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Spatial biases in motion extrapolation for manual interception

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Research Article

Spatial biases in motion extrapolation for manual interception

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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.

45 Statement of Public Significance

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

56 Spatial biases in motion extrapolation for manual interception
57 Even our simplest interactions with the environment, such as picking up a cup of coffee,
58 require complex movement planning and coordination. Our brain must determine where
59 the cup is relative to our body, the hand movement required to reach the cup, and what
60 force needs to be applied to grasp and lift it. The processes involved have fascinated
61 scientists from numerous fields (e.g., Georgopoulos, 2002; Beek, Dessing, Peper & Bullock,
62 2003; Wolpert & Ghahramani, 2000). Reaching is even more complex when objects move in
63 space (e.g., catching a ball), because the reach must end anywhere along the path of the
64 object. To intercept the object at the right place at the right time we must account for its
65 continuous positional changes (Peper, Bootsma, Mestre & Bakker, 1994; Dessing, Bullock,
66 Peper & Beek, 2002; Dessing, Peper, Bullock & Beek, 2005; Brouwer, Brenner & Smeets,
67 2002; Cesqui, d'Avella, Portone & Lacquaniti, 2012; Tresilian, 1993; Caljouw, van der Kamp
68 & Savelsbergh, 2004). Although the mechanisms for reaching movements towards
69 stationary objects are relatively well understood, the exact mechanisms by which humans
70 successfully perform manual interception of moving objects are still elusive.

71 Research on interception has consistently reported that movement features depend
72 on details of the target's motion.¹ For instance, targets initially moving at a high speed cause
73 the effector to move directly to the interception point, arriving well in advance of the target
74 (although not always at the accurate location; Arzamarski , Harrison, Hajnal, & Michaels,
75 2007; Port, Lee, Dassinville & Georgopoulos, 1997; Bosco, Delle Monache & Lacquaniti,
76 2012). Moreover, when enough time is available the effector is not always moved directly
77 towards the interception point, but undergoes 'unnecessary', excess displacement. When

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.

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

90 The aforementioned effects have informed thinking about the control of manual
91 interception (Beek et al., 2003; Bootsma, Fayt, Zaal & Laurent 1997; Dessing et al., 2002,
92 2005; Ledouit et al., 2013; Montagne et al., 1999; Peper et al., 1994; Zhao & Warren, 2015).
93 Early arrival of the effector at the interception location has been taken as evidence for the
94 use of spatial predictions (Arzamarski et al., 2007; Port et al., 1997; Bosco et al., 2012).
95 Conversely, the effects of angle-of-approach and curvature argue for the use of
96 non-predictive interception strategies (Bootsma et al., 1997, 2015; Montagne et al., 1999;
97 Peper et al., 1994) or the use of initially inaccurate spatial predictions with online
98 corrections (Arzamarski et al., 2007; Smeets & Brenner, 1995; Brenner & Smeets, 1996).
99 One problem with such inferences is that behavioural features of the type discussed are not
100 always unique to a control strategy (Beek et al., 2003; Brouwer et al., 2003; Dessing et al.,
101 2005). Specific experimental manipulations are needed to uncover the perception-action

102 coupling underlying interception (e.g., nature of the information used, use of online
103 control). Visual target occlusion is a good candidate in this respect.

104 Target occlusion has been used to examine target motion extrapolation and the
105 (continuous) use of visual information about the target during interception (e.g., Dessing et
106 al., 2009a; Mazyn, Savelsbergh, Montagne & Lenoir, 2007; Mrotek & Soechting, 2007a;
107 Teixeira, Chua, Nagelkerke & Franks, 2006). Target occlusion, particularly in the final phase,
108 necessitates some form of prediction or extrapolation (Zago, Iosa, Maffei & Lacquaniti,
109 2010; Dessing et al., 2009a; Mrotek & Soechting 2007b; Katsumata & Russell, 2012; see also
110 Bosco et al., 2015). Successful catching is possible if a ball is visible until at least 240ms
111 before interception (Whiting & Sharp, 1974; Sharp & Whiting, 1975). After training,
112 occlusion causes strategic/qualitative changes in performance (i.e., catching closer to the
113 body and delaying movement initiation; Mazyn et al., 2007). In the current study, we will
114 vary the duration of the final occlusion to control the last visible target motion (Teixeira et
115 al., 2006), to highlight how behaviour is continuously modulated by information about
116 target motion.

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

125

126 Experiment 1: Manual interception with Occlusion

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

133

134 Materials and Methods

135 Participants

136 12 right-handed participants with normal or corrected-to-normal vision (average laterality
137 quotients: 0.93, range: 0.81-1; Oldfield, 1971) were included, recruited mainly through a
138 voluntary research participation scheme that awarded credit to students for participation in
139 research experiments. Participants provided written informed consent before participating.

140

141 Experimental Set-up

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

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).

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

165 The experiment took place in a dark room; the only light sources were the stimulus
166 presentation screen and a small lamp that switched on briefly between blocks of trials.
167 Vision of the arm and hand was blocked by a piece of white cardboard stretching from the
168 chinrest to the far edge of the reflector. To reduce friction of the finger on the glass touch
169 screen, a piece of thin foam was taped to the palmar side of the right index finger (without
170 this material the touch screen had difficulty detecting fast finger movements). Stimulus

171 presentation was controlled through Matlab (The Mathworks, Nattick, MA, USA) by Version
172 3 of the Psychophysics Toolbox (Brainard, 1997).

173

174 Procedures

175 Participants provided informed consent, completed the handedness questionnaire, and sat
176 in the height-adjustable chair before the experimenter placed the foam on the fingertip.
177 They then placed their head in the chin rest and fastened the Velcro strap so that the trials
178 could start. To start a trial, participants held the cursor (a small yellow circle; 6.7 mm
179 diameter; see Figure 2A) inside the predefined starting zone in the centre of the screen (a
180 larger green circle; 10.0mm diameter) for 250ms. Importantly, the cursor was presented
181 122.2mm above the finger in this phase. This manipulation was deemed necessary to ensure
182 participant's visual attention was in the centre of the screen at trial onset.³ If the finger was
183 initially positioned inside the starting zone the cursor was blue, informing the participant to
184 first exit the zone, upon which the cursor turned yellow. A horizontal white line was shown
185 in the middle of the screen (spanning the entire screen width) throughout the trial. Once
186 the trial started the cursor turned red and appeared at the exact finger position (i.e.,
187 122.2mm below screen centre). Simultaneously, a light pink target (5.6mm diameter)
188 appeared 122.2mm above the white line, moving at a constant downward speed
189 (122.2mm/s; movement time to reach the line: 1000ms), see Figure 2B. Target trajectories

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).

190 varied in terms of initial zone (111.0mm left or right of screen centre), final zone (111.0mm
191 left or right of screen centre), and curvature (leftward, none, rightward; Figure 1B). The
192 exact initial and final sideward target positions were randomly varied within a range of
193 194.4mm centred on the aforementioned zone centres. In the remainder of this manuscript,
194 we will refer to trajectories without curve as 'straight' trajectories and trajectories that start
195 and end on different sides of the screen as 'diagonal' trajectories. Relative to downward on
196 the screen, target motion directions for non-diagonal trajectories were 0° (possible range -
197 57.8° to 57.8°) and for diagonal trajectories they were -61.2° (possible range -73.7° to -12.8°)
198 or 61.2° (possible range 12.8° to 73.7°). New random initial/final positions were created for
199 each participant to avoid inducing systematic variations/deviations in our data. Trajectories
200 were generated by fitting a second-order polynomial through the initial, halfway and final
201 sideward target positions as a function of time; curve was generated by adding a 27.8mm
202 leftward or rightward offset to the halfway position. Participants intercepted the target on
203 the horizontal line using the red cursor. The target disappeared after it had reached the line
204 (or earlier for occlusion conditions), while the cursor was shown for a further 500ms;
205 participants thus never received explicit visual feedback on their performance for more than
206 a single frame.

207

208 Insert Figure 1 & 2 about here

209

210 Time of target occlusion was manipulated by having the target disappear after
211 250ms, 500ms, 750ms or 1000ms (i.e., no occlusion). Each participant completed five
212 repetitions of all 12 trajectories (2 initial zones x 2 final zones x 3 curvatures) for all
213 occlusion conditions. Occlusion conditions were presented in randomly ordered blocks of 60

214 trials. Our touchscreen did not always function perfectly, resulting in occasional jumps in the
215 cursor positions. To determine whether this happened, after each trial we fitted a cubic
216 spline through the sideward and upward cursor positions from trial onset until 500ms after
217 interception. If at any frame from target onset to interception the fitted 2D position was
218 further than 5 pixels from the measured position, the touchscreen was judged to have
219 missed finger displacement. In this case, as well as when the cursor exited the starting zone
220 within 100ms of target appearance the trial was repeated at a random position within the
221 remainder of the block; this ensured that we collected five valid trials for all conditions.
222 Based on this criterion, on average 10 trials were repeated for each participant.⁴ All
223 procedures were approved by the School of Psychology Research Ethics Committee of
224 Queen's University Belfast.

225

226 Data Analysis

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

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.

236 We conducted Shapiro-Wilk tests of composite normality to determine whether the
237 data was normally distributed. Even though Analysis of Variance (ANOVA) is relatively
238 robust to deviations from normality, we used an arbitrary cut-off to determine whether we
239 would run a parametric ANOVA. If the data for 20% or more of the conditions were not
240 normally distributed (i.e., Shapiro-Wilk test significant at an uncorrected alpha-level of
241 0.05), we would not use a full factorial repeated measures ANOVA, but a Friedman ANOVA
242 to analyze the main effects. As a result, CE and $T_{arrival}$ were analysed using a repeated
243 measures ANOVA, while SM was analysed using a Friedman ANOVA. When the Sphericity
244 assumption was violated for CE and $T_{arrival}$, corrected degrees of freedom were used (and
245 will be reported; epsilon < 0.75: Greenhouse-Geisser; epsilon > 0.75: Huyn-Feldt, Field,
246 2013).

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

256

257 **Results**

258 In this experiment, we examined the effects of visual occlusion of target trajectories with
259 varying initial/final positions and curvature on manual interception. In general, interceptive

260 behaviour was consistently influenced by all these factors, inducing spatial biases in the
261 movements and inaccurate interceptive behaviour; this can be appreciated from the
262 averaged trajectories shown in Figure 3. Figure 3 also illustrates that the interceptive
263 movements for all times of target occlusion are qualitatively similar to previously reported
264 movements for interception without occlusion (Arzamarski et al., 2007; Dessing et al., 2005;
265 Ledouit et al., 2013; Smeets & Brenner, 1995). Our exploratory analyses are discussed next;
266 to afford readability we will first present all main effects before discussing the interactions.

267

268 Insert Figure 3 about here

269

270 The main effect of curvature on SM was significant, $X^2(2, N=12) = 15.2$, $p = 0.5 \cdot 10^{-3}$;
271 participants used more excess movement to intercept curved than straight trajectories
272 (Figure 4B). There was also a significant effect of curvature on CE, $F(1.3, 13.9) = 364.5$, $p <$
273 $0.5 \cdot 10^{-6}$, $\eta_p^2 = 0.94$, which revealed a bias in the direction of the curve (Figure 4C). In
274 combination, these effects suggest participants had difficulty accurately extrapolating and
275 successfully intercepting curved target trajectories. Earlier target occlusion motivated earlier
276 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),
277 and more direct movement paths, $X^2(3, N=12) = 18.8$, $p = 0.3 \cdot 10^{-3}$ (Figure 4E). The cursor
278 arrived earlier at the right final zone than at the left ($T_{arrival}$) $F(1, 11) = 14.9$, $p = 0.0026$, $\eta_p^2 =$
279 0.58 (Figure 4A). On average, the interception point was undershot, which amounts to a bias
280 towards the left for right final target positions and vice versa (effect of Final Zone on CE),
281 $F(1, 11) = 41.5$, $p = 0.5 \cdot 10^{-4}$, $\eta_p^2 = 0.79$ (Figure 4F). Besides these main effects, interception
282 behaviour was influenced by several interactions, as discussed next.

283

284

Insert Figure 4 about here

285

286 There was a significant Final Zone x Curvature interaction for $T_{arrival}$, $F(2,22) = 10.0$, p
287 $= 0.8 \cdot 10^{-3}$, $\eta_p^2 = 0.48$, which appeared to be due to the effect of curvature being in opposite
288 direction for the two final zones (see Supplementary Figure 1).). This effect was modulated
289 by occlusion (i.e., significant Final Zone x Curvature x Time of Target Occlusion interaction,
290 $F(6,66) = 13.7$, $p < 0.5 \cdot 10^{-6}$, $\eta_p^2 = 0.56$). The effect of occlusion appeared to be stronger for
291 rightward curving targets (than for the other curve conditions) ending on the left and for
292 leftward curving targets ending on the right (Figure 5A&B).

293

294

Insert Figure 5 about here

295

296 The effect of curvature on CE (endpoints deviating in the direction of curvature)
297 increased with longer occlusion (significant Curvature x Time of Target Occlusion
298 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
299 Initial Zone x Time of Target Occlusion interaction, $F(2.1,23.3) = 9.6$, $p = 0.8 \cdot 10^{-3}$, $\eta_p^2 = 0.47$
300 (Figure 6B); post-hoc tests did not demonstrate significant differences, but a bias in the
301 direction of the initial zone appeared to increase with more occlusion. The significant Final
302 Zone x Time of Target Occlusion interaction, $F(3,33) = 24.8$, $p < 0.5 \cdot 10^{-6}$, $\eta_p^2 = 0.69$, revealed
303 an inward bias (i.e., errors towards the screen centre) that increased with longer occlusion
304 (Figure 6C). These occlusion-dependent effects highlight that imperfect performance is

305 accentuated by the removal of visual information, suggesting that with unconstrained
306 viewing participants relied on continuous target motion information.

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

312

313 Insert Figure 6 about here

314

315 There was a significant Final zone x Curvature x Time of Target Occlusion interaction
316 for CE, $F(6,66) = 4.1$, $p = 0.0014$, $\eta_p^2 = 0.27$, which showed that the effect of target curvature
317 for the longer occlusion is asymmetric: larger errors for rightward curving targets ending on
318 the left and leftward curving targets ending on the right (see Figure 7). Finally, we also
319 observed a significant Final zone x Initial Zone x Curvature interaction, $F(2,22) = 27.8$, $p =$
320 $0.1 \cdot 10^{-5}$, $\eta_p^2 = 0.72$, which showed that the effect of curvature is somewhat larger for
321 diagonal trajectories (Supplementary Figure 2).

322

323 Insert Figure 7 about here

324

325 **Discussion**

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

339 We observed several specific effects related to the target trajectory. Large biases in
340 the direction of curve increased with increasing occlusion. The effect of curve replicates
341 previous findings and suggests that humans have problems perceiving and accounting for
342 effects of curve (Craig et al., 2006; Dessing & Craig, 2010; Mrotek & Soechting, 2007a).
343 However, we mainly observed an effect of curve-related outward target motion at
344 interception, which suggests a modulating effect of trajectory configurations (see below).
345 Participants never received explicit feedback on the occluded target's final position,
346 preventing them from correcting for their errors (Mrotek & Soechting, 2007a). The later
347 arrival times and more excess movements for curved trajectories and less target occlusion
348 suggest that our participants adopted a strategy involving online adjustments to correct for

349 initial inaccuracies when possible (Brenner & Smeets, 2009a, 2009b, 2011; Brenner, Driesen
350 & Smeets, 2014; Montagne et al., 1999; Peper et al., 1994; Dessing et al., 2002, 2005, 2009a;
351 Arzamarski et al., 2007; Ledouit et al., 2013).

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

364 It is possible that expectations influence interceptive behaviours (Brouwer,
365 Middelburg, Smeets & Brenner, 2003) particularly when information is limited, such as after
366 target occlusion. The expectation of gravitational acceleration is a particular example of this;
367 it has been suggested that humans use an internal model of gravity (possibly shaped by
368 experience) to generate expectations regarding the motion of objects (Zago et al., 2010; de
369 Ruy, Marinovic & Wallis, 2012). Other research has shown that events in previous trials can
370 influence expectations of what is to come in the current trial (Dessing et al., 2009a; De
371 Lussanet, Smeets & Brenner, 2001; Brenner & Smeets, 2011). This may also result in

372 expectations concerning sequences of conditions (Gray, 2002; Zelaznik, Hawkins &
373 Kisselburgh, 1983; Tijtgat, Bennett, Savelsbergh, De Clercq & Lenoir, 2011).

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

393

394

Insert Figure 8 about here

395

396 Experiment 2: Occlusion with Additional Eccentric Dummy Trajectories

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

404

405 Methods

406 This experiment was conducted with eight right-hand participants (average laterality
407 quotient: 0.95; range: 0.86-1; Oldfield, 1971), two of whom had participated in Experiment
408 1.⁵ The experiment and analyses slightly differed from the previous experiment. To make
409 space on the screen for the dummy final zones, the initial and final zones were slightly
410 smaller (118.0mm) and their centres were located closer to screen centre (67.3mm) than in
411 previous experiments. Relative to downward on the screen, target motion directions for
412 non-diagonal trajectories were 0° (possible range -44.0° to 44.0°) and for diagonal
413 trajectories they were -47.8° (possible range -64.2° to -7.8°) or 47.8° (possible range 7.8° to
414 64.2°). Only three Times of Target Occlusion were used (333ms, 667ms, 1000ms [i.e., no
415 occlusion]). The critical manipulation was the introduction of additional dummy trajectories
416 without curve that started in one of the initial zones and moved towards one of two
417 additional, more eccentric final zones on the same side of the screen (i.e., the centres of

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

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

422 Trajectories were generated in the same manner as in Experiment 1 for the two final
423 zones closest to the screen centre. For the experimental conditions, 10 repetitions were run
424 for each of the two initial zones, two final zones, three curves, and three target occlusion
425 conditions; the number of dummy trajectories was set such that across all trials there was a
426 25% chance of a target landing in any of the four zones (and a 50% chance of the dummy
427 trajectory starting in either initial zone). On average 80 trials were repeated for each
428 participant (see Experiment 1 for criteria). We conducted customized repeated measure
429 ANOVAs that included only the Curvature x Time of Target Occlusion, Initial Zone x Time of
430 Target Occlusion, Final Zone x Time of Target Occlusion and Final Zone x Curvature x Time of
431 Target Occlusion interactions for CE, and the Final Zone x Curvature x Time of Target
432 Occlusion interaction for T_{arrival} . Across all tested effects we applied a Holm-Sidak correction
433 to the 0.05 alpha-level (for 5 effects); post-hoc analyses (using paired-samples *t*-tests) used
434 an additional Holm-Sidak correction on the corrected alpha-level associated with each
435 effect.

436

437 **Results/Discussion**

438 Our analyses showed that the presence of dummy trajectories removed only a single effect.
439 The Final Zone x Curvature x Time of Target Occlusion interaction for CE was not significant
440 ($p = 0.45$). The same interaction was significant for T_{arrival} , $F(4,28) = 27.7$, $p < 0.5 \cdot 10^{-6}$, $\eta_p^2 =$
441 0.80, and showed a distinct effect of early occlusion (i.e., earlier arrival at the final position)

442 for rightward curving trajectories ended in the left final zone and for leftward curving
443 trajectories ending in the right final zone (see Figure 5C&D). The directional interception
444 error was modulated by a significant Curvature x Time of Target Occlusion interaction,
445 $F(1.3,9.1) = 20.9$, $p = 0.8 \cdot 10^{-3}$, $\eta_p^2 = 0.75$, reflecting a bias in the direction of curve that
446 increased with more target occlusion (see Figure 9A). Similarly, the significant Initial Zone x
447 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
448 Target Occlusion, $F(2,14) = 28.6$, $p = 0.1 \cdot 10^{-4}$, $\eta_p^2 = 0.80$, interactions showed similar patterns
449 to the main experiment (see Figures 9B and C). Again, we examined the latter interactions
450 for CE (Figure 9D), which mainly illustrated a larger increase in errors with longer occlusion
451 mainly for diagonal target trajectories.

452 We thus observed that the asymmetry in the effects of curve for longer occlusion
453 between final zones was not observed in Experiment 2; this strongly suggests that the
454 *absence* of effects of curve for targets moving inward at interception due to curve was due
455 to expectations concerning the range of final target positions (see also Dessing & Craig,
456 2010). Because all other effects were present again in Experiment 2, we conclude that these
457 were not due to a lack of eccentric final target zones. Given that the spatial errors were
458 mainly present for curved and diagonal trajectories and increased with increasing occlusion,
459 it seems likely that with full vision, online control was used to correct for any biases in initial
460 motion processing for curved and diagonal trajectories. Target occlusion prevented effective
461 online corrections and thus resulted in spatial biases (i.e., not fully accounting for unseen
462 target motion). This is most evident for the increasing effect of curve with longer occlusion,
463 which can be largely explained by participants not taking future effects of curve (due to
464 sideward acceleration) into account and thus only using the last seen motion direction
465 (Dessing & Craig, 2010).

466

467

Insert Figure 9 & 10 about here

468

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

489 target to have passed; the idea was that performance in this task would reflect movement
490 aiming, but not online information-based modulations of movement speed.

491

492 **Experiment 3: Occlusion-induced biases in motion extrapolation**

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

499

500 **Method**

501 We examined the effects of curvature, initial and final target zone and target occlusion on
502 CE (twelve right-handed participants [average laterality quotient: 0.91; range: 0.75-1;
503 Oldfield, 1971]). Experimental parameters were unchanged from Experiment 1, with the
504 exception that participants were no longer required to move to intercept the target landing
505 on the central line. Rather, participants were instructed to observe the moving target until it
506 disappeared. Half a second after the target crossed the line the cursor appeared at the
507 centre, coupled with an auditory cue informing participants to move the cursor (controlled
508 by a computer mouse with standard gain settings; position recorded at mouse click). The
509 cursor was constrained to move along the central line; participants positioned the cursor
510 where they judged the target to have passed. On average 4 trials were repeated for each
511 participant, in case the cursor started moving prior to the auditory cue. Each participant
512 completed a block of 40 practice trials with randomized target visibility, followed by four

513 blocks of 60 trials (one for each Time of Target Occlusion, presented in random order), with
514 conditions randomized within the blocks. We predicted that if the spatial biases in
515 Experiment 1 were associated with online information-based modulations of movement
516 speed (Dessing et al., 2009a, b), these biases should disappear in our judgment task. Our
517 analyses focused on the Initial Zone x Time of Target Occlusion and Final Zone x Time of
518 Target Occlusion interactions, although we also considered the Curvature x Time of Target
519 Occlusion interaction for comparison with the previous experiments; we only analysed the
520 spatial error in the judgment (CE). Statistical analyses were the same as in Experiment 2,
521 with the exception that the within-ANOVA alpha-level correction was only done for 3
522 effects.

523

524 **Results/Discussion**

525 Data analyses showed that the spatial judgment error was significantly affected by an Initial
526 Zone x Time of Target Occlusion, $F(2.0,22.3) = 15.8$, $p = 0.5 \cdot 10^{-4}$, $\eta_p^2 = 0.59$, and Final Zone x
527 Time of Target Occlusion interaction, $F(1.9,21.3) = 20.5$, $p = 0.1 \cdot 10^{-4}$, $\eta_p^2 = 0.65$. Both
528 interactions showed the same pattern as in Experiment 1 (Figure 11B & C; plotted together
529 in Figure 11D), which strongly suggests that the spatial biases during interception were due
530 to target motion-related variations in movement aiming (e.g., imperfect motion
531 extrapolation), rather than in movement speed. Further confirmation of this came from the
532 significant Curvature x Time of Target Occlusion interaction, $F(1.7,18.3) = 101.5$, $p < 0.5 \cdot 10^{-6}$,
533 $\eta_p^2 = 0.90$, which revealed a bias in the direction of curvature increasing with increasing
534 target occlusion (Figure 11A).

535 Imperfect/biased motion extrapolation could result in deviations in movement
536 aiming. We realized that one specific aspect of our design could influence such effects: the

537 cursor was shown initially and reappeared in the centre of the screen after target
538 disappearance. This constant cursor position could provide a reference for motion
539 extrapolation, although we are not aware of any evidence for this. If motion extrapolation
540 would be biased toward the visual reference position, this could induce inward biases. We
541 thus conducted a judgment experiment in which the cursor appeared at the start of the
542 response period at a random position along the central line.

543

544 **Experiment 4: Occlusion-induced biases in motion extrapolation II**

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

547

548 **Method**

549 This experiment included twelve right-handed participants (average laterality quotient:
550 0.93; range: 0.75-1; Oldfield, 1971). The experimental set-up and procedures were the same
551 as Experiment 3, with the exception that the cursor was invisible during target motion and
552 appeared at a random position along the line when participants were cued to indicate the
553 judged final target position. On average 9 trials were repeated for each participant. Our
554 analyses again focused on the Initial Zone x Time of Target Occlusion, Final Zone x Time of
555 Target Occlusion interactions for CE. Even though the Curvature x Time of Target Occlusion
556 interaction should not have been influenced by the central cursor position, it was included
557 in our analyses for comparison with the previous Experiments.

558

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.

559 **Results/Discussion**

560 Just like in Experiment 3, directional error was modulated by significant Initial Zone x Time
561 of Target Occlusion, $F(1.6,18.1) = 24.2$, $p = 0.2 \cdot 10^{-4}$, $\eta_p^2 = 0.68$, and Final Zone x Time of
562 Target Occlusion, $F(3,33) = 19.3$, $p < 0.5 \cdot 10^{-6}$, $\eta_p^2 = 0.64$, interactions, which showed the
563 same pattern as before (Figure 12B-D). We also replicated the Curvature x Time of Target
564 Occlusion interaction, $F(2.9,31.4) = 164.1$, $p < 0.5 \cdot 10^{-6}$, $\eta_p^2 = 0.94$, showing a bias in the
565 direction of curvature increasing with increasing target occlusion (Figure 12A). This confirms
566 that the aforementioned spatial biases were not due to the visible central starting position
567 of the cursor.

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

582 could be pursued for longer, which should thus reduce any part of the errors for early
583 occlusion related to the limited pursuit duration.

584

585 **Experiment 5: Pursuit duration-dependent biases in motion extrapolation**

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

590

591 **Method**

592 Twelve right-handed participants gave their informed consent (average laterality quotient:
593 0.92; range: 0.75-1; Oldfield, 1971). We showed the target at its initial position for one
594 second, allowing participants to shift their gaze toward the target before it started to move,
595 and thus track it for longer before it disappeared (in the early occlusion condition). All other
596 experimental parameters and analyses remained the same as the previous experiments
597 (N.B., the initial cursor position and time of appearance matched Experiment 3). On average
598 5 trials were repeated for each participant.

599

600 **Results/Discussion**

601 Just like in the previous experiments, the spatial judgment error (CE) was modulated by a
602 significant Curvature x Time of Target Occlusion interaction, $F(2.1,22.7) = 183.4$, $p < 0.5 \cdot 10^{-6}$,
603 $\eta_p^2 = 0.94$, due to a bias in the direction of curvature that increased with increasing target
604 occlusion (see Figure 13A). The Initial Zone x Time of Target Occlusion, $F(1.8,20.7) = 37.7$, $p <$
605 $5 \cdot 10^{-7}$, $\eta_p^2 = 0.77$, and Final Zone x Time of Target Occlusion, $F(3,33) = 34.2$, $p < 5 \cdot 10^{-7}$, $\eta_p^2 =$

606 0.76, interactions also showed the same pattern as before (see Figure 13B-D). These results
607 suggest that limited pursuit did not increase the errors in the long occlusion condition in the
608 previous experiments.

609

610 **General Discussion**

611 Many studies have considered the information and strategies for manual interception
612 (Chapman, 1968; Bootsma et al., 1997; Montagne et al., 1999; Beek et al., 2003; Dessing et
613 al., 2005; Zago, McIntyre, Senot & Lacquaniti, 2009; Smeets & Brenner, 1995; Peper et al.,
614 1994) and which task features influence which behavioural features. Here, we explored
615 interception behaviour in situations with incomplete target motion information (target
616 occlusion) for a range of different target trajectories. We observed very direct movements
617 and long waiting times at interception with early target occlusion and straight target
618 trajectories. However, arrival times were later for curved trajectories and for shorter
619 occlusion. Spatial biases increased with occlusion when the target crossed the screen during
620 the trajectory. This suggests that when more of the trajectory was visible participants used
621 the available viewing time to correct for initial inaccuracies where possible and update their
622 interceptive movement online (Brenner & Smeets, 2009a, 2009b, 2011; Brenner et al., 2014;
623 Montagne et al., 1999; Peper et al., 1994; Dessing et al., 2002, 2005, 2009a; Tresilian et al.,
624 2009; Arzamarski et al., 2007; Ledouit et al., 2013). However, based on this data we cannot
625 determine whether the movement updates depended on updated spatial predictions or on
626 another type of non-predictive continuous control (Dessing et al., 2005). Curved target
627 trajectories consistently resulted in large biases in the curve direction that increased with
628 increasing occlusion; straight trajectories only resulted in very small errors across all target

629 occlusion conditions. The observed pattern was consistent with the suggestion that
630 participants did not account for effects of curve (Dessing & Craig, 2010; Ledouit et al., 2013;
631 Mrotek & Soechting, 2007a), which has been ascribed to the limited sensitivity to
632 acceleration of the human visual system (i.e., sideward curve occurred due to sideward
633 acceleration; Dessing & Craig, 2010; Craig et al., 2006; Brouwer et al., 2002; Rosenbaum,
634 1975; Schmerler, 1976). However, in Experiment 2, which included a wider range of final
635 target positions (i.e., using dummy trajectories), we showed that expectations concerning
636 this range could reduce this effect (see also Dessing & Craig, 2010).

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

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

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

665 Our experiments highlight that humans can quite accurately intercept targets
666 moving on straight trajectories and any target that is visible throughout its entire trajectory.
667 Performance is greatly diminished when accurate extrapolation of curved and occluded
668 target trajectories is required and time pressure is added. After occlusion, spatial biases
669 occur because unseen target motion is not adequately accounted for (e.g., Mrotek &
670 Soechting, 2007a; Dessing et al., 2009a; Ledouit et al., 2013; see also Bosco et al., 2012).
671 Biases could arise within motion direction perception, which have been reported both for
672 motion in depth (Harris & Dean, 2003; Harris & Drga, 2005; Duke & Rushton, 2012;
673 Welchman, Tuck, & Harris, 2004) and in the frontal plane (Hubbard, 1990; Souman, Hooge,
674 & Wertheim, 2005; Post & Chaderjian, 1987; Tynan & Sekuler, 1982). Besides in the actual
675 information used, biases may depend on how motion signals are coded and combined
676 (Baddeley & Tripathy, 1998; Barlow & Tripathy, 1997; Kwon, Tadin, & Knill, 2015; Leclercq,

677 Lefèvre, & Blohm, 2012; Mudison, Leclercq, Lefèvre, & Blohm, 2015; Weiss, Simoncelli, &
678 Andelson, 2002). Evidently, if motion extrapolation is based on biased motion signals, it
679 should show systematic biases in absence of compensatory mechanisms. Mechanisms for
680 motion extrapolation, however, could also cause biases, for instance through the 'model'
681 used for extrapolation (Bosco et al., 2012, 2015; Fulvio, Green, & Schrater, 2014; Fulvio,
682 Maloney, & Schrater, 2015). The biases observed here are trajectory-dependent, which
683 seems to favour an explanation in terms of biased motion signals (rather than biased
684 extrapolation mechanisms). However, a definitive conclusion about this requires more
685 dedicated experiments on motion perception.

686 Our findings have some potential practical implications. The effects of occlusion in
687 this study were pivotal for our interpretation of the observed target trajectory-dependent
688 movement biases (see also, Dessing et al., 2009a; Mazyn et al., 2007; Mrotek & Soechting,
689 2007a; Teixeira et al., 2006). Visual occlusion has been forwarded as useful technique for
690 sports training (Fadde, 2006; Farrow, Chives, Hardingham, & Saucedo, 1998), but it is known
691 that certain biases can only be corrected for through terminal feedback (Mrotek &
692 Soechting, 2007a), which cannot be guaranteed in such scenarios. In combination with our
693 findings, this suggests that the usefulness of visual occlusion for training purposes may well
694 be very situation-dependent.

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

SPATIAL BIASES IN INTERCEPTION

700 trajectories, the most likely explanation is that they are present within motion signals

701 feeding into the extrapolation mechanism.

702

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SPATIAL BIASES IN INTERCEPTION

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884 **Figure Captions**

885

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

891

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

896

897 Figure 3: Averaged lateral movement trajectories in Experiment 1. Figure 3 illustrates the
898 movement trajectories averaged across all participants for curved target trajectories during
899 each target occlusion condition for the Left (panel **A**) and Right (panel **B**) initial target zone.
900 Within each panel, trajectories veering to the left are for the left final target zone and
901 trajectories veering to the right are for the right final target zone. The vertical dashed lines
902 indicate the average final target position. The width of the shaded areas around the average
903 trajectory is 1 Standard Error. Figure reproduced with permission (doi:
904 [10.6084/m9.figshare.4626013](https://doi.org/10.6084/m9.figshare.4626013)).

905

906 Figure 4: Significant main effects in Experiment 1. This figure shows the effects of final
907 target zone on the arrival time (T_{arrival} ; **A**) and constant error (CE; **F**), the effects of target
908 curvature on the surplus movement (SM; **B**) and constant error (CE; **C**) and the effects of
909 time of target occlusion on the arrival time (T_{arrival} ; **D**) and surplus movement (SM; **E**). For all
910 error bars, the length of each whisker represents one standard deviation (SD, i.e., total
911 length of 2 SDs for panels **C** and **F**). Significant levels differences are indicated by lines in the
912 graphs (except for effects with two levels). Figure reproduced with permission (doi:
913 10.6084/m9.figshare.4626016).

914

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

920

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

929 between symbols denote significant differences between the curvature levels. In panels **B**
930 and **C**, the significant differences between initial and final target zones, respectively, are
931 indicated for each time of target occlusion using asterisks. The schematic inset in each panel
932 explains the used colors and symbols. Figure reproduced with permission (doi:
933 10.6084/m9.figshare.4626022).

934

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

938

939 Figure 8: Trajectories used in Experiment 2. In addition to the trajectories used in
940 Experiment 1, straight 'Dummy' trajectories landed at more eccentric positions on the
941 screen. The horizontal bars depict the initial and final target zones (from which the actual
942 positions for each trial were randomly selected). Figure reproduced with permission (doi:
943 10.6084/m9.figshare.4626028).

944

945 Figure 9: The relevant interactions for the constant error (CE) in Experiment 2. For
946 explanation, see caption of Figure 6. Figure reproduced with permission (doi:
947 10.6084/m9.figshare.4626034).

948

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

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

954

955 Figure 11: The relevant interactions for the constant error (CE) in Experiment 3. For
956 explanation, see caption of Figure 6. Figure reproduced with permission (doi:
957 10.6084/m9.figshare.4626040).

958

959 Figure 12: The relevant interactions for the constant error (CE) in Experiment 4. For
960 explanation, see caption of Figure 6. Figure reproduced with permission (doi:
961 10.6084/m9.figshare.4626043).

962

963 Figure 13: The relevant interactions for the constant error (CE) in Experiment 5. For
964 explanation, see caption of Figure 6. Figure reproduced with permission (doi:
965 10.6084/m9.figshare.4626046).

966

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

971

972 Supplementary Figure 2: Final Zone x Initial x Curvature interaction for CE in Experiment 1.
973 For all error bars, the length of each whisker represents one standard deviation. Differences

974 between final zones and initial zones for each level of curvature are indicated by asterisks
975 within the inset on the right of the figure. Note that for all combinations of initial and final
976 zones all levels of curvature differed significantly. Figure reproduced with permission (doi:
977 10.6084/m9.figshare.4626052).

978