Hand interception of occluded motion in humans: a test of model-based vs. on-line control

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La Scaleia B, Zago M, Lacquaniti F. Hand interception of occluded motion in humans: a test of model-based vs. on-line control. J Neurophysiol 114: 1577–1592, 2015. First published July 1, 2015; doi:10.1152/jn.00475.2015.—Two control schemes have been hypothesized for the manual interception of fast visual targets. In the model-free on-line control, extrapolation of target motion is based on continuous visual information, without resorting to physical models. In the model-based control, instead, a prior model of target motion predicts the future spatiotemporal trajectory. To distinguish between the two hypotheses in the case of projectile motion, we asked participants to hit a ball that rolled down an incline at 0.2 g and then fell in air at 1 g along a parabola. By varying starting position, ball velocity and trajectory differed between trials. Motion on the incline was always visible, whereas parabolic motion was either visible or occluded. We found that participants were equally successful at hitting the falling ball in both visible and occluded conditions. Moreover, in different trials the intersection points were distributed along the parabolic trajectories of the ball, indicating that subjects were able to extrapolate an extended segment of the target trajectory. Remarkably, this trend was observed even at the very first repetition of movements. These results are consistent with the hypothesis of model-based control, but not with on-line control. Indeed, ball path and speed during the occlusion could not be extrapolated solely from the kinematic information obtained during the preceding visible phase. The only way to extrapolate ball motion correctly during the occlusion was to assume that the ball would fall under gravity and air drag when hidden from view. Such an assumption had to be derived from prior experience.

gravity; internal model; visual motion; visual extrapolation

MANUAL INTERCEPTION OF VISUAL TARGETS moving rapidly can be very accurate (Bootsma and van Wieringen 1990; Regan 1997). This accuracy implies that interception is anticipatory, that is, the observed spatiotemporal trajectory of the target is extrapolated in the near future (Nijhawan 2008; Soechting and Flanders 2008; Soechting et al. 2009). Without extrapolation, the hand would be misplaced where the target was 100–200 ms earlier, due to visuomotor delays (Bootsma and van Wieringen 1990; Brenner et al. 1998; Day and Lyon 2000; Marinovic et al. 2009; McLeod 1987; Vishton et al. 2010).

The mechanisms underlying the extrapolation of target motion to control interceptive movements are still under dispute (Baurès et al. 2007; Bosco et al. 2015; Katsumata and Russell 2012; Merchant et al. 2009; Tresilian 2005; Zago et al. 2008, 2009; Zhao and Warren 2015). In particular, two control schemes have been contrasted, the model-free on-line control and the model-based control. In the former scheme, extrapolation is based on continuous visual information about target kinematics, without any prior model of target motion (e.g., Arzamarski et al. 2007; Bastin et al. 2006; Baurès et al. 2007; Bootsma and van Wieringen 1990; Bootsma et al. 2010; Dressing et al. 2002; Fink et al. 2009; Jacobs and Michaels 2006; Ledouit et al. 2013; Lee et al. 1983; Lee 1998; Peper et al. 1994; Warren 2006; Zhao and Warren 2015). In the latter scheme, instead, a prior model of target motion contributes to predict the future spatiotemporal trajectory (e.g., Battaglia et al. 2013; de Rugy et al. 2012; Franklin and Wolpert 2011; Gómez and López-Moliner 2013; Lacquaniti et al. 1993; McIntyre et al. 2001; Mischiati et al. 2015; Mrotek and Soechting 2007; Tramper et al. 2013; van Soest et al. 2010; Zago et al. 2004).

Distinguishing between the two hypotheses has proved difficult so far. In particular, for predictable target trajectories under normal visual conditions, one may expect similar outcomes under both hypotheses, provided reliable inputs are available for extrapolation of target motion. Thus, in line of principle, the usage of either time derivatives of target position or model-based control might yield accurate responses.

One way to distinguish between the two hypotheses is to employ a target that undergoes two different but predictable types of motion in two consecutive phases and to mask its view during the last phase, just before interception. In this case, the extrapolation of target motion during the last phase cannot be derived from visual information about the first phase but requires an internal representation of the last phase as derived from prior knowledge. Accordingly, on-line control would lead to substantial spatiotemporal errors of the interception movements, with a systematic bias in the direction of the trajectory extrapolated from the first phase. Instead, motion extrapolation provided by a prior model of the occluded trajectory of the target might lead to successful interception.

In the present study we tested these hypotheses using a ball that rolled down a rectilinear incline with an acceleration of about 0.2 g (first phase) and then fell in air at an acceleration of 1 g along a quasi-parabolic trajectory (last phase; see Figs. 1 and 2). With randomization of the starting position along the incline, ball velocity and trajectory differed from trial to trial. The first phase of rectilinear motion was always visible, whereas the last phase of quasi-parabolic motion was made either visible or occluded in separate sessions by interposition of a transparent or opaque panel, respectively. Participants
were asked to hit the ball as soon as it emerged from behind the panel, but the exact position of interception was not specified in advance. Importantly, the target interception zones associated with different parabolas were well spaced between each other and relative to the rectilinear trajectory that virtually extended the inclined plane.

This design allows a direct test of the predictions stemming from on-line and model-based control. Both modes of control may allow interception of the experimental targets in the visible condition. However, the expected outcomes differ for the occluded condition. On-line control should drive the hand in retard and in a wrong direction, for instance, toward the rectilinear trajectory extending the visible inclined plane, because kinematic information from the visible phase specified rectilinear motion at about one-fifth of gravitational acceleration. By contrast, model-based control might be able to drive the hand in time to the targets if the prior model took into account gravity and air drag effects (Battaglia et al. 2013; Bosco et al. 2012; De Sá Teixeira et al. 2013; Gómez and López-Moliner 2013; Hubbard 2005; Lacquaniti et al. 1993; Saxberg 1987; Zago et al. 2004).

METHODS

Participants

Ten subjects (7 females and 3 males, 31 ± 9 yr old, mean ± SD) participated in the experiments. All participants gave written informed consent to procedures approved by the Institutional Review Board of Santa Lucia Foundation, in conformity with the Declaration of Helsinki on the use of human subjects in research. All participants were right-handed (as assessed by a short questionnaire based on the Edinburgh scale), had normal or corrected-to-normal vision and no past history of psychiatric or neurological diseases, and were naive to the specific purpose of the experiments. One participant (subject ME) was an amateur volleyball player, whereas none of the others had any ball game as a hobby.

Experimental Setup

Participants sat on a chair placed in front and to the right of the incline made of smooth inox steel (Fig. 2A). A soft, homogenous rubber ball (9-cm diameter, 30-g weight) rolled down the incline, without slipping or bouncing. After exiting from the incline, it fell under gravity and air drag along a quasi-parabolic trajectory (Fig. 1). At the lower end of the incline, there was one of two types of panels depending on the experimental condition: a transparent panel for the visible condition and a white, opaque panel for the occluded condition. Both panels were like soft curtains that could be hit by the participants without any harm. They were the same size (65 × 50 cm, width × height) and were located in the same position to match the interception region across visual conditions. In this position, the lower border of the panels was 40.5 cm below the center of the ball at the exit position from the incline.

The 2.1-m-long, 0.2-m-wide incline, supported by three tripod stands, was tilted by 20° relative to the horizontal, with the long axis roughly parallel to the frontal plane of the subject. The lower end of the incline was at 1.1-m height above the floor. The incline was equipped with six electromechanical lever arms spaced along the track, which allowed the release of the ball from different starting positions. These devices were located on the side of the incline opposite to that facing the subject and did not prevent the view of the descending ball. Each lever consisted of a thin steel bar whose position (up or down) was set by a solenoid (G.W. Lisk, Clifton Springs, NY) under computer control. The time accuracy of ball release was better than 1 ms. An on-axis laser transmitter/receiver (transceiver) was placed at a 5-cm distance from the lower end of the incline, orthogonal to the direction of ball descent, to monitor the descent time of the ball in each trial. The back of the chair, supporting the head and torso of the subject, was adjusted at about 25° relative to the vertical, allowing a comfortable position and full view of the incline. In this posture, the eyes of the participant were located at a horizontal distance of about 50 cm from the frontal plane of motion of the ball center, 22 cm to the right and 5 cm above the lower end of the incline. By protracting the arm forward, each participant could easily reach the interception region at the lower border of the panel.

Participants held an instrumented plastic box (2 × 6.5 × 3.2 cm, width × height × depth, 65-g weight) in their right hand. The box had a steel rod (4.2-cm length, 0.4-cm diameter) on the front side and a steel winged frame fixed over the horizontal side. The box was grasped by the subject so that the rod protruded between the index and middle finger, and the winged frame was roughly parallel to the back of the hand (Fig. 2A, inset). Inside the box, there was a triaxial piezoelectric accelerometer that measured box (and hand) acceleration (Isotron 63-B100; Endevco, San Juan Capistrano, CA; ±50-g dynamic range, amplitude nonlinearity <1%). The accelerometer and the laser receiver were sampled by the acquisition system at 1 kHz. The position of the box in three dimensions (3D) was recorded at 200 Hz by means of the Optotrak 3020 system (Northern Digital, Waterloo, ON, Canada; RMS accuracy better than 0.2 mm in all directions). To this end, three infrared-emitting markers were attached to the winged frame of the box. Two additional markers were placed on the incline to determine the position of its lower end. Data logging was controlled by the real-time system PXI-1010 (National Instruments, Austin, TX), which directly acquired accelerometer and laser receiver data and synchronously triggered the system control unit of the Optotrak system. Optotrak data were recorded using NDI First Principles motion capture software (Northern Digital) starting at trigger time. In each trial, data acquisition started before ball release (see below) and lasted 3 s.

Task

Shortly before each trial, the experimenter placed the ball at the starting position on the incline, and the participant was asked to
look at the ball and to place the right arm in the initial posture on a foam box (26 x 12 x 16 cm, width x height x depth). With the adducted shoulder, the upper arm was roughly vertical, the forearm tilted down by about 20° relative to the horizontal, the wrist mid-pronated, and the hand and fingers clenched around the box (see Fig. 2A). The tip of the rod had to be placed at a distance of about 16 cm from the plane of motion of the ball’s center, 46 cm below and 43 cm to the right of the lower end of the incline, 10 cm below the lower border of the panel. After a pseudorandom delay between 150 and 400 ms (50-ms steps) from an alert tone, the ball was released, rolled down the incline, and fell with the kinematics described in the Appendix. Ball acceleration was about 2.075 m/s² on the incline and 9.795 m/s² during free fall. Participants were asked to hit the ball as soon as it emerged from behind the panel, but neither the position nor the time of interception were specified in advance, resulting instead from the interceptive action performed in individual trials.

Protocol

Before the experiment, participants received general instructions and were familiarized with the setup. They were informed that in each trial the ball would descend from a different starting position along the incline and would fall behind the panel. Participants were tested in a counterbalanced order in the visible and occluded sessions about 15 days apart. In each session, there were six possible starting positions of the ball along the incline, resulting in six durations of ball motion from the release to the lower end of the incline and six quasi-parabolic paths (in the following denoted as targets) during free fall, numbered 1 to 6 from the shortest to the longest (Table 1 and Fig. 1). These targets were randomized across trials, avoiding identical starting conditions in consecutive trials. The nominal occlusion time corresponded to the motion duration of the ball center from the lower end of the incline to the lower border of the occluding panel. Each target was presented 15 times for a total of 90 trials per session. Participants were allowed to pause any time they wished during the experiment. The approximate duration of each session was 40 min.

Data Analysis

Of a total of 1,800 trials (90 trials x 2 sessions x 10 subjects), 25 trials were excluded (1.39%) from the analysis due to the presence of artifacts or lack of subject’s attention (as marked in the experiment’s notebook).

Contact rate. The contact between the ball and the hand generated a brief burst of high-frequency oscillations in the accelerometer signals (La Scaleia et al. 2014; Zago et al. 2004, 2005). To isolate these oscillations from the lower frequency oscillations due to the voluntary arm movement, the raw data from the acceleration component along the longitudinal axis of the hand-held rod were filtered with a bidirectional 25-Hz high-pass Butterworth filter. Contact was then identified when the filtered acceleration exceeded a threshold of 22 m/s² and was further verified by visual inspection. The contact rate was then computed as the percentage of all trials with detectable contact oscillations over the total number of trials for any given condition for each subject.

Endpoint analysis. Optotrak data were numerically low-pass filtered (bidirectional, 25-Hz cutoff, 2nd-order Butterworth filter) to eliminate high-frequency oscillations due to contact. The time-varying 3D coordinates (x, y, z) of the tip of the hand-held rod were...
derived from the known geometry of the box and rod and from the measured 3D position and orientation of the box. For each trial, we computed the instantaneous distance between the rod tip and the ball surface. The 3D trajectory of the latter was estimated from the calibration trials (see Appendix). An intersection point (and time) was then defined as either the position (time) in which the rod tip first contacted the ball surface when their relative distance became null or the position (time) in which the rod tip first arrived at the minimum distance from the ball trajectory (considering the ball surface and the entire ball trajectory) when the rod tip did not contact the ball (Fig. 2B). We estimated the position of the ball when it first reached the minimum distance from the intersection point and the time at which this occurred (ball interception time). To check for possible biases introduced by estimating the intersection points relative to the ball trajectory, we also computed the intersection of the rod tip trajectory with the frontal plane tangent to the ball surface during free fall.

**Hand movements.** Hand movements were analyzed in terms of the spatiotemporal trajectory of the tip of the hand-held rod. Time-varying tangential velocity was computed as \( v_T = \sqrt{\dot{x}^2 + \dot{y}^2 + \dot{z}^2} \). To quantify the presence of submovements, we low-pass filtered (10-Hz cutoff) the tangential velocity and counted the number of peaks with a magnitude >50% of the maximum. Mean curvature was computed as the mean of the perpendicular distances of all sampled points along the trajectory (from movement onset to intersection point) relative to a straight line connecting the position of the rod tip at movement onset and intersection point (Arce et al. 2009). Movement onset was computed according to the following algorithm. First, we normalized tangential velocity to the maximum: \( v = v_T/v_{max} \); then, going back from the sample at which \( v = 1 \), we defined the first sample for which \( v < 0.08 \) as the onset. We computed the interval between the onset time of hand movements and the exit time of the ball from the incline (corresponding to the onset of the occlusion in the corresponding visual condition). A positive (negative) value of this interval indicates (corresponding to the onset of the occlusion in the corresponding visual condition). A positive (negative) value of this interval indicates

\[
\Delta v^o_j = IP_s^o - IP_s^o,
\]

The 3 \times 3 covariance matrix of subject \( s \) is expressed by the equation

\[
S^o_{v/o,k} = \sum_{i,j} \frac{\delta v^o_{i,j} (\delta v^o_{i,j})^T}{n_{v/o,k} - 1},
\]

where \( n_{v/o,k} \) represents the number of trials of subject \( s \) for \( v/o \) condition and target \( k \). By pooling the intersection points across all subjects, the estimate of the combined covariance matrix for a visual condition and target is

\[
S^o_{v/o,k} = \frac{1}{n_{v/o,k}} \sum_{i=1}^{n_{v/o,k}} \sum_{j=1}^{n_{v/o,k}} \frac{\delta v^o_{i,j} (\delta v^o_{i,j})^T}{n_{v/o,k} - 1},
\]

where \( n_{v/o,k} = n_{v/o,k} \) is the number of subjects (\( n = 10 \)). The spatial precision (variability of performance) of all subjects for visual condition and target was computed by means of the 95% tolerance ellipsoid for each condition. This ellipsoid, based on the data from all trials of all subjects for a given condition, is obtained by scaling the combined covariance matrix

\[
T^o_{0.95} = \frac{\chi^2(n-1)(n-n_s)}{n(n-n_s-p+1)} F^o_{0.95},
\]

where \( n = \sum_{k} n_{v/o,k} \) is the total number of trials of all subjects for a given condition, and \( p = 3 \) is the dimensionality of the Cartesian vector space (Diem 1963). Eigenvalues and eigenvectors of the \( T^o_{0.95} \) matrix were used to characterize the shape, size, and orientation of the ellipsoid (McIntyre et al. 1997; Morrison 1990). The three axes of the ellipsoid have the same orientation as the three eigenvectors of the \( T^o_{0.95} \) matrix, and the lengths of the three semi-axes correspond to the square roots of the three corresponding eigenvalues. We tested whether the eigenvalues were statistically different from each other by means of a \( \chi^2 \) test at 95% confidence level (\( \chi^2 > \chi^2_{0.05,2} \)), where \( \chi^2 \) has the form (Morrison 1990, p. 336)

\[
\chi^2 = -(n-1)\sum_i \ln \lambda_i + (n-1)\ln \sum_{k} \frac{n_{v/o,k}}{r},
\]

where \( \lambda_k \) are the \( r = 2 \) eigenvalues being compared for a given covariance matrix \( T^o_{0.95} (k = 1/2 \text{ or } k = 2/3) \). \( \chi^2 \) has \( q = 0.5(r+1) - 1 = 2 \) degrees of freedom. We separately carried out the same analyses described above to compute the spatial distribution of intersection points relative to the frontal plane tangent to the ball surface.

**Spatial error.** For each trial, we computed the spatial error (SE) as the Euclidean distance between the intersection point and the surface of the ball when it first reached the minimum distance from the intersection point. If the tip of the rod intercepted the ball trajectory (considering the ball surface and the entire ball trajectory), the spatial error was null. To characterize the rate at which subjects decreased their spatial error during an experiment, we fitted an exponential function to the series of SE values across successive repetitions (nonlinear least-squares fitting):

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### Table 1. Parameters of ball motion

<table>
<thead>
<tr>
<th>Target</th>
<th>Motion Duration, ms</th>
<th>Distance Traveled, m</th>
<th>Incline</th>
<th>Motion Duration, ms</th>
<th>Horizontal Distance Traveled, m</th>
<th>Horizontal</th>
<th>Vertical</th>
<th>Total Motion Duration, ms</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>486</td>
<td>0.245</td>
<td>256</td>
<td>0.246</td>
<td>0.96</td>
<td>2.79</td>
<td>742</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>671</td>
<td>0.467</td>
<td>241</td>
<td>0.320</td>
<td>1.31</td>
<td>2.82</td>
<td>912</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>847</td>
<td>0.792</td>
<td>232</td>
<td>0.383</td>
<td>1.63</td>
<td>2.84</td>
<td>1,079</td>
<td></td>
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<tr>
<td>4</td>
<td>1,029</td>
<td>1.098</td>
<td>223</td>
<td>0.444</td>
<td>1.95</td>
<td>2.86</td>
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<td></td>
</tr>
<tr>
<td>5</td>
<td>1,206</td>
<td>1.508</td>
<td>212</td>
<td>0.485</td>
<td>2.45</td>
<td>2.91</td>
<td>1,418</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>1,390</td>
<td>2.00</td>
<td>206</td>
<td>0.538</td>
<td>2.56</td>
<td>2.93</td>
<td>1,596</td>
<td></td>
</tr>
</tbody>
</table>

Motion duration and distance traveled on the incline are from the starting position until the end of the incline. Motion duration and distance traveled in air are until the lower border of the panel (vertical distance traveled was 0.405 m for all targets). Speed is at the lower border of the panel.
where \( SE_i \) is the median value of \( SE \) values for the corresponding repetition (\( i = 0 \) for the first repetition) and \( b_0 \), \( b_1 \), and \( b_2 \) are the offset, gain, and learning constant, respectively.

**Timing error.** For each trial, we computed the timing error as the difference between the time at intersection of the rod tip and ball intersection (see Endpoint analysis). If the minimum of the instantaneous distance was null, the timing error was considered null. A positive (negative) value of timing error corresponds to a response later (earlier) than that theoretically expected if the rod arrived at the intersection time at the same time as the ball did.

**Statistics**

The distributions of percentages of trials with contact (contact rate) were arcsin(sqrt) transformed prior to statistical analysis. Results are means ± SD, and uncertainty is reported using 95% confidence interval (CI). Statistical differences between group means were analyzed in one of two ways, always with a significance level of 0.05. For contact rate and hitting movement parameters, the differences between conditions were assessed using repeated-measures analysis of variance (RM-ANOVA) with target and visual condition as within-subjects factors and block order as a between-subjects factor. The degrees of freedom for the within-subjects comparisons were corrected (Greenhouse-Geisser) in case of deviation from sphericity. Whenever RM-ANOVA detected a significant difference, we performed post hoc Bonferroni corrections for multiple comparisons. Effect size was assessed as partial \( \eta^2 \). We performed multivariate analysis of variance (MANOVA) to examine whether the target and the visual conditions significantly affected the center (\( x \) and \( y \) coordinates) of the spatial distribution of intersection points. This MANOVA treated the \( x \) and \( y \) coordinates as the dependent variable and the target and visual condition as the fixed factors, and we used Wilk’s \( \lambda \) as the test statistic. Timing errors were not normally distributed, and we report their median and interquartile range. Data preprocessing was performed with custom software in MATLAB (The MathWorks, Natick, MA), and statistical analyses were performed with MATLAB and SPSS (IBM, Armonk, NY).

**RESULTS**

**Overall Success Rate**

As an estimate of the success rate, we computed the percentage of trials in which a contact occurred between the hand and the ball. Strikingly, the overall contact rate was very similar in the visible condition and the occluded condition, despite the lack of visual information about the quasi-parabolic trajectory of the target during the >200-ms epoch preceding interception in the latter case. The mean contact rate was 87% (CI [79%, 93%], 6 targets × 10 subjects, \( n = 60 \)) in the visible condition and 86% (CI [79%, 92%]) in the occluded condition (\( n = 60 \)). The contact rate was not homogenous across different targets and visual conditions (Fig. 3). Thus the mean contact rate was higher with occlusion than without for targets 4 and 5, whereas the opposite result was found for targets 1 and 6, and no appreciable difference existed between visual conditions for targets 2 and 3. However, the differences between visual conditions were not statistically significant. RM-ANOVA (2 visual conditions × 6 targets as within-subjects factors and 2 block orders as between-subjects factor) showed that the contact rate did not depend significantly on the visual condition (\( F_{1,8} = 0.267, P = 0.619 \)), target (\( F_{2,041,16,329} = 3.323, P = 0.061 \)), or block order (\( F_{1,8} = 4.278, P = 0.071 \)).

Instead, contact rate depended significantly on the interaction between visual condition and target (\( F_{2,860,22,945} = 3.470, P = 0.034, \eta^2 = 0.303 \)), but post hoc tests showed that the differences between each pair of conditions were not significant (all \( P > 0.51 \)). Contact rate also depended significantly on the interaction between visual condition and block order (\( F_{1,8} = 31.047, P = 0.001, \eta^2 = 0.795 \)). In this case, post hoc tests showed that the contact rate in the occluded condition was significantly smaller when the first session was occluded than when the first session was visible (mean contact rate = 74%, CI [62%, 85%] and 95%, CI [87%, 99%], respectively; \( P = 0.03 \)). Importantly, however, there were no significant differences (all \( P > 0.48 \)) in the contact rate between the two visual conditions in both block orders.

It is noteworthy that in most of the cases (91.4%) in which a contact between the hand and the ball was detected, this occurred within the time interval between the positive peak and the negative peak of acceleration (mean interval = 133 ms, SD = 42 ms, \( n = 1,350 \), pooling results across repetitions, targets, sessions, and subjects). This indicates that participants generated maximum momentum to hit the incoming ball at about the right time, because the zero-crossing of acceleration corresponds to peak speed.

**Hand Movements**

Figure 4 plots the trajectories of the tip of the hand-held rod for all repetitions of all participants with a central target (target 3), and Fig. 5 plots the corresponding trajectories with the most medial and the most lateral target (targets 1 and 6, respectively). Because the panel placed in front of the participants was like a soft curtain (see METHODS), in some cases the participants touched its lower border to reach the falling ball (see subject ME in Figs. 4 and 5). It can be noticed that the hand generally traced curved trajectories from a relatively constant starting position to a hitting position that varied considerably across trials, due to the fact that the ball could be hit at several different locations scattered along the quasi-parabolic path (see Spatial distribution of endpoints). Moreover, there was intersubject variability in the trajectories, especially those directed to the most medial and most lateral target (Fig. 5). Some participants (for instance, subjects AT, II, CG, and VM) moved the hand roughly along the direction from the starting to the...
hitting point, whereas other participants (e.g., subjects GC, ME, and LM) moved the hand initially in the medial or lateral direction (depending on the target) and then toward the hitting point. However, there was no systematic correlation between the specific type of movement used by the participants and the success rate. Thus the mean contact rate was very high for both subject VM (93% and 96% in the visible and occluded conditions, respectively) and subject...
LM (97% and 98% in the visible and occluded conditions, respectively) despite their different trajectories of the hand.

Global path curvature was quantified in terms of the mean distance of the rod tip from a straight line joining the position of the rod tip at movement onset and at intersection point. Mean curvature was 2.47 cm (SD = 1.29 cm, n = 891, pooling results across repetitions, targets, and subjects) in the visible condition and 1.97 cm (SD = 1.37 cm, n = 884) in the occluded condition. RM-ANOVA (2 visual conditions × 6 targets as within-subjects factors and 2 block orders as between-subjects factor) showed that the mean curvature depended significantly on the visual condition (F<sub>1,8</sub> = 37.679, P << 0.001, η<sup>2</sup><sub>p</sub> = 0.825). Mean curvature did not depend significantly on any other factor or interaction (all P > 0.250).

Movement speed was computed in terms of the tangential velocity of the rod tip from the start of the trial until the maximum extension of the arm. Mean maximum speed was 2.16 m/s (SD = 1.29 m/s, n = 891) in the visible condition and 2.16 m/s (SD = 0.68 m/s, n = 884) in the occluded condition. RM-ANOVA (2 visual conditions × 6 targets as within-subjects factors and 2 block orders as between-subjects factor) showed that the maximum speed did not depend significantly on the visual condition (F<sub>1,8</sub> = 1.500, P = 0.256) but depended significantly on block order (F<sub>1,8</sub> = 7.062, P = 0.029, η<sup>2</sup><sub>p</sub> = 0.469), being smaller when the first session was occluded than when it was visible, and on the target (F<sub>1,772,14,179</sub> = 5.191, P = 0.02, η<sup>2</sup><sub>p</sub> = 0.407). Post hoc tests showed that only the movement speed for target 1 was higher than that for target 2; all other differences were not significant (all other P > 0.240).

Mean motion duration was 238 ms (SD = 78 ms, n = 891) in the visible condition and 248 ms (SD = 88 ms, n = 884) in the occluded condition. RM-ANOVA (2 visual conditions × 6 targets as within-subjects factors and 2 block orders as between-subjects factor) showed that the motion duration did not depend significantly on the visual condition (F<sub>1,8</sub> = 0.404, P = 0.543) or any other factor or interaction (all P > 0.084).

A simple strategy would be to synchronize the onset of hand movements with the time the rolling ball crossed a visible landmark on the incline, but this would not guarantee a correct timing because the duration of the subsequent ball motion in free fall differed across targets. In fact, we found that hand movements generally started before the ball reached the exit point from the incline (and the onset of the occlusion in the corresponding visual condition). The mean difference between the onset time of hand movements and the exit time of the ball was −27 ms (SD = 89 ms, n = 891) in the visible condition and −38 ms (SD = 94 ms, n = 884) in the occluded condition (Fig. 6). This time interval did not depend significantly on the visual condition (F<sub>1,8</sub> = 0.450, P = 0.521) but depended significantly on the target (F<sub>2,526,20,207</sub> = 14.714, P << 0.001, η<sup>2</sup><sub>p</sub> = 0.648). Post hoc tests showed that the interval was significantly shorter for target 1 than that for targets 5 and 6 (all P < 0.033) and was shorter for target 2 than for targets 4–6 (all P < 0.025). Therefore, the onset of hand movements was not time-locked to the exit of the ball from the incline or the onset of the occlusion, thus refuting the spatial landmark strategy mentioned above.

Spatial Scatter of Endpoints

To analyze the detailed spatial characteristics of the endpoints of the hitting movements, we considered the position of the tip of the rod at the intersection time (see Fig. 2B and METHODS). Figure 8 plots the intersection points for all trials with a central target (target 3). Remarkably, most intersection points are scattered along the trajectory of the ball for both visual conditions, indicating that subjects were generally able to extrapolate the target trajectory even when this was occluded from view.

Figure 9 plots the intersection points for all targets, along with the horizontal (A) and frontal projections (B) of the tolerance ellipsoids including 95% of the points for each experimental condition. Each ellipsoid has been centered on the intersection point averaged across repetitions and subjects. The mean x and y coordinates of the intersection points depended significantly on the target (MANOVA, 2 visual conditions × 6 targets, P << 0.001, η<sup>2</sup><sub>p</sub> = 0.643) but were independent of the visual condition (P = 0.737) and the interaction between visual condition and target (P = 0.053). The magnitude of the variable error (spatial precision) is provided by the square root of the eigenvalues of the ellipsoids (Table 2). The eigenvalues (and the volume of the ellipsoids) for the occluded condition were greater than the corresponding eigenvalues for the visible condition for all targets, indicating...
that the intersection points were more variable across trials in
the former than in the latter condition. On average, the ratio
between the major (first) eigenvalue of the occluded condition
and the corresponding eigenvalue of the visible condition was
1.320 (range: 1.076–1.434) across all targets, whereas the
 corresponding ratio for the second eigenvalue was 1.278
(range: 1.087–1.395).

For all the ellipsoids, the three eigenvalues were signifi-
cantly different from each other, implying that the distribution
of the intersection points was not isotropic but tended to align
along specific directions. Thus, when we consider the hori-
zontal projections of the ellipsoids (Fig. 9A), we notice that the
95% confidence limits of the first eigenvector (which is aligned
with the major axis of the ellipsoid) include the tangent line to
the quasi-parabolic trajectory of the ball at the mean intersec-
tion point only in the case of target 2 under visible conditions
but for all 6 targets under occluded conditions (Table 3). As for
the frontal projections of the ellipsoids in the plane of motion
of the ball’s center (Fig. 9B), the 95% confidence limits of the
first eigenvector include the tangent line to the ball’s trajectory
for all targets except target 5 under visible conditions and for
all targets except targets 1 and 2 under occluded conditions.
Irrespective of these small deviations, the tolerance ellipsoids
overlapped the quasi-parabolic trajectories for all conditions.
By contrast, the endpoint of hand movements did not intersect
the rectilinear trajectory that virtually extended the inclined
plane in any trial (Fig. 9).

Remarkably, this trend also applied to the very first repeti-
tion of movements directed to each individual target in both the
visual and the occluded conditions (Fig. 10), although an
improvement in performance with repetition was found for
targets 1 and 6 in the occluded condition (see Effect of
practice). In Fig. 10 it can be seen that a larger proportion of
intersection points fall outside the envelopes of ball trajectories
for targets 1, 2, 5, and 6 in the occluded session than in the
visible one.

Intersection with the Frontal Plane

So far, we have reported the analysis of the intersection
points relative to the ball trajectory. In line of principle, this
analysis may bias the results toward the quasi-parabolic paths
actually traced by the ball and away from other paths poten-
tially extrapolated by the subjects. To address this issue, we
also computed the intersection of the rod tip trajectory with the frontal plane tangent to the ball surface during free fall, thus eliminating any bias toward specific trajectories. We found that the 95% confidence limits of the first eigenvector of the tolerance ellipses computed with this latter method included the corresponding eigenvectors of the frontal projections of the ellipsoids computed with the first method for each target and visual condition. Moreover, on average (over all targets), the area of the ellipses computed with the two methods differed by 13.6% for the visible condition and by 3.6% for the occluded condition. Overall, the new analysis confirmed the results described above.

### Potential Feasibility of Movement Corrections Once the Ball Emerged from Below the Occluding Panel

It could be argued that although the longest part of the free-fall trajectory of the ball occurred behind the panel, there was still sufficient time to correct hand movements for interception after the ball emerged from below the panel. Several observations exclude this possibility. First, we found little evidence for corrective submovements in the profiles of tangential velocity (see Submovements). Second, although the participants were instructed to hit the ball as soon as it emerged from behind the panel, in most trials they actually intersected the trajectory (and hit the ball in the successful cases) before the ball emerged from the lower border of the panel, that is, when the ball was still behind the panel. This was possible because the hand could easily reach behind and above the lower border of the soft curtain (see Fig. 2A). In Figs. 8–10, the vertical position of the individual intersection points can be compared with the corresponding position of the lower

### Table 2. Variable error magnitude

<table>
<thead>
<tr>
<th>Target</th>
<th>Visible</th>
<th>Occluded</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1st</td>
<td>2nd</td>
</tr>
<tr>
<td>First</td>
<td>18.40</td>
<td>17.71</td>
</tr>
<tr>
<td>Second</td>
<td>8.41</td>
<td>7.32</td>
</tr>
<tr>
<td>Third</td>
<td>4.49</td>
<td>4.74</td>
</tr>
<tr>
<td>First</td>
<td>23.49</td>
<td>23.77</td>
</tr>
<tr>
<td>Second</td>
<td>11.74</td>
<td>7.96</td>
</tr>
<tr>
<td>Third</td>
<td>5.48</td>
<td>5.15</td>
</tr>
</tbody>
</table>

Values (in cm) are magnitude of the variable error for each condition, provided by the square root of the 3 eigenvalues of the 95% tolerance ellipsoids (rank ordered), which correspond to the semi-axes of the ellipsoids.
Table 3. Orientation of the first eigenvectors and of the tangents to ball trajectory

<table>
<thead>
<tr>
<th>Target</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Frontal projection</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Visible Eigenvector</td>
<td>65.25</td>
<td>67.23</td>
<td>55.18</td>
<td>48.52</td>
<td>43.59</td>
<td>40.50</td>
</tr>
<tr>
<td>Visible Tangent</td>
<td>71.07</td>
<td>67.56</td>
<td>58.86</td>
<td>53.17</td>
<td>49.06</td>
<td>44.65</td>
</tr>
<tr>
<td>Occluded Eigenvector</td>
<td>56.63</td>
<td>55.44</td>
<td>54.71</td>
<td>49.53</td>
<td>44.83</td>
<td>39.45</td>
</tr>
<tr>
<td>Occluded Tangent</td>
<td>70.07</td>
<td>64.56</td>
<td>58.54</td>
<td>53.14</td>
<td>49.22</td>
<td>45.14</td>
</tr>
<tr>
<td><strong>Horizontal projection</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Visible Eigenvector</td>
<td>15.94</td>
<td>2.21</td>
<td>-12.55</td>
<td>-13.97</td>
<td>-10.33</td>
<td>-7.76</td>
</tr>
<tr>
<td>Visible Tangent</td>
<td>1.85</td>
<td>4.15</td>
<td>-6.04</td>
<td>-4.92</td>
<td>-4.52</td>
<td>-1.40</td>
</tr>
</tbody>
</table>

Values (in deg) of the angle (relative to the horizontal) of the major axis of the frontal and horizontal projections of the 95% tolerance ellipsoids and of the tangents to ball trajectory at the mean intersection points. For the horizontal projection, the angle of the tangent to ball trajectory relative to the horizontal is always 0.

border of the panels. Table 4 reports the mean values (and 95% confidence intervals) of the vertical position of the intersection points: all mean values corresponded to positions higher than that of the lower border of the panel (–40.5 cm). In occluded conditions, the percentage of trials in which the intersection points were located below the position of the lower border of the panel was always less than 30% of the total (see Table 5). Finally, we estimated the theoretical time window over which the ball became visible after emerging from below the occluding panel and before it was hit (or intersected) by the hand. Table 5 reports the worst-case estimate for each target, corresponding to the trial with the lowest intersection point out of all trials and subjects. The longest time window of estimated visibility was 46 ms for the occluded condition, clearly a time interval much too short to allow any movement correction. Notice that this time interval is probably overestimated, because we did not account for the visual parallax extending further down the occluded field of view (see Fig. 2A).

Timing

As expected from the high contact rates reported above, interception timing was very often close to the ideal for both visual conditions. Thus the median of timing errors was 0 ms in both the visible and occluded condition, with an interquartile range of 11.5 ms (n = 891, pooling the results across repetitions, targets, and subjects) and 13.9 ms (n = 884), respectively.

Effect of Practice

We did not find any major effect of practice on any spatial or temporal parameter related to hitting performance under both visual conditions. Thus, when we included repetition as a within-subjects factor in the RM-ANOVA (2 visual conditions × 6 targets × 15 repetitions as within-subjects factors and 2 block orders as between-subjects factor), this factor did not affect significantly hand movement speed, duration, or onset. The mean curvature depended significantly on repetition.
Table 4. Vertical coordinates of intersection points

<table>
<thead>
<tr>
<th>Target</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td>Visible Mean</td>
<td>−40.3</td>
<td>−38.6</td>
<td>−36.9</td>
<td>−34.0</td>
<td>−32.9</td>
<td>−32.3</td>
</tr>
<tr>
<td>CI</td>
<td>[−39.3, −41.2]</td>
<td>[−37.7, −39.5]</td>
<td>[−35.9, −37.9]</td>
<td>[−33.3, −34.7]</td>
<td>[−32.1, −33.6]</td>
<td>[−31.5, −33.0]</td>
</tr>
<tr>
<td>Occluded Mean</td>
<td>−37.6</td>
<td>−37.5</td>
<td>−36.4</td>
<td>−35.2</td>
<td>−34.5</td>
<td>−34.2</td>
</tr>
<tr>
<td>CI</td>
<td>[−36.4, −38.8]</td>
<td>[−36.4, −38.6]</td>
<td>[−35.3, −37.4]</td>
<td>[−34.2, −36.3]</td>
<td>[−33.5, −35.6]</td>
<td>[−33.1, −35.3]</td>
</tr>
</tbody>
</table>

Values (in cm) are means and 95% confidence intervals (CI; over all repetitions and subjects) of the vertical coordinates of intersection points. The vertical coordinate of the lower border of the panel was always −40.5 cm.

\( F_{4,477,35.818} = 2.728, \, P = 0.039, \, \eta_p^2 = 0.254 \), but post hoc tests showed that these differences were not significant (all \( P > 0.99 \)). Moreover, we did not find any significant effect of repetition on the spatial errors for any target of the visible condition, and for most targets (targets 2–5) of the occluded condition. However, we found an effect of repetition for the occluded condition when we considered the median of spatial errors (see METHODS) over targets 1 and 6 of all subjects. An exponential function (Eq. 1) fitted well \( (r^2 = 0.997) \) the values of this parameter across successive repetitions. The learning constant \( b_2 \) was 0.58 repetition (CI [0.52, 0.64]), indicating a very rapid decrement of the error. The other fitting parameters were offset, \( b_0 = 0.017 \) cm (CI [−0.01, 0.04]), and gain, \( b_1 = 3.03 \) cm (CI [2.9, 3.1]).

DISCUSSION

In agreement with previous reports (Bosco et al. 2012; Cesqui et al. 2012; Fink et al. 2009; Savelsbergh et al. 1992), we found that participants were able to accurately intercept projectile trajectories under continuous visual guidance. The novel finding is that participants were equally successful at hitting the falling ball when its quasi-parabolic trajectory was completely occluded prior to interception, consistent with the hypothesis of model-based control. Most interception parameters we assessed did not differ significantly between the visible and the occluded condition. In particular, for both visual conditions we found high contact rates, correct timings of interception, and distinct interception clusters for different target trajectories.

By design, ball path and speed during the occluded period could not be extrapolated solely from the kinematic information obtained during the preceding visible phase, when the ball rolled down along the incline at a fraction of gravitational acceleration. The only way to extrapolate ball motion correctly during the occlusion period was to assume that the ball would fall under gravity and air drag, when hidden from view. Such an assumption had to be derived from prior experience. Our results are thus inconsistent with the hypothesis of on-line control, according to which extrapolation of target motion is based exclusively on continuous visual information about target kinematics, without any prior model of target motion. If such an on-line control had been used during the occlusion period, participants should have directed the hand in retarding (because the previous visible phase was at about one-fifth of the subsequent gravitational acceleration) and in a wrong direction, for instance, toward the rectilinear trajectory extending the visible inclined plane.

---

**Table 5. Potential visibility of the ball below the panel**

<table>
<thead>
<tr>
<th>Target</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trials below the panel, %</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Visible</td>
<td>55</td>
<td>38</td>
<td>28</td>
<td>7</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Occluded</td>
<td>27</td>
<td>28</td>
<td>24</td>
<td>22</td>
<td>24</td>
<td>19</td>
</tr>
<tr>
<td>Maximum duration of ball motion below the panel, ms</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Visible</td>
<td>36</td>
<td>41</td>
<td>31</td>
<td>15</td>
<td>6</td>
<td>20</td>
</tr>
<tr>
<td>Occluded</td>
<td>46</td>
<td>42</td>
<td>41</td>
<td>33</td>
<td>30</td>
<td>45</td>
</tr>
</tbody>
</table>

Values are the percentage of trials (of all repetitions and subjects) in which the intersection points of Fig. 9B were located below the position of the lower border of the transparent or opaque panels and the maximum duration of ball motion below the panel before being intersected by the hand, for the visible and occluded conditions, respectively. This corresponds to the trial with the lowest intersection point of all repetitions and subjects.

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**Internal Model of Target Motion**

In a recent critical review, Zhao and Warren (2015) acknowledged the lack of reliability of on-line control under occluded conditions but rejected the hypothesis of model-based control. As an alternative to model-based strategies, they suggested less accurate off-line strategies derived from previous experience with the task, such as heuristics, visual-motor mappings, or spatial memory. For the present experiments, such strategies could predict that once participants have learned from previous trials that a ball rolling down the incline from a greater height (and longer time) tends to fall more to the right than balls rolling down from a lower height (see Figs. 1 and 2), they would make arm movements in approximately the appropriate direction after the ball goes out of sight. However, two sets of findings run against this ad hoc solution. First, interceptions in the occluded condition were similar to those under the visible condition from the very first repetition. Second, arm movements were not just in the appropriate direction but resulted in intersection positions distributed along the trajectory of the falling balls.

The latter finding is especially significant, in so far as it meets the stringent requirement that has been formulated by Zhao and Warren (2015) to distinguish between model-based control and simpler heuristics: only an internal model of projectile motion should be able to represent intervening states of a ball’s trajectory. Consistent with this prediction, we found that in different trials the intersection points were distributed along the quasi-parabolic trajectories of the ball for both visual conditions (Figs. 8 and 9), indicating that subjects were able to...
extrapolate an extended segment (about 30–50 cm) of the target trajectory both with and without visual cues. Remarkably, this trend was found even at the very first repetition of movements aimed to each target (Fig. 10), indicating that the internal model of projectile motion was largely independent of any feedback from previous trials of the same session. Indeed, we found no significant effect of practice on hitting performance for any target of the visible condition and for all but two targets of the occluded condition. Instead, the spatial errors over the most medial and most lateral target did improve very rapidly with repetition in the occluded condition.

The results demonstrate the role of an internal model of target motion for the occluded condition, but what about the visible condition? Although the evidence is indirect, there are important hints for a critical role of model-based control even in the latter case. First and foremost, as remarked above, most interception parameters did not differ significantly between the visible and the occluded condition, underlining a fundamental similarity between the two sets of hitting movements. Moreover, in both visual conditions the hitting movements lacked the typical features that are considered indicative of continuous visual guidance. Thus the presence of submovements is often taken as evidence for corrective actions produced in response to feedback-detected errors in the unfolding action (Elliott et al. 2010; Lee et al. 1997; Tresilian 2005). Instead, in the vast majority of trials of the present experiments, arm movements started before the ball reached the exit point from the incline, lasted <300 ms, and had a monophasic, bell-shaped speed profile without submovements. These are typical features of ballistic movements under limited sensory feedback (Tresilian 2004, 2005).

Visual Signals About Target Motion

In addition to the internal model, visual information about ball kinematics very likely played a role in the present experiments. First, the path and speed of the ball during the free fall phase depended on ball speed at the exit from the incline. In turn, the latter speed parameter depended on the starting position of the ball on the incline, which was randomized across trials. Therefore, to correctly predict the ensuing trajectory, the internal model of projectile motion had to be input with on-line estimates of ball speed obtained some time before the exit from the incline. We did not record eye movements, but it is likely that in addition to retinal signals also extraretinal signals related to an efference copy of eye movements contributed toward extrapolating target motion. Indeed, it is known that when a target becomes occluded, subjects are able to make predictive saccades to the expected point of target reappearance, even when the target follows curved trajectories or is deflected during the occlusion (Bennett and Barnes 2006; Delle Monache et al. 2015; Ferrera and Barboricu 2010; Mrotek and Soechting 2007; Orban de Xivry et al. 2009). Oculomotor predictions may also include visual acceleration information, as well as experience-based models of physical interactions between the visual target and the environment (Bennett and Benguigui 2013; Brouwer et al. 2002; Delle Monache et al. 2015; Diaz et al. 2013; Souto and Kerzel 2013; Tramper et al. 2013).

Despite the broad similarity of performance between the visible and the occluded condition, there were nevertheless some notable differences. Thus, although the overall success rate (measured as contact rate) was not significantly different between the two conditions, the interception of fully visible targets was generally more precise. Indeed, the intersection points of the rod tip were scattered along a significantly smaller area in the visible condition than in the occluded one. This suggests that, perhaps unsurprisingly, the arm movement parameters were better calibrated to the free-fall phase of ball motion with full vision than with partial occlusion of ball trajectory.

Prior Experience

We argued above that the internal model of projectile motion was largely independent of any feedback from previous trials of the same session, in so far as the hand often intersected the quasi-parabolic trajectories of the ball already at the first attempt, and very little effect of practice was observed. However, prior visual experience with the quasi-parabolic trajectories of the ball did have a measurable effect on the performance in the occluded session, presumably because visual signals on the actual free-fall of the target fine-tuned the parameters of the internal model. In fact, we found a significant interaction between visual condition and block order for the contact rate: this performance parameter was worse in the occluded session when this was the first session compared with when it was preceded by the visible session. Because the two sessions were performed about 15 days apart, this order effect is compatible with a long-term memory of the model parameters. Indeed, familiarity with a specific trajectory has been shown to facilitate the interpretation of physical forces when intercepting a moving target (Mijatović et al. 2014) or when tracing a contour under haptic guidance (Tramper and Flanders 2013). Experience with gravity effects has been shown to shape human behavior since early infancy. Thus, before 1 yr of age, infants expect that an unsupported object falls, that an object moving down an inclined plane accelerates, and that an upwardly moving object decelerates, and they are surprised to see artificial violations of these expectations (Kim and Spelke 1992; Stahl and Feigenson 2015). It is then conceivable that model-based extrapolation of visual motion under gravity is in place already at an early age.

Comparison with Previous Work

In a previous study (La Scaleia et al. 2014), we asked participants to hit a ball after it rolled down an incline tilted by 30°, 45°, or 60°. In contrast with the present experiments, in the previous ones the hitting endpoint was constrained experimentally by providing participants with a continuous visual feedback about the current hand position relative to the required final position for interception. Moreover, the required interception position was located just below the exit point from the incline, so that the main extrapolation concerned the rectilinear trajectory along the incline, whereas the subsequent free-fall phase was very short compared with the present one. La Scaleia et al. (2014) found that interception performance was excellent under full visual guidance, roughly comparable to that reported presently for the visible condition. Thus the average contact rate was 88% in La Scaleia et al. (2014) compared with 85% in the present experiments.

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In another experiment of the previous study, the ball rolled down along the incline as before, but it was stopped just before the end of the track. Participants were asked to imagine that the ball kept moving and to hit it at the same nominal interception point as before. Again, a continuous visual feedback was provided about the current hand position relative to the required final position for interception. Spatial errors were small as expected (given the visual feedback), but timing errors were substantial (on average, 51 ms) for the incline angle (30°) more comparable with the present one (20°). In light of these timing errors as well as other performance deficiencies detailed in La Scaleia et al. (2014), the accurate performance in the present occluded experiments appears striking, especially if one considers that the length and duration of target motion that had to be extrapolated was much greater here than in the previous study. One possible explanation for this apparent discrepancy is that although visual information about the last phase of target motion prior to interception was missing in both the previous and the present occluded experiments, haptic feedback of the hand with a real falling ball was available in the present experiment but not in the previous experiment. In this regard, it has been shown that the interception performance with targets accelerated by gravity is better in the presence of haptic feedback from contact with a real ball than in its absence with virtual interceptions (Zago et al. 2004). Haptic object size sensations also improve visual distance estimates used in interception tasks (Battaglia et al. 2011). Another factor that may account for the discrepancy noted above is given by the fact that the interception point was specified in advance in the previous experiments (La Scaleia et al. 2014) but not in the present ones. In this respect, it has been shown that the temporal precision of interception is much poorer when the point of interception is specified in advance (Brenner and Smeets 2015).

De Sá Teixeira et al. (2013) presented a linearly moving target that suddenly disappeared and asked participants to indicate the location on the screen where the target had vanished. They introduced temporal delays between the target’s disappearance and the response to track changes in the remembered location over time. They found that the remembered vanishing positions evolved with time in a pattern that mimics a parabolic trajectory, reminiscent of some of the present findings and consistent with an internalization of gravity in the visual representation of projectiles.

Putative Neural Substrates for Extrapolation of Occluded Target Motion

To our knowledge, there are no published neurophysiological data directly pertinent to the present task involving the extrapolation of relatively complex trajectories. However, extensive research has been carried out on the neural mechanisms correlated with extrapolation of simpler occluded trajectories (for a recent review, see Bosco et al. 2015). Thus both electrophysiological and functional neuroimaging studies point to a critical role of the posterior parietal cortex (the lateral intraparietal sulcus in monkeys, Eskandar and Assad 1999; the posterior part of the intraparietal sulcus in humans, O’Reilly et al. 2008), premotor cortex (frontal eye fields, Ferrera and Barboriga 2010; Nagel et al. 2006), and cerebellum (Beudel et al. 2009; Cerminara et al. 2009; O’Reilly et al. 2008) in the extrapolation of linear motion at constant speed. Neural activity in these regions is maintained during extended periods of motion occlusion, suggesting the use of an internal model of target motion (Cerminara et al. 2009).

Neuroimaging and transcranial magnetic stimulation have shown that the effects of gravity on target motion elicit neural responses in a distributed cortical-subcortical network including the vestibular cortex, putamen, cerebellum, and vestibular nuclei (Bosco et al. 2008; Indovina et al. 2005; Maffei et al. 2010; Miller et al. 2008), but occluded motion affected by gravity has yet to be studied. Nevertheless, it appears plausible that some of the same regions involved in detecting the effects of gravity on a visible target may also encode an internal model of gravitational motion (Indovina et al. 2005) to be used with occluded trajectories.

Conclusions

We have shown that a model-based control of interception incorporating prior knowledge of gravity and air drag effects, as well as visual and gaze signals about target motion, can account for the interception of projectile motion under both fully visible and partly occluded conditions. The present results with occluded conditions refute the hypothesis of on-line control involving continuous visual information about target kinematics without any prior model of target motion. Although the hypothesis of model-free on-line control cannot be dismissed for the fully visible condition, a contribution of internal models also appears very likely in this case. A brain that is able to mimic target kinematics so well under occluded conditions would be wasteful to not use both the model and the on-line signals under full visibility. In fact, when the kinematics of a vertically descending ball departs from the expected gravitational acceleration in the unusual conditions of real or simulated microgravity and the resulting on-line visual signals are incongruent with the prior gravity model, the interceptive behavior conforms with the prior gravity model, rather than with the visual evidence (McIntyre et al. 2001; Zago et al. 2004). Experience with the new environment progressively leads to an adjustment of the model parameters based on sensory evidence (Zago et al. 2005; Zago and Lacquaniti 2005). On the other hand, on-line control is the only option for completely unpredictable targets (Elliott et al. 2010; Soechting et al. 2009).

APPENDIX

Here we describe the kinematics of the ball as derived from a series of calibration trials performed before the experiments. The equations of motion of a sphere in air (such as ball motion after exiting from the lower end of the incline) under gravity and drag (quadratic in speed) are

\[ m\ddot{x} = -\frac{1}{2}C_pS\dot{v}^2 \]  
\[ m\ddot{y} = mg - \frac{1}{2}C_pS\dot{v}^2, \]  

where \( \ddot{x} \) (or \( \ddot{y} \)) is the linear acceleration of the center of mass of the sphere along the horizontal (or vertical) axis, \( m \) is the sphere mass, \( g \) is the acceleration due to gravity, \( \rho \) is the density of air, \( S \) is the reference area, \( \dot{v} \) is the speed of the sphere relative to air, and \( C \) is the...
To assess the adequacy of the estimated parameters, we computed a spatial error and a temporal error. If $P(T)$ denotes the instantaneous position (time) of the ball recorded by the video camera and $P^*$ ($T^*$) denotes the corresponding theoretical position (time) predicted by the estimated parameters $\tilde{g}, \tilde{v}_L, \tilde{v}_0$, and $\tilde{v}_0$, the distance between $P^*$ and $P$ defines the spatial error of the model, and the difference between $T^*$ and $T$ defines the temporal error. We found that the mean spatial error was 0.001 m (SD = 0.0005 m, $n = 18$) and the mean temporal error was $-0.08$ ms (SD = 0.72 ms, $n = 18$).

To assess the consistency of the parameter estimates over time, we performed a second, identical session of video recordings 10 days after the first session. We then evaluated the spatial and the temporal error using the parameters $\tilde{g}, \tilde{v}_L, \tilde{v}_0$, and $\tilde{v}_0$ estimated in the first session and the kinematics of the ball recorded in the second session. We found that the new mean spatial error was 0.0019 m (SD = 0.0012 m, $n = 18$) and the new mean temporal error was 0.19 ms (SD = 0.67 ms, $n = 18$).

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DISCLAIMERS

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

B.L.S., M.Z., and F.L. conceived and designed research; B.L.S. performed experiments; B.L.S. and M.Z. prepared figures; B.L.S., M.Z., and F.L. drafted manuscript. B.L.S., M.Z., and F.L. analyzed data; B.L.S., M.Z., and F.L. interpreted results of experiments; B.L.S. and M.Z. performed data analysis; B.L.S. and M.Z. prepared figures; B.L.S. and M.Z. performed data analysis and wrote the draft manuscript. B.L.S., M.Z., and F.L. designed research; B.L.S., M.Z., and F.L. drafted manuscript; B.L.S., M.Z., and F.L. performed experiments; B.L.S., M.Z., and F.L. interpreted results of experiments; B.L.S., M.Z., and F.L. wrote the draft manuscript; B.L.S., M.Z., and F.L. edited and revised manuscript; B.L.S., M.Z., and F.L. approved final version of manuscript.

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