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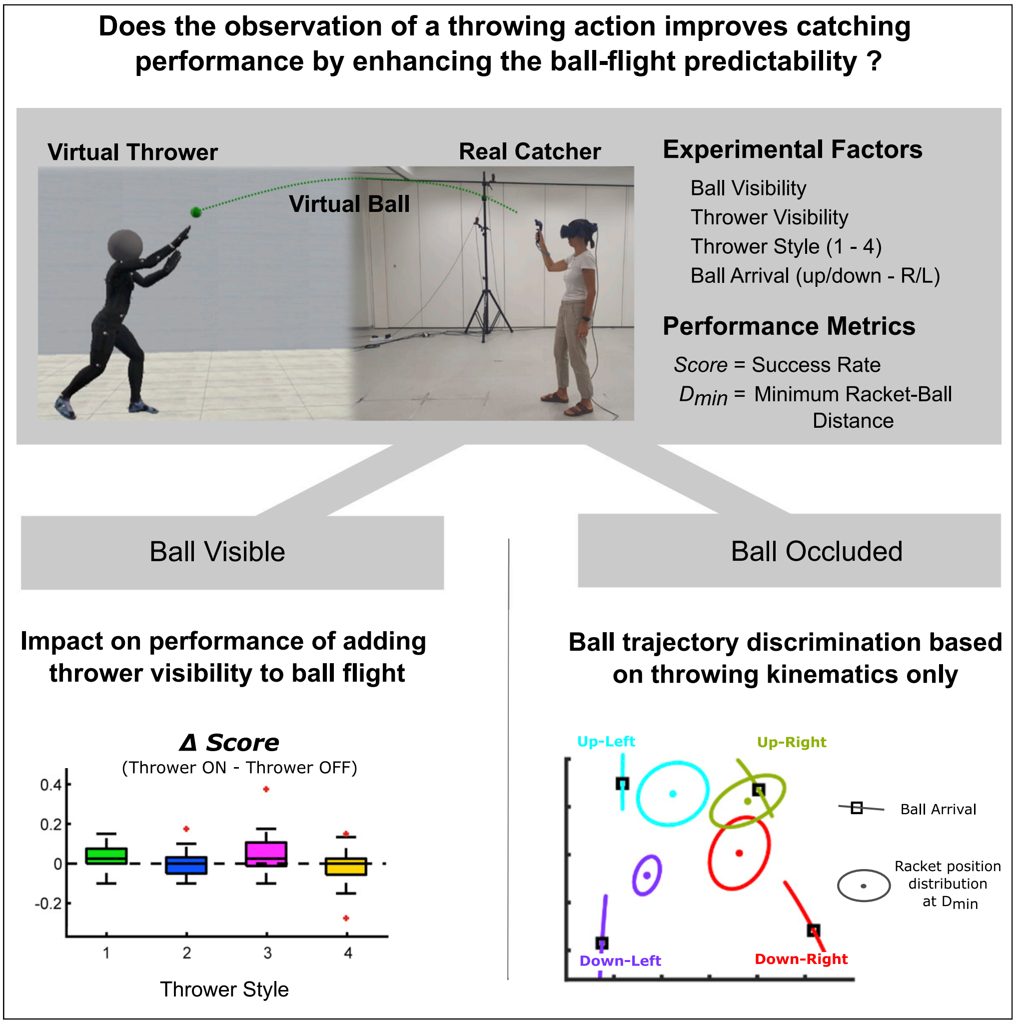

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Highlights

Predictive skills based on throwing observation were tested in a VR catching task

Visibility of the throwing action in addition to ball flight improves performance

Throwing kinematics alone allows catchers to correctly predict the ball direction

The impact of throwing kinematics on catching depends on the thrower's style

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Interception of virtual throws reveals predictive skills based on the visual processing of throwing kinematics

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SUMMARY

Predicting the outcome of observed actions is fundamental for efficient interpersonal interactions. This is evident in interceptive sports, where predicting the future ball trajectory could make apart success and fail. We quantitatively assessed the predictive abilities of non-trained adults intercepting thrown balls in immersive virtual reality. Participants performed better when they could see the complete throwing action in addition to the ball flight, and they were able to move toward the correct direction when the ball flight was occluded. In both cases, performance varies with the individual motor style of the thrower. These results prove that humans can effectively predict the unfolding of complex full-body actions, with no need to extensively practice them, and that such predictions are exploited online to optimize interactive motor performance. This suggests that humans hold a functional knowledge of how actions recurrent in the human motor repertoire map into the changes brought to the environment.

INTRODUCTION

Intercepting fast objects requires predictive abilities. Sensorimotor control of interception is affected by latencies intrinsic to the processing of sensory information and to the planning and execution of motor commands (Zago et al., 2009). Altogether, these latencies may sum up to several hundreds of milliseconds, a temporal window in which a fast object may travel distances of the order of a few meters. It is, therefore, clear that successful interception must rely on predictive processes that anticipate the future trajectory of the flying object.

Predictions of flying ball trajectories can be made based on information from the ball's flight itself. Evidence from previous studies suggested that the human brain integrates information from the ball trajectory with an internal model of the physical laws of motion under gravity to predict successful interception points (Russo et al., 2017; Zago et al., 2008). Alternatively, prospective models assume that in interceptive tasks the hand is continuously guided by the visual information from the moving object (Peper et al., 1994). Both cases hold that predictions are continuously updated during the projectile's flight (Brenner and Smeets, 2018).

In addition to the ball trajectory, the throwing action can provide information for predicting the ball trajectory (Maselli et al., 2017). The kinematics of intentional actions, namely the way our body segments move in space and time, provide information about the goal of the action ahead of its completion. This has been shown for simple actions, such as reaching for a bottle to pour water into a glass or to move it to another location (Ansuini et al., 2008). Importantly, such modulation in the kinematics of executed actions can be decoded by human observers who are able to anticipate appropriate responses (Ansuini et al., 2015; Cavallo et al., 2016; Soriano et al., 2018). Similar results have been found for more complex motor behaviors. The full-body kinematics of tennis serve (Huys et al., 2009) or of an overarm throw (Maselli et al., 2017) delivers information about the future direction of the hit or thrown ball. Elite sports players can use this information for enhancing their interceptive performance, but only in the context of the sports they have extensively trained (Abernethy, 1990; Aglioti et al., 2008; Mann et al., 2010). Most studies to date investigated how predictive skills based on the observation of complex actions depend on motor expertise. However, whether non-experts can readout information from complex but ecological relevant actions, like throwing, remains unclear. In the current study, we addressed this issue.

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Our aim was to assess whether untrained adults can extract information from observed overarm throwing actions to improve their interceptive performance. We considered overarm throwing because, besides being a complex full-body motor behavior well studied in sport science, it is part of the repertoire of universal human motor behaviors (Payne, 2017) observed across cultures and geographical regions (Lombardo and Deaner, 2018; Young, 2009). Still further, throwing as a fundamental motor behavior has been associated with the shaping of the biomechanical bodily structure, and with the development of cognitive skills throughout human evolution (Calvin, 1982; Roach et al., 2013; Roach and Richmond, 2015). It is, therefore, plausible that, along with the innate ability to perform overarm throws, humans have developed skills to decode information from observed throwing actions to enhance their performance in interpersonal interactions involving throwing and catching objects, also a pervasive behavior in humans.

In previous studies, we examined overarm motor behavior in untrained adults (Maselli et al., 2017, 2019) who were instructed to perform free overarm throws at different targets placed at six meters distance. By combining dimensionality reduction and machine learning techniques we could characterize the predictability of individual throwers by quantifying advanced (i.e. preceding ball release) information that would permit an observer to anticipate the outgoing direction of the projectile (Maselli et al., 2017). In particular, we extracted the spatiotemporal profile of advanced information in the kinematics of individual throwers, by computing the accuracy with which it is possible to distinguish throws directed to the right, rather than to the left when looking at specific body segments and at different temporal phases of the throwing action. Results revealed how the full-body kinematics of throwing actions encodes information about the outgoing ball direction well ahead of ball release (up to 600 ms in advance). Large interindividual differences were found across participants, with advanced information distributed dishomogeneously in time and throughout body segments in a way that varies across individuals. So, while some throwers deliver most of the relevant information from their stepping trajectories, for others trunk rotations may be more informative. The question then arises whether non-expert observers can extract information from a thrower with the same efficiency as data-driven classifiers and whether they are better tuned to extract information from specific patterns of movement which may be present in some throwers but not others.

The marked interindividual variability in the predictability of throwing action is in line with the heterogeneity that emerged from a complementary analysis of the full-body throwing kinematics aimed at characterizing and categorizing throwing actions across genders and individuals (Maselli et al., 2019). The motor pattern adopted in an unconstrained overarm throwing task was, indeed, found to be specific to individual throwers, to the extent that it is possible to recognize the identity and gender of a thrower from the pattern of joint trajectories characterizing a single throw. Despite this, there are similarities in the motor behavior observed across individuals. Four main classes of throwing strategies were identified across a pool of untrained throwers (n = 20), mainly differing in their stepping pattern and, to a lesser degree, in the trajectory of the throwing arm. The emergence of individual throwing strategies (or styles), above the overall background motor variability characterizing the unconstrained throwing task, finds resonance in the more general view that redundancy in complex motor tasks implies the existence of multiple solutions (Ganesh et al., 2010; Ganesh and Burdet, 2013; Maselli et al., 2019) and with the evidence that individuals tend to adhere to one of the possible solutions (Vidal and Lacquaniti, 2021). These results further motivate and generalize the question above, namely if non-expert throwers can equally extract information from different throwers or are better attuned to a specific class of throwing strategies.

Here we present an experiment designed to assess predictive skills based on the observation of throwing actions in untrained adults. In particular, we wondered whether advanced information, i.e., the information available ahead of ball release that provides hints about the outgoing ball trajectory, can be read out by non-expert observers and exploited in real-time to improve performance in interceptive tasks. In addition, we tested whether interceptive performance based on the observation of throwing actions depends on the throwing strategy of the individual throwing strategy adopted by the observed thrower. For this, we selected four non-expert throwers (with no specific training in throwing and catching sports) from our earlier study (Maselli et al., 2019), each representative of a different throwing style.

RESULTS

Participants, wearing an immersive virtual reality (VR) headset, were instructed to intercept a virtual ball under three different visibility conditions, using a virtual racket. In two conditions they could see a virtual character facing them and executing a throwing action (see Figure in STAR Methods and Videos S1-S4). In one

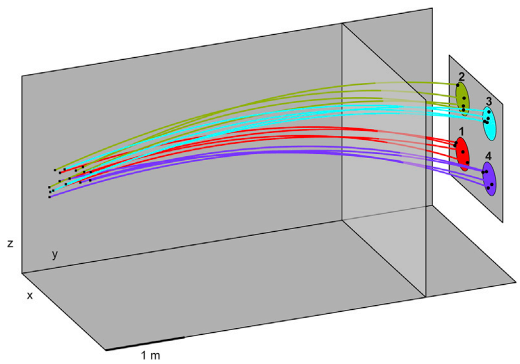

Figure 1. Ball trajectories

The trajectories selected for the four throwers are shown and colored according to the corresponding target. The four targets are circles of 20 cm radius arranged on a vertical plane placed at a distance of 6 m from the initial position of the thrower. The location of the vertical semitransparent gray plane corresponds to the mean y-coordinate of interceptions across trials and participants. The interception point of the different trajectories with this plane clearly shows how, for each target, differences in the impact point of throws from different throwers are not negligible.

case the flight of the ball released by the virtual character was visible (*AllVisible*), while in the other the ball was not rendered during its flight (*ThrowerOnly*). The third condition included only the ball flight, starting after an unpredictable interval in which the ball was shown still at a position corresponding to the location of ball release (*BallOnly*). Both the thrower's kinematics and the ball trajectories displayed in the virtual environment accurately reproduced the kinematics of real throws recorded in our previous studies (Maselli et al., 2017, 2019). We included successful throws directed to four different targets (arranged as in Figure 1) and executed by four throwers, representative of the four previously identified throwing strategies (Maselli et al., 2019). The four throwers were selected so to minimize differences in their predictability temporal profiles. For each of them, four throws, one for each target, were selected so as to minimize the variability in their flight time (see STAR Methods and Table 1 for more details). Altogether the experimental design included three factors: the throw visibility (*BallVisibility*), the hit target (*Target*), and the thrower identity (*Thrower*).

Comparing interception performance across conditions allowed to address the research questions in our agenda by testing the following hypotheses. First, we hypothesize that interceptive performance improves when the thrower kinematics is visible in addition to the ball trajectory, i.e., performance in *AllVisible* is better than in *BallOnly* (H1). In addition, we hypothesize that the interception kinematics observed in the *ThrowerOnly* condition allows us to disentangle the direction of the invisible ball (H2). If confirmed, both hypotheses would imply that non-expert participants are able to extract and use information from the observed throwing kinematics to prepare favorable conditions for successful interception and to effectively improve performance. We further hypothesize that, when the throwing action is visible, interceptive performance systematically varies with the throwing style of the opponent (H3). To test this, we inspected interceptive performance in the *ThrowerOnly* condition, for which performances are not dominated and saturated by information from the ball trajectory. Interception performance was assessed based on two variables: the *success rate* of interception (*Score*) and the *minimum distance* between the ball trajectory and the racket (D_{min}). The hypotheses under scrutiny were tested by contrasting *Score* and D_{min} across experimental conditions using, respectively, generalized linear mixed models (GLMM) and linear mixed models (LMM).

Differences in the ball trajectory alone affect performance

The use of ecological stimuli, namely using visual stimuli replicating the throwing kinematics and ball trajectories from real throws, poses the issue of a possible confound associated with unavoidable differences in the trajectories of the different throws. In fact, although the selection of the throws from different throwers and to different targets have been selected so to minimize the variance in the ball release velocity and in the spatial distribution of the ball trajectories (see Table 1 and STAR Methods for details), such differences in ball trajectories across conditions cannot be completely suppressed. The potential impact of such differences on performance should be then taken into account when comparing performances associated with individual throwers.

The trajectories selected for the different combinations of thrower and target are shown in Figure 1, where differences across conditions can be clearly appreciated. We thus tested whether these differences in the ball flight alone (so in the *BallOnly* condition) affected interceptive performances. Both performance variables, *Score* and D_{min}, exhibit a noticeable modulation by *Thrower* (Figure 2). The performance showed a similar level of modulation by *Target* (Figure 3). *Score* data were fitted with the GLMM model in Equation 1

Table 1. Ball flight time and impact speed by thrower

Thrower ID	Flight Time [s]	Impact Speed [m/s]
1	0.457 ± 0.010	9.178 ± 0.221
2	0.449 ± 0.006	8.290 ± 0.142
3	0.442 ± 0.006	8.979 ± 0.205
4	0.451 ± 0.013	8.638 ± 0.456

The table reports mean and standard deviations across throws to the four targets of ball flight time (from ball release to impact with the plane of average interception shown in Figure 1) and impact speed for the four throwers included in the experiment.

in STAR Methods (R^2 = 0.19), which revealed a significant main effect of *Target* ($p = 0.008$) and a significant interaction between *Target* and *Thrower* ($p < 10^{-10}$). Post-hoc analysis, based on the comparisons of the coefficients of the dummy variables and their interactions (values for the dummy variables were defined with respect to the reference condition Target 4 – Thrower 2, which has the highest mean *Score* value in the *BallOnly* condition) revealed that: i) *Score* for Target 2 were significantly lower with respect to *Score* for Target 4 ($p = 0.003$), and ii) *Target* by *Thrower* interactions were significant for all throwers and both Targets 2 and 3, with *Score* values in all the 6 conditions lower than in the reference condition ($p < 0.01$ for all comparisons).

The corresponding LMM model was fitted on D_{min} (R^2 = 0.25). In this case, the main effect of *Target* ($p = 0.009$) and the *Target* × *Thrower* interactions ($p < 10^{-10}$). Post-hoc analysis revealed that the *Target* by *Thrower* significant interaction is associated with D_{min} values being significantly larger than in the reference condition (Target 4 – Thrower 2) in the following conditions: Targets 2/3 – Thrower 1 ($p = 0.001$ and $p < 10^{-10}$, respectively), Targets 2/3 – Thrower 3 ($p < 10^{-10}$ and $p = 0.02$, respectively), Targets 1/3 – Thrower 4 ($p = 0.007$ and $p < 10^{-4}$, respectively).The detailed output from both the GLMM and LMM models discussed above can be found in the supplemental information.

The performances of individual participants (panels B and D of both Figures 2 and 3) clearly show how modulations of performance by both *Thrower* and *Target* are dominated by participants with the worst performance. It is interesting that among the worst performing participants a consistent pattern of performance modulation is observed, which indicates that some trajectories are easier to intercept. In particular, trajectories hitting the bottom targets (1 and 4) are easier to intercept than those hitting the top targets. Top left trajectories (to Target 3) are the most difficult, as to be expected given that all participants used right hand to intercept the ball.

The significant differences in performance reported here are attributed to differences in the ball trajectories alone, as the throwing action is occluded in the *BallOnly* condition. As this could be a possible source of confound when testing the impact of thrower visibility on interceptive performance, we considered performance differences between throws in the *AllVisible* and *BallOnly* conditions for each combination of target and thrower.

Thrower visibility improves interceptive performance

To test whether viewing the throwing action in addition to the ball trajectory improves interceptive performance (H1) we compared performance (both *Score* and D_{min}) in the *AllVisible* and *BallOnly* conditions, treating *Thrower* and *Target* as additional independent factors. To take into account the impact of different ball trajectories on performance, we considered the performance difference between the two *ThrowVisibility* conditions, i.e. $\Delta S = Score(AllVisibile) - Score(BallOnly)$ and $\Delta D_{min} = D_{min}(AllVisibile) - D_{min}(BallOnly)$. By doing so it is possible to appreciate the effect of thrower visibility on the performance in the same set of ball trajectories. Distributions of these differences across participants are shown in Figure 4 for the different *Throwers* and in Figure 5 for the different *Targets*.

Despite the large interindividual variability and the small absolute values of ΔS and ΔD_{min}, they both appear to be skewed, toward positive and negative values respectively. Both trends point to an overall improvement in the performance when viewing the throwing action in addition to the ball trajectory. This can be better appreciated for the participants performing the worst in the *BallOnly* condition, for

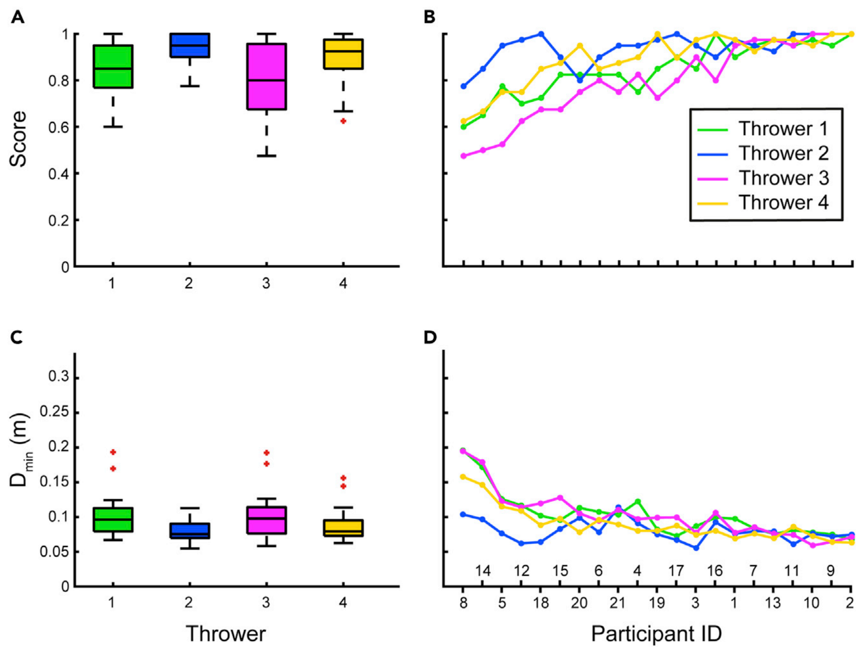

Figure 2. Performance in the BallOnly condition: the effect of Thrower

(A and C) The boxplots show the distributions across participants of *Score* and D_{min} for the four throwers included in the study.

(B and D) The *Score* and D_{min} values from individual participants are shown, with participants ordered along the x axis by decreasing levels of overall (across all targets and throwers) *Score* in the *BallOnly* condition.

which there was more space for improvement. In particular, the larger improvements were observed for participants 8 and 14, when intercepting throws from *Thrower* 1 and 3 directed to *Target* 3.

Statistical significance of the differences across visibility conditions was tested using the GLMM model in Equation 2 in STAR Methods for *Score* (R^2 = 0.14) and the corresponding LMM model for D_{min} (R^2 = 0.23). The model includes three main factors, *Target*, *Thrower*, and *Trial-Type*, and their interactions. The *Tiral-Type* factor was included to test the effect of thrower visibility by comparing the *AllVisible* versus *BallOnly* conditions.

For *Score,* we found a significant main effect of *Thrower* ($p < 0.001$) and significant effects for all the two-way interactions tested, i.e., between *Target* and *Thrower* ($p < 10^{-10}$), between *Target* and *Trial-Type* (p = 0.018), and between *Thrower* and *Trial-Type* (p = 0.032). In addition, a significant three-way interaction of *Trial-Type* with *Thrower* and *Target* ($p < 0.001$) was found. Post-hoc analysis revealed that *Score* values for Thrower 1 and 3 were significantly lower than for the reference Thrower 2 (p = 0.004 and p = 0.032, respectively), and that *Score* values for Target 1 are significantly lower than for reference Target 4. The effect of thrower visibility was instead significant only for a subset of conditions: *Score* values were higher in the *AllVisibile* conditions for throws to Target 2 (p = 0.01), in particular for Thrower 3 and 4 (p = 0.040 and 0.042, respectively), as well as for throws to Target 3 but only for Thrower 4 (p = 0.034). In addition, a number of significant two-way interactions between *Target* and *Thrower* were found (see the complete output of the model in the supplemental information).

Similar results were obtained for D_{min}, for which, in addition to the significant effects reported for *Score*, we found a significant effect of *Target* (p = 0.02). The effect of thrower visibility was significant only in its interaction with the *Target* and *Thrower* factors. The complete output from the model can be found in the supplemental information.

These outcomes support the observation drawn above in discussing Figures 4 and 5, and thus confirm hypothesis H1 showing how interceptive performance improves when viewing thrower kinematics in addition to ball trajectory, although the effect could be appreciated only for some combinations of *Thrower* and

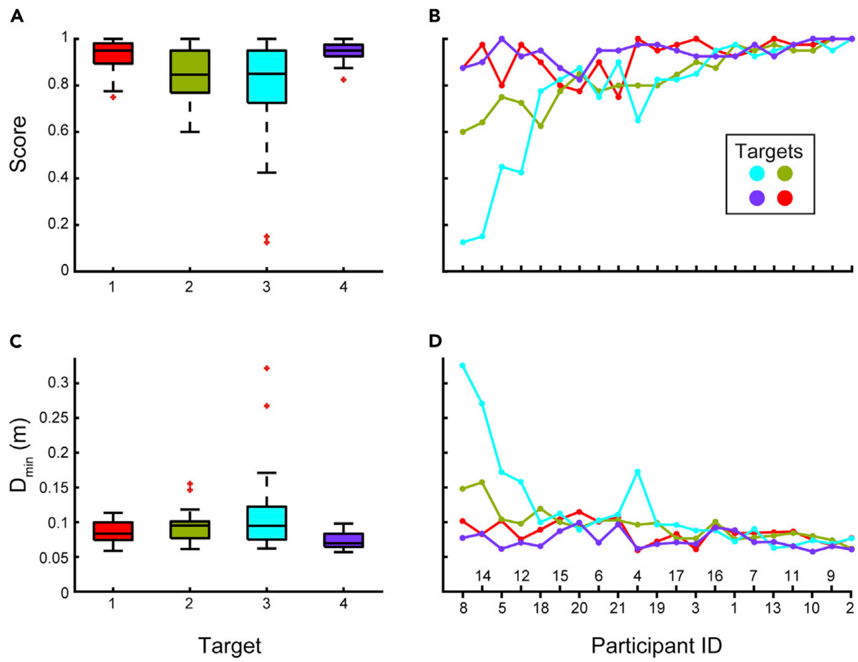

Figure 3. Performances in the BallOnly condition: the effect of Target

(A and C) The boxplots show the distributions across participants of *Score* and D_{min} for the four targets included in the study.

(B and D) The *Score* and D_{min} values from individual participants are shown, with participants ordered along the x axis by decreasing levels of overall (across all targets and throwers) *Score* in the *BallOnly* condition.

Targets, and in particular for ball trajectories that cannot be intercepted with optimal performance (*Score* > 0.8) in the *BallOnly* condition.

Improvement in performance associated with the vision of the throwing action may derive from the ability to extract advanced information about the future direction of the outgoing ball that can be used to prepare more effectively the interceptive movement, for example by directing the hand in the region of interest and/or taking a preparatory posture allowing for better hand control. To corroborate this interpretation we looked at interceptive performance in the *ThrowerOnly* condition to test whether participants could discriminate the direction of the invisible ball based on the throwing kinematics alone (H2).

Untrained adults can extract information about the outgoing ball direction based only on the throwing kinematics

Effective interception of the invisible ball trajectory with the racket surface is an extremely difficult task. For this, for each trial, we estimated *extended interception point*, defined as the location of the center of the virtual racket at the time of its minimum distance (D_{min}) from the ball's trajectory. We then inspected the difference in the distribution of the *extended interception points* across the four targets. The distributions of the extended interception points for throws to each of the four targets are represented in Figure 6. Here the distributions are shown as the 2D ellipses obtained by projecting the extended interception points onto the frontal (xz) plane, separately for the different throwers (columns) and for four representative participants (rows). The latter were chosen among all participants as the ones performing better and worse in the Right-vs-Left (P19 and P7, respectively) and Up-vs-Down discrimination (P6 and P2, respectively), as revealed by the linear discriminant analysis (LDA) presented below. For participant 6 the ellipses associated with different targets tend to occupy different regions of the space, with a spatial arrangement that corresponds to the target positions both in elevation and laterally, indicating a capacity to correctly discriminate the direction of the occluded balls based on information extracted exclusively from the throwing kinematics. Participant 19 instead is characterized by a clear separation of the ellipses by side but not in elevation, therefore by the ability to discriminate the lateral direction of the occluded balls, but not their

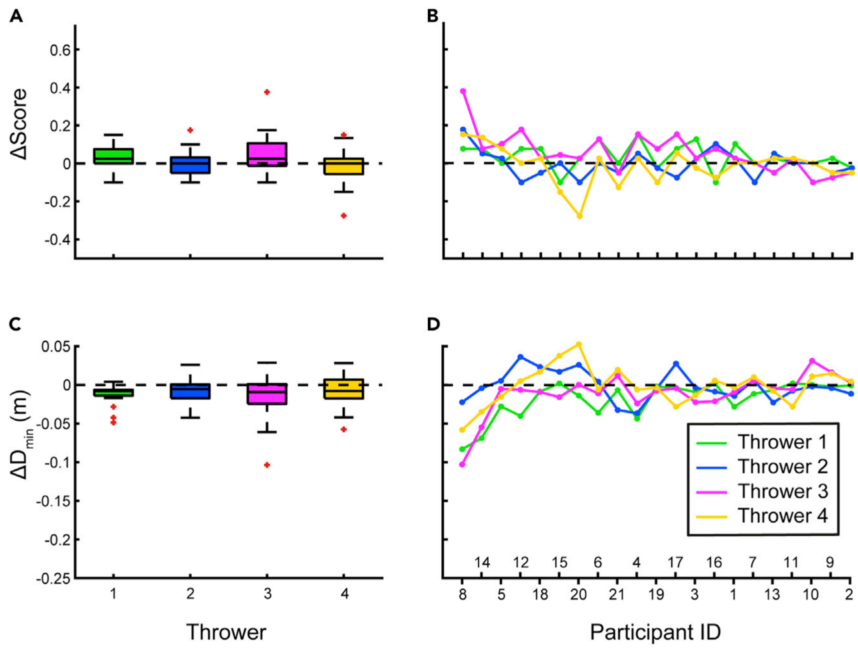

Figure 4. Difference in performance between AllVisible and BallOnly conditions: the effect of Thrower

(A and C) The boxplots show the distributions across participants of ΔS and ΔD_{min} (differences across visibility conditions) for the four throwers included in the study.

(B and D) The corresponding values from individual participants are shown, with participants ordered along the x axis by decreasing levels of overall (across all targets and throwers) *Score* in the *BallOnly* condition.

elevation. A similar trend, but with a lower degree of ellipses separation is observed for participant 2. The discrimination ability drops drastically for participant 7, characterized by larger ellipses (indicating a larger variability in the extended interception points' distributions) and a higher degree of overlap among them. For most participants (Figure S1), the separation between targets at different sides (Right-vs-Left) appears to be larger than for targets at different elevations (Up-vs-Down), suggesting overall better predictability of the ball directly on the horizontal (mediolateral) direction, rather than on the vertical direction. Interestingly, differences in the ellipses' geometry and spatial arrangement can be clearly noticed when comparing different throwers.

As a quantitative assessment, we used a linear discriminant analysis (LDA) to test whether the interception kinematics can effectively discriminate the ball direction. Horizonal and vertical discrimination were tested separately by considering two 2-class problems: Right-vs-Left and Up-vs-Down. For each participant (catcher), the analysis was conducted on the four subsets of trials associated with the different throwers. The LDA model was trained with the positions of the extended interception points, each labeled according to the belonging class (Right/Left, Up/Down) of the corresponding throw. Results are shown in Figure 7A, in terms of misclassification errors (MEs) estimated with the one-leave-out method (see STAR Methods for more details). Figure 7B shows the summary boxplots corresponding to the MEs distributions across all participants for the different throwers. In the horizontal classification problems, the ME values for all possible combinations of catcher and thrower are well below the chance level (50 per cent for the 2-class discrimination problems), with an average value of 11.43 and a standard deviation of 7.58. The misclassification errors for the vertical discrimination problem are larger, with an average value of 32.92 and a standard deviation of 12.42. Indeed, for this problem not all combinations of catchers and throwers have misclassification rates below the chance level, implying that some participants were not able to correctly infer the vertical arrival position of the outgoing ball for one or more throwers.

We next tested whether the extraction of information of the outgoing ball trajectory from the throwing kinematics depended on the thrower. For this, we fit *Score* and D_{min}, in the *ThrowerOnly* condition, with GLMM and LMM, respectively, adopting the models in Equation 1 of STAR Methods. For both, we found a significant main effect of *Target* and *Thrower*, and a significant interaction between the two; all p-values

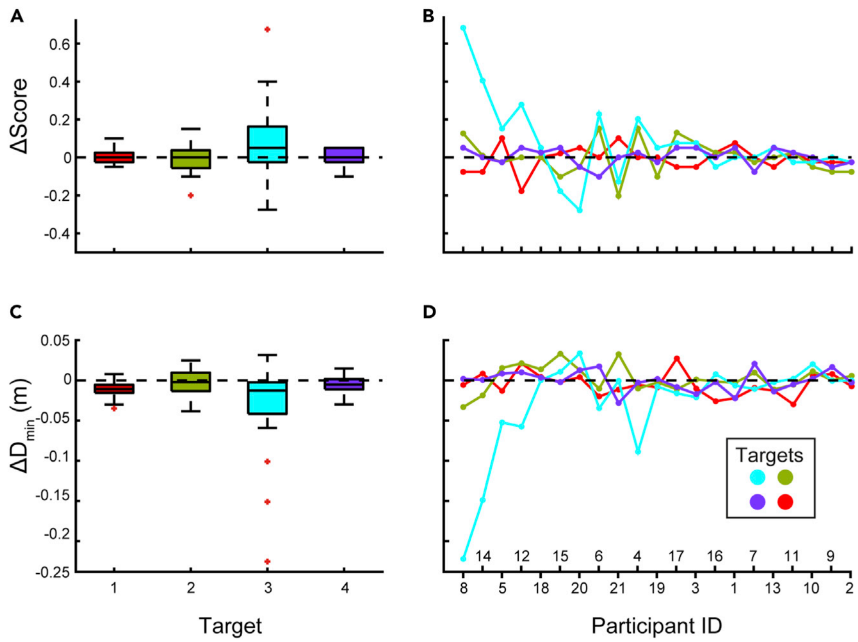

Figure 5. Difference in performance between AllVisible and BallOnly conditions: the effect of Target

(A and C) The boxplots show the distributions across participants of ΔS and ΔD_{min} (differences across visibility conditions) for the four targets included in the study.

(B and D) The corresponding values from individual participants are show, with participants ordered along the x axis by decreasing levels of overall (across all targets and throwers) *Score* in the *BallOnly* condition.

are below 10^{-6}, but for the main effect of *Thrower* on *Score*, which is 0.016. The detailed output of both models can be found in the supplemental information.

In sum, these results indicate i) that untrained individuals are able to extract information about the future ball direction on the basis of the throwing kinematics alone, thus confirming our hypothesis H2, and ii) that the ability to extract information is significantly modulated by the thrower kinematics strategy, thus confirming H3.

DISCUSSION

The current study shows that human adults, not specifically trained in throwing sports, are able to extract information from the observed kinematics of a throwing action and to use online this information to enhance their interceptive performance. Participants who had to intercept a thrown ball in an immersive virtual reality setup, performed better when they could see the complete throwing action in addition to the ball flight. Moreover, when the ball was occluded during its flight, participants were able to correctly direct the interceptive action using the information provided by the throwing action alone. In addition, our results highlight how the reported predictive skills based on the observation of naturalistic throwing actions are modulated by the thrower, as the throwing pattern adopted by some throwers could be read out better than the pattern adopted by others. Crucially, these effects are most evident for participants having poor interceptive skills, and in general, for those conditions in which the baseline performance (i.e. performance in trials with only the ball flight visible) was poor, leaving room for improvements associated with the visibility of the throwing action.

These results extend our current knowledge on the nature of predictive skills for action, and in particular for interceptive behavior. Studies focusing on interceptive performance have demonstrated how humans make use of internal predictions about projectiles trajectories to successfully intercept flying objects, plausibly based on an internal model of how objects move under the effect of gravity (Dayan et al., 2007; Russo et al., 2017; Zago et al., 2008). Our results show that untrained adults are able to correctly predict the direction of projected objects also based on the kinematics of the throwing action. Notably, this implies a more complex ability for predictions with respect to the processing of a ball flight. Previous

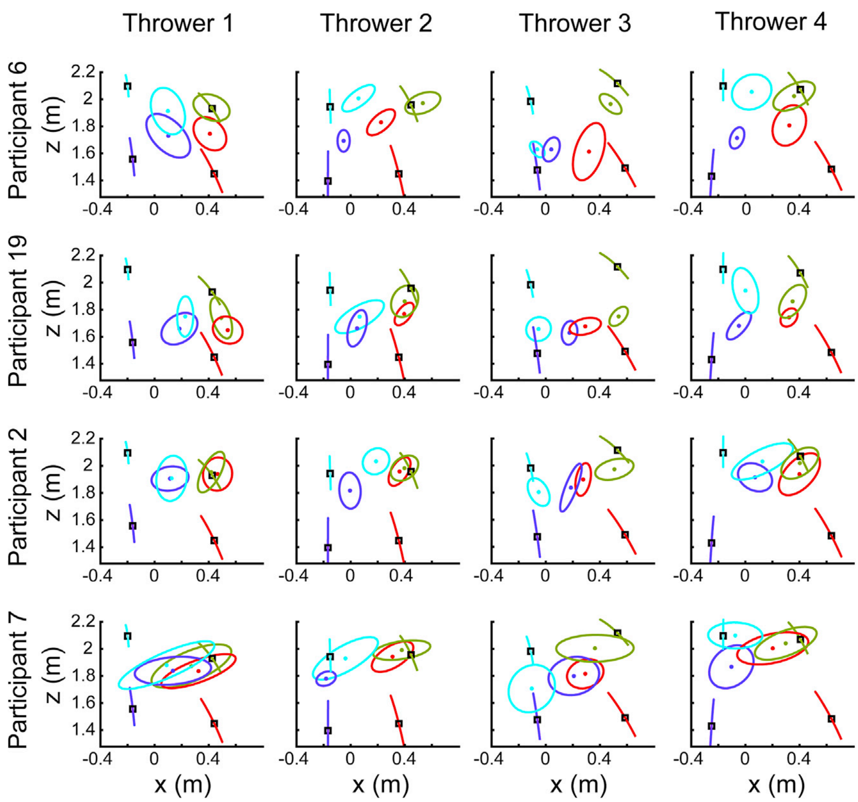

Figure 6. Distributions of extended interception points

The four ellipses in each panel represent the distribution of the projection of the extended intercepting points onto the frontal (xz) plane for throws directed to the different targets, coded by color. The center of each ellipse corresponds to mean (averaging extended interception positions across the corresponding subset of trials), whereas the principal semi-axes correspond to one standard deviation of the distributions along the two directions of higher variability. Panels in the four rows represent performance from four representative participants selected based on the best (P6 and P19) and worst (P2 and P7) anticipation skills in the Up-vs-Down and Right-vs-Left discrimination as from LDA results. Panels along the four columns correspond to participants performance in the subset of throws from individual throwers. See also Figures S1–S3 for all showing the same for all participants.

studies have demonstrated the ability of elite sports athletes to correctly infer the future direction of a thrown ball based on the observed throwing movement of an opponent, but this ability has been so far considered a skill learned throughout extensive and sport-specific training. So, anticipatory skills based on action observations have been shown to be higher for elite athletes than for non-experts (Abernethy, 1990; Farrow et al., 2005; Müller and Abernethy, 2012), but only if they were specifically trained in the observed throwing or kicking technique (Aglioti et al., 2008; Mann et al., 2010). Although these results demonstrated that specific training enhances predictive skills, our results provide direct evidence that humans have the ability to extract and use online advanced information from observed throwing actions for the successful interception of projected objects even without training. It may be possible that such predictive ability evolved together with throwing (Calvin, 1982; Lombardo and Deaner, 2018; Roach et al., 2013; Young, 2009) and catching skills, although this is a speculation that needs to be further explored in dedicated studies.

Results from the current study are also interesting in the context of social neuroscience. Humans are known to extensively rely on predictions based on the observation of biological motion for inferring other intentions and anticipating the future unfolding of observed actions (Ambrosini et al., 2015; Ansuini et al., 2015; Cavallo et al., 2016). These predictive mechanisms are thought to be key to guaranteeing a smooth and effective interpersonal interaction based on non-verbal communication (Flanagan and Johansson, 2003; Giese and Rizzolatti, 2015; Pezzulo et al., 2019). Still, established experimental evidence for these overall conclusions are largely based on the examination of simple actions, such as reaching for an object to grasp

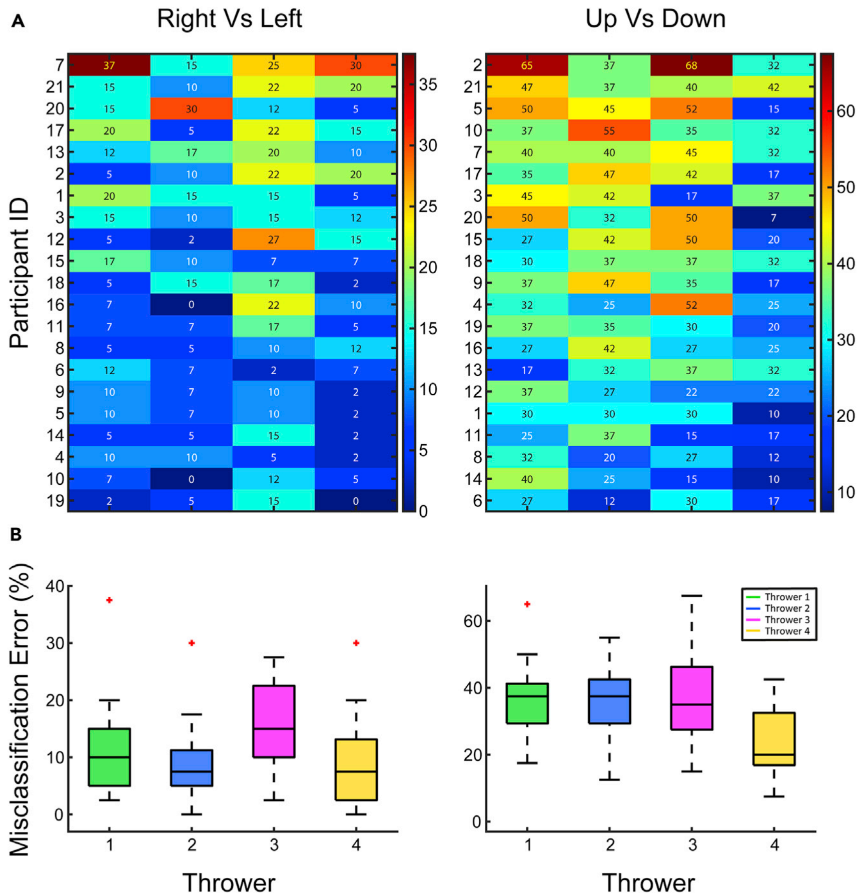

Figure 7. Results from the linear discriminant analysis (LDA) applied to the problem of ball side and elevation discrimination in the ThrowerOnly condition trials

(A) Heat map show the resulting misclassification errors from LDA applied to the Right-vs-Left (left panel) and Up-vs-Down (right panel) problems, for all participants (rows) and for the different throwers (columns); participants are ordered from top to bottom in decreasing order of average misclassification errors across throwers.

(B) Boxplots provide the summary statistics (across participants) of the misclassification errors from LDA applied to the Right-vs-Left (left panel) and Up-vs-Down (right panel) problems, associated with the four throwers.

and/or move it (Ansuini et al., 2008; Donnarumma et al., 2017; Flanagan and Johansson, 2003; Urgesi et al., 2010). Here we showed that similar mechanisms are at play in complex forms of interpersonal interactions, demonstrating that humans are able to predict the unfolding of complex full-body actions involving the manipulation of external objects, and that they are furthermore able to use online these predictions to optimize the interaction. So, our results extend previous research on interpersonal communication by including quantitative assessments of the critical role played by predictive mechanisms associated with action observation in complex and full-body motor behavior.

Importantly, the experimental evidence from the current study are grounded in a scrupulous experimental design, in which the visual stimuli—namely the throwing actions shown to participants in the interceptive task—have been selected based on a previous analysis in which the information content about the outgoing direction of the projected ball has been fully characterized (Maselli et al., 2017). That study showed large interindividual variability in throwing predictability, so that individual throwers differ not only in how early (before ball release) they become predictable but also in the set and sequence of body segments that deliver the most relevant information. Having quantified and characterized the information about the outgoing ball direction encoded in the selected throws, we could then assess the extent to which such information could be decoded by a human observer and make grounded comparisons across different throwers' conditions.

In particular, the current study addressed the issue of how differences in the predictability profile of throwers adopting different motor strategies impact on prediction skills and on the ensuing interceptive performance. Results show that interceptive performance varies with the opponent thrower: despite the large interindividual differences, a consistent trend was found across participants for individual throwers being less predictable (e.g., Thrower 3 for side discrimination) or more predictable (e.g., Thrower 4 for elevation discrimination) than others. Although the four throwers were selected so as to have comparable temporal profiles of their predictability, differences in their motor strategies and therefore in the kinematics cues (body segments) that convey the relevant information could explain the different degrees of information readout from individual throwers. This suggests that not all information encoded in the kinematics of action is equally easy to decode, and thus that the human brain may be better tuned to specific bodily cues when decoding observed actions for predicting their incoming unfolding. On the other hand, it is interesting to notice that interceptive performances revealed better discrimination of the side rather than the elevation of the outgoing ball trajectory, which reflects the corresponding differences found in the related information encoding (Maselli et al., 2017).

Noticeably, the grounded comparison of different ecologically valid experimental conditions (in this case different throwing styles) has been granted by the introduction of a novel methodology to quantitatively characterize complex motor behavior (Maselli et al., 2019) and kinematics-driven predictability with a small set of parameters. These quantitative approaches allow for further sophisticated analysis. For example, one could look at the relation of interceptive performance with the detailed spatiotemporal structure of each thrower's predictability, so as to point out which are the kinematics cues (e.g., specific body segments) that are easier to decode. One could also wonder whether there is an individual tuning to specific bodily cues and whether this tuning reflects the individual motor expertise and styles (Vidal and Lacquaniti, 2021), as mirror neurons theories would suggest (Calvo-Merino et al., 2010; Casile and Giese, 2006; Giese and Rizzolatti, 2015). In this case, a match in the throwing styles of catcher and thrower would facilitate the decoding of the observed throwing action. Although these questions go beyond the aim of the current study, we plan to address them in future studies.

In sum, the results of the present study highlight the ability of humans to formulate detailed predictions about the unfolding of complex full-body actions and to use online these predictions to optimize interactions. Differently from what was suggested by previous studies, our results show that such predictive skills do not require extensive exposure to, or motor training in, the observed action. This suggests that, at least to some extent, predictive skills based on action observation may be rooted in an intrinsic internal knowledge of how common actions in the human-motor repertoire maps into changes in the physical state of the surrounding environment. The combination of ecologically valid stimuli, immersive technologies, and new methods for describing and categorizing complex actions that allowed to achieve these results, may pave the way for a research agenda that aims at exploring in more detail the sensorimotor mechanisms underlying the role of prediction skills in real-life multi-agents interactions.

Limitations of the study

The current study has some intrinsic limitations associated with the use of immersive virtual reality (IVR). In fact, IVR exposure may affect motor behavior in a way that is still not straightforward to predict (Thomas et al., 2016; Zhang and Sternad, 2021). However, IVR grants the otherwise impossible chance of adopting complex but perfectly reproducible visual stimuli, in our case reproducing with high fidelity the full-body kinematics of throwing actions from real throwers. In this respect, we believe that IVR provides a precious experimental tool for state-of-art research on non-verbal interpersonal interaction, affording a valid compromise between systematic experimental designs and the use of complex ecologically valid stimuli.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2022.105212.

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AUTHOR CONTRIBUTIONS

A.M. and A.dA. conceived and designed the experiment. A.M. implemented the Unity project and the experimental setup. A.M. and P.DP. conducted the experiments. P.DP. and A.M. analyzed the data. All authors discussed and interpreted the results. A.M. wrote the article and all authors provided inputs to its final version.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Pseudo-anonymized source data from human subjects	This paper	https://doi.org/10.5281/zenodo.7050093
Software and algorithms		
Unity Version 2018.2.21	Unity Technologies	https://unity.com/
Matlab 2019	MathWorks	https://www.mathworks.com/
HTC Vive Pro	HTC Corporation	https://www.vive.com/

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Antonella Maselli (antonella.maselli@istc.cnr.it).

Materials availability

Videos of the visual stimuli are given in the supplemental information file.

Data and code availability

- Pseudo-anonymized source data (hand and ball kinematics) has been deposited at https://doi.org/10.5281/zenodo.7050093 and are publicly available as of the date of publication.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Participants performed a task in immersive virtual reality (IVR), in which they had to intercept a virtual ball thrown by a virtual character. Before this, participants were asked to perform a real throwing session, replicating the task and the experimental procedure adopted in our previous studies (Maselli et al., 2017, 2019). This part of the data collection served for a complementary study in which we aimed at exploring how interceptive performance are affected by the relation between the throwing styles of the catcher and the thrower.

The experiment consisted in a 3 × 4 × 4 within-subjects design, the three factors being the *ThrowVisibility*, *Thrower* and *Target*. All factors modulate the visual stimuli to which participants were exposed in the virtual catching task. The *ThrowVisibility* factor had three levels: *BallOnly*, in which only the ball trajectory was displayed; *ThrowerOnly*, in which the throwing kinematics was displayed but the ball disappeared at the ball-release time; and *AllVisible*, in which both the throwing kinematics and the full ball trajectory was available to participants. The *Thrower* factor had four levels in which the throwing kinematics was modulated: each level corresponded to one of the four throwing styles identified and described in our previous work (Maselli et al., 2019). For each thrower, we further considered throws to four different targets arranged with respect to the thrower as in (Maselli et al., 2017).

The virtual catching session included 10 repetitions for each condition, summing up to a total of 480 trials presented to participants in a pseudorandom order: trials were grouped in 10 blocks of 48 trials (one for each condition), and trials within each group were arranged in a random order.

Twenty-two participants (11 female; age: 26.5 ± 4.9 years, mean ± std) took part to the experiment. They were all right handed according to the laterality score given by the Edinburgh questionnaires (L: 0.86 ± 0.14). They were informed that they could leave the experiment and/or could ask for breaks at any time.

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All but one participant (who only performed the throwing session for technical problems) completed the whole experiment. A second participant, despite completing the experiment was excluded from the analysis because they failed in following properly the task instructions.

METHOD DETAILS

Throwing stimuli selection

The virtual throws stimuli, including both the throwing kinematics and the ball trajectories, faithfully reproduced the real throwing kinematics recorded from real subjects (Maselli et al., 2017, 2019). First, we selected four throwers among the twenty subjects available, each representative of a throwing style. The four throwers were selected so to match as close as possible the temporal profile of their characteristic "throwing predictability", as computed and reported in (Maselli et al., 2017). To this aim, we minimized the variance of the time intervals before ball release at which the thrower becomes predictable in the groups of four throwers each representative of a specific throwing style. According to this criterium, the selected subjects were P4, P5, P6 and P13 from (Maselli et al., 2017) (here renamed in order as Thrower 1, Thrower 2, Thrower 3, Thrower 4), representative respectively of the *No-Step*, *Left-Step*, *Right-Step* and *Double-Step* throwing styles identified in (Maselli et al., 2019). The throwing kinematics and corresponding predictability profiles are shown in Figures 3 and 7 of (Maselli et al., 2017), while the animated kinematics as displayed through the HMD can be seen in the Videos S1–S4 (showing the throws to Target 1 for all throwers). For each thrower we next selected four throws, one for each target. The throws selected were those that, among the successful trials (i.e. throws hitting the intended target of 20 cm radius), minimized (i) the reciprocal distance of the impact locations on the target board, and (ii) the variance of the flight time across the four throwers. Following these criteria the mean and standard deviation of the flight time across participants, averaged across target, was 0.595 ± 0.02 s, while the mean distance of the same-target arrival locations was 0.17 cm. The kinematics recoded in the selected trials was used to create the virtual throwing stimuli (more details in the "Virtual Scene" subsection). As a sanity check, we computed the differences in flight times and speed at impact of the virtual balls thrown by the different throwers to the four targets in the Unity scenario. Flight time was estimated as the time interval between ball release and the virtual impact of the ball with the plane of average interception (i.e., the vertical xz plane placed at the mean y-coordinate of interceptions across trials and participants shown in Figure 1). Impact speed was estimated as the ball tangential velocity at the time of intersection with the same plane. Mean and standard deviation across throwers and targets were 0.450 ± 0.01 s for the flight time, and 8.771 ± 0.431 m/s for the ball speed. The corresponding values for each single thrower are given in Table 1. The reported differences across throwers have been taken into account when assessing the impact of the individual throwing strategy on interceptive performance by looking at the difference in performances between *AllVisible* and *BallOnly* conditions.

Experimental setup

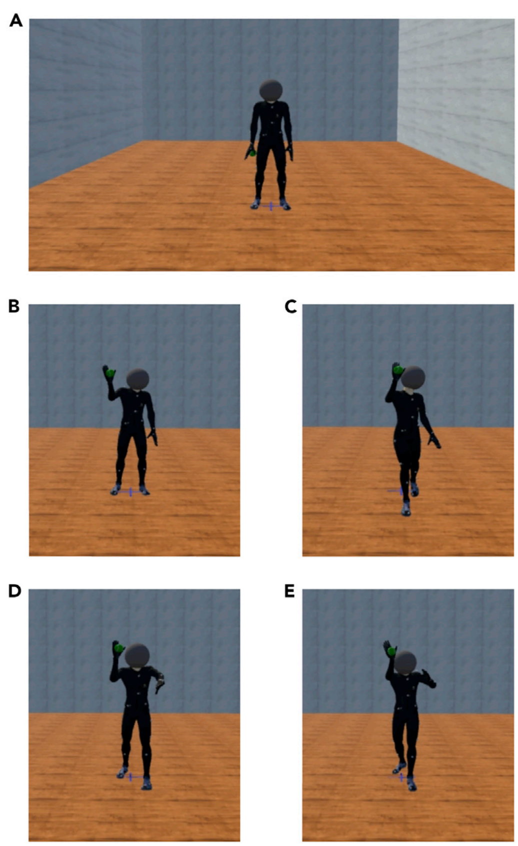
The experimental setup included a Vive system for IVR and the motion capture optical system OptiTrack for the recordings of full-body kinematics.

The Vive system (HTC Europe Co. Ltd, Slough, Berkshire, U.K), includes two base stations emitting infrared pulses which create a "room scale" tracking area where the headset and the controllers can be tracked with sub-millimeter precision. The headset streams the interactive virtual scenario designed for the virtual catching task, at a refresh rate of 90Hz and a 110° field of view, with a display resolution of 1080×1200 pixels per eye. For the experiment we further used one Vive controller, which participants held in their right hand and used to control a virtual racket for intercepting the virtual ball. The controller was also used to track the hand kinematics during the interceptive task. The Vive system was integrated via SteamVR with the Unity Engine running on a personal computer.

The OptiTrack (NaturalPoint, Inc., Oregon, USA) optoelectronic motion capture system, including its data acquisition and processing software Motive Body, was used to track the full-body kinematics during both the real throwing task and the virtual catching task. Participants were instrumented with 57 retroreflective markers that allowed to track the whole body. The experimental setup for the throwing task replicated exactly the one described in (Maselli et al., 2017).

Virtual scenario

The virtual scene has been implemented on the Unity platform. It included an empty room of 8 × 15 m^2 floor size and 5 m height, a 9 cm diameter ball, four virtual characters, and a racket. The latter was generated by attaching a white disk (20 cm diameter, 3 cm thickness) to a virtual replica of the hand-held controller. The four virtual characters were created by resizing the skeleton's body segments of a standard virtual character, so to match the bodily proportion and the high of the real participants selected as throwers. This assured that when loading the kinematics of a specific throw onto the corresponding virtual character as an animation (which is controlled by the joint angles kinematics) the spatial trajectories of the single joints accurately matched the one recorded in the motion capture session. The characters head was occluded by an opaque sphere, in order to remove possible implicit cues about the intended target present in the head movement of the thrower (see Figure). For each throw the ball was animated according to the trajectory of the real ball, also tracked by the motion capture system. Each trial was associated with a single trial and therefore a single thrower. The participant started the throwing stimuli by pressing a button on the hand-held controller while being in a fixed initial position and holding a neutral A-pose, with the feet slightly spread and the arm along the sides of the body. According to the experimental condition, each trial either began either with the thrower appearing in the initial A-pose as in Figure A, facing the participants (*AllVisible*, *ThrowerOnly*), or with the ball appearing at the location corresponding to the throwing release point of the specific trial (*BallOnly*). The animation of the throwing action or the ball flight was started after an average interval of 1 s with a uniformly distributed random jitter of 0.5 s, included to make the start unpredictable. In the *AllVisible* condition both the throwing action and the complete ball flight were shown, while in the *BallOnly* and the *ThrowerOnly* condition only the ball trajectory and the avatar throwing action respectively were displayed.



Virtual scene: throwing stimuli

(A) The figure shows virtual thrower initial A-pose.

(B–E) Snapshots of the different throwers at the moment of ball release (B: Thrower 1; C: Thrower 2; D: Thrower 3; E: Thrower 4). The corresponding animations of the complete throwing action can be seen in the supplemental videos.

The controller position and orientation were tracked by the HTC Vive system. If the actual ball trajectory was successfully intercepted, a haptic feedback of the event was rendered as a vibration of the controller.

Procedure

Participants were instructed about the experimental procedure and signed a consent form before taking part to the experiment. They then filled the Edinburgh handedness questionnaire for assessing hand preference (Oldfield, 1971), a brief questionnaire about their experience with sport activity, and their previous exposure to immersive virtual reality. Participants were then instrumented with the retroreflective markers for full-body kinematics recording. This preparation phase took on average 20 min.

The experiment started with a brief familiarization with the throwing task followed by the experimental throwing session consisting in 80 throws, 20 for each of four targets arranged on a vertical plane at a distance of 6 m, see (Maselli et al., 2017) for more details. After the throwing session, participants took a break of about five to 10 min, after which the virtual interception session started. After being fit the head-mounted display (HMD) and provided with the Vive controller, participants performed few trials for getting familiar with task in the three visibility conditions. The experimental session started next and consisted of 480 trials in which the 48 conditions were presented pseudo-randomly, in 10 consecutive blocks each including all 48 conditions. Participants took one to two breaks in which they could remove the HMD and rest. All together the experiment including both the throwing and virtual interception tasks, plus breaks, lasted on average 90 min.

In both throwing and interceptive sessions we recorded full-body kinematics. In addition, in the virtual session we recorded the kinematics of the controller held by the intercepting hand (always the right hand) and of the head with the Vive system. In the current study we focus our analysis on the kinematics of the intercepting hand from the controller. The full-body kinematics of the throwing and interceptive actions will be analyzed in future studies.

The experimental design and protocol were approved by the Ethical Review Board of the Santa Lucia Foundation (Prot. CE/PROG.542).

QUANTIFICATION AND STATISTICAL ANALYSIS

Data collection and pre-processing

For each trial, the kinematics of the hand-held controller and the position of the virtual racket were recorded from the start of the trial to the time at which the ball impacted the racket or exceeded 5.5 m along antero-posterior axis (y axis) in the VR environment (moving so behind the participant). For each trial, we analyzed the kinematics of the virtual racket position, which is automatically extracted from Unity as a fixed roto-translation of the tracked controller, and sampled at 90 Hz. Positional data were filtered with a digital low pass-filter (a 5th order Butterworth filter with 10 Hz cutoff frequency). Each trial was labeled as successful, or failed, according to whether there was, or was not, a collision between the ball and the virtual racket. *Scores* values for each combination of participant and experimental condition were computed as the fraction of successful trials. In addition, D_{min} was estimated as the distance at which the position difference between the racket and ball was minimal. For each trial, we also extracted the extended interception point as the position of the virtual racket center at the time of minimum distance between the ball and the racket. Data were processed in MATLAB.

Statistical analysis

The dependence of the *Score* and the D_{min} on the experimental factors was tested with generalized linear mixed models (GLMM) and linear mixed models (LMM) that account for interindividual variability by including the participant as a random effect. Different mixed models were adopted according to the metric under scrutiny. The experimental factors, i.e. *BallVisibility* (*BV*), the hit target (*Ta*), and the thrower identity (*Th*)) were treated as fixed effect factors with categorical (dummy) variables. Data from the *BallOnly* and *ThrowerOnly* conditions were fitted with the model described in Equation 1. Instead, when comparting the impact of the thrower visibility by contrasting the *AllVisible* and *BallOnly* conditions data were fitted with the model in Equation 2.

$$Y = g\,(u_0 + \alpha_0 Ta + \beta_0 Th + \lambda_0 TaTh + \epsilon) \quad \text{(Equation 1)}$$

$$Y = g\,(u_0 + \alpha_0 Ta + \beta_0 Th + \gamma_0 BV + \lambda_0 Ta\ Th + \zeta_0 Ta\ BV + \Delta_0 Th\ BV + \delta_0 Ta\ Th\ BV + \epsilon) \quad \text{(Equation 2)}$$

In Equations 1 and 2, u_0 represents the individual intercept and accounts for interindividual differences. The coefficients α_0, β_0, γ_0, λ_0, ζ_0, Δ_0 and δ_0 represent fixed-effects, thus the modulation of the response variable by the main factors *Ta, Th,* and *BV,* and their interactions.

In both equations, *g* represents the link function. As *Score* data have a binomial distribution (as it could take only two possible outcomes: Y = 1 for hits, and Y = 0 for missed balls), they were fitted with a GLMM using a logit link function (MATLAB function *fitglme*). For D_{min}, which represents a continuous variable, data were instead fit with an LMM (thus with *g* representing the identity functions, MATLAB function *fitlme*). In all cases the estimation of model parameters were based on the maximum likelihood using Laplace approximation.

Dummy variables for *Th* and *Ta* fixed effect were defined with respect to the corresponding conditions with the highest mean *Score* in the *BallOnly* visibility condition. Post-hoc comparisons could be then performed by assessing the p-values of the regression coefficients for the dummy variables and their interactions.

In order to test the hypothesis that participants were able to make reliable predictions about the direction of the outgoing ball based on information from the throwing kinematics alone, we run a linear discriminant analysis (LDA) on the points of extended interception for the *ThrowerOnly* condition (MATLAB function *fitcdiscr*). LDA is a standard supervised classification technique that may be used to quantify the degree of separation of observations in different groups (or classes). The method consists in finding discriminant functions that divide the space in which observations are defined in a number of predefined regions, by maximizing the ratio of the between-groups to the within-group variabilities in the training set (Mardia et al., 1979). By applying LDA to the distribution of extended interception points for throws directed to different targets it is possible then to quantify the ability of the catcher to discriminate the direction of the invisible ball. We specifically tested the ability to discriminate the lateral direction (Right-vs-Left) and the vertical direction (Up-vs-Down), with different 2-classes LDA tests. LDA performance for both classification problems have been run separately for all combinations of participants and throwers. The data given in input to train the model were the 3D positions of the extended interception points labeled according to the class of belonging of the associated throw (Up/Down, Right/Left). Results are reported in terms of misclassification errors (MEs) computed with the leave-one-out cross-validation procedure. The latter consists in performing the classification assignment of each single observation (the one left out) based on the training set defined by the rest of the observations, repeating the same procedure for all observations in the dataset, and defining ME as the percentage of misclassified observations.