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Research Article

Spatial biases in motion extrapolation for manual interception

Sinéad A. Reid & Joost C. Dessing
School of Psychology
Queen’s University Belfast

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Correspondence concerning this article should be addressed to Joost C. Dessing, David Keir Building, 18-30 Malone Road, BT9 5BN Belfast, Northern Ireland. Contact: j.dessing@qub.ac.uk, Tel: 0044-28-90975650.

Abstract

The exact mechanisms by which humans control the manual interception of moving targets are currently unknown. Here, we explored the behaviours associated with the spatial control for manual interception. The examined task required controlling a cursor to intercept moving targets on a touch screen. We explored the effects of target motion direction, curvature and occlusion on manual interception. We observed occlusion-dependent spatial errors and arrival times for curved and diagonal trajectories (larger errors and earlier arrival of the finger at its final position with longer occlusion. These effects were particularly apparent for targets moving away from screen centre at interception due to curve. In a follow-up experiment we showed that the outward curve effects on spatial errors were absent because the associated trajectories appears to move towards positions that participants could expect the target to never reach. Our analyses also revealed occlusion-dependent spatial errors for diagonal trajectories, which is well-known angle-of-approach effect. Follow-up experiments demonstrated that this effect was not due to the central initial cursor position acting as a visual reference point or the initial ocular pursuit. Most importantly, the angle-of-approach effect persisted in a judgment task. We thus conclude that this effect does not stem from online information-based modulations of movement speed, but from target information used to control aiming (i.e., movement direction). Moreover, processing for diagonal target motion appears to be biased towards straight downwards.

Statement of Public Significance

This study examines the control of manual interception, for a range of target trajectories, using visual occlusion. We show that occlusion causes spatial biases in the movements because unseen target motion is not fully accounted for. Participants quite accurately intercepted targets moving on straight trajectories and targets continuously visible; spatial biases arose, however, when unseen target motion must be accounted for. Because these effects were present irrespective of the time pressure inherent to manual interception, we interpret these to originate from target information used to control where to move rather than how fast to move. This research has implications in sports training, suggesting that the usefulness of visual occlusion training may be dependent on exactly how occluded objects are moving.

Spatial biases in motion extrapolation for manual interception

Even our simplest interactions with the environment, such as picking up a cup of coffee, require complex movement planning and coordination. Our brain must determine where the cup is relative to our body, the hand movement required to reach the cup, and what force needs to be applied to grasp and lift it. The processes involved have fascinated scientists from numerous fields (e.g., Georgopoulos, 2002; Beek, Dessing, Peper & Bullock, 2003; Wolpert & Ghahramani, 2000). Reaching is even more complex when objects move in space (e.g., catching a ball), because the reach must end anywhere along the path of the object. To intercept the object at the right place at the right time we must account for its continuous positional changes (Peper, Bootsma, Mestre & Bakker, 1994; Dessing, Bullock, Peper & Beek, 2002; Dessing, Peper, Bullock & Beek, 2005; Brouwer, Brenner & Smeets, 2002; Cesqui, d'Avella, Portone & Lacquaniti, 2012; Tresilian, 1993; Caljouw, van der Kamp & Savelsbergh, 2004). Although the mechanisms for reaching movements towards stationary objects are relatively well understood, the exact mechanisms by which humans successfully perform manual interception of moving objects are still elusive.

Research on interception has consistently reported that movement features depend on details of the target's motion.[1] For instance, targets initially moving at a high speed cause the effector to move directly to the interception point, arriving well in advance of the target (although not always at the accurate location; Arzamarski , Harrison, Hajnal, & Michaels, 2007; Port, Lee, Dassonville & Georgopoulos, 1997; Bosco, Delle Monache & Lacquaniti, 2012). Moreover, when enough time is available the effector is not always moved directly towards the interception point, but undergoes 'unnecessary', excess displacement. When

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[1] To clarify, from this point on we will use the term 'movement' only when discussing human movement and 'motion' when referring to the movement of a target or object.

the hand initiates from a future position of a target approaching under an angle, it is frequently moved away from and then back to the same initial position to intercept it (Montagne, Laurent, Durey & Bootsma, 1999; Dessing & Craig, 2010; Dessing et al., 2005; Dessing, Oostwoud Wijdenes, Peper & Beek, 2009a; Jacobs & Michaels, 2006). This angle-of-approach effect also occurs for different initial hand positions: initial hand movements are biased to the right for targets approaching the interception point from the right compared to those approaching it from the left (see also Ledouit, Casanova, Zaal & Bootsma, 2013; Peper et al., 1994). These initial biases are largely corrected through feedback control. For curved target trajectories, which involve continuous changes in the angle-of-approach, initial movements are similarly biased towards the initial approach direction (Craig, Berton, Rao, Fernandez, & Bootsma, 2006; Dessing & Craig, 2010; Bootsma, Ledouit, Cassanova, & Zaal, 2015).

The aforementioned effects have informed thinking about the control of manual interception (Beek et al., 2003; Bootsma, Fayt, Zaal & Laurent 1997; Dessing et al., 2002, 2005; Ledouit et al., 2013; Montagne et al., 1999; Peper et al., 1994; Zhao & Warren, 2015). Early arrival of the effector at the interception location has been taken as evidence for the use of spatial predictions (Arzamarski et al., 2007; Port et al., 1997; Bosco et al., 2012). Conversely, the effects of angle-of-approach and curvature argue for the use of non-predictive interception strategies (Bootsma et al., 1997, 2015; Montagne et al., 1999; Peper et al., 1994) or the use of initially inaccurate spatial predictions with online corrections (Arzamarski et al., 2007; Smeets & Brenner, 1995; Brenner & Smeets, 1996). One problem with such inferences is that behavioural features of the type discussed are not always unique to a control strategy (Beek et al., 2003; Brouwer et al., 2003; Dessing et al., 2005). Specific experimental manipulations are needed to uncover the perception-action coupling underlying interception (e.g., nature of the information used, use of online control). Visual target occlusion is a good candidate in this respect.

Target occlusion has been used to examine target motion extrapolation and the (continuous) use of visual information about the target during interception (e.g., Dessing et al., 2009a; Mazyn, Savelsbergh, Montagne & Lenoir, 2007; Mrotek & Soechting, 2007a; Teixeira, Chua, Nagelkerke & Franks, 2006). Target occlusion, particularly in the final phase, necessitates some form of prediction or extrapolation (Zago, Iosa, Maffei & Lacquaniti, 2010; Dessing et al., 2009a; Mrotek & Soechting 2007b; Katsumata & Russell, 2012; see also Bosco et al., 2015). Successful catching is possible if a ball is visible until at least 240ms before interception (Whiting & Sharp, 1974; Sharp & Whiting, 1975). After training, occlusion causes strategic/qualitative changes in performance (i.e., catching closer to the body and delaying movement initiation; Mazyn et al., 2007). In the current study, we will vary the duration of the final occlusion to control the last visible target motion (Teixeira et al., 2006), to highlight how behaviour is continuously modulated by information about target motion.

Visually occluded target trajectories with varying approach directions and curvatures – manipulations not studied in combination before to our knowledge - should yield interesting behavioural effects. We therefore *explored* interceptive behaviour in a paradigm that included a range of target trajectories and various target occlusion durations. To anticipate, we found effects of angle-of-approach and trajectory curvature that were modulated by target occlusion; confirmatory follow-up experiments showed these effects are associated with the control of movement direction (i.e., aiming), rather than movement speed. This implies that visual processing was biased for diagonal target motion.

Experiment 1: Manual interception with Occlusion

Experiment 1 involved a computer screen-based interception paradigm in which we varied target trajectories in terms of their initial and final position and curvature, while manipulating target visibility through occlusion at different times during the approach.[2] The effects observed in Experiment 1 motivated the confirmatory experiments discussed hereafter, which thus employ the experimental set-up and procedures similar or equivalent to those used for this experiment.

Materials and Methods

Participants

12 right-handed participants with normal or corrected-to-normal vision (average laterality quotients: 0.93, range: 0.81-1; Oldfield, 1971) were included, recruited mainly through a voluntary research participation scheme that awarded credit to students for participation in research experiments. Participants provided written informed consent before participating.

Experimental Set-up

Participants sat in a height-adjustable chair behind a table on which the set-up was mounted (see Figure 1A). The head was fixed comfortably in a padded chinrest with a thick strap stretching over the head and attached with Velcro to restrict excessive movement. The head was tilted slightly forward, so that participants faced a piece of transparent Perspex, the top of which was coated with a darkened film (Defender Auto Window Film, Car Accessories Ltd., Buckingham, UK). The film reflected images displayed on a downward

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[2] This experiment was the control condition within a larger study examining the spatial control of manual interception for two different mappings between finger and cursor movement (Dessing & Reid, 2013).

facing Dell LCD computer screen (533x300mm, 1920x1080 pixels, 60Hz) fixed 290mm above it. A touchscreen (32’’ Intelli Touch Plus, Elo Touch Systems, Milpitas, CA, USA) was placed parallel to but 290mm below the reflective film to record finger movements. Because touchscreen and stimulus screen differed in size, we performed a calibration before the experiment (once, not for each participant) based on 8 touches of 20 circular targets (placed in a 5 x 4 grid spanning 80% and 83% of the screen width and height, respectively). A linear regression model was used to map the recorded 2D touch coordinates (in pixels) to target location on the stimulus screen (in pixels); separate models were used for the sideward and upward dimensions. The calibration accounted for the differences between the stimulus screen and touchscreen in terms of pixel size (0.28mm vs. 0.35mm, respectively) and in terms of relative position and orientation of both screen surfaces. This meant that the cursor could be presented exactly at the 2D touch position and participants had full control over the cursor. Because delays can influence behaviour in interception paradigms (de la Malla, López-Moliner & Brenner, 2015), we measured/estimated the delay between finger and cursor movements in our system to be minimal (maximally 25ms). This matched our personal experience of unnoticeable delay and veridical representation of the finger position.

The experiment took place in a dark room; the only light sources were the stimulus presentation screen and a small lamp that switched on briefly between blocks of trials. Vision of the arm and hand was blocked by a piece of white cardboard stretching from the chinrest to the far edge of the reflector. To reduce friction of the finger on the glass touch screen, a piece of thin foam was taped to the palmar side of the right index finger (without this material the touch screen had difficulty detecting fast finger movements). Stimulus presentation was controlled through Matlab (The Mathworks, Nattick, MA, USA) by Version 3 of the Psychophysics Toolbox (Brainard, 1997).

Procedures

Participants provided informed consent, completed the handedness questionnaire, and sat in the height-adjustable chair before the experimenter placed the foam on the fingertip. They then placed their head in the chin rest and fastened the Velcro strap so that the trials could start. To start a trial, participants held the cursor (a small yellow circle; 6.7 mm diameter; see Figure 2A) inside the predefined starting zone in the centre of the screen (a larger green circle; 10.0mm diameter) for 250ms. Importantly, the cursor was presented 122.2mm above the finger in this phase. This manipulation was deemed necessary to ensure participant’s visual attention was in the centre of the screen at trial onset.[3] If the finger was initially positioned inside the starting zone the cursor was blue, informing the participant to first exit the zone, upon which the cursor turned yellow. A horizontal white line was shown in the middle of the screen (spanning the entire screen width) throughout the trial. Once the trial started the cursor turned red and appeared at the exact finger position (i.e., 122.2mm below screen centre). Simultaneously, a light pink target (5.6mm diameter) appeared 122.2mm above the white line, moving at a constant downward speed (122.2mm/s; movement time to reach the line: 1000ms), see Figure 2B. Target trajectories

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[3] Pilot measurements suggested that participants had particular problems intercepting targets with long occlusion if we presented the cursor at the finger position in this phase of the trial. This was judged to be due to the gaze initially being too far from the target (i.e., at the initial finger position at the bottom of the screen), leaving insufficient time for participants to change their gaze to the target and shortly track it before the target disappeared. Offsetting the cursor vertically only while the finger was moved to the initial position reduced this problem (even though the long occlusion condition remained the most challenging).

varied in terms of initial zone (111.0mm left or right of screen centre), final zone (111.0mm left or right of screen centre), and curvature (leftward, none, rightward; Figure 1B). The exact initial and final sideward target positions were randomly varied within a range of 194.4mm centred on the aforementioned zone centres. In the remainder of this manuscript, we will refer to trajectories without curve as 'straight' trajectories and trajectories that start and end on different sides of the screen as 'diagonal' trajectories. Relative to downward on the screen, target motion directions for non-diagonal trajectories were 0° (possible range -57.8° to 57.8°) and for diagonal trajectories they were -61.2° (possible range -73.7° to -12.8°) or 61.2° (possible range 12.8° to 73.7°). New random initial/final positions were created for each participant to avoid inducing systematic variations/deviations in our data. Trajectories were generated by fitting a second-order polynomial through the initial, halfway and final sideward target positions as a function of time; curve was generated by adding a 27.8mm leftward or rightward offset to the halfway position. Participants intercepted the target on the horizontal line using the red cursor. The target disappeared after it had reached the line (or earlier for occlusion conditions), while the cursor was shown for a further 500ms; participants thus never received explicit visual feedback on their performance for more than a single frame.

<u>Insert Figure 1 & 2 about here</u>

Time of target occlusion was manipulated by having the target disappear after 250ms, 500ms, 750ms or 1000ms (i.e., no occlusion). Each participant completed five repetitions of all 12 trajectories (2 initial zones x 2 final zones x 3 curvatures) for all occlusion conditions. Occlusion conditions were presented in randomly ordered blocks of 60 trials. Our touchscreen did not always function perfectly, resulting in occasional jumps in the cursor positions. To determine whether this happened, after each trial we fitted a cubic spline through the sideward and upward cursor positions from trial onset until 500ms after interception. If at any frame from target onset to interception the fitted 2D position was further than 5 pixels from the measured position, the touchscreen was judged to have missed finger displacement. In this case, as well as when the cursor exited the starting zone within 100ms of target appearance the trial was repeated at a random position within the remainder of the block; this ensured that we collected five valid trials for all conditions. Based on this criterion, on average 10 trials were repeated for each participant.[4] All procedures were approved by the School of Psychology Research Ethics Committee of Queen’s University Belfast.

Data Analysis

Data analyses were conducted offline using Matlab. The data was filtered using a recursive, fourth-order Butterworth filter (low-pass, 10Hz cut-off). The surplus movement (SM) of the cursor was calculated by subtracting the shortest potential movement path length between the initial (the point at which the cursor exited the starting zone) and final cursor position (the position of the cursor in the final frame) from the actual path length taken. The arrival time, $T_{arrival}$, was defined as how long before interception the cursor last arrived within ± 30 pixels of the final cursor position (i.e., values were always positive). Constant error (CE) was determined by subtracting the final target position from the final cursor position (positive is rightward).

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[4] This experiment initially did not include an algorithm for rerunning trials online. We thus reran the experiment after Experiment 2 *for the sole purpose* of using the same algorithm.

We conducted Shapiro-Wilk tests of composite normality to determine whether the data was normally distributed. Even though Analysis of Variance (ANOVA) is relatively robust to deviations from normality, we used an arbitrary cut-off to determine whether we would run a parametric ANOVA. If the data for 20% or more of the conditions were not normally distributed (i.e., Shapiro-Wilk test significant at an uncorrected alpha-level of 0.05), we would not use a full factorial repeated measures ANOVA, but a Friedman ANOVA to analyze the main effects. As a result, CE and $T_{arrival}$ were analysed using a repeated measures ANOVA, while SM was analysed using a Friedman ANOVA. When the Sphericity assumption was violated for CE and $T_{arrival}$, corrected degrees of freedom were used (and will be reported; epsilon < 0.75: Greenhouse-Geisser; epsilon > 0.75: Huyn-Feldt, Field, 2013).

As these exploratory analyses involved a large number of effects, we corrected for multiple comparisons implicit to multiway ANOVAs (Cramer et al., 2015); we used a step-down Holm-Sidak procedure, which ranks all *p*-values from lowest to highest and compares them to the rank-specific Sidak-adjusted alpha-level (see Tables S1-3 in Supplementary information for *p*-sorted ANOVA results for all effects including corrected alpha-levels). Post-hoc analyses involved paired-samples *t*-tests (for CE and $T_{arrival}$) or Wilcoxon Signed Ranks tests (for SM) with additional Holm-Sidak corrections on the already corrected alpha-level associated with the effect. Note that we present figures for all significant effects, which also visualize all significant post-hoc differences.

Results

In this experiment, we examined the effects of visual occlusion of target trajectories with varying initial/final positions and curvature on manual interception. In general, interceptive behaviour was consistently influenced by all these factors, inducing spatial biases in the movements and inaccurate interceptive behaviour; this can be appreciated from the averaged trajectories shown in Figure 3. Figure 3 also illustrates that the interceptive movements for all times of target occlusion are qualitatively similar to previously reported movements for interception without occlusion (Arzamarski et al., 2007; Dessing et al., 2005; Ledouit et al., 2013; Smeets & Brenner, 1995). Our exploratory analyses are discussed next; to afford readability we will first present all main effects before discussing the interactions.

<u>Insert Figure 3 about here</u>

The main effect of curvature on SM was significant, $X^2(2,N=12) = 15.2$, $p = 0.5{\cdot}10^{-3}$; participants used more excess movement to intercept curved than straight trajectories (Figure 4B). There was also a significant effect of curvature on CE, $F(1.3,13.9)=364.5$, $p < 0.5{\cdot}10^{-6}$, $\eta_p^2 = 0.94$, which revealed a bias in the direction of the curve (Figure 4C). In combination, these effects suggest participants had difficulty accurately extrapolating and successfully intercepting curved target trajectories. Earlier target occlusion motivated earlier arrival at the interception line ($T_{arrival}$), $F(1.1,1.7)= 27.9$, $p = 0.4{\cdot}10^{-5}$, $\eta_p^2 =0.72$ (Figure 4D), and more direct movement paths, $X^2(3,N=12) = 18.8$, $p = 0.3{\cdot}10^{-3}$ (Figure 4E). The cursor arrived earlier at the right final zone than at the left ($T_{arrival}$) $F(1,11) = 14.9$, $p = 0.0026$, $\eta_p^2 = 0.58$ (Figure 4A). On average, the interception point was undershot, which amounts to a bias towards the left for right final target positions and vice versa (effect of Final Zone on CE), $F(1,11) = 41.5$, $p = 0.5{\cdot}10^{-4}$, $\eta_p^2 = 0.79$ (Figure 4F). Besides these main effects, interception behaviour was influenced by several interactions, as discussed next.

Insert Figure 4 about here

There was a significant Final Zone x Curvature interaction for T_{arrival}, $F(2,22) = 10.0$, $p = 0.8 \cdot 10^{-3}$, $\eta_p^2 = 0.48$, which appeared to be due to the effect of curvature being in opposite direction for the two final zones (see Supplementary Figure 1).). This effect was modulated by occlusion (i.e., significant Final Zone x Curvature x Time of Target Occlusion interaction, $F(6,66) = 13.7$, $p < 0.5 \cdot 10^{-6}$, $\eta_p^2 = 0.56$). The effect of occlusion appeared to be stronger for rightward curving targets (than for the other curve conditions) ending on the left and for leftward curing targets ending on the right (Figure 5A&B).

Insert Figure 5 about here

The effect of curvature on CE (endpoints deviating in the direction of curvature) increased with longer occlusion (significant Curvature x Time of Target Occlusion interaction, $F(1.9,21.7) = 72.1$, $p < 0.5 \cdot 10^{-6}$, $\eta_p^2 = 0.87$; see Figure 6A). There was a significant Initial Zone x Time of Target Occlusion interaction, $F(2.1,23.3) = 9.6$, $p = 0.8 \cdot 10^{-3}$, $\eta_p^2 = 0.47$ (Figure 6B); post-hoc tests did not demonstrate significant differences, but a bias in the direction of the initial zone appeared to increase with more occlusion. The significant Final Zone x Time of Target Occlusion interaction, $F(3,33) = 24.8$, $p < 0.5 \cdot 10^{-6}$ $\eta_p^2 = 0.69$, revealed an inward bias (i.e., errors towards the screen centre) that increased with longer occlusion (Figure 6C). These occlusion-dependent effects highlight that imperfect performance is accentuated by the removal of visual information, suggesting that with unconstrained viewing participants relied on continuous target motion information.

We plotted the latter interactions in combination (Final Zone x Initial Zone x Time of Target Occlusion; Figure 6D), which highlighted that the two interactions (with similar sized effects of initial and final zone) mainly captured effects of the diagonal trajectories. These trajectories resulted in a much larger error with increasing occlusion duration than trajectories that appeared and ended on the same side of the screen.

Insert Figure 6 about here

There was a significant Final zone x Curvature x Time of Target Occlusion interaction for CE, $F(6,66) = 4.1$, $p = 0.0014$, $\eta_p^2 = 0.27$, which showed that the effect of target curvature for the longer occlusion is asymmetric: larger errors for rightward curving targets ending on the left and leftward curving targets ending on the right (see Figure 7). Finally, we also observed a significant Final zone x Initial Zone x Curvature interaction, $F(2,22) = 27.8$, $p = 0.1 \cdot 10^{-5}$, $\eta_p^2 = 0.72$, which showed that the effect of curvature is somewhat larger for diagonal trajectories (Supplementary Figure 2).

Insert Figure 7 about here

Discussion

We explored interception performance in situations with incomplete target trajectory information (target occlusion). We observed very direct movements and early arrival for straight target trajectories. The finger arrived at the final position earlier for fully visible targets that appeared and ended on the same side of the screen, suggesting that these trajectories may have been easier to intercept than curved or diagonal trajectories. Furthermore, surplus movement increased and the cursor arrived later with less target occlusion (i.e., more target information) suggesting participants used the available viewing time to update their interceptive movement. These effects show that participants at any moment did not fully account for the future curve, which influenced interception movements with target occlusion (when no more visual information about target motion was available). Finally, participants were relatively successful when extrapolating and intercepting targets moving within the same side of the screen (i.e., non-diagonal trajectories).

We observed several specific effects related to the target trajectory. Large biases in the direction of curve increased with increasing occlusion. The effect of curve replicates previous findings and suggests that humans have problems perceiving and accounting for effects of curve (Craig et al., 2006; Dessing & Craig, 2010; Mrotek & Soechting, 2007a). However, we mainly observed an effect of curve-related outward target motion at interception, which suggests a modulating effect of trajectory configurations (see below). Participants never received explicit feedback on the occluded target's final position, preventing them from correcting for their errors (Mrotek & Soechting, 2007a). The later arrival times and more excess movements for curved trajectories and less target occlusion suggest that our participants adopted a strategy involving online adjustments to correct for initial inaccuracies when possible (Brenner & Smeets, 2009a, 2009b, 2011; Brenner, Driesen & Smeets, 2014; Montagne et al., 1999; Peper et al., 1994; Dessing et al., 2002, 2005, 2009a; Arzamarski et al., 2007; Ledouit et al., 2013).

The two-way interactions between Time of Target Occlusion and Initial and Final Zone, respectively, showed that the errors were mainly associated with diagonal trajectories and increased with increasing occlusion. Errors for target trajectories that initiated and landed on the same side of the screen were much smaller (Figure 6D). In other words, we observed the well-known angle-of-approach effect (i.e., errors depending on the direction of target approach) for both final positions. Although this effect has mostly been reported for early features of the hand movements (Dessing et al., 2005, 2009a, 2009b; Jacobs & Michaels, 2006; Ledouit et al., 2013; Montagne et al., 1999; Peper et al., 1994; Duke & Rushton, 2012), occlusion in our experiment prevented online movement adjustments to correct for these early biases. While this effect has been associated with visual information used to control interception, we realized that certain non-visual aspects could also have contributed in our experiment.

It is possible that expectations influence interceptive behaviours (Brouwer, Middelburg, Smeets & Brenner, 2003) particularly when information is limited, such as after target occlusion. The expectation of gravitational acceleration is a particular example of this; it has been suggested that humans use an internal model of gravity (possibly shaped by experience) to generate expectations regarding the motion of objects (Zago et al., 2010; de Rugy, Marinovic & Wallis, 2012). Other research has shown that events in previous trials can influence expectations of what is to come in the current trial (Dessing et al., 2009a; De Lussanet, Smeets & Brenner, 2001; Brenner & Smeets, 2011). This may also result in expectations concerning sequences of conditions (Gray, 2002; Zelaznik, Hawkins & Kisselburgh, 1983; Tijtgat, Bennett, Savelsbergh, De Clercq & Lenoir, 2011).

In Experiment 1, expectations may have influenced the observed occlusion-dependent biases in two ways. Firstly, the use of online information may be influenced by conditions in the previous trial. To examine this potential effect, we analysed the constant errors using a linear mixed model that included all factors the ANOVA did (and Subject as a random variable [to implement the 'repeated measures']), with final target position on the previous trial as an additional factor. None of the effects involving this additional factor were significant, demonstrating that none of the effects discussed above were influenced by expectations based on conditions or behaviour in the previous trial. Secondly, expectations may have influenced behaviour because trajectories tended to be leftward from the right initial position and right of the leftward initial position. Because the initial motion direction of some curved trajectories was aimed at a position outside of the screen, participants could expect/know they never needed to move to such eccentric positions based on the previous trials or knowledge of the screen size (see also Dessing & Craig, 2010). This might have induced a bias towards the average final position and caused the earlier arrival and larger spatial errors for the earlier occlusion conditions when targets moved outward at interception due to curve. To evaluate whether the lack of eccentric final target positons induced such effects, we conducted a follow-up experiment that included additional straight 'dummy' trajectories from either initial position to more eccentric zones (Figure 8).

Insert Figure 8 about here

Experiment 2: Occlusion with Additional Eccentric Dummy Trajectories

As discussed above, expectations associated with the absence of eccentric final target positions could have biased the reach endpoints inward and induced an earlier arrival and larger errors for inward curving targets occluded early. We thus conducted an experiment that included trajectories towards more eccentric final target positions; our analysis did not include these 'dummy' trajectories (i.e., the factor final target zone only included two positions, akin Experiment 1) and focused solely on the occlusion-dependent biases and arrival times observed as a function of curvature, initial and final target zone.

Methods

This experiment was conducted with eight right-hand participants (average laterality quotient: 0.95; range: 0.86-1; Oldfield, 1971), two of whom had participated in Experiment 1.[5] The experiment and analyses slightly differed from the previous experiment. To make space on the screen for the dummy final zones, the initial and final zones were slightly smaller (118.0mm) and their centres were located closer to screen centre (67.3mm) than in previous experiments. Relative to downward on the screen, target motion directions for non-diagonal trajectories were 0° (possible range -44.0° to 44.0°) and for diagonal trajectories they were -47.8° (possible range -64.2° to -7.8°) or 47.8° (possible range 7.8° to 64.2°). Only three Times of Target Occlusion were used (333ms, 667ms, 1000ms [i.e., no occlusion]). The critical manipulation was the introduction of additional dummy trajectories without curve that started in one of the initial zones and moved towards one of two additional, more eccentric final zones on the same side of the screen (i.e., the centres of

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[5] We confirmed that these participants did not influence the results of Experiment 2.

these zones were located 202.0mm on either side of the centre of the screen, Figure 8). Importantly, these trials were not analysed, but we predicted that if the trajectory-dependent and occlusion-dependent inward biases were due to the absence of extreme final positions, these effects should disappear in the presence of the dummy trajectories.

Trajectories were generated in the same manner as in Experiment 1 for the two final zones closest to the screen centre. For the experimental conditions, 10 repetitions were run for each of the two initial zones, two final zones, three curves, and three target occlusion conditions; the number of dummy trajectories was set such that across all trials there was a 25% chance of a target landing in any of the four zones (and a 50% chance of the dummy trajectory starting in either initial zone). On average 80 trials were repeated for each participant (see Experiment 1 for criteria). We conducted customized repeated measure ANOVAs that included only the Curvature x Time of Target Occlusion, Initial Zone x Time of Target Occlusion, Final Zone x Time of Target Occlusion and Final Zone x Curvature x Time of Target Occlusion interactions for CE, and the Final Zone x Curvature x Time of Target Occlusion interaction for $T_{arrival}$. Across all tested effects we applied a Holm-Sidak correction to the 0.05 alpha-level (for 5 effects); post-hoc analyses (using paired-samples *t*-tests) used an additional Holm-Sidak correction on the corrected alpha-level associated with each effect.

Results/Discussion

Our analyses showed that the presence of dummy trajectories removed only a single effect. The Final Zone x Curvature x Time of Target Occlusion interaction for CE was not significant (p = 0.45). The same interaction was significant for $T_{arrival}$, $F(4,28) = 27.7$, $p < 0.5\cdot10^{-6}$, η_p^2 = 0.80, and showed a distinct effect of early occlusion (i.e., earlier arrival at the final position) for rightward curving trajectories ended in the left final zone and for leftward curving trajectories ending in the right final zone (see Figure 5C&D). The directional interception error was modulated by a significant Curvature x Time of Target Occlusion interaction, $F(1.3,9.1) = 20.9$, $p = 0.8 \cdot 10^{-3}$, $\eta_p^2 = 0.75$, reflecting a bias in the direction of curve that increased with more target occlusion (see Figure 9A). Similarly, the significant Initial Zone x Time of Target Occlusion, $F(2,14) = 40.7$, $p = 0.1 \cdot 10^{-5}$, $\eta_p^2 = 0.85$, and Final Zone x Time of Target Occlusion, $F(2,14) = 28.6$, $p = 0.1 \cdot 10^{-4}$, $\eta_p^2 = 0.80$, interactions showed similar patterns to the main experiment (see Figures 9B and C). Again, we examined the latter interactions for CE (Figure 9D), which mainly illustrated a larger increase in errors with longer occlusion mainly for diagonal target trajectories.

We thus observed that the asymmetry in the effects of curve for longer occlusion between final zones was not observed in Experiment 2; this strongly suggests that the *absence* of effects of curve for targets moving inward at interception due to curve was due to expectations concerning the range of final target positions (see also Dessing & Craig, 2010). Because all other effects were present again in Experiment 2, we conclude that these were not due to a lack of eccentric final target zones. Given that the spatial errors were mainly present for curved and diagonal trajectories and increased with increasing occlusion, it seems likely that with full vision, online control was used to correct for any biases in initial motion processing for curved and diagonal trajectories. Target occlusion prevented effective online corrections and thus resulted in spatial biases (i.e., not fully accounting for unseen target motion). This is most evident for the increasing effect of curve with longer occlusion, which can be largely explained by participants not taking future effects of curve (due to sideward acceleration) into account and thus only using the last seen motion direction (Dessing & Craig, 2010).

Insert Figure 9 & 10 about here

Dessing et al., (2009a, b) argued that target motion information may modulate the angle-of-approach effect in two ways. The first would involve variations in aiming (i.e., movement direction/endpoint), while the second would involve variations in movement speed due to information-based variations in the motor drive (i.e., the strength of the continuous coupling between target and hand; see Dessing et al., 2009a for a detailed discussion). This is illustrated in Figure 10, which presents essential features of the model for interception they employed (see also Dessing et al., 2002, 2005). Dessing et al., hypothesized the angle-of-approach effect is mainly due to variations in movement aiming, but did not explicitly test this. Along a similar line, Ledouit et al., (2013) described the angle-of-approach effect as reflecting a combination of current and future target position information influencing aiming (see Bootsma et al., 2015 for an advanced account of this combination). They showed that the angle-of-approach effect persisted with trajectories for which the separate behavioural effects of general motion direction and curve cancelled each other out. Importantly, however, the trajectories were generated based on a line extrapolation task, which might not be reflective of target motion extrapolation. We thus set out to directly test whether the angle-of-approach and curve effects described above were purely associated with movement aiming (see Figure 10) or whether these are (also) influenced by target motion-related modulations of movement speed. We conducted several follow-up experiments that required motion extrapolation but not interception. In these experiments participants had to indicate, after a short delay, where they judged the target to have passed; the idea was that performance in this task would reflect movement aiming, but not online information-based modulations of movement speed.

Experiment 3: Occlusion-induced biases in motion extrapolation

In Experiment 1 larger spatial biases were observed after occlusion for diagonal target trajectories, when less trajectory information was available. To examine whether this was due to movement aiming or online information-based modulations of movement speed we repeated Experiment 1 without time pressure. Participants were thus required to indicate where they judged the target to have passed without the online modulations in movement speed associated with interception.

Method

We examined the effects of curvature, initial and final target zone and target occlusion on CE (twelve right-handed participants [average laterality quotient: 0.91; range: 0.75-1; Oldfield, 1971]). Experimental parameters were unchanged from Experiment 1, with the exception that participants were no longer required to move to intercept the target landing on the central line. Rather, participants were instructed to observe the moving target until it disappeared. Half a second after the target crossed the line the cursor appeared at the centre, coupled with an auditory cue informing participants to move the cursor (controlled by a computer mouse with standard gain settings; position recorded at mouse click). The cursor was constrained to move along the central line; participants positioned the cursor where they judged the target to have passed. On average 4 trials were repeated for each participant, in case the cursor started moving prior to the auditory cue. Each participant completed a block of 40 practice trials with randomized target visibility, followed by four blocks of 60 trials (one for each Time of Target Occlusion, presented in random order), with conditions randomized within the blocks. We predicted that if the spatial biases in Experiment 1 were associated with online information-based modulations of movement speed (Dessing et al., 2009a, b), these biases should disappear in our judgment task. Our analyses focused on the Initial Zone x Time of Target Occlusion and Final Zone x Time of Target Occlusion interactions, although we also considered the Curvature x Time of Target Occlusion interaction for comparison with the previous experiments; we only analysed the spatial error in the judgment (CE). Statistical analyses were the same as in Experiment 2, with the exception that the within-ANOVA alpha-level correction was only done for 3 effects.

Results/Discussion

Data analyses showed that the spatial judgment error was significantly affected by an Initial Zone x Time of Target Occlusion, $F(2.0,22.3) = 15.8$, $p = 0.5\cdot10^{-4}$, $\eta_p^2 = 0.59$, and Final Zone x Time of Target Occlusion interaction, $F(1.9,21.3) = 20.5$, $p = 0.1\cdot10^{-4}$, $\eta_p^2 = 0.65$. Both interactions showed the same pattern as in Experiment 1 (Figure 11B & C; plotted together in Figure 11D), which strongly suggests that the spatial biases during interception were due to target motion-related variations in movement aiming (e.g., imperfect motion extrapolation), rather than in movement speed. Further confirmation of this came from the significant Curvature x Time of Target Occlusion interaction, $F(1.7,18.3) = 101.5$, $p < 0.5\cdot10^{-6}$, $\eta_p^2 = 0.90$, which revealed a bias in the direction of curvature increasing with increasing target occlusion (Figure 11A).

Imperfect/biased motion extrapolation could result in deviations in movement aiming. We realized that one specific aspect of our design could influence such effects: the cursor was shown initially and reappeared in the centre of the screen after target disappearance. This constant cursor position could provide a reference for motion extrapolation, although we are not aware of any evidence for this. If motion extrapolation would be biased toward the visual reference position, this could induce inward biases. We thus conducted a judgment experiment in which the cursor appeared at the start of the response period at a random position along the central line.

Experiment 4: Occlusion-induced biases in motion extrapolation II

Experiment 4 was conducted to test the potentially biasing effect of the visible central starting position of the cursor.[6]

Method

This experiment included twelve right-handed participants (average laterality quotient: 0.93; range: 0.75-1; Oldfield, 1971). The experimental set-up and procedures were the same as Experiment 3, with the exception that the cursor was invisible during target motion and appeared at a random position along the line when participants were cued to indicate the judged final target position. On average 9 trials were repeated for each participant. Our analyses again focused on the Initial Zone x Time of Target Occlusion, Final Zone x Time of Target Occlusion interactions for CE. Even though the Curvature x Time of Target Occlusion interaction should not have been influenced by the central cursor position, it was included in our analyses for comparison with the previous Experiments.

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[6] This experiment was conducted prior to Experiment 3, but we realized that we changed two things at once (reverting to a judgment task and changing the location of cursor appearance) and thus needed an intermediate experiment.

Results/Discussion

Just like in Experiment 3, directional error was modulated by significant Initial Zone x Time of Target Occlusion, $F(1.6,18.1) = 24.2$, $p = 0.2\cdot10^{-4}$, $\eta_p^2 = 0.68$, and Final Zone x Time of Target Occlusion, $F(3,33) = 19.3$, $p < 0.5\cdot10^{-6}$, $\eta_p^2 = 0.64$, interactions, which showed the same pattern as before (Figure 12B-D). We also replicated the Curvature x Time of Target Occlusion interaction, $F(2.9,31.4) = 164.1$, $p < 0.5\cdot10^{-6}$, $\eta_p^2 = 0.94$, showing a bias in the direction of curvature increasing with increasing target occlusion (Figure 12A). This confirms that the aforementioned spatial biases were not due to the visible central starting position of the cursor.

In Experiment 1, we adjusted a specific aspect of our task (getting the cursor to the starting position) to reduce the initial saccade amplitude in the hope of increasing the time the target could be tracked (see footnote 3). Research suggests it takes around 200ms to saccade to a moving target as the target's position and velocity need to be accounted for (Bieg, Chuang, Bülthoff & Bresciani, 2015). This would mean that for the earliest occlusion conditions in our experiments (250ms of target visibility) there was little available time to track/extrapolate the target motion compared to the other target occlusion conditions. This limited pursuit duration might have affected the perception of target motion, given the known link between pursuit and motion perception (Orban de Xivry & Lefevre, 2007; Beutter & Stone, 1998, 2000; Braun, Pracejus & Gegenfurtner, 2006; for review see Schütz, Braun & Gegenfurtner, 2011). This could have contributed to the large spatial biases observed for the earliest occlusion condition. Therefore, we conducted one last experiment in which the target appeared stationary at its initial position for 1000ms before starting to move (see Ledouit et al., 2013 for a similar approach). This manipulation ensured the target could be pursued for longer, which should thus reduce any part of the errors for early occlusion related to the limited pursuit duration.

Experiment 5: Pursuit duration-dependent biases in motion extrapolation

In Experiment 5, we provided participants with vision of the stationary target at its initial position for 1000ms before it began to move. The idea was that this should allow them to look at this position and subsequently track the target for longer prior to its disappearance, and thereby reduce any initial eye movement-related contributions to the spatial biases.

Method

Twelve right-handed participants gave their informed consent (average laterality quotient: 0.92; range: 0.75-1; Oldfield, 1971). We showed the target at its initial position for one second, allowing participants to shift their gaze toward the target before it started to move, and thus track it for longer before it disappeared (in the early occlusion condition). All other experimental parameters and analyses remained the same as the previous experiments (N.B., the initial cursor position and time of appearance matched Experiment 3). On average 5 trials were repeated for each participant.

Results/Discussion

Just like in the previous experiments, the spatial judgment error (CE) was modulated by a significant Curvature x Time of Target Occlusion interaction, $F(2.1,22.7) = 183.4$, $p < 0.5 \cdot 10^{-6}$, $\eta_p^2 = 0.94$, due to a bias in the direction of curvature that increased with increasing target occlusion (see Figure 13A). The Initial Zone x Time of Target Occlusion, $F(1.8,20.7) = 37.7$, $p < 5 \cdot 10^{-7}$, $\eta_p^2 = 0.77$, and Final Zone x Time of Target Occlusion, $F(3,33) = 34.2$, $p < 5 \cdot 10^{-7}$, $\eta_p^2 =$

0.76, interactions also showed the same pattern as before (see Figure 13B-D). These results suggest that limited pursuit did not increase the errors in the long occlusion condition in the previous experiments.

General Discussion

Many studies have considered the information and strategies for manual interception (Chapman, 1968; Bootsma et al., 1997; Montagne et al., 1999; Beek et al., 2003; Dessing et al., 2005; Zago, McIntyre, Senot & Lacquaniti, 2009; Smeets & Brenner, 1995; Peper et al., 1994) and which task features influence which behavioural features. Here, we explored interception behaviour in situations with incomplete target motion information (target occlusion) for a range of different target trajectories. We observed very direct movements and long waiting times at interception with early target occlusion and straight target trajectories. However, arrival times were later for curved trajectories and for shorter occlusion. Spatial biases increased with occlusion when the target crossed the screen during the trajectory. This suggests that when more of the trajectory was visible participants used the available viewing time to correct for initial inaccuracies where possible and update their interceptive movement online (Brenner & Smeets, 2009a, 2009b, 2011; Brenner et al., 2014; Montagne et al., 1999; Peper et al., 1994; Dessing et al., 2002, 2005, 2009a; Tresilian et al., 2009; Arzamarski et al., 2007; Ledouit et al., 2013). However, based on this data we cannot determine whether the movement updates depended on updated spatial predictions or on another type of non-predictive continuous control (Dessing et al., 2005). Curved target trajectories consistently resulted in large biases in the curve direction that increased with increasing occlusion; straight trajectories only resulted in very small errors across all target occlusion conditions. The observed pattern was consistent with the suggestion that participants did not account for effects of curve (Dessing & Craig, 2010; Ledouit et al., 2013; Mrotek & Soechting, 2007a), which has been ascribed to the limited sensitivity to acceleration of the human visual system (i.e., sideward curve occurred due to sideward acceleration; Dessing & Craig, 2010; Craig et al., 2006; Brouwer et al., 2002; Rosenbaum, 1975; Schmerler, 1976). However, in Experiment 2, which included a wider range of final target positions (i.e., using dummy trajectories), we showed that expectations concerning this range could reduce this effect (see also Dessing & Craig, 2010).

We also observed specific effects of occlusion associated with the overall motion direction of the target. Further examination of the Initial Zone x Time of Target Occlusion and Final Zone x Time of Target Occlusion interactions showed that the errors (and thus their increase with more occlusion) mainly occurred for diagonal target trajectories. We showed that the occlusion-dependent biases for curved and diagonal trajectories were not associated with an effect of expectations of the interception point based on the preceding trial (for examples of such effects, see Dessing et al., 2009a; de Lussanet et al., 2001). The effects of diagonal trajectories were also not associated with expectations due to the absence of more eccentric final target positions, confirmed in Experiment 2. In Experiment 3 we removed time-pressure implicit in manual interception, and showed that the spatial biases were not associated with online information-based modulations of movement speed. Using random initial positioning of the cursor (only appearing after the target disappeared), Experiment 4 refuted that these spatial biases were due to the central cursor acting as a visual reference point for motion extrapolation. Finally, Experiment 5 showed that the large biases with long occlusion were not a result of insufficient time to track the target. This leaves us to conclude that the observed angle-of-approach effect (Arzamarski et al., 2007;

Duke & Rushton, 2012; Jacobs & Michaels, 2006; Ledouit et al., 2013; Montagne et al., 1999) reflects target motion-related variations in movement aiming.

In the interception experiment, significant inward biases were apparent for fully visible targets (in addition to the biases for the other occlusion conditions; see Figure 6B-D). These biases were reduced to near zero in Experiment 2, suggesting that they were potentially associated with expectations due to the lack of eccentric final target positions. However, for the judgment tasks, these errors were also reduced to near zero for fully visible targets, or even reversed (i.e., Experiment 5), which might suggest the effect during interception reflects modulations of movement speed (i.e., an insufficient motor drive, or effort, resulting in undershooting even for fully visible targets). Tentatively, in combination these findings may suggest an effect of expectations on online modulations of movement speed.

Our experiments highlight that humans can quite accurately intercept targets moving on straight trajectories and any target that is visible throughout its entire trajectory. Performance is greatly diminished when accurate extrapolation of curved and occluded target trajectories is required and time pressure is added. After occlusion, spatial biases occur because unseen target motion is not adequately accounted for (e.g., Mrotek & Soechting, 2007a; Dessing et al., 2009a; Ledouit et al., 2013; see also Bosco et al., 2012). Biases could arise within motion direction perception, which have been reported both for motion in depth (Harris & Dean, 2003; Harris & Drga, 2005; Duke & Rushton, 2012; Welchman, Tuck, & Harris, 2004) and in the frontal plane (Hubbard, 1990; Souman, Hooge, & Wertheim, 2005; Post & Chaderjian, 1987; Tynan & Sekuler, 1982). Besides in the actual information used, biases may depend on how motion signals are coded and combined (Baddeley & Tripathy, 1998; Barlow & Tripathy, 1997; Kwon, Tadin, & Knill, 2015; Leclercq, Lefèvre, & Blohm, 2012; Mudison, Leclercq, Lefèvre, & Blohm, 2015; Weiss, Simoncelli, & Andelson, 2002). Evidently, if motion extrapolation is based on biased motion signals, it should show systematic biases in absence of compensatory mechanisms. Mechanisms for motion extrapolation, however, could also cause biases, for instance through the 'model' used for extrapolation (Bosco et al., 2012, 2015; Fulvio, Green, & Schrater, 2014; Fulvio, Maloney, & Schrater, 2015). The biases observed here are trajectory-dependent, which seems to favour an explanation in terms of biased motion signals (rather than biased extrapolation mechanisms). However, a definitive conclusion about this requires more dedicated experiments on motion perception.

Our findings have some potential practical implications. The effects of occlusion in this study were pivotal for our interpretation of the observed target trajectory-dependent movement biases (see also, Dessing et al., 2009a; Mazyn et al., 2007; Mrotek & Soechting, 2007a; Teixeira et al., 2006). Visual occlusion has been forwarded as useful technique for sports training (Fadde, 2006; Farrow, Chives, Hardingham, & Sauces, 1998), but it is known that certain biases can only be corrected for through terminal feedback (Mrotek & Soechting, 2007a), which cannot be guaranteed in such scenarios. In combination with our findings, this suggests that the usefulness of visual occlusion for training purposes may well be very situation-dependent.

In sum, we have reported a range of severe spatial biases in manual interception of occluded targets moving on diagonal and/or curved trajectories. We have shown that these biases are not unique to interception, but occur in judgment tasks as well. This suggests that they reflect deficiencies in motion extrapolation, which during manual interception feeds into movement aiming. More specifically, because the biases occur mainly for diagonal trajectories, the most likely explanation is that they are present within motion signals feeding into the extrapolation mechanism.

References

Arzamarski, R., Harrison, S. J., Hajnal, A., & Michaels, C. F. (2007). Lateral ball interception: hand movements during linear ball trajectories. *Experimental Brain Research, 177(3)*, 312-323.

Baddeley, R. J., & Tripathy, S. (1998). Insights into motion perception by observer modelling. *Journal of the Optical Society of America [A], 15*, 289 –296.

Barlow, H., & Tripathy, S.P. (1997). Correspondence noise and signal pooling in the detection of coherent visual motion. *Journal of Neuroscience*, *17(20),* 7954-7966.

Beek, P. J., Dessing, J. C., Peper, C. E., & Bullock, D. (2003). Modelling the control of interceptive actions. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences, 358,* 1511-1523.

Beutter, B. R., & Stone, L. S. (1998). Human motion perception and smooth eye movements show similar directional biases for elongated apertures. *Vision Research, 38,* 1273–1286.

Beutter, B. R., & Stone, L. S. (2000). Motion coherence affects human perception and pursuit similarly. *Visual Neuroscience, 17,* 139-153.

Bieg, H. J., Chuang, L. L., Bülthoff, H. H., & Bresciani, J. P. (2015). Asymmetric saccade reaction times to smooth pursuit. *Experimental Brain Research, 233(9)*, 2527–2538.

Bootsma, R. J., Fayt, V., Zaal, F. T., & Laurent, M. (1997). On the information-based regulation of movement: What Wann (1996) may want to consider. *Journal of Experimental Psychology: Human Perception and Performance, 23,* 1282-1289.

Bootsma, R. J., Ledouit, S., Casanova, R., & Zaal, F. T. J. M. (2015). Fractional-order information in the visual control of lateral locomotor interception. *Journal of Experimental Psychology: Human Perception and Performance, 42(4)*, 517-529.

Bosco, G., Delle Monache, S., & Lacquaniti, F. (2012). Catching what we can't see: Manual interception of occluded fly-ball trajectories. *PLoS ONE, 7,* e49381.

Bosco, G., Delle Monache, S. D., Gravano, S., Indovina, I., La Scaleia, B., Maffei, V., Zago, M., & Lacquaniti, F. (2015). Filling gaps in visual motion for target capture. *Frontiers in Integrative Neuroscience, 9*, 1-17.

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision, 10*, 433-436.

Braun, D. I., Pracejus, L., & Gegenfurtner, K. R. (2006). Motion aftereffect elicits smooth pursuit eye move-ments. *Journal of Vision, 6(7),* 671–684.

Brenner, E., & Smeets, J. B. (1996). Hitting moving targets: co-operative control of 'when' and 'where'. *Human Movement Science, 15(1)*, 39-53.

Brenner, E., & Smeets, J. B. J. (2009a). Sources of variability in interceptive movements. *Experimental Brain Research, 195*, 117-133.

Brenner, E., & Smeets, J. B. J. (2009b). Modifying one's hand trajectory when a moving target's orientation changes. *Experimental Brain Research, 196,* 375-383.

Brenner, E., & Smeets, J. B. J. (2011). Continuous visual control of interception. *Human Movement Science, 30,* 475–494.

Brenner, E., Driesen, B., & Smeets, J. B. J. (2014). Precise timing when hitting falling balls. *Frontiers in Human Neuroscience, 8*, 342: 1-8.

Brouwer, A. M., Brenner, E., & Smeets, J. B. (2002). Perception of acceleration with short presentation times: can acceleration be used in interception? *Perception and Psychophysics, 64,* 1160-1168.

Brouwer, A. M., Brenner, E., Smeets, J. B. (2003). When is behavioral data evidence for a control theory? Tau-coupling revisited. *Motor Control, 7*, 103-110.

Brouwer, A. M., Middelburg, T., Smeets, J. B. J., & Brenner, E. (2003). Hitting moving targets: A dissociation between the use of the target's speed and direction of motion. *Experimental Brain Research, 152*, 368-375.

Caljouw, S. R., van der Kamp, J., & Savelsberg, G. J. P. (2004). Catching optical information for the regulations of timing. *Experimental Brain Research, 155,* 427-438.

Cesqui, B., d'Avella, A., Portone, A., & Lacquaniti, F. (2012). Catching a ball at the right time and place: individual factors matter*. PLoS One, 7,* e31770.

Chapman, S. (1968). Catching a baseball. *American Journal of Physics, 36,* 868-870.

Cramer, A. O. J., van Ravenzwaaij, D., Matzke, D., Steingroever, H., Wetzels, R., Grasman, R. P. P. P., Waldorp, L. J., & Wagenmakers, E. J. (2015). Hidden multiplicity in exploratory multiway ANOVA: Prevalence and remedies. *Psychonomic Bulletin & Review*, 1-8.

Craig, C. M., Berton, E., Rao, G., Fernandez, L., & Bootsma, R. J. (2006). Judging where a ball will go: The case of curved free kicks in football. *Naturwissenschaften*, *93*, 97-101.

De la Malla, C., López-Moliner, J., & Brenner, E. (2014). Dealing with delays does not transfer across sensorimotor tasks. *Journal of Vision*, *14(12):8,* 1-17.

de Lussanet, M. H. E., Smeets, J. B. J., & Brenner, E. (2001). The effect of expectations on hitting moving targets: influence of the preceding target's speed. *Experimental Brain Research, 137*, 247-248.

de Rugy, A., Marinovic, W., & Wallis, G. (2012). Neural prediction of complex accelerations for object interception. *Journal of Neurophysiology, 107*, 766–71.

Dessing, J. C., Bullock, D., Peper, C. L., & Beek, P. J. (2002). Prospective control for manual interceptive actions: comparative simulations of extant and new model constructs. *Neural Networks, 15,* 163-179.

Dessing, J. C., Peper, C. E., Bullock, D., & Beek, P. J. (2005). How position, velocity and temporal information combine in the prospective control of catching: data and model. *Journal of Cognitive Neuroscience, 17,* 668-686.

Dessing, J. C., Oostwoud Wijdenes, L., Peper, C. E., & Beek, P. J. (2009a). Adaptations of lateral hand movements to early and late visual occlusion in catching. *Experimental Brain Research, 192,* 669-682.

Dessing, J. C., Oostwoud Wijdenes, L., Peper, C. E., & Beek, P. J. (2009b). Visuomotor transformation for interception: catching while fixating. *Experimental Brain Research, 196*, 511-527.

Dessing, J. C., & Craig, C. M. (2010). Bending it like Beckham: how to visually fool the goalkeeper. *PLoS One, 5(10)*, e13161.

Dessing, J. C., & Reid, S. A. (2013, November). *Spatial eye-hand coordination for manual interception.* Poster presented at the annual Society for Neuroscience Meeting, San Diego, CA, USA.

Duke, P. A., & Rushton, S. K. (2012). How we perceive the trajectory of an approaching object. *Journal of Vision, 12(3):9,* 1–16.

Fadde, P. J. (2006). Interactive video training of perceptual decision-making in the sport of baseball. *Technology, Instruction, Cognition, and Learning, 4*(3), 265–285.

Farrow, D., Chives, P., Hardingham C. & Sauces, S. (1998). The effect of video-based perceptual training on the tennis return of serve. *International Journal of Sport Psychology*, *29*, 231-242.

Field, A. P. (2013). *Discovering statistics using SPSS: (and sex and drugs and rock 'n' roll)* (4th ed.). Los Angeles, CA: SAGE Publications.

Fulvio, J. M., Green, C. S., & Schrater, P. R. (2014). Task-specific response strategy selection on the basis of recent training experience. *PLoS Computational Biology, 10(1)*, e1003425.

Fulvio, J. M., Maloney, L. T., & Schrater, P. R. (2015). Revealing individual differences in strategy selection through visual motion extrapolation. *Cognitive Neuroscience, 6(4)*, 169-79.

Georgopoulos, A. P. (2002). Cognitive motor control: spatial and temporal aspects. *Current Opinion in Neurobiology, 12,* 678-683.

Gray, R. (2002). “Markov at the bat”: A model of cognitive processing in baseball batters. *Psychological Science, 13(6),* 542-547.

Harris, J. M., & Dean, P. J. A. (2003). Accuracy and precision of binocular 3D motion perception. *Journal of Experimental Psychology: Human Perception and Performance*, 29, 869–881.

Harris, J. M., & Drga, V. F. (2005). Using visual direction in three-dimensional motion perception. *Nature Neuroscience, 8(2):* 229-33.

Hubbard, T. L. (1990). Cognitive representation of linear motion: possible direction and gravity effects in judged displacement. *Memory & Cognition, 18(3)*, 299-309.

Jacobs, D. M., & Michaels, C. F. (2006). Lateral interception I: operative variables, attunement, and calibration. *Journal of Experimental Psychology: Human Perception and Performance, 32*, 343-458.

Katsumata, H., & Russell, D. M. (2012). Prospective versus predictive control in timing of hitting a falling ball. *Experimental Brain Research, 216*, 499–514.

Kwon, O. S., Tadin, D., & Knill, D. C. (2015). Unifying account of visual motion and position perception. *Proceedings of the National Academy of Sciences USA, 112(26)*, 8142-7.

La Scaleia, B., Zago, M., & Lacquaniti, F. (2015). Hand interception of occluded motion in humans: A test of model-based versus on-line control. *Journal of Neurophysiology, 114,* 1577–1592.

Leclercq, G., Blohm, G., & Lefèvre, P. (2012). Accurate planning of manual tracking requires a 3D visuomotor transformation of velocity signals. *Journal of Vision*, 12(5), 6, 1–21,

Ledouit, S., Casanova, R., Zaal, F. T., & Bootsma, R. J. (2013). Prospective control in catching: the persistent angle-of-approach effect in lateral interception. *PloS one, 8*, e80827.

Mazyn, L. I. N., Savelsbergh, G. J. P., Montagne, G., & Lenoir, M. (2007). Planning and on-line control of catching as a function of perceptual-motor constraints. *Acta Psychologica, 126*, 59-78.

Montagne, G., Laurent, M., Durey, A., & Bootsma, R. (1999). Movement reversals in ball catching. *Experimental Brain Research, 129*, 87-92.

Mrotek, L. A., & Soechting, J. F. (2007a). Predicting curvilinear target motion through an occlusion. *Experimental Brain Research, 178(1)*, 99-114.

Mrotek, L. A., & Soechting, J. F. (2007b) Target interception hand-eye coordination and strategies. *The Journal of Neuroscience, 27*, 7297-7309.

Murdison, T. S., Leclercq, G., Lefèvre, P., & Blohm, G. (2015). Computations underlying the visuomotor transformation for smooth pursuit eye movements. *Journal of Neurophysiology*, *113*, 1377-1399.

Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia, 9*, 97-113.

Orban de Xivry, J. J., & Lefèvre, P. (2007). Saccades and pursuit: two outcomes of a single sensorimotor process. *The Journal of Physiology, 584(1),* 11-23.

Peper, L., Bootsma, R. J., Mestre, D. R., & Bakker, F. C. (1994). Catching balls: how to get the hand to the right place at the right time. *Journal of Experimental Psychology: Human Perception and Performance, 20(3),* 591-612.

Port, N. L., Lee, D., Dassonville, P., & Georgopoulos, A. P. (1997). Manual interception of moving targets. I. Performance and movement initiation. *Experimental Brain Research, 116*, 406-420.

Post, R. B., & Chaderjian, M. (1987). Perceived path of oblique motion: horizontal-vertical and stimulus-orientation effects. *Perception, 16(1)*, 23-8.

Rosenbaum, D. A. (1975). Perception and extrapolation of velocity and acceleration. *Journal of Experimental Psychology: Human Perception & Performance, 1,* 395-403.

Schmerler, J. (1976). The visual perception of accelerated motion. *Perception, 5,* 167-185.

Schütz, A. C., Braun, D. I., & Gegenfurtner, K. R. (2011). Eye movements and perception: A selective review. *Journal of Vision, 11(5):9*, 1-30.

Sharp, R. H., & Whiting, H. T. A. (1975). Information processing and eye movement behaviour in a ball catching skill*. Journal of Human Movement Studies, 1*, 124-131.

Smeets, J. B. J., & Brenner, E. (1995). Perception and action are based on the same visual information: distinction between position and velocity. *Journal of Experimental Psychology: Human Perception and Performance, 21,* 19–31.

Souman, J. L., Hooge, I. T. C., & Wertheim, A. H. (2005). Perceived motion direction during smooth pursuit eye movements. *Experimental Brain Research, 164*, 376–386.

Teixeira, L. A., Chua, R., Nagelkerke, P., & Franks, I. M. (2006). Use of visual information in the correction of interceptive actions. *Experimental Brain Research, 175*, 758-763.

Tijtgat, P., Bennett, S. J., Savelsbergh, G. J. P., De Clercq, D., & Lenoir, M. (2011). To know or not to know: influence of explicit advance knowledge of occlusion on interceptive actions. *Experimental Brain Research, 214,* 483-490.

Tresilian, J. R. (1993). Four questions of time-to-contact: an analysis of research in interceptive timing. *Perception, 22,* 653-680.

Tynan, P. D., & Sekuler, R. (1982). Motion processing in peripheral vision: Reaction time and perceived velocity. *Vision Research, 22(1)*, 61–68.

Weiss, Y., Simoncelli, E. P., & Adelson, E. H. (2002). Motion illusions as optimal percepts. *Nature Neuroscience*, *5(6),* 598-604.

Welchman, A. E., Tuck, V. L. & Harris, J. M. (2004). Human observers are biased in judging the angular approach of a projectile. *Vision Research, 44*, 2027–2042.

Whiting, H. T. A., & Sharp, R. H. (1974). Visual occlusion factors in a discrete ball-catching task. *Journal of Motor Behaviour, 6*, 11-16.

Wolpert, D. M., & Ghahramani, Z. (2000). Computational principles of movement neuroscience. *Nature Neuroscience, 3*, 1212-1217.

Zago, M., McIntyre, J., Senot, P., & Lacquaniti, F. (2009). Visuo-motor coordination and internal models for object interception. *Experimental Brain Research, 192*, 571-604.

Zago, M., Iosa, M., Maffei, V., & Lacquaniti, F. (2010). Extrapolation of vertical target motion through a brief visual occlusion. *Experimental Brain Research, 201(3)*, 365-84.

Zelaznik, H. N., Hawkins, B., & Kisselburgh, L. (1983). Rapid visual feedback processing in single-aiming movements. *Journal of Motor Behavior, 15*, 217-236.

Figure Captions

Figure 1: Experimental set-up and target trajectory shapes. **A**: Participant viewing images from a downward-facing computer screen via reflective Perspex. Finger movements were recorded by the touchscreen. **B**: Target trajectories (curved and straight) appearing in one of two initial zones (upper horizontal bars) and moving towards either of the final zones (lower horizontal bars). Figure reproduced with permission (doi: 10.6084/m9.figshare.4626007).

Figure 2: Trial view. **A**: Participant moves yellow cursor into predefined zone (green circle) to initiate a trial. **B**: Participant cursor appears closer to the bottom of the screen in red and pink target appears at the top simultaneously. The target must be intercepted at the line in the centre. Figure reproduced with permission (doi: 10.6084/m9.figshare.4626010).

Figure 3: Averaged lateral movement trajectories in Experiment 1. Figure 3 illustrates the movement trajectories averaged across all participants for curved target trajectories during each target occlusion condition for the Left (panel **A**) and Right (panel **B**) initial target zone. Within each panel, trajectories veering to the left are for the left final target zone and trajectories veering to the right are for the right final target zone. The vertical dashed lines indicate the average final target position. The width of the shaded areas around the average trajectory is 1 Standard Error. Figure reproduced with permission (doi: 10.6084/m9.figshare.4626013).

Figure 4: Significant main effects in Experiment 1. This figure shows the effects of final target zone on the arrival time ($T_{arrival}$; **A**) and constant error (CE; **F**), the effects of target curvature on the surplus movement (SM; **B**) and constant error (CE; **C**) and the effects of time of target occlusion on the arrival time ($T_{arrival}$; **D**) and surplus movement (SM; **E**). For all error bars, the length of each whisker represents one standard deviation (SD, i.e., total length of 2 SDs for panels **C** and **F**). Significant levels differences are indicated by lines in the graphs (except for effects with two levels). Figure reproduced with permission (doi: 10.6084/m9.figshare.4626016).

Figure 5: Significant Final Zone x Curvature x Time of Target Occlusion interactions for $T_{arrival}$ in Experiments 1 (**A** and **B**) and 2 (**C** and **D**). For all error bars, the length of each whisker represents one standard deviation. Horizontal lines show significant differences within the panels; asterisks represent significant differences between final target zones (i.e., between panels). Figure reproduced with permission (doi: 10.6084/m9.figshare.4626019).

Figure 6: The relevant interactions for the constant error (CE) in Experiment 1. Panel **A** shows the Curvature x Time of Target Occlusion interaction, panel **B** the Initial Zone x Time of Target Occlusion interaction, panel **C** the Final Zone x Time of Target Occlusion interaction, and panel **D** the Final Zone x Initial Zone x Time of Target Occlusion interaction. Note that the latter interaction was not significant, but is shown to illustrate that the interactions in **B** and **C** are mainly due to the diagonal trajectories. For all error bars, the length of each whisker represents one standard deviation. Colored vertical lines represent significant differences between times of target occlusion. On the right of panel **A**, lines

between symbols denote significant differences between the curvature levels. In panels **B** and **C**, the significant differences between initial and final target zones, respectively, are indicated for each time of target occlusion using asterisks. The schematic inset in each panel explains the used colors and symbols. Figure reproduced with permission (doi: 10.6084/m9.figshare.4626022).

Figure 7: Significant Final Zone x Curvature x Time of Target Occlusion interaction for CE in Experiment 1. For all error bars, the length of each whisker represents one standard deviation. Figure reproduced with permission (doi: 10.6084/m9.figshare.4626025).

Figure 8: Trajectories used in Experiment 2. In addition to the trajectories used in Experiment 1, straight 'Dummy' trajectories landed at more eccentric positions on the screen. The horizontal bars depict the initial and final target zones (from which the actual positions for each trial were randomly selected). Figure reproduced with permission (doi: 10.6084/m9.figshare.4626028).

Figure 9: The relevant interactions for the constant error (CE) in Experiment 2. For explanation, see caption of Figure 6. Figure reproduced with permission (doi: 10.6084/m9.figshare.4626034).

Figure 10: Schematic of two routes by which target motion information can influence manual interception. Target motion information can influence aiming/movement direction and online modulations of movement speed. This represents an essential feature of

interception model forwarded by Dessing et al., 2002, 2005, 2009a, b). Figure reproduced with permission (doi: 10.6084/m9.figshare.4626037).

Figure 11: The relevant interactions for the constant error (CE) in Experiment 3. For explanation, see caption of Figure 6. Figure reproduced with permission (doi: 10.6084/m9.figshare.4626040).

Figure 12: The relevant interactions for the constant error (CE) in Experiment 4. For explanation, see caption of Figure 6. Figure reproduced with permission (doi: 10.6084/m9.figshare.4626043).

Figure 13: The relevant interactions for the constant error (CE) in Experiment 5. For explanation, see caption of Figure 6. Figure reproduced with permission (doi: 10.6084/m9.figshare.4626046).

Supplementary Figure 1: Significant Final Zone x Curvature interaction for $T_{arrival}$ in Experiment 1. Vertical lines represent significant differences between level of curvature levels and final. For all error bars, the length of each whisker represents one standard deviation. Figure reproduced with permission (doi: 10.6084/m9.figshare.4626049).

Supplementary Figure 2: Final Zone x Initial x Curvature interaction for CE in Experiment 1. For all error bars, the length of each whisker represents one standard deviation. Differences between final zones and initial zones for each level of curvature are indicated by asterisks within the inset on the right of the figure. Note that for all combinations of initial and final zones all levels of curvature differed significantly. Figure reproduced with permission (doi: 10.6084/m9.figshare.4626052).