjects (five males, seven females) participated in the experiments. Of these, two participated in all of the experiments, two others participated in two sessions, and eight were tested in only one session. Each session was conducted on a separate day and was typically completed in 1 h. None of the subjects had a history of neurological disorders and all had normal vision corrected to 20/20. The procedures were approved by the University of Minnesota Institutional Review Board and all subjects provided informed consent.

The subjects were seated in front of a computer monitor (Mitsubishi Diamond Scan 20M, refresh rate of 60 Hz, and resolution of 640 × 480 pixels). The monitor was at eye height, 40 cm in front of the eyes. Subjects watched a small circular target (0.6°) that moved predictably at a constant speed (17 cm/s, 24.3°/s), following either a circular or an oval path. Target location was replaced on every frame and thus there

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Address for reprint requests and other correspondence: J. F. Soechting, Department of Neuroscience, University of Minnesota, 6-145 Jackson Hall, 321 Church St. SE, Minneapolis, MN 55455 (E-mail: soech001@umn.edu).

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was no permanent trace of the target's path on the screen. Each trial began when the subject's extended right index finger contacted the monitor's screen. This contact point was indicated by a red rectangle that disappeared as soon as contact was made. Subjects were instructed to intercept the moving target by sliding their finger along the surface of the screen as soon as the target's color changed from cyan to yellow. Successful interception occurred when the finger was within 1 cm of the target. Subjects were given no instructions concerning the eye movements they were to make and there were no constraints on the hand's speed at the time of interception. Thus the finger was permitted to cross the target's path.

Data recording

The computer monitor was equipped with a touch-sensitive screen (Elo TouchSystems, Menlo Park, CA) with a spatial resolution of about 0.01 cm. This device was used to record the finger motion at a temporal resolution of 100 Hz. We also recorded eye movements (SMI Eye Link System, SR Research, Mississauga, Ontario, Canada) at a rate of 250 Hz, the head being stabilized with a chin rest. For the eye position data, saccades were identified using standard procedures (Barnes 1982; Mrotek et al. 2006). Data recording ended 200 ms after the target was intercepted. Hand and eye data were calibrated at the beginning of each experimental session (Mrotek and Soechting 2007b).

Experimental procedures

We conducted two experiments. In the first, the target always followed a circular path; in the second, the path was either circular or oval in randomly interspersed trials.

EXPERIMENT 1. In this experiment, the target followed a circular path centered on the display screen, with a radius of 8.1 cm and a period of 3.0 s. In one experimental series (*experiment* 1A, seven sessions), the signal to initiate interception was given at one of six locations, equally spaced in six increments along the path and the initial location of the hand was in the middle of the bottom of the monitor's screen. The earliest signal was provided 1.8 s after motion onset (60% of the period) and the latest signal occurred at 4.3 s after motion onset (143% of the period). There were 20 trials for each of the six experimental conditions and the experimental conditions were randomized from trial to trial. In five of the seven sessions, the target always moved in a clockwise (CW) direction, beginning at the 3 o'clock position.

In two other sessions (involving two of the initial five subjects), the target moved in a counterclockwise (CCW) direction, beginning at the 9 o'clock position. Thus when the signal to initiate interception was given, the target's locations were mirror symmetric about the vertical axis for the CCW versus the CW motions.

Finally, in 10 more sessions (*experiment* 1B), the direction of target motion (CW vs. CCW) varied randomly from trial to trial. In these sessions, the time of the signal also varied randomly from trial to trial in the second cycle of target motion (i.e., throughout the period from 3.0 to 6.0 s after the onset of target motion). There were 75 trials each for CW and for CCW target motions. In five sessions, the initial hand location was also at the bottom of the screen, requiring predominantly upward hand movements. In the other five sessions, the hand started in the middle of the right border, requiring predominantly leftward hand movements to intercept the target.

EXPERIMENT 2. This experiment was designed to determine the extent to which subjects incorporated information about the curvature of the target's motion into the planning of the hand movement. In one third of the trials, the target moved along a CW circular path (radius 8.1 cm, period 3 cm), as in *experiment* 1. In the other trials, the target followed one of two oval paths (Fig. 1*A*, dotted and dashed lines), also in a CW motion. The ovals were constructed from two semicircles, and the ends of the two semicircles were connected by straight lines. The centers of each of the two semicircles (radii of 5.4 and 4.05 cm) were located such that they were tangent to the larger circle at its top and bottom. The speed of the target's motion (17 cm/s) was the same for all three target paths.

For each of the three target paths, in one third of the trials the signal was given such that the target was at the bottom of its trajectory when the hand began to move and in another one third of the trials it was given when the target was at the top (filled circles in Fig. 1*A*). In *experiment* 1, we found that the reaction time to initiate hand movement was typically 300 ms. Accordingly, the target's color changed 300 ms before it reached the top or bottom. To prevent subjects from anticipating the start signal, the target's color changed at random times in the last one third of the trials (randomly interleaved). In all cases, the signal to initiate interception was provided only after the target had completed one cycle of motion. There were 20 trials for each of the nine conditions (3 target paths × 3 signal times).

For the two locations indicated in Fig. 1*A*, we reasoned that if subjects did not take the curvature of target motion into account and merely planned the interception movement based on the target's location and velocity, the initial direction of finger motion should be the same for all three target paths. At these locations, the target always moved horizontally at the same speed, to the left at the bottom and to the right at the top. Conversely, if hand motion planning incorporated information about curvature of target motion, the initial direction of finger movement should differ for the three paths.

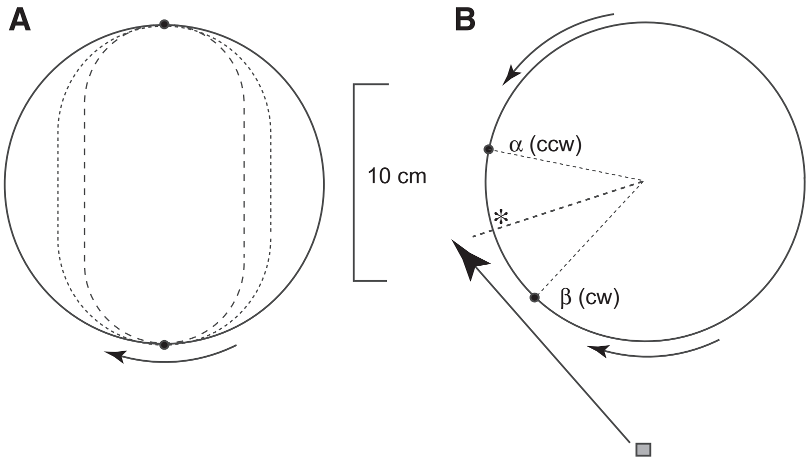

FIG. 1. Experimental design for *experiment* 2 (*A*) and for *experiment* 1B (*B*). In *experiment* 2, the target could follow one of 3 possible paths: a circle (solid line), a wider oval (dotted line), or a narrower oval (dashed line). The semicircles comprising the top and bottom parts of the ovals had radii that were one half or two thirds of the radius of the circle. On two thirds of the trials, hand movements to intercept the target were initiated when the target was at the apogee or perigee of the target's path (filled circles). On the other third of the trials, the signal to initiate hand movement was presented at random times. In *experiment* 1B, the target followed a circular path, clockwise (CW) or counterclockwise (CCW). For trials in which the initial direction of hand movement (large arrow) was the same, the location of the target at movement onset for CCW (filled circle at α) and CW (β) trials was identified. Those movements were assumed to be directed to a common point, either on the target's trajectory or on the radial line from the center to that point (denoted by *). The amount by which the hand movement led the target corresponds to the time required for the target to travel from α (or β) to *.

Data analysis

Hand speed was computed numerically by differentiating the *x*- and *y*-finger position data after double-sided exponential filtering (time constant 10 ms). Onset of the finger movement was defined as the time at which speed first exceeded 5% of its maximum. We computed the initial direction of finger motion (φ_{init}), using the first 100 or 150 ms of the movement, 0° being defined as straight up (or to the left in part of *experiment* 1B). Over these intervals, the finger's motion should be uninfluenced by visual feedback. Since both measures led to the same conclusions—although the longer interval provided a more reliable measure of direction—we report only the results using the 150-ms interval. We defined a "successful" interception as one in which the subject intercepted the target on the first try, hand speed being bell-shaped with a single peak. For these "successful" trials, we also computed the distance and direction (φ_{final}) from the finger location at movement onset and at the time of interception, the movement time (defined as the time from movement onset to target interception), and hand speed at the time of interception. Standard statistical procedures (ANOVA and multiple linear regression) were used to analyze these data, with the level of significance set at $P < 0.05$.

In the first series of experiments we found that the initial direction of finger movements did not always intersect the target motion and that, when it did, the amount by which the finger movement was directed in advance of the target varied considerably, but showed no consistent relation to movement distance or movement time. Those results suggested that subjects sometimes actually planned a curved hand trajectory and that, in contrast to arm movements to stationary targets (Georgopoulos and Massey 1988), the initial direction of movement was not a reliable indicator of the intended point of target interception.

Thus to determine how far in advance of the target's position the finger was aimed, we conducted a second series of experiments in which the circular target motion alternated between clockwise and counterclockwise on random trials, in which the position of the signal to initiate interception was also randomized. We reasoned that pairs of trials, one for CW motion and the other for CCW motion, in which the initial direction of hand motion was the same, would provide a measure of the intended point of interception, even if curved trajectories were planned.

This analytical design is illustrated schematically in Fig. 1*B*, where the points α and β denote target locations for two trials in which the initial direction of hand motion was the same. As drawn schematically, this initial direction does not intersect the target's motion but, from geometry, it is clear that the planned point of interception lies somewhere along a line that is equidistant from α and β, the radial line denoted by an asterisk (*). Thus the planned time of interception (the amount of time by which the hand movement leads the target motion) is one half of the time the target requires to move from point α to point β. This analysis assumes that the initial direction of finger motion depends only on the intended point of interception, but not directly on the direction of the target's motion, an assumption supported by a recent report by Brenner and Smeets (2007).

For the purpose of defining comparable initial finger movement directions for CW and CCW target motions, we first fit the distribution of initial directions with a sum of sines. We found that using the fundamental and the first two harmonic components gave an excellent fit to the data. Then we found the angular phase difference of this fit for CW and CCW motions as a function of the phase in the cycle at which hand movement started. Since a 360° phase corresponded to 3.0 s, the duration of one cycle, we could convert this phase difference to a time lead and we correlated this computed time lead with the actual movement time required to intercept the target.

RESULTS

General characteristics

Subjects followed the circular target motion using mainly smooth pursuit eye movement. Figure 2*A* shows typical results from one subject. The plot at the *left* shows the target path

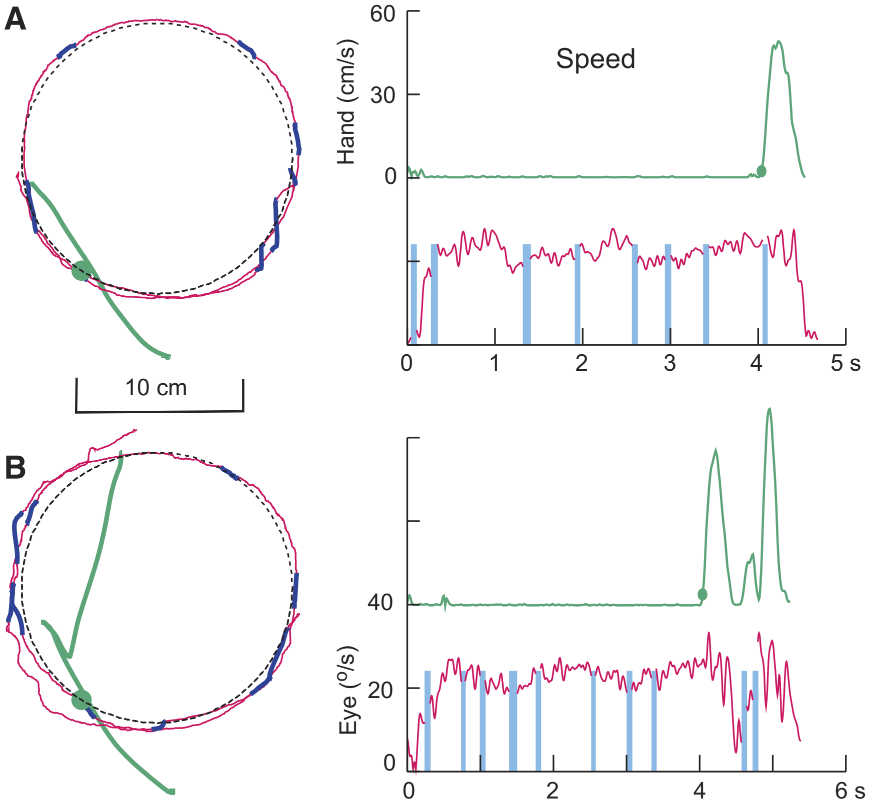

FIG. 2. Representative successful (*A*) and unsuccessful trials (*B*) from subject 3. A successful trial was defined as one in which the target was intercepted in one continuous movement. *Left panels* in *A* and *B* show the target's path (black dashed lines), eye position (red corresponding to smooth pursuit and blue to saccades), and the hand path (green trace). The target's location at the onset of finger movement is denoted by the filled green dot. The *right panels* show eye (red) and hand (green) velocities. Saccadic episodes (indicated by light blue shading) have been removed from the eye velocity traces.

(black dashed line) and the finger's path (green trace). The large green dot indicates the location of the target at hand movement onset. Eye tracking is also shown, the red portions of the trace corresponding to smooth pursuit and the dark blue segments to saccades. Pursuit was maintained up until the point of interception and saccades were sparse. This behavior was observed in all trials from all subjects and, in agreement with our observations when subjects intercepted targets moving less predictably (Mrotek and Soechting 2007b), we found no evidence for predictive saccades directed to the anticipated point of interception. The traces in the *right panel* show the temporal profiles of hand (green trace) and smooth pursuit eye speed (red trace). The onset of finger movement, defined as the time at which hand speed first exceeded 5% of its peak value, is shown by the filled green circle. In this trial, the finger began to move about 240 ms after the signal to initiate interception was presented.

The trial in Fig. 2*A* was classified as "successful" since hand speed was bell-shaped with a single peak. By contrast, the trial in Fig. 2*B*, which was from the same subject and had the same time of hand movement onset, was classified as "unsuccessful." The initial finger movement did not intercept the target and there was a second movement, initiated at about 4.8 s, that was redirected to intercept the target at a new location. Unsuccessful trials were rare. On average, in the first series of experiments (*experiment* 1A, circular target motion with go signal at one of six times) 93.5% of the trials were classified as successful. Success rates in the other series (*experiments* 1B and 2) were comparable, but there was considerable variability from subject to subject, with success rates ranging from 73 to 99%.

Characteristics of the interception movement

On average, the reaction time to initiate the finger movement was 358 ms, with a range for different subjects from 281 to 433 ms. Individual subjects were typically very consistent in their reaction times, with intrasubject SDs of about 40 ms. The reaction times tended to be shorter when the signal to initiate the movement was presented later in the trial. Averaged over all 17 sessions, the slope of reaction time, regressed on the time of the go signal measured from the start of target motion, was negative (-0.018 ± 0.005 SD, $t_{16} = -3.50$, $P < 0.01$). Thus on average, the reaction time decremented by about 54 ms over one cycle of the target motion (3.0 s). However, for those subjects in which the trend was significant, reaction time increased as the experiment progressed (i.e., the slope of the regression of reaction time on trial number tended to be positive). These findings suggest that the decrease in latency did not arise because subjects became more certain about the target's trajectory as the trial progressed. Instead, we suggest that reaction time decreased because the probability that a go signal would be presented soon increased as time progressed in a given trial (Carpenter and Williams 1995; Ghose 2006).

On successful trials, the movement time (time from movement onset to the time of interception) and the peak hand speed depended on the distance from the hand to the target at the point of interception. On average, in *experiment* 1, the subjects took 330 ms to intercept the target, with an intersubject range of 280 to 450 ms. The closest target was reached as early as 160 ms after movement onset in the fastest subject, whereas the time to intercept the distalmost targets ranged from 370 to 630 ms (Fig. 3*A*). In all subjects, movement time and distance were strongly correlated (average $r^2 = 0.631$, range 0.32–0.80), with an average slope of 13.2 ms/cm. Similarly, peak finger speed was also positively correlated with distance (average $r^2 = 0.728$, range 0.51–0.88) with a slope that averaged $2.97 \pm 0.56\ \mathrm{s}^{-1}$ (Fig. 3*B*).

The peak finger speed was attained in 190 ± 30 ms (SD computed on subject averages) and this time also depended reliably on movement distance (average $r^2 = 0.728$, slope = 4.4 ± 1.7 ms/cm; Fig, 3*C*). In almost all instances the target was intercepted while the hand was still moving at an appreciable speed. Average hand speed at the time of interception was 28.6 ± 7.4 cm/s, corresponding to 46.4 ± 8.0% of the peak speed. Typically, the target was intercepted when the hand velocity was proportionally closer to its peak for closer targets. Thus the peak speed occurred at about 75% of the movement time for the closest target, but at about 55% of movement time for the most distant targets (Fig. 3*D*).

The movement kinematics for the interception movements resemble those described previously for movements to stationary targets in that speed and movement time were proportional to distance (Buneo et al. 1994; see also Viviani and McCollum 1983). Since the peak speed generally occurred within 200 ms of movement onset, these results suggest that the amplitude of the interception movement was planned by taking into account the predicted distance from the hand at movement onset to the position of the target at the time of interception. We base this conclusion on the reasoning that, during the first 200 ms of the hand movement, the influence of on-line visual feedback of target and hand motion would be negligible.

Initial direction of finger motion

The question now arises: did the initial direction of the interception movement also take into account the distance from the hand to the target, as the target moved along the circular path? If so, and assuming the interception movement was planned to be straight (Morasso 1981), one would expect that the point at which the initial hand trajectory intercepts the target's trajectory would lead the target by an amount that depended on distance.

We tested this by first computing the direction of the finger movement in the first 150 ms and we extrapolated this direction to the point at which it intersected the target's path. If the hypothesis was correct, then this point of intersection should lead the target's position at movement onset by an amount that depended on distance and time to interception. An alternative would be that direction was planned assuming a constant movement time, i.e., that the amount by which the point of intersection leads the target should be constant.

The results were not in accord with either hypothesis. The amount by which the initial direction of the hand movement led the target was not constant but it also did not vary in any consistent manner with movement time or distance. Furthermore, in some instances the initial direction of hand movement was along a line that did not intersect the target's path at all. Typical results from one subject are shown in Fig. 4. The plots show the results for all six locations at which the signal to

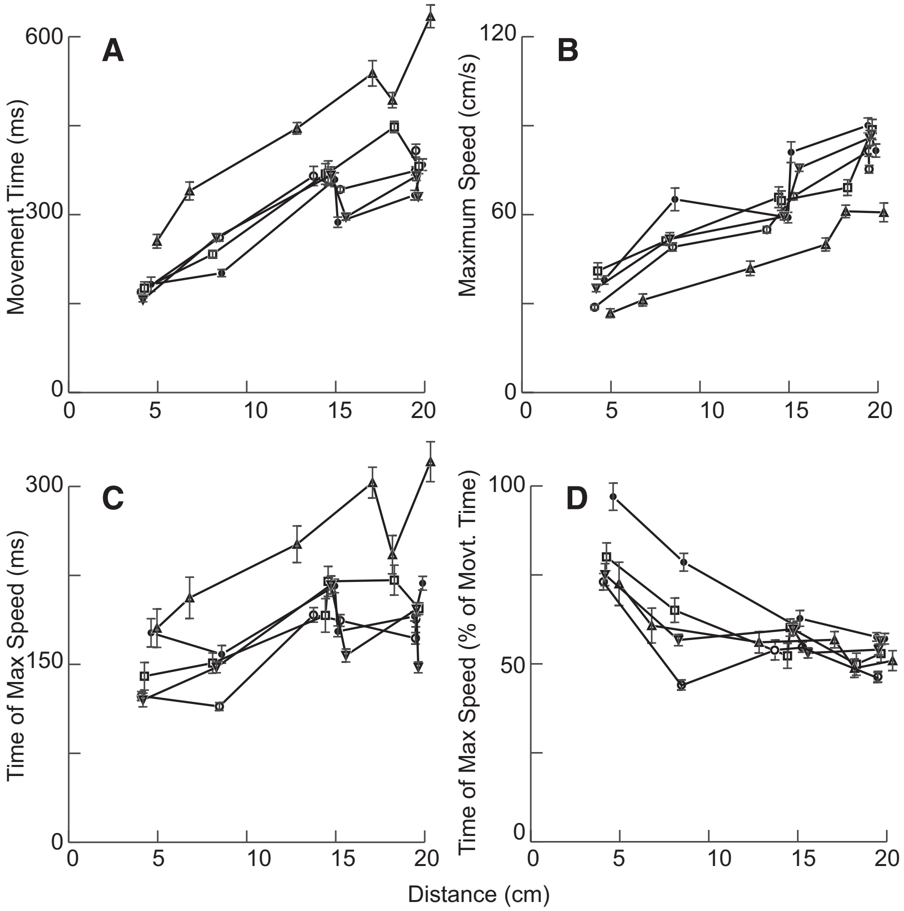

FIG. 3. Dependence of various movement parameters on the distance to the target at the time of interception. Plots show the dependence of movement time (*A*), the maximum speed (*B*), the time of maximum speed (*C*), and this time measured as a percentage of movement time. Data are for successful trials in *experiment* 1A for CW target motion from each of the 5 subjects. The error bars bracket 1SE.

intercept (▾) was presented. In some instances (Fig. 4, *C* and *D*), the extrapolation of the initial direction of finger movement coincided with the target's location at the time of interception (■). In other instances, however, the movement was initially directed to the target's location at movement onset (●, Fig. 4, *A* and *F*) and, finally, in Fig. 4*E*, the initial direction of finger movement was lateral to the target's trajectory (see also Fig. 2).

Conceivably, subjects made errors in the initial direction of finger movement because the prediction of target motion failed to take into account the target motion's curvature, i.e., the extrapolation was made based solely on the target's position and velocity near the time of movement onset. Note that such an extrapolation would be consistent with the bias in movement direction in Fig. 4*E*. If this third hypothesis were correct, then the results obtained for CCW target motion should be mirror symmetric with those in Fig. 4, obtained for the CW target motion. Specifically, one would expect a rightward bias in finger motion direction when the "go" signal was presented at 6 o'clock (as in Fig. 4*E*), but the target moved CCW. To test this, we repeated the experiment in two of the five subjects using CCW target motions. The results showed that failure to account for curvature did not explain the initial movement direction (Fig. 5). The subjects still showed a leftward bias, this time when the go signal occurred at the 12 and 10 o'clock positions (corresponding to Fig. 4, *B* and *C*).

A regression of the initial movement direction (φ_{init}) on the direction to the target at the time of interception (φ_{final}) showed that in four of the five subjects, the slope was reliably >1.0, with a negative intercept, indicative of a leftward bias (Table 1). Only trials in which the target was intercepted successfully on the first try were included in the analysis. Importantly, neither the slope nor the intercept differed substantially between CW and CCW target motions. The results of this analysis and the data shown in Figs. 4 and 5 suggest that subjects did not plan linear finger motions. Rather, they suggest that curved trajectories were planned, in a clockwise direction for most of the subjects (i.e., for four of the five). If so, the intended point of interception cannot be deduced from the initial direction of finger motion.

The last experimental series in *experiment* 1 was designed to make our analysis independent of the assumption that subjects planned linear movements. In this series, we randomly interleaved trials with CW and CCW circular target motions and presented the go signal at random times. We tested two starting locations of the hand: one in which the finger started at the bottom of the screen and the movement was primarily upward and a second one, requiring primarily leftward movements, in which the finger started at the right edge of the screen. We reasoned that two trials (one CW and one CCW) having the same initial direction of finger movement would have the same planned point of interception (Fig. 1*B*). Furthermore, this point should be halfway in between the targets' locations at the time of movement onset (α and β in Fig. 1*B*). Accordingly, the time by which the hand movement led the target at movement onset should correspond to one half of the target's transit time from α to β. This analysis assumes that the time to intercept the target at a given location was the same irrespective of the direction of target motion. This was indeed the case; neither

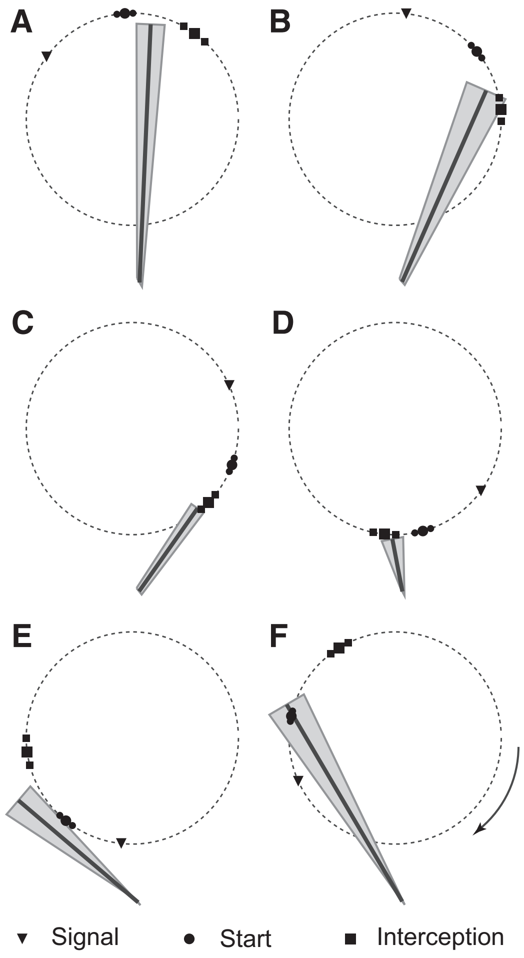

FIG. 4. Initial direction of finger movement to intercept a target moving CW along a circle (dotted line), the go signal occurring when the target was at the location denoted by ▼. The solid lines denote the initial direction of finger movement, computed from the first 150 ms after movement onset and the shaded area brackets ±1SD of this value. Target location at the mean onset times of interception are denoted by ● and the mean time of interception on successful trials is denoted by ■. Smaller symbols show ±1SD of these times. The plots show all of the results from subject 1. Note that there is not a consistent relation between the initial direction of finger movement and the target's location at movement onset or at the time of interception.

movement time nor maximum speed depended on the direction of target motion (ANOVA, $P > 0.1$), whereas, as presented earlier (Fig. 3, *A* and *B*), these parameters did depend on the distance to the target ($P < 0.001$).

Figure 6 shows the results of this analysis for one subject with the starting location at the lower border. The *top panels* show the initial movement directions for trials in which the target moved CW (*left*) and CCW (*right*) as a function of the phase in the target motion's cycle at the time the hand movement was initiated (0° corresponding to the 3 o'clock position, and phase always increasing in the CW direction). These data were fitted with sums of sinusoids (fundamental and two harmonics) and the results of this fit are shown by the solid black lines. Results of this fit for motion in the other direction are shown superimposed with the light blue traces. For each value of initial movement direction (*y*-axis), we computed the phase difference (*x*-axis) between the two fitted curves and then we converted this phase difference to a time difference (Prediction Time). Results for only one movement direction (CW) are shown in Fig. 7 for two other subjects, the movements in Fig. 7*A* being primarily vertical (bottom starting location) and those in Fig. 7*B* being primarily horizontal (right side starting location).

The prediction time is shown in the black curves in the *bottom panels* in Figs. 6 and 7. The movement time (red) and distance from the initial finger position to the target at the time of interception (green) are also shown for comparison for all of the successful trials. Since the estimate of the prediction time is less reliable when φ_{init} changes slowly (i.e., at the peaks and troughs), these portions of the estimate are shown as lighter and dashed (black). However, all data points were included in the regression of prediction time on movement time and distance (below).

From a close inspection of the *top panels* in Figs. 6 and 7 one can see that the prediction time varied as a function of the phase in the target's motion cycle, since the solid black and blue curves are not offset by a constant amount. This is highlighted in the *bottom panels*, which also show that the prediction time was reliably correlated with the time required to intercept the target. In Fig. 6 (subject 1), the slope of the correlation of prediction time on movement time was 0.87 ($r^2 = 0.59$, $P < 0.001$, Table 2). The corresponding results for Fig. 7 are 7*A*: slope = 0.47, $r^2 = 0.59$, and for 7*B*: slope =

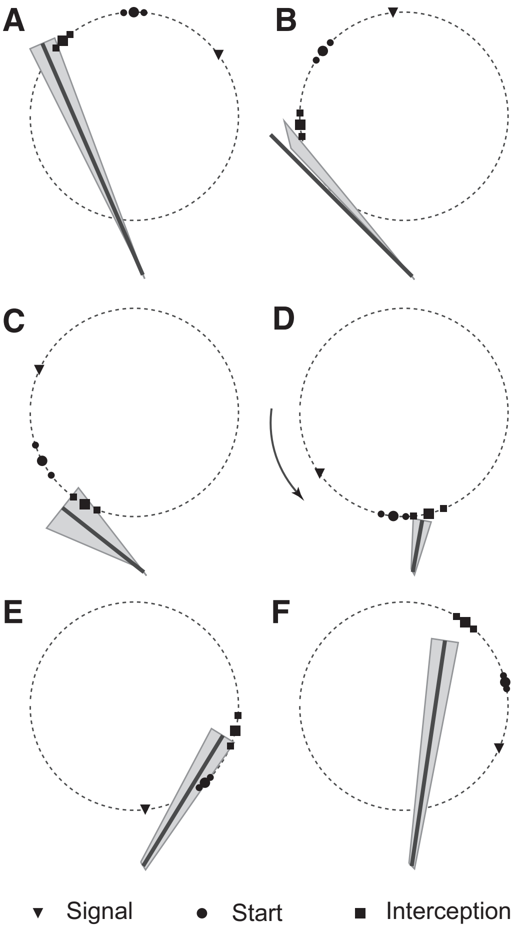

FIG. 5. Initial direction of finger movement to intercept a target moving CCW along a circle. Results are plotted in the same format as in Fig. 4 and are from the same subject.

TABLE 1. *Slope and intercept of regression of initial movement direction (φ_{init}) on the direction to the target at interception (φ_{final})*

Subject	Direction	Number of Trials	Intercept, deg	Slope	R^2
1	CW	108	−9.00 ± 0.60	1.15 ± 0.02	0.958
2	CW	117	−6.12 ± 1.23	1.13 ± 0.01	0.982
3	CW	115	−4.24 ± 0.58	1.21 ± 0.02	0.965
4	CW	108	2.81 ± 0.99	1.08 ± 0.03	0.899
5	CW	87	−7.18 ± 0.85	1.00 ± 0.03	0.921
1	CCW	99	−5.98 ± 0.62	1.13 ± 0.02	0.965
2	CCW	110	−4.853 ± 0.46	1.19 ± 0.02	0.974

Values are coefficients ± SE. CW, clockwise; CCW, counterclockwise.

0.83, $r^2 = 0.56$. The slope of this regression was positive, but less than unity and significantly different from zero ($P < 0.001$), for all 10 sessions. Furthermore, on average, the prediction time tended to slightly underestimate the time required to intercept the target, by 13% (range from 3 to 30% for individual subjects).

Initial direction depends on curvature of target motion

The results in Figs. 6 and 7 show that subjects did indeed take into account the time required to intercept the target in planning the initial direction of the finger movement. They leave open the question of whether this planning incorporates an estimate of the curvature of the target trajectory. As discussed in METHODS, the interception movement could have been aimed at any point along the radial line that bisects points α and β in Fig. 1*B*. The second experiment was designed to more directly address the question of target curvature prediction. We used three different motion profiles randomly presented (Fig. 1*A*) and, in two thirds of the trials, we timed the go signal such that the hand movement would begin when the target was at its apogee or its perigee. At those points, the target was traveling horizontally, at the same speed for all three target trajectories. Consequently, an extrapolation of target motion based solely on velocity would yield the same result in all three instances and the initial direction of hand motion should be the same.

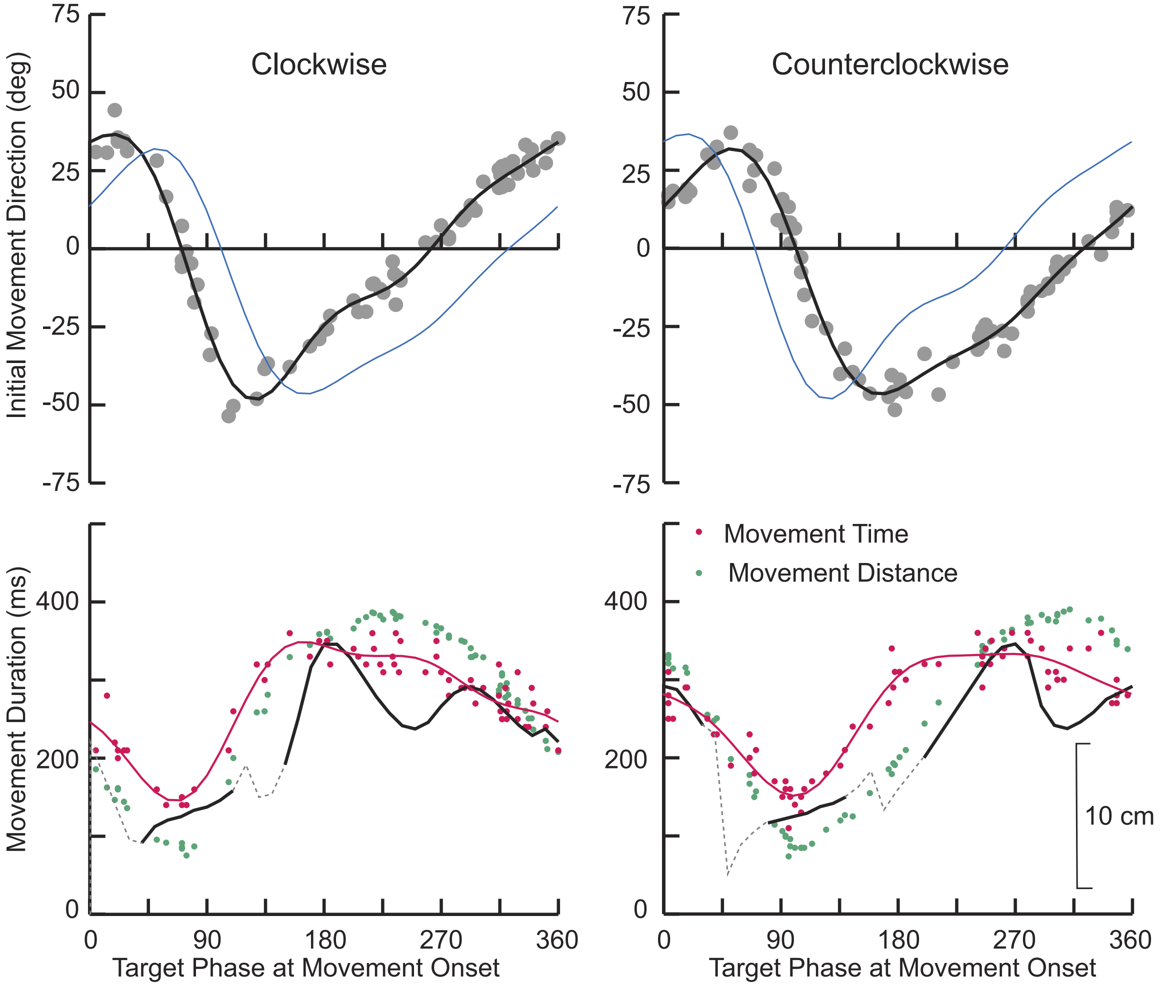

FIG. 6. Initial finger movement direction as a function of the target's location at the onset of the interception movements for CW (*left*) and CCW (*right*) circular target motion for subject 1 in *experiment* 1B. The gray circles depict the initial movement directions for individual trials, plotted as a function of the cyclic phase of target motion (0° corresponding to the 3 o'clock position, with phase increasing in the CW direction). In the *top panels*, the solid black lines denote a fit to the data and the lighter blue lines show for comparison the fit for the motion in the opposite direction. Note that there is not a constant horizontal offset between these 2 traces. This variable offset is shown as the black trace in the *bottom panels*, converted to time. The heavy solid portion corresponds to segments where the offset could be estimated reliably. The lighter dashed portions show the remainder, where the reference movement direction (black line in *top panels*) differed by <10% from the minimum or maximum. The red dots show movement time to intercept the target (on successful trials) and the red solid line is a fit to these data. The green dots show the movement distance for the same trials. Note the correlation between the time by which the initial movement direction leads the target and the time required to intercept the target.

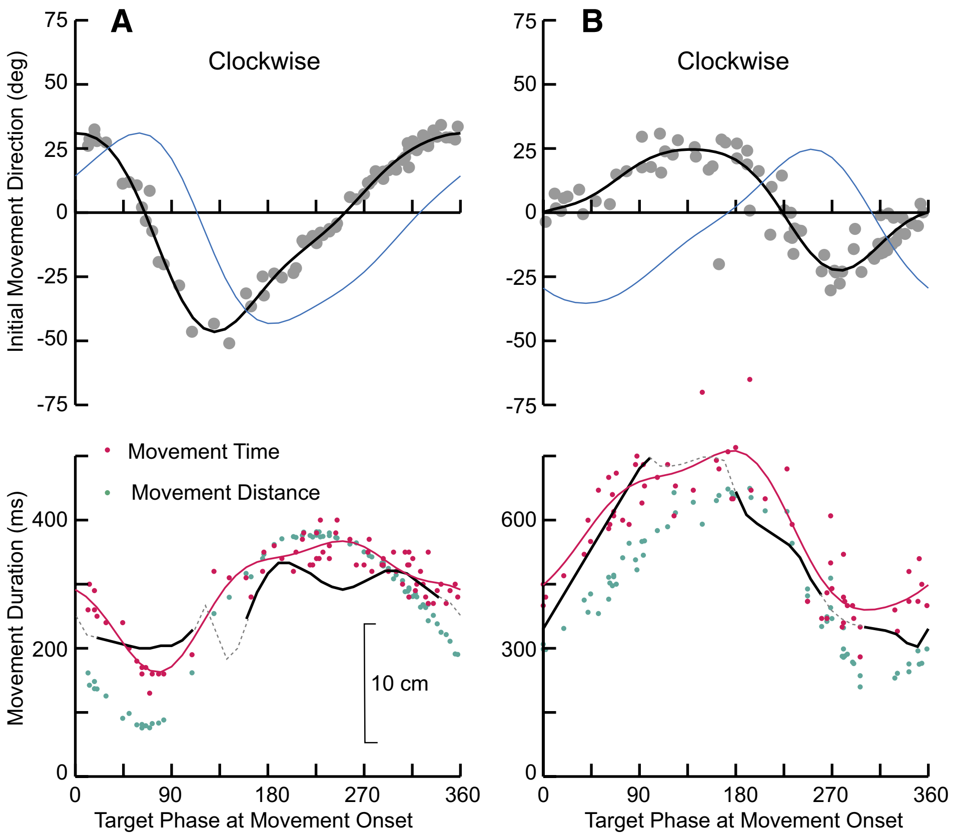

FIG. 7. Initial finger movement direction as a function of the target's location. Results are plotted in the same format as in Fig. 6 and are for subject 2 (*A*) and for subject 9 (*B*). In *A*, the initial finger location was at the bottom of the screen, whereas in *B*, it was at the right border. Results are shown from individual trials in which the target moved in the CW direction and the blue trace in the *top panels* shows the fit to the corresponding data for CCW target motion.

Conversely, if target motion curvature was incorporated into the prediction, the initial direction of finger motion should be closer to vertical for the narrow oval than it is for the circle.

This was indeed the case as illustrated in Fig. 8, which shows representative results from two subjects (1 and 9) for the case when the target was at its perigee. In both subjects, the initial direction was closer to the vertical when the target followed the narrower oval than when it followed the circular path (compare red and blue traces in the *rightmost panels* of Fig. 8, *A* and *B*). Over all subjects, this effect was significant statistically for both target locations: perigee [$F_{(2,281)} = 14.1$, $P < 0.001$] and apogee [$F_{(2,282)} = 3.35$, $P = 0.037$]. On average, for the target at the perigee the initial direction of finger movement moved closer to the vertical by 1.7° (wider oval) and 4.6° (narrow oval) with respect to the average value of 29.2° for circular motion. The effect was smaller when the target was at its apogee, the decrement being 0.7 and 1.9°, respectively. By comparison, the decrement in the direction to the target at its point of interception was 3.8 and 6.7° at the perigee and 0.9 and 2.9° at the apogee. Thus on average, the initial direction of finger movement (φ_{init}) changed by 64% of the amount of the change in final direction (φ_{final}). This result is consistent with a model in which curvature of target motion is incorporated into the prediction of target motion but the amount of curvature is underestimated.

TABLE 2. *Regression of prediction time on movement time for successful trials*

Subject	Number of Trials	Intercept, ms	Slope	R^2
1—V	136	−8.063 ± 17.5	0.871 ± 0.063	0.587
2—V	147	134.1 ± 12.8	0.469 ± 0.041	0.468
5—V	140	146.1 ± 21.1	0.613 ± 0.044	0.581
6—V	135	54.5 ± 12.8	0.660 ± 0.044	0.626
7—V	109	218.2 ± 12.3	0.131 ± 0.030	0.149
1—H	110	143.4 ± 22.8	0.337 ± 0.072	0.168
2—H	138	262.1 ± 26.7	0.338 ± 0.062	0.179
9—H	128	47.4 ± 37.7	0.829 ± 0.065	0.563
11—H	135	115.4 ± 15.9	0.492 ± 0.055	0.376
12—H	121	388.2 ± 27.4	0.341 ± 0.052	0.265

Values are coefficients ± SE. V refers to experiments in which the starting position was at the lower border of the screen; H refers to experiments in which it was on the right border.

Tracking target motion

Even though subjects were not instructed to do so, they generally used smooth pursuit eye movements to track the target's motion. Since eye tracking also involves prediction (Bennett and Barnes 2004; Kowler et al. 1981, 1984; Mrotek and Soechting 2007a), the ocular trajectories can provide additional information about the parameters that entered into the extrapolation of target motion. Figure 9 shows the average eye position traces (solid black) for two subjects (A and B) in *experiment* 2. These traces were obtained by binning eye position in 1° increments of radial angle and averaging over all of the trials, beginning 200 ms after the onset of the trial. The results show that the tracking was not entirely precise. Espe-

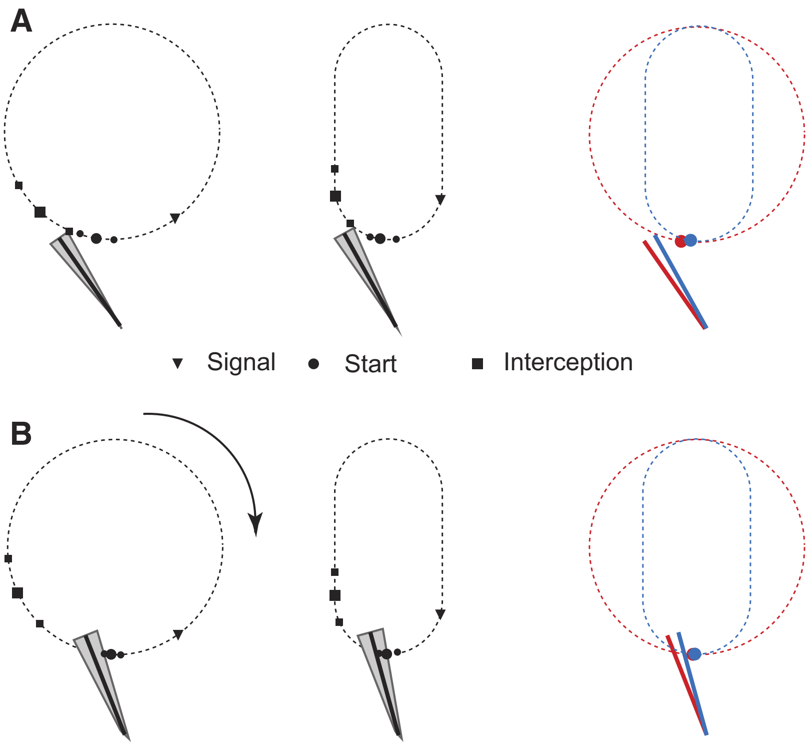

FIG. 8. Initial movement directions to intercept targets moving along a circular path (*left*) or along an oval (*middle*). Start signals (▼) were presented at times such that finger movements would be initiated (●) when the target was at its perigee and moving horizontally at the same speed for both target motions. The overlay of the 2 results in the *right panel* shows that the initial direction of finger movement is closer to vertical when the target moved along an oval, indicating that curvature of target motion was incorporated into the movement plan. Data are for 2 representative subjects (2 in *A* and 9 in *B*).

cially in the case of the ovals, the eye's trajectory did not reproduce the target's path.

We consider first the results for circular target motion (Fig. 9, *top row*). In agreement with previous results (cf. Mrotek and Soechting 2007b), tracking gain was slightly higher for the horizontal component than it was for the vertical, eye paths being slightly elongated in the horizontal direction. Most notably, however, the eye followed a radius that was slightly larger than the target's radius (by 6.2% on average in Fig. 9*A* and by 1.5% in Fig. 9*B*, $P < 0.001$, *t*-test). This was true in *experiments* 1A and 2; on average the radius of the eye's gaze was 3.2% larger. For smooth pursuit, the average gain (the ratio of pursuit speed to target speed) was slightly less than unity (0.97 ± 0.06) and pursuit lagged the target by a small amount (14 ± 18 ms). This lag was computed by comparing the direction of pursuit eye velocity to the direction of the target's velocity at each point in time and it corresponded to a lag of about 2° radial angle. The values for gain and lag are similar to values reported previously (Barnes and Ruddock 1989; Collewijn and Tammiga 1984; Kettner et al. 1996) and indicate the presence of a predictive component in ocular tracking.

Two of the ten subjects were excluded from this analysis because they did not always maintain pursuit throughout the trial. Instead, they sometimes initiated pursuit, then paused, made a large catch-up saccade, and then reinitiated pursuit that was maintained until interception. In those instances, the pause occurred early during the first cycle, when the probability of the signal for the initiation of interception was zero.

When subjects tracked the two ovals (Fig. 9, *middle* and *bottom rows*), average pursuit gain was slightly less (0.94 ± 0.06 for the wider oval and 0.91 ± 0.08 for the narrower one) and the direction of smooth pursuit lagged the direction of target by slightly more (7.7 ± 0.9° for the wider oval and 3.5 ± 0.5° for the narrow oval compared with 2° for the circle). However, this directional lag was not uniform throughout the cycle. As can be appreciated in Fig. 9, the eye's trajectory continued to curve as the target began to move straight down or straight up (i.e., at the end of each semicircle). Consequently, for a period of time the direction of eye movement dramatically led the direction of target motion. This phenomenon was observed in all five subjects. Immediately following the transition from curvilinear to rectilinear target motion, the direction of eye velocity lagged the direction of target motion. This lag decreased steadily and reversed to a lead by about 80 ms. For the interval from 100 to 300 ms after the transition, this angular lead was significantly different from zero (*t*-test on data binned in 20-ms intervals, $P < 0.001$).

Because the direction of pursuit did not correspond precisely to the direction of the target's motion, the path followed by the eye was distorted relative to the target's path. In fact, the two subjects who had previously participated in *experiment* 1 (tracking only circular motion) reported that this second experiment was more difficult because the target appeared to "wiggle." Thus it appears that the trajectory followed by the eyes influenced their perception of the target's motion, this perception corresponding more closely to the eye's motion than it did to the target's spatial trajectory. It has been reported that motions that deviate from the power-law relation between speed and curvature (Lacquaniti et al. 1983) can lead to misperception of the trajectory (Viviani et al. 1997). However, in the present experiments, this relation was always obeyed, since speed and curvature were constant.

More generally, these results suggest that the predictive component of the pursuit eye movements was not based on a synthesis of the overall shape (i.e., an oval) but that it was based on an extrapolation of local motion cues (i.e., if the target was following a curve, it should continue on a curved path). Furthermore, the fact that the eye followed along a

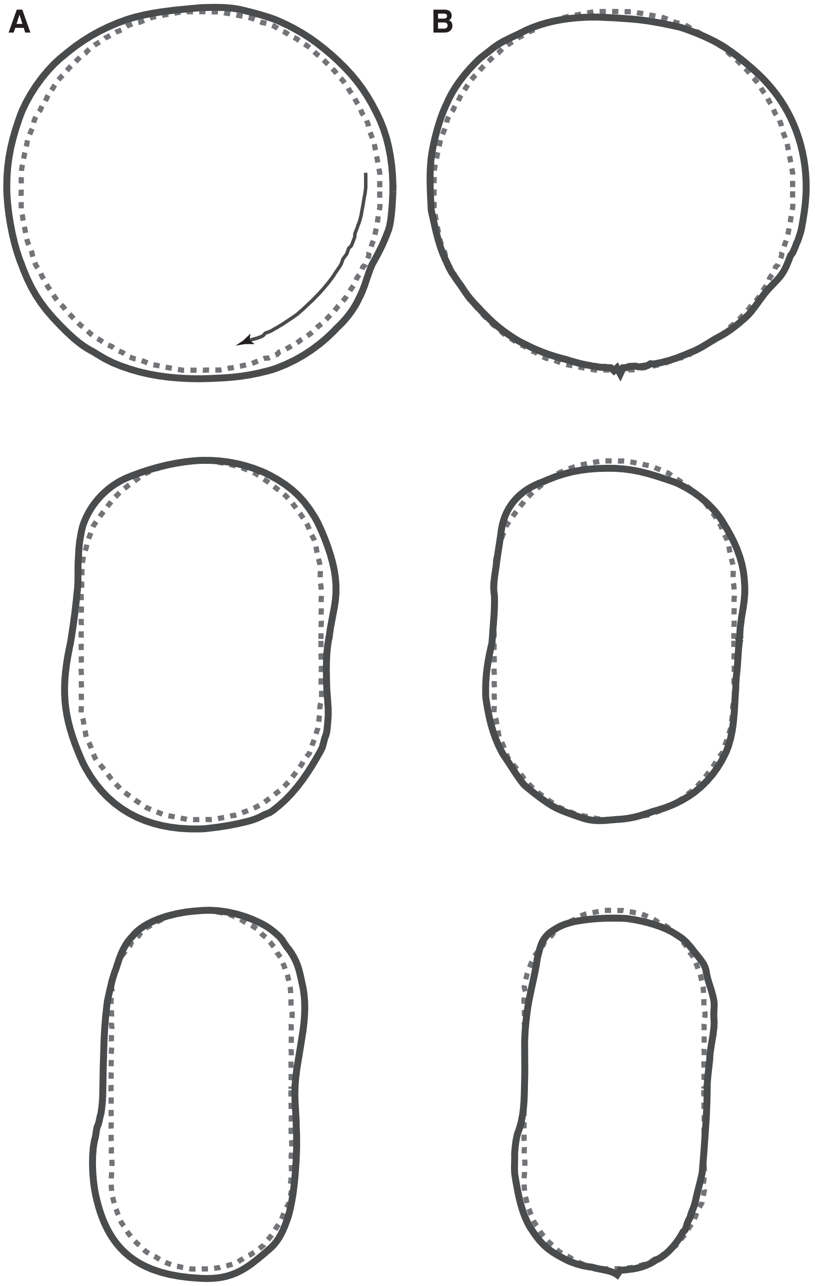

FIG. 9. Average paths of eye tracking in *experiment* 2. Dashed lines show target paths (circular motion in *top panels*, along wide or narrow ovals in the *bottom 2 panels*) and the solid lines depict average eye position (computed from all trials for one subject) for these target motions. Note that the eye followed a larger radius than that of the target for circular motion and that the eye's path was distorted when the target moved along an oval. Data are for subjects 1 (*A*) and 8 (*B*).

radius that was slightly larger than that of the target suggests that curvature was underestimated.

DISCUSSION

In the experiments described here we sought to ascertain some of the parameters that are used to predict target motion for the purpose of interception. We assumed that the amplitude and direction of a manual interception movement would be planned so as to intercept the target at a location that was based on an extrapolation from its motion prior to the onset of the hand movement. Specifically, we focused on the direction of the interception movement and we found that this direction was influenced by the time required to intercept the target as well as the curvature of the target's trajectory. Since the movement time was proportional to the distance to the target, these results indicate that the extrapolation of target motion is based on its location, velocity, and angular velocity (or curvature). Our results also suggest that this extrapolation is based on an underestimation of movement time and curvature and is thus not entirely accurate. Furthermore, the pattern of pursuit eye movements suggests that the extrapolation is based on local motion cues around the time of the onset of the interception movement rather than on a synthesis of the target's motion (i.e., using cognitive cues), even for very simple trajectories. Finally, the results suggest that, in agreement with some previous observations on interception movements (Smeets and Brenner 1995b), curved hand movements may be planned.

In our initial experiments, in which the target followed a circle in the CW direction, we found a marked leftward bias in the initial direction of finger movement (Figs. 2 and 4 and Table 1). Because this same bias persisted when the target moved in the opposite, CCW direction (Fig. 5), this bias could not be attributed to a faulty prediction of target motion, for example, one that ignored curvature. Rather, those results suggested that subjects planned a curved hand movement. This was somewhat unexpected since pointing movements are often assumed to be planned as straight-line movements (Flash and Hogan 1985; Gordon et al. 1995; Morasso 1981). However, reaching movements in the sagittal and frontal planes show a consistent pattern of CW and CCW curvature, which may be due to musculoskeletal considerations (Flanders et al. 1996; Pellegrini and Flanders 1996). It is also possible that in our experimental conditions, subjects planned movements that curved in a clockwise direction to minimize the chance that the arm would obscure vision of the target. (Subjects always used their right arm to intercept the target.) Independently of the explanation for this phenomenon, it became clear that the initial direction of finger movement was not an accurate indicator of the planned point of interception.

We overcame this by comparing trials with the same initial direction of finger movement, but for which the target moved in opposite directions (Fig. 1*B*). The amount of time by which the direction of finger movement anticipated the target's motion corresponds to one half the time it would take the target to traverse the distance from the target's location at the onset of the two interception movements. We found that this time was significantly correlated with the time required to intercept the target and thus with the distance from the finger to the point of interception. However, since the slope of this regression was consistently <1, variations in movement time were found to be underestimated.

The results of the second experiment showed that the curvature of the target's trajectory also influenced the initial direction of the interception movement (Fig. 8). The results of the first experiment, in which we found comparable biases in movement direction for CW and CCW target motions, indirectly confirm this conclusion. As was the case for movement time, the amount of curvature appears to have been underestimated by about a third. An analysis of eye trajectories (Fig. 9) also suggests an underestimation of target path curvature, since the eye followed a radius that was consistently larger than that of the target motion. However, since the eye movements reflect a combination of feedback (minimizing disparities between target velocity and eye velocity) and predictive elements (Bennett and Barnes 2004; Churchland et al. 2003) errors in predicting target motion are difficult to quantify.

Our experiments were aimed primarily at delineating the factors influencing the direction of the planned interception movement. However, in agreement with previous results (Eggert et al. 2005), we found that the planned amplitude of the interception movement was also based on a prediction of target motion, specifically on the distance to the target at the time of interception. We base this argument on the fact that peak velocity, which occurred about 200 ms after movement onset, was strongly correlated with distance to the target at the time of interception. Our experiments did not test effects of target speed on the interception movement, since this parameter was constant in all the experiments. However, previous experiments in which subjects had to intercept circular target motion at the 12 o'clock position showed that the onset of interception was related to the target's speed (Port et al. 1997). Furthermore, experiments in which the target became invisible suggested that a combination of a default speed and the actual target speed were used in controlling the direction of the interception movement (Brouwer et al. 2002).

Finally, our experiments also did not address the question of whether the extrapolation of target motion depended on an estimate of motion parameters at one instant in time or whether they reflected an average of those parameters over an interval of time. Previous reports have claimed that an interval of 200 to 300 ms or more was required to obtain a reliable estimate of speed (Brenner et al. 1998; de Lussanet et al. 2004; Merchant et al. 2003; Smeets and Brenner 1995a). However, in those experiments interception was initiated at times close to the onset of target motion. In smooth pursuit tracking, even though the speed of smooth pursuit is scaled with the target's speed at longer latencies, the initial response to the onset of target motion also is not scaled to speed (Krauzlis and Lisberger 1994b). However, the smooth pursuit response to brief, 50-ms perturbations applied during ongoing motion is scaled to the amplitude of the perturbation (Kerrigan and Soechting 2007; Schwartz and Lisberger 1994). Consequently, it is likely that an interval considerably <200 ms is adequate to estimate target speed, provided that this estimate is obtained some time after the onset of the motion (van Donkelaar et al. 1992).

An exposure of 50 ms is also adequate to estimate the direction of target motion (Hohnsbein and Mateeff 1998; Mrotek et al. 2004). Furthermore, subjects maintain smooth pursuit along a curved trajectory after the target has disappeared behind an occlusion, even for viewing times as short as 150 ms (Mrotek and Soechting 2007a). Since the angular velocity of smooth pursuit was graded with the target's angular velocity, those results indicate that an estimate of the rate of change in direction can also be obtained from local cues. Thus on the basis of these behavioral observations, extrapolation of target motion based on sensed target motion over an interval as short as 50 ms appears to be feasible.

Neurons in the medial temporal area (MT) are responsible for processing visual motion signals, being tuned to the speed and the direction of a moving target (Maunsell and Van Essen 1983; Mikami et al. 1986). Using randomly moving gratings and spike-triggered averaging, Bair and Movshon (2004) showed that MT neurons integrate motion signals over intervals of 20–40 ms, whereas Perge et al. (2005) found that directional information was averaged over a slightly longer (40- to 50-ms) interval. Furthermore, Osborne et al. (2004) found that spike activity in a 20-ms bin provided >50% of the information about stimulus motion that was contained in a much longer (250-ms) interval. Thus there is evidence that MT has the temporal resolution to encode target motion even when this motion changes rapidly. However, the processes whereby this information is used to extrapolate the motion into the future remain to be defined.

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REFERENCES

Bair W, Movshon JA. Adaptive temporal integration of motion in direction-selective neurons in macaque visual cortex. *J Neurosci* 18: 7305–7323, 2004.

Barnes GR. A procedure for the analysis of nystagmus and other eye movements. *Aviat Space Environ Med* 53: 676–682, 1982.

Barnes GR, Ruddock CJ. Factors affecting the predictability of pseudo-random motion stimuli in the pursuit reflex of man. *J Physiol* 408: 137–165, 1989.

Bennett SJ, Barnes GR. Predictive smooth ocular pursuit during the transient disappearance of a visual target. *J Neurophysiol* 92: 578–590, 2004.

Brenner E, Smeets JB. Flexibility in intercepting moving objects. *J Vision* 7: 1–17, 2007.

Brenner E, Smeets JB, de Lussanet MH. Hitting moving targets. Continuous control of the acceleration of the hand on the basis of the target's velocity. *Exp Brain Res* 122: 467–474, 1998.

Brouwer A-M, Brenner E, Smeets JBJ. Hitting moving objects: is target speed used in guiding the hand? *Exp Brain Res* 143: 198–221, 2002.

Buneo CA, Soechting JF, Flanders M. Muscle activation patterns for reaching: the representation of distance and time. *J Neurophysiol* 71: 1546–1558, 1994.

Carpenter RH, Williams ML. Neural computation of log likelihood in control of saccadic eye movements. *Nature* 377: 59–62, 1995.

Churchland MM, Chou IH, Lisberger SG. Evidence for object permanence in the smooth-pursuit eye movements of monkeys. *J Neurophysiol* 90: 2205–2218, 2003.

Collewijn H, Tamminga EP. Human smooth and saccadic eye movements during voluntary pursuit of different target motions on different backgrounds. *J Physiol* 351: 217–250, 1984.

de Lussanet MHE, Smeets JBJ, Brenner E. The quantitative use of velocity information in fast interception. *Exp Brain Res* 157: 181–196, 2004.

Eggert T, Rivas F, Straube A. Predictive strategies in interception tasks: differences between eye and hand movements. *Exp Brain Res* 160: 433–449, 2005.

Flanders M, Pellegrini JJ, Geisler SD. Basic features of phasic activation for reaching in vertical planes. *Exp Brain Res* 110: 67–79, 1996.

Flash T, Hogan N. The coordination of arm movements: an experimentally confirmed mathematical model. *J Neurosci* 5: 1688–1703, 1985.

Georgopoulos AP, Massey JT. Cognitive spatial-motor processes. 2. Information transmitted by the direction of two-dimensional arm movements and by neuronal populations in primate motor cortex and area 5. *Exp Brain Res* 69: 315–326, 1988.

Ghose GM. Strategies optimize the detection of motion transients. *J Vision* 6: 429–440, 2006.

Gordon J, Ghilardi MF, Ghez C. Impairments of reaching movements in patients without proprioception. I. Spatial errors. *J Neurophysiol* 73: 347–360, 1995.

Hohnsbein J, Mateeff S. The time it takes to detect changes in speed and direction of visual motion. *Vision Res* 38: 2569–2573, 1998.

Kerrigan SJ, Soechting JF. Anisotropies in the gain of smooth pursuit during two-dimensional tracking as probed by brief perturbations. *Exp Brain Res* 180: 435–448, 2007.

Kettner RE, Leung H-C, Peterson BW. Predictive smooth pursuit of complex two-dimensional trajectories in monkey: component interactions. *Exp Brain Res* 108: 221–235, 1996.

Kowler E, Martins AJ, Pavel M. The effect of expectations on slow oculomotor control. IV. Anticipatory smooth eye movements depend on prior target motions. *Vision Res* 24: 197–210, 1984.

Kowler E, Steinman RM. The effect of expectations on slow oculomotor control—III. Guessing unpredictable target displacements. *Vision Res* 21: 191–203, 1981.

Krauzlis RJ, Lisberger SG. A model of visually-guided smooth pursuit eye movements based on behavioral observations. *J Comput Neurosci* 1: 265–283, 1994a.

Krauzlis RJ, Lisberger SG. Temporal properties of visual motion signals for the initiation of smooth pursuit eye movements in monkeys. *J Neurophysiol* 72: 150–162, 1994b.

Lacquaniti F, Terzuolo C, Viviani P. The law relating the kinematic and figural aspects of drawing movements. *Acta Psychol* 54: 115–130, 1983.

Lisberger SG, Movshon JA. Visual motion analysis for pursuit eye movements in area MT of macaque monkeys. *J Neurosci* 19: 2224–2246, 1999.

Maunsell JH, Van Essen DC. Functional properties of neurons in middle temporal visual area of the macaque monkey. I. Selectivity for stimulus direction, speed, and orientation. *J Neurophysiol* 49: 1127–1147, 1983.

Merchant H, Battaglia-Mayer A, Georgopoulos AP. Interception of real and apparent motion targets: psychophysics in humans and monkeys. *Exp Brain Res* 152: 106–112, 2003.

Mikami A, Newsome WT, Wurtz RH. Motion selectivity in macaque visual cortex. I. Mechanisms of direction and speed selectivity in extrastriate area MT. *J Neurophysiol* 55: 1308–1327, 1986.

Morasso P. Spatial control of arm movements. *Exp Brain Res* 42: 223–237, 1981.

Mrotek LA, Flanders M, Soechting JF. Interception of targets using brief directional cues. *Exp Brain Res* 156: 94–103, 2004.

Mrotek LA, Flanders M, Soechting JF. Oculomotor responses to gradual changes in target direction. *Exp Brain Res* 172: 175–192, 2006.

Mrotek LA, Soechting JF. Predicting curvilinear target motion through an occlusion. *Exp Brain Res* 178: 99–114, 2007a.

Mrotek LA, Soechting JF. Target interception: hand-eye coordination and strategies. *J Neurosci* 27: 7297–7309, 2007b.

Osborne LC, Bialek W, Lisberger SG. Time course of information about motion direction in visual area MT of macaque monkeys. *J Neurosci* 24: 3210–3222, 2004.

Pellegrini JJ, Flanders M. Force path curvature and conserved features of muscle activation. *Exp Brain Res* 110: 80–90, 1996.

Perge JA, Borghuis BG, Bours RJ, Lankheet MJ, van Wezel RJ. Temporal dynamics of direction tuning in motion-sensitive macaque area MT. *J Neurophysiol* 93: 2104–2116, 2005.

Port NL, Lee D, Dassonville P, Georgopoulos AP. Manual interception of moving targets. I. Performance and movement initiation. *Exp Brain Res* 116: 406–420, 1997.

Schwartz JD, Lisberger SG. Initial tracking conditions modulate the gain of visuo-motor transmission for smooth pursuit eye movements in monkeys. *Visual Neurosci* 11: 411–424, 1994.

Smeets JBJ, Brenner E. Prediction of moving target's position in fast goal-directed action. *Biol Cybern* 73: 519–528, 1995a.

Smeets JBJ, Brenner E. Perception and action are based on the same visual information: distinction between position and velocity. *J Exp Psychol Hum Percept Perform* 21: 19–31, 1995b.

Soechting JF, Mrotek LA, Flanders M. Smooth pursuit tracking of an abrupt change in target direction: vector superposition of discrete responses. *Exp Brain Res* 160: 245–258, 2005.

van Donkelaar P, Lee RG, Gellman RS. Control strategies in directing the hand to moving targets. *Exp Brain Res* 91: 151–161, 1992.

Viviani P, Baud-Bovy G, Redolfi M. Perceiving and tracking kinesthetic stimuli: further evidence of motor-perceptual interactions. *J Exp Psychol Hum Percept Perform* 23: 1232–1252, 1997.

Viviani P, McCollum G. The relation between linear extent and velocity in drawing movements. *Neuroscience* 10: 211–218, 1983.