Neural prediction of complex accelerations for object interception

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HUMANS ARE CAPABLE OF PRODUCING astonishingly fine tolerance motor movements demanding both high spatial and temporal accuracy. It has been demonstrated that we can easily hit falling balls with a bat within a time window of ±10 ms (McLeod et al. 1985), and the temporal accuracy to hit a home run in a baseball match may be as little as ±2 ms (Regan 1992). The processes by which the human brain converts visual information into motor movements of this kind remains poorly understood, but however it is done, the system needs to contend with internal delays between visual detection and motor movement, which can run to the order of 100 ms (Marinovic et al. 2008, 2009; McLeod 1987). There is gathering evidence that part of the process of honing motor behavior involves the development of an internal model for motion extrapolation, and recent studies have looked into the neural substrate of such a model (Bosco et al. 2008; Cerminara et al. 2009; Indovina et al. 2005; Miller et al. 2008; O’Reilly et al. 2008) and how timing might be controlled (Billington et al. 2011; Field and Wann 2005). An active area of current debate is the form this model takes and the types of information about a target and its motion that such a model might contain. What we do know from the smooth pursuit eye movement literature is that humans are relatively good at tracking objects moving at a fixed velocity, but that we are actually poor at detecting and estimating changes in velocity, i.e., accelerations (Watamaniuk and Heinen 2003; Werkhoven et al. 1992). This is a problem because, in real life, even inanimate moving objects experience changes in velocity due to wind resistance, gravity, changes in terrain, etc. It would therefore seem expedient to be able to internalize predictions about velocity changes. To date, what little evidence we do have has come from the study of objects falling under gravity. Evidence points to the fact that we take the effects of gravity-driven acceleration into account when timing the interception of a falling ball, for example (Indovina et al. 2005; McIntyre et al. 2001; Zago et al. 2009). The question remains, however, as to whether this is a system that has developed especially for this purpose. Free fall involves a simple linear acceleration, which permits extrapolation of location at any point along the object line of movement (Zago et al. 2009). However, perhaps humans possess a much more flexible system for dealing with accelerations in a more general manner. Here, we show that a human observer’s internal model of target motion is capable of predicting the effects of far more complex variations in acceleration that result from interaction of an object with its environment in both ecological and unecological, but lawful, ways.

MATERIALS AND METHODS

Participants. Ten participants (6 of them male, aged 22–43 yr) volunteered for this experiment. All were right handed with normal or corrected-to-normal vision. They all gave written informed consent before the experiment, and the experiment itself was approved by the local ethics committee and conformed to the Declaration of Helsinki.

Task. The task required the participant to time precisely a discrete action (i.e., an abduction force produced with the index finger) when a moving ball passed through a specific location. Participants sat in a chair with their eyes at 85 cm from a computer display (48 × 30 cm, 1,920–×1,200-pixel resolution, 66-Hz refresh rate) positioned at eye level (Fig. 1A). The participants were required to abduct their right index finger against a force transducer, placed beside their right hand on the hand rest, at the precise moment they judged the red moving ball (30-pixel diameter) would pass through a green stationary line (6-pixel width) positioned on the right-hand side of the screen (Fig. 1B and C). The movement of the ball corresponded to a ball rolling under the effects of gravity within a tube (32-pixel width) of varying slope. The effects of rolling resistance were also accurately simulated.

After each trial, the onset of the abduction force was determined using a standard onset peaking algorithm (Teasdale et al. 1993), as described in Tresilian et al. (1997): 1) locate the sample (sample 1) at which the force time series first exceeds 10% of its maximum value (Vmax); 2) working back from this point, stop at the first sample.
Rolling ball simulations. Because the ball was restricted to move along the path of the tube, its motion was determined from Newton’s second law of physics using the projections of all forces acting along the direction of motion. In our case, gravity ($F_g$) and rolling resistance ($F_r$, the resistance associated with surface deformation, which is a function of the normal force at the rolling object) were the only forces considered as having a component in that direction. The equation of motion is therefore given by:

$$mp = F_g - F_r,$$

which develops into:

$$mp = m \cdot g \cdot \sin(\alpha) - C_r \cdot m \cdot g \cdot \cos(\alpha),$$

where $p$ is the acceleration (and $p$ is the position) of the ball along the tube path, $m$ is its mass, $\alpha$ is the slope of the tube, and $C_r$ is the rolling resistance coefficient.

The acceleration of the ball was therefore determined by the slope of the tube. Figure 2 shows typical examples of tube configurations used. These configurations can be separated into three phases: a small initial ramp, followed by a constant slope for most of the trajectory, and finally a Gaussian deflexion (upward in Fig. 1B and downward in Fig. 1C) just before the crossing of the target line. With the ball released at zero velocity, the initial ramp was designed to accelerate the ball until it reached a fixed velocity (960 pixels/s), which was maintained constant by the specific inclination of the flat section of tubing (i.e., at this velocity, the force of gravity was exactly compensated by the rolling resistance such that overall acceleration was nil). Then, the deflexion was introduced to elicit the pattern of varying acceleration. The starting position was determined randomly for each trial between the left edge of the screen (e.g., Fig. 1B) and 672 pixels on its right, such that the movement time associated with a particular tube profile was varied by up to 700 ms from one trial to the next.

In addition to a profile $d_{\text{up}}$ that has no deflection, 10 conditions of upward deflection (from $d_1$ to $d_{\text{up}}$) and 30 conditions of downward deflection (from $d_{\text{up}}$ to $d_{\text{down}}$) were used. There was therefore a total of 41 simulated profiles used between the highest upward deflexion ($d_{\text{up}}$, in Fig. 1B, which represents a deflexion of 96 pixels) and the lowest downward deflexion ($d_{\text{down}}$, in Fig. 1C, which represents a deflexion of 288 pixels). Figure 2 displays the profiles of velocity (Fig. 2A) and acceleration (Fig. 2B) associated with each deflexion. As can be seen from this figure, upward deflexions undergo a phase of deceleration followed by a phase of acceleration, whereas the opposite occurs for downward deflexions. Overall, the average velocity for an upward (downward) deflexion is therefore lower (higher) than the constant velocity operating with no deflexion, and the passage of the target line will be delayed (advanced) compared with what it would have been under constant velocity.

Catch trials and predictions. To test whether the pattern of varying acceleration of the ball dictated by its interaction with the environment was taken into consideration by the participants to time their responses, we conducted constant velocity catch trials for four specific tube profiles ($d_{8}$, $d_{18}$, $d_{28}$, and $d_{38}$) within a block of normal trials (velocity and acceleration profiles are indicated in Fig. 2) on their direct images. Figure 2C indicates that for upward deflexion, the ball should take longer to go through the deflexion part of the tube than if the tube were flat (e.g., $\delta t = 164$ ms for $d_{28}$ black arrow, Fig. 2C). This is due to the combined effect of changes in tube length and kinematics over the deflexion. Conversely, the ball takes less time to go through small downward deflexions and longer time again for more important downward deflexion (e.g., $\delta t = 6$, 76, and 155 ms for $d_{28}$, $d_{18}$, and $d_{28}$, respectively). This is because for these higher downward deflexions, the increase in tube length over-
Participants to correct their behavior partially on the bases of ongoing information, and we therefore expect only a fraction of the error predicted in Fig. 3A.

Procedures and design. Each participant was tested two times with the same protocol. On one occasion, the scene was projected normally, with gravity pointing down (i.e., normal gravity), and on another, upside down, as if gravity were acting upward (i.e., reversed gravity). These two sessions were conducted on separated days interspersed by at least 1 wk, and the order of the sessions was counterbalanced between participants.

Before each experimental session, the participants were given 2 blocks of practice trials to familiarize themselves with the task. The 1st consisted of 20 trials with no deflexion (d0) to enable them to experience the apparatus and the task (i.e., synchronize their response with the ball) in the simple case of constant velocity. The 2nd familiarization block consisted of 3 consecutive sets of 41 trials (i.e., 1 trial per each of the 41 different deflexions) presented in a randomized order (total 123 trials). Then, the main experimental session was conducted. This session consisted of 8 consecutive sets of 20 trials (160 trials total), including 4 catch trials of different profiles (d8, d9, d17, and d28) and 16 non-catch trials consisting of the 4 closest neighbor profiles of each catch trial (e.g., neighbor profiles d7, d8, and d9 for catch trial d8) presented in a randomized order.

Data reduction and analysis. For each trial, the timing error was calculated as the difference between the onset of the force response and the passage of the ball through the target line, with negative errors indicating early responses. For each participant, the mean of the timing errors was then calculated separately for each of the 4 different profiles of catch trials and their associated normal trial neighbors. The resulting values were analyzed using 3-way repeated-measures ANOVAs [2 gravity (normal vs. reverse) × 2 trial type (normal vs. catch) × 4 deflexion (d8, d9, d17, and d28)]. For each deflexion condition, paired-sample t-tests were conducted to compare timing error between trial types (i.e., catch and normal) within the same gravity condition (i.e., normal or reverse) and between gravity conditions within the same trial type. Because biases of variable magnitudes were observed in averaged timing error for the different participants, averaged errors for each deflexion and trial type were difficult to interpret individually, and we concentrated our analysis on relative changes between deflexions and trial types as indicated before. This intersubject variability might be due to the nature of the task, with a virtual interception providing less realistic feedback than hitting a real object (e.g., Zago et al. 2005). This variability should, however, not affect our results because of the repeated-measure design used.

The time course of the timing error was also assessed on both the familiarization block and the main experimental session. For the familiarization block, the summed squared error was calculated over each consecutive set of 10 trials, giving 12 time values per participant (covering 120 trials, the last 3 trials were discarded). The resulting values were analyzed using a 2-way repeated-measures ANOVA [2 gravity (normal vs. reverse) × 12 times]. For the main experimental session, the summed squared error was calculated separately on normal and catch trials over each consecutive set of 20 trials (i.e., 16 normal and 4 catch trials), giving 8 time values per participant. The resulting values were analyzed using 2-way repeated-measures ANOVAs [2 gravity (normal vs. reverse) × 8 times]. Sphericity was tested using Mauchly’s test, and the degrees of freedom were corrected using the Greenhouse-Geisser estimates of sphericity when the assumption for sphericity was violated. The significance level was set to α = 0.01 for all tests.

The averaged patterns of error obtained for normal trials and for catch trials were also fitted with the patterns of errors indicated by arrows in Fig. 2C. First, the errors for normal trials were fitted with the pattern of error expected should participants neglect the differences in time taken by the ball to go through the various deflexions (black arrows, Fig. 2C). Second, the errors for catch trials were fitted with the pattern of error predicted should the participants expect the correct effect of acceleration (red arrows, Figs. 2C and 3A). The values

Fig. 2. Velocity (A) and acceleration (B) profiles for the 41 different deflexions used. The profiles that correspond to the deflexions used for the catch trials are highlighted in red (i.e., d8, d9, d17, and d28). C: Difference in time (Δt) taken by the ball to go through the various deflexion compared with a flat tube (i.e., no deflexion) for trials with normal acceleration (black square) and constant velocity catch trials (red circle). Black arrows indicate timing errors expected should participants neglect the differences in time taken by the ball to go through the various deflexions, and red arrows indicate timing errors expected should participants expect normal acceleration on catch trials.

Each participant was tested two times with the same protocol.
obtained for the first fit of the normal trials were used as a baseline to perform this second fit of the catch trials. In both cases, two parameters were varied to obtain the best fit (i.e., minimal residual variance): a bias and a proportion.

**Control experiment 1 methods.** Ten new participants (5 of them female, aged 25–53 yr) volunteered in this control experiment. The protocol was the same as each session of the main experiment. The only difference was that the tube that determines the path of the ball, and therefore its kinematics, was made invisible. This manipulation withdrew any cue that could be used to predict in advance the ball trajectory and time course based on its interaction with the environment. This control was designed to test whether the differences between normal trials and catch trials observed in the main experiment were genuinely due to a prediction of the ball kinematics based on its path.

**Control experiment 2 methods.** Eight new participants (3 of them female, aged 23–44 yr) volunteered in this control experiment. The same protocol was employed again, but this time with the ball acceleration that corresponded to the different simulated deflexions was played on a flat path with no apparent deflexion (i.e., visible but flat tube). As for the precedent control experiment, any cue that could allow participants to predict the ball acceleration has been removed, but here, the additional confound induced by the altered path length that is due to the deflexion was also removed. This control was designed to test whether any effect on the previous control experiment could be due to the altered path length.

**RESULTS**

**Pattern of error.** Figure 3, B and D, shows a pattern of error that resembles that predicted in Fig. 3A, whether the visual scene was projected normally (i.e., normal gravity) or upside down (i.e., reversed gravity). Statistical analyses reveal that the effects predicted are all significant and that there is no difference between conditions of normal and reversed gravity. The 3-way repeated-measures ANOVA (2 gravity × 2 trial type × 4 deflexion) indicates a main effect of trial type [F(1, 9) = 55.87, P < 0.0005], deflexion [F(3, 9) = 17.70, P < 0.0005], and an interaction between them [F(3, 27) = 25.41, P < 0.0005]. No other main effect or interaction was detected. The difference between catch trials and normal trials was significant for all deflexions of the 2 gravity conditions [all ts (9) > 3.57, all Ps < 0.006]. On the other hand, no differences were found between timing errors of the 2 gravity conditions within each trial type and deflexion [all ts (9) < 1.46, all Ps > 0.18].

There are, however, noticeable differences from the pattern predicted in Fig. 3A. These include a pattern of errors for normal trials that is overall negative (i.e., early responses) and that varies with deflexion. A fit indicates that 98.0% variance of the errors is explained by a proportion of only 15.4% of the full pattern of error expected should participants neglect the effect of acceleration over normal trials and should they expect normal acceleration on catch trial (cf. MATERIALS AND METHODS and RESULTS). Negative errors indicate early responses.
could be easily explained by the fact that the very onset of the force was used to prevent eventual benefits from modulating the force response when too early or too late.

Another noticeable difference is the size of the errors predicted for catch trials, which is more important than the actual errors observed (notice the different scale use for Fig. 3A than for the 3 other panels). The best fit performed on catch trials accounts for 95.4% of error variance using a proportion of 29% of the pattern of error predicted should participants mistime their response by an amount that corresponds to the full effect of normal acceleration. This means that participants were building up an expectation of the effects of acceleration dictated by the interaction of the ball and the tube and were unable to overcome that expectation completely during unexpected constant velocity catch trials despite the availability of visual information throughout.

*Time course of the performance.* The 2-way repeated-measures ANOVA (2 gravity × 12 time) conducted on the summed squared error calculated over the 12 consecutive sets of 10 trials of the familiarization block did not reveal any main effect or interaction (all P > 0.77). Similarly, the 2-way repeated-measures ANOVAs (2 gravity × 8 time) conducted on summed squared error calculated over the 8 consecutive sets of 20 trials of the main block did not reveal any main effect or interaction for normal trials (all P > 0.48) nor for catch trials (all P > 0.54). These analyses indicate that overall performance was stable throughout the experiment, although some degree of adaptation could have been masked by the trial-by-trial variability.

*Control experiment 1: invisible path.* Figure 4A shows a pattern of error that resembles that of the normal trial of the main experiment but for both the normal and the catch trials. Statistical analyses reveal a significant effect of deflexion [F(3, 30) = 14.40, P < 0.0005] but no effect of trial type [F(1, 10) = 5.34, P = 0.043] and no interaction [F(1.99, 19.9) = 3.87, P = 0.038]. That normal trials and catch trials were no longer different when the path of the ball was made invisible indicates that differences observed in the main experiment are due to a prediction of the ball kinematics based on its interaction with the environment. The remaining effect of deflexion on timing error could be related to the altered path length induced by the deflexions, which has been removed in control experiment 2.

*Control experiment 2: flat path.* Figure 4B shows that when the acceleration profiles were played on a flat path, there was no longer difference with deflexion types. There was no effect of deflexion [F(3, 7) = 2.91, P = 0.058], only a marginal effect of trial type [F(1, 7) = 9.75, P = 0.017] and no significant interaction [F(3, 21) = 1.24, P = 0.32]. This indicates that the effect of deflexion on normal trials of the previous control, and part of the effect observed in the main experiment, were indeed related to changes in path length with deflexion. That performance was close for normal and catch trials also indicates that participants were somehow able to compensate for the effect of unexpected acceleration based on online visual information.

**DISCUSSION**

Here, we show that when timing an object interception, humans are building up an expectation of the effects of complex, varying accelerations that result from interactions with the environment. The errors produced by participants timing their responses with the arrival of a ball rolling under gravity within a tube of various shapes indicates that, within a relatively short practice (~300 trials), they were able to compensate for most (~85%) of the effects of a complex acceleration dictated by the movement of the ball within its tube. Errors on catch trials in which the velocity of the ball was unexpectedly maintained constant confirmed that participants were expecting the effect of acceleration normally induced by the shape of the tube. Control experiments in which predictive cues about the environment were removed also indicate that the task could be resolved, to a certain degree, by online feedback only. Yet, participants were not able to overcome their expectation of the effect of gravity when reliable predictive cues were available in the main experiment. Furthermore, we showed that these effects were identical whether the visual scene was projected normally or upside down, which indicates that the mechanism of this prediction is flexible and not confined to ecologically valid interactions.

A critical feature of the present finding is that the acceleration of the ball was induced by the interaction with its particular environment in a predictable fashion. This situation resembles the study of Brown et al. (2007) in which learning to move in a force field was shown to improve timing interception...
of an object accelerating in the same direction as the force field. In this case, knowledge of the environment acquired through motor learning influenced predictions of the motion of the object as if the object were interacting with the same environment. However, an important difference with the present study is that in Brown and colleagues’ study (2007), no visual information about the environment was available to assist in the prediction of the outcome of its action on the object. In this context, the knowledge developed during motor practice might have been sufficient to elicit a meaningful effect because of the relatively restricted scenario used (i.e., only 1 constant acceleration of the object, tested after practice of 1 of 2 possible force field environments that differed, or not, in direction). Here, the patterns of accelerations were complex and variable, both within and between the multiple tube shapes tested, but each was entirely predictable from a projection of the behavior of the ball onto its visible environment (i.e., the shape of the tube).

The present results are also in line with important studies that have demonstrated that we are able to take the effects of gravity-driven acceleration into account when timing the interception of falling objects (Indovina et al. 2005; McIntyre et al. 2001; Zago et al. 2009). However, the extension of this finding to a much broader range of cases and situations has important implications for the mechanism underlying the prediction. In the case of a free-falling object, acceleration is constant, and an internal model could simply be composed of a single (constant) estimate of gravity acceleration combined with online retinal information (Zago et al. 2009; see also Tresilian 1999). An internal model of this kind, however, would fail short in the present context in which the variations of acceleration result from specific interactions with the environment. The fact that we obtained similar results whether the visual scene was projected normally or upside down further indicates that the mechanism of this prediction is flexible and not confined to an evolutionarily prepared version of gravity. Previous studies investigating this issue in the context of free-falling objects found an effect of the direction of gravity on both the behavior and the neural substrate involved in the prediction (Bosco et al. 2008; Indovina et al. 2005; Miller et al. 2008). It was also found, however, that the inclusion of more realistic scenery amplified this effect (Miller et al. 2008). In our case, the scenery was kept very sparse, and this might have contributed to the apparent ease with which subjects were able to learn to cope with reverse gravity.

In summary, our findings demonstrate that for object interception, humans are capable of predicting complex interactions with the environment in a manner that is much more flexible than previously thought. However, the overall capabilities and the precise form of a putative internal model responsible for this type of prediction remain largely unknown. We believe that the task set presented here constitutes a novel paradigm that has great potential to address these issues.

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS


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Billington J, Wilkie RM, Field DT, Wann JP. Neural processing of imminence of an object accelerating in the same direction as the force field. In this case, knowledge of the environment acquired through motor learning influenced predictions of the motion of the object as if the object were interacting with the same environment. However, an important difference with the present study is that in Brown and colleagues’ study (2007), no visual information about the environment was available to assist in the prediction of the outcome of its action on the object. In this context, the knowledge developed during motor practice might have been sufficient to elicit a meaningful effect because of the relatively restricted scenario used (i.e., only 1 constant acceleration of the object, tested after practice of 1 of 2 possible force field environments that differed, or not, in direction). Here, the patterns of accelerations were complex and variable, both within and between the multiple tube shapes tested, but each was entirely predictable from a projection of the behavior of the ball onto its visible environment (i.e., the shape of the tube).

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