

# **The predictability of a target's motion influences gaze, head and hand movements when trying to intercept it**

Cristina de la Malla<sup>1,2,\*</sup>, Simon K. Rushton<sup>3</sup>, Kait Clark<sup>3,4</sup>, Jeroen B.J. Smeets<sup>2</sup> and Eli Brenner<sup>2</sup>

<sup>1</sup> Vision and Control of Action (VISCA) Group, Department of Cognition, Development and Psychology of Education, Institut de Neurociències, Universitat de Barcelona (\*contact author: c.delamalla@ub.edu)

<sup>2</sup> Department of Human Movement Sciences, Vrije Universiteit Amsterdam

<sup>3</sup> School of Psychology, Cardiff University

<sup>4</sup> Department of Health and Social Sciences, University of the West of England

## **Abstract**

Does the predictability of a target's movement and of the interception location influence how the target is intercepted? In a first experiment, we manipulated the predictability of the interception location. A target moved along a haphazardly curved path, and subjects attempted to tap on it when it entered a hitting zone. The hitting zone was either a large ring surrounding the target's starting position (Ring condition) or a small disk that became visible before the target appeared (Disk condition). The interception location gradually became apparent in the Ring condition, whereas it was immediately apparent in the Disk condition. In the Ring condition subjects pursued the target with their gaze. Their head and hand gradually moved in the direction of the future tap position. In the Disk condition subjects immediately directed their gaze towards the hitting zone by moving both their eyes and heads. They also moved their hands to the future tap position sooner than in the Ring condition. In a second and third experiment we made the target's movement more predictable. Although this made the targets easier to pursue, subjects now shifted their gaze to the hitting zone soon after the target appeared in the Ring condition. In the Disk condition they still usually shifted their gaze to the hitting zone at the beginning of the trial. Together, the experiments show that predictability of the interception location is more important than predictability of target movement in determining how we move to intercept targets.

33 **New and Noteworthy**

34       We show that if people are required to intercept a target at a known location they direct  
35 their gaze to the interception point as soon as they can, rather than pursuing the target with their  
36 eyes for as long as possible. The predictability of the interception location rather than the  
37 predictability of the path to that location largely determines how the eyes, head and hand move.

## 38 **Introduction**

39

40       When interacting with objects people normally direct their gaze towards them (Land and  
41 Hayhoe, 2001; Johansson et al., 2001; Pelz et al., 2001; Mennie et al., 2007; Smeets, et al.,  
42 1996; for reviews see Hayhoe and Ballard, 2005; Land, 2006). When objects move in the  
43 environment, people almost automatically track them with their gaze (Lisberger et al., 1987;  
44 Dorr et al., 2010), often with a combination of eye and head movements (Orban de Xivry and  
45 Lefevre, 2007; Bahill and McDonald, 1983; Brenner and Smeets, 2007; 2009; Mrotek and  
46 Soechting, 2007; Soechting and Flanders, 2008). This allows them to keep the object of interest  
47 foveated, providing the maximal spatial resolution at the target (Schütz et al., 2009). Other  
48 advantages of looking at targets when one needs to interact with them are that it helps predict  
49 the target's future trajectory (Spering et al., 2011) leading to more precise interception (Brenner  
50 and Smeets, 2011; Fookien et al., 2016), and reduces the effects that irrelevant target features  
51 have on the object's apparent motion (Braun et al., 2008; de la Malla, et al., 2018; 2019) leading  
52 to more accurate performance (de la Malla et al., 2017).

53       An important factor that has received little attention in relation to how people interact  
54 with moving targets is how the predictability of the target's movement influences action. Most  
55 of what is known about intercepting moving objects is based on studying how targets such as  
56 balls with highly predictable movement trajectories are intercepted. However, predicting how a  
57 target will continue to move is not always so straightforward. Imagine for example that the wind  
58 blows away some notes that you were carrying to the other side of a lawn. The notes will be  
59 moving haphazardly across the lawn so you will probably try to track them with your gaze  
60 while gathering them. However, the notes probably cannot be tracked very smoothly, because  
61 inevitable inaccuracy in anticipating a note's future position will lead to tracking errors when  
62 this anticipated position is used to overcome the latency that is inherent in gaze control (van den  
63 Berg, 1988; Robinson, 1965).

64       If a target is moving predictably, the observer has the option of predicting where it will be  
65 some time in the future and moving their gaze to wait at that location. This would explain the  
66 anticipatory gaze shifts that are found when a target moves back and forth (Lisberger et al.,  
67 1981; Bahill and McDonald, 1983) or bounces off a hard surface (Land and McLeod, 2000;  
68 Diaz et al., 2013). Anticipating where a target will be a considerable time in the future makes it  
69 possible to successfully intercept targets even if they are not tracked accurately (Cesqui et al.,  
70 2015) or gaze is intentionally diverted from the target (López-Moliner et al., 2016). If a target is  
71 moving unpredictably, anticipating where it will be a considerable time in the future is not a  
72 reliable option, unless for some reason the future location is known. Here we systematically  
73 examine how being confronted with unpredictable target motion influences pursuit and

interceptive behaviour, and the extent to which knowing where the target will be at some time in the future influences this.

In a first experiment we measured gaze, head and hand movements as subjects attempted to hit unpredictably moving targets. They were asked to hit the targets when the targets crossed into a hitting zone that was visible from the beginning of the trial. In one condition (the Ring condition) the hitting zone was a large ring so that the exact position at which the target will cross the ring gradually became clearer as time progressed (Graf et al., 2005). In the other condition (the Disk condition) the hitting zone was indicated by a small disk so the exact hitting position was evident from the start. In a second experiment the targets moved at a constant speed on straight paths to the same hitting zones, which made it easier to pursue the targets as well as always making it possible to predict where the targets had to be hit from the moment they started to move. In a last experiment the targets moved on a limited number of (straight) trajectories to make the target's motion even more predictable.

## Methods

### *Subjects*

Eight subjects (1 author, 1 male) took part in the first experiment (age range 26-39). Two of the subjects reported being left-handed. Five subjects (1 male, 1 left-handed) took part in both the second and third experiments (age range 27-33). Two of the subjects took part in all three experiments. Except for the author that took part in the first experiment, all subjects were naïve to the purposes of the experiments. All subjects had normal or corrected-to-normal vision. None had evident motor abnormalities. All subjects gave written informed consent. The study was part of a program that was approved by the ethical committee of the Faculty of Behavioural and Movement Sciences at the Vrije Universiteit Amsterdam. The experiments were carried out in accordance with the approved guidelines.

### *Apparatus*

The three experiments were conducted in a normally illuminated room. Subjects stood in front of a large screen (Techplex 150, acrylic rear projection screen; width: 1.25 m; height: 1.00 m; tilted backwards by 30° to make tapping more comfortable) onto which the stimuli were projected (In-Focus DepthQ Stereoscopic Projector; resolution 800 by 600 pixels; screen refresh rate: 120 Hz; Figure 1A). The setup gave subjects a clear view of the stimuli as well as of their arm, hand and finger. Subjects were not restrained in any way and had to intercept the projected targets by tapping on them. An infrared camera (Optotrak 3020, Northern Digital) that was

110 positioned at about shoulder height to the left of the screen measured (at 250 Hz) the position of  
111 an infrared marker attached to the nail of the index finger of the subjects' dominant hand.

112 Subjects were free to move in any way they wanted during the experiments. To measure  
113 their head movements, we had subjects use their teeth to hold a biteboard with a dental imprint.  
114 The positions of three infrared markers attached to the biteboard were monitored by the  
115 Optotrak. The movement of the head was inferred from the movement of the biteboard. The use  
116 of personal dental imprints means that the position of the head (and thus of the eyes) relative to  
117 the biteboard never changes, so their relative positions only need to be determined once.

118 Eye movements (rotations) with respect to the head were registered with a head-  
119 mounted eye-tracking system (Eyelink II, SR Research) at 500 Hz. Where subjects were looking  
120 on the screen was determined by combining the measurements of eye in head orientation from  
121 the eye tracking system with the position of the eyes and orientation of the head from the  
122 recorded biteboard marker positions.

123

#### 124 *Calibration*

125 In order to relate our gaze measurements to positions of stimuli on the screen (details  
126 described in the next paragraph), we needed to know the spatial coordinates of the images on  
127 the screen. We used a pointer consisting of a rod with one tapered end and three infrared  
128 markers attached to a surface on the other end to calibrate the screen. This pointer was first  
129 calibrated by placing an additional marker at the tip of the tapered end to determine the position  
130 of the tip relative to the three markers. The rendering of images on the screen was then  
131 calibrated by placing the tip of the pointer at five consecutively indicated image positions on the  
132 screen. The coordinates of the image positions were determined from the positions of the three  
133 markers attached to the pointer.

134 The pointer and calibrated screen were used to determine the positions of the eyes  
135 relative to the biteboard. The pointer was attached to a tripod and was placed between the  
136 subject and the screen. Subjects were asked to look with one eye and move their head until the  
137 tip of the pointer was aligned with a small white dot presented on the calibrated screen. The  
138 markers of both the biteboard and the pointer were recorded by the Optotrak. Subjects could  
139 move their heads however they wanted. Once they considered the tip of the pointer to be aligned  
140 with the current dot on the screen, they had to press the button of a mouse that they were  
141 holding in their hand. If they had moved less than 1 mm during the last 300 ms before doing so,  
142 a new dot appeared at a different position and they had to repeat the procedure. Otherwise they  
143 had to press again after making sure that the alignment was still fine. Subjects had to align the  
144 tip of the pointer with 20 dots using only the left eye and then with 20 dots using only the right  
145 eye. Each time they considered the tip of the pointer and the dot to be aligned with one of their  
146 eyes, we converted the coordinates of the tip of the pointer and of the dot on the screen into a

147 line with respect to the markers attached to the biteboard. These lines all pass through the eye,  
148 but with each measurement providing a different line with respect to the markers of the  
149 biteboard. The position with respect to the biteboard that minimized the sum of the distances to  
150 all lines was considered to be the position of the eye. From then on, we could determine the  
151 positions of the two eyes from measured positions of the markers on the biteboard.

152         Next, we calibrated the eye movement recordings. To do so, we presented a dot at the  
153 centre of the screen, and asked subjects to move their heads for 30 s while maintaining fixation  
154 on the dot. By combining the coordinates of the pupil with respect to the head from the Eyelink  
155 data with the position of the dot relative to the head (based on the calibrated screen and the  
156 biteboard marker coordinates), we determined the scaling of Eyelink coordinates that minimized  
157 the deviations in calculated gaze position throughout this period (for each eye). We verified this  
158 calibration by asking subjects to look at the screen and rendering dots at the positions at which  
159 we considered the subjects to be looking with their left and right eyes. If the two dots were at  
160 about the same place, and subjects reported that the dots were at the positions they were  
161 looking, the calibration was considered correct. If not, the calibration was repeated.

162         The final step in the calibration was to relate the position of the fingertip marker to  
163 where the subject perceived his or her finger to be relative to the projected images on the screen.  
164 For this, we measured the position of the marker on the fingertip when the subject placed the  
165 fingertip at four indicated positions on the screen. This step was performed to correct for the  
166 fact that the marker was attached to the nail rather than to the tip of the finger.

167         We synchronized the Optotrak recordings with the images projected on the screen by  
168 flashing a disk in the upper left corner of the screen whenever a new target appeared. A  
169 photodiode that was directed towards that part of the screen was used to briefly inactivate an  
170 additional Optotrak marker attached to the side of the screen (using custom built hardware with  
171 a delay of 1 ms). Detecting this inactivation provided information (to within the 4 ms sampling  
172 interval) about when the target appeared relative to the movement data, and allowed us to  
173 determine that the average latency with which we could adjust the images to events extracted  
174 from the online Optotrak data was 24 ms. All delays were accounted for, both in the analysis  
175 and in the feedback provided during the trials. Subjects did not notice that the target continued  
176 to move for about 24 ms before feedback about their hitting performance was provided,  
177 presumably partly because their own finger occluded the target and partly through backward  
178 masking (Breitmeyer and Ogmen, 2000).

179         Combining all these steps provided synchronized arm, head and gaze information in a  
180 common coordinate system. For convenience, we used a coordinate system that was aligned  
181 with the screen on which the target was moving, so that the target and gaze could be specified  
182 by two coordinates.

183

184 *Stimulus and procedure*

185

186 Experiment 1:

187       The experiment was performed in a single session with two randomly interleaved  
188 conditions. Subjects started each trial by placing their index finger at an indicated starting point  
189 (Figure 1A). The starting point was a 2 cm diameter red disk that was 35 cm below the screen  
190 centre. One of two possible hitting zones appeared at the same time as the starting point. The  
191 hitting zone was white and was 4 cm wide. It was either a ring (Ring condition, Figure 1B) or a  
192 disk (Disk condition, Figure 1C). After a random period between 0.5 and 0.7 s from when the  
193 subject placed his or her index finger on the starting position, the target appeared at the centre of  
194 the screen. The target moved along a seemingly unpredictable trajectory. The target was a 2 cm  
195 diameter black disk. We chose a target that was smaller than the hitting zones, because this  
196 often elicits pursuit of the target for at least part of its trajectory when intercepting predictably  
197 moving targets (Brenner and Smeets, 2011; de la Malla et al., 2017).

198       Subjects had to try to intercept the target by tapping on it when it was within the hitting  
199 zone. Taps were detected on-line. A tap was considered to have occurred if the deceleration of  
200 the movement orthogonal to the screen was at least  $50 \text{ m/s}^2$  while the finger was less than 5 mm  
201 above the screen. To avoid inadvertently interpreting motion onset as a tap, we also checked  
202 that the finger was moving towards the screen, and that it had been lifted to at least 1 cm off the  
203 screen since being placed at the starting position. Whenever they wanted, subjects could rest  
204 between trials by not placing their finger at the starting position.

205       In the Ring condition (Figure 1B), the white ring always appeared at the same place,  
206 centred on the screen. The ring had a radius of 25 cm and was 4 cm wide. Consequently, it  
207 extended from 23 to 27 cm from the screen centre. Subjects had to hit the target when it was  
208 within the ring.

209       In the Disk condition (Figure 1C), the white disk appeared at one of twenty-four  
210 possible positions. The disk had a diameter of 4 cm (the same width as the ring) and its centre  
211 was 25 cm from the screen centre. The possible positions of the centres of these hitting zones  
212 were separated by 15 degrees. Subjects had to hit the target when it was within the disk. The  
213 same target trajectories were presented in the two conditions.

214

215

216

217

218

219

220

Figure 1 here

**Figure 1.** Schematic representation of the task and conditions. (A) Subjects started with their index finger at the red dot and had to intercept a moving target (black dot) by tapping on it when it reached the white hitting zone. (B) In the Ring condition, the hitting zone was always the same large white ring. (C) In the Disk condition, it was a small white disk at one of 24 possible positions. The white dashed lines in C indicate the other possible positions. They were not visible during the experiment. The six curves in B and C show the six possible paths that the target could take to one of the 24 hitting zones.

The target always appeared at the centre of the screen and could follow one of six possible trajectories in one of 24 directions. The different trajectories were constructed in polar coordinates using a constant increase in distance from the screen centre, with the polar angle  $\varphi$  changing according to Equation 1:

$$\varphi = D + \left( a + b \sin \left( 2\pi \frac{t}{T} \right) \right) \left( \frac{t}{T} \right)^2 \quad (\text{Equation 1})$$

where the  $D$  is one of the 24 directions to the hitting zone (equally spaced),  $t$  is time to reach the centre of the hitting zone and  $T$  is the movement time of the target (1.2 s). There were six combinations of values of  $a$  and  $b$ :  $[-2\pi/3, \pi/2]$ ,  $[\pi/3, -\pi/2]$ ,  $[2\pi/3, -\pi/2]$ ,  $[-\pi/3, \pi/2]$ ,  $[\pi/2, \pi/2]$ ,  $[-\pi/2, -\pi/2]$ . The six possible target trajectories are shown in Figures 1B and 1C. All six trajectories crossed the centres of the hitting zones after 1.2 s. In trials of the Ring condition, subjects only gradually realised where the target would pass through the large hitting zone as the trial progressed, with the target approaching the ring along a curvy path. In trials of the Disk condition, subjects knew that the target was going to pass through the small hitting zone even before the target appeared.

Feedback was provided after each attempt to hit the target. A target was considered to have been hit if the tip of the finger (as calibrated) was within the outline of the target. If subjects hit the target, the target stopped moving and remained at the position at which it had been hit for 500 ms. If the tip of the finger was also within the hitting zone a sound indicated that the target was hit. If subjects missed the target, the target was deflected away from the finger at 1 m/s, remaining visible for 500 ms. All the trajectories and conditions were presented in random order in a single session. In total, there were 288 trials per subject: 2 conditions, 24 directions to the hitting zone, 6 trajectories for each direction. It took about 25 minutes to complete the experiment.



257  
258  
259  
260  
261  
262  
263  
264  
265  
266  
267  
268  
269  
270  
271  
272  
273  
274  
275  
276  
277  
278  
279  
280  
281  
282  
283  
284  
285  
286  
287  
288  
289  
290  
291  
292  
293

Experiment 2:

The second experiment was identical to the first, except that the targets followed a straight trajectory towards either the Ring or the Disk ( $a$  and  $b$  in Equation 1 were both zero). The purpose of this experiment was to determine which differences between how subjects intercepted the targets in the Disk and Ring conditions of Experiment 1 were due to the Disk revealing where the target could be hit even before the target appeared, and to determine which aspects of how subjects intercepted the targets in Experiment 1 were specific to targets that move unpredictably. In total there were 192 trials per subject: 2 conditions, 24 directions to the hitting zone, and 4 repetitions for each hitting zone. It took about 15 minutes to complete the experiment.

Experiment 3:

The third experiment was identical to the second, except that targets only moved in four of the 24 possible directions (0°, 90°, 180° or 270°). This made it even easier to judge where the target would cross the Ring. In total there were 40 trials per subject: 2 conditions, 4 directions to the hitting zone, and 5 repetitions for each hitting zone. It took about 8 minutes to complete the experiment.

*Data analysis*

All analyses were performed with custom written programs using RStudio (RStudio Team, 2018). In Experiment 1 we excluded 76 trials (3.3%) in which subjects clearly did not follow the instruction. These were 52 trials in which no tap was detected, 12 trials in which the distance between where subjects tapped (the tap position) and where the target was at the moment of the tap was larger than 20 cm, and 12 trials in which the distance between the tap position and the position at which the target's path crossed the centre of the hitting zone was larger than 20 cm. No trials were excluded due to missing data. In Experiments 2 and 3 we excluded 6 (0.5%) and 2 (0.8%) trials, respectively, all because subjects did not tap on the screen within 1.5 seconds.

The next step in our analysis was to align the Optotrak and Eyelink data with the presentation of the images on the screen using the timing signal from the photodiode. Since the data acquisition itself was not synchronised with the image projection, and was at different frequencies for the Optotrak and Eyelink, the first step in our analysis was to align the signals in time using linear interpolation to obtain a target position (on the screen), eye orientations (with respect to the head), eye positions (in space), head orientation (in three dimensions with respect

294 to the world) and hand position (position of the finger with respect to the screen) at each  
295 moment from when the targets appeared until the moment of the tap. We refer to the average  
296 position of the two eyes as the head position, so the reported changes in head position include  
297 influences of both displacements and rotations of the head. We combined the temporally aligned  
298 positions of the eyes in space with the orientations of the eyes with respect to the head and the  
299 orientation of the head in space to calculate the line of sight for each eye.

300 We determined where subjects were looking on the screen (gaze) by averaging the  
301 estimates of where the lines of sight of the two eyes intersected the screen (except for 22 trials  
302 of Experiment 1 in which only one of the eyes was measured correctly, probably due to some  
303 light reflecting on glasses; for those trials we only used the estimates of one eye). We calculated  
304 the instantaneous speed and acceleration of gaze, head and hand movements by using finite  
305 difference approximations. We divided the change in position between 10 ms before and 10 ms  
306 after the moment in question by the 20 ms time difference between them. We calculated the  
307 gaze acceleration by dividing the difference between the gaze speeds 10 ms after and 10 ms  
308 before the moment in question by the 20 ms time difference between them. When calculating  
309 the speed of the head and of the hand we only considered the motion component parallel to the  
310 screen, because we wanted to determine the peak in the speed at which the hand moved towards  
311 the vicinity of the target. Including the motion component orthogonal to the screen would  
312 include the final tapping movement, which was often very fast so that the peak velocity would  
313 often be just before the tap. We also report the component parallel to the screen when reporting  
314 head and hand positions and distances moved.

315 To evaluate whether gaze, the head and the hand were following the target we examined  
316 how the distance from the interception point decreased during each trial. Given that the hand's  
317 starting position is below all possible target locations, the hand's initial distance differed  
318 considerably between hitting zones at the top and bottom of the screen (Figure 1B and 1C). To  
319 prevent changes in the hand's distance from the upper target locations from overshadowing  
320 those from the lower target locations when averaging across target locations, we averaged  
321 normalized distances. We obtained the latter by dividing the distance from the hand position to  
322 the tap position at each moment of time by the initial distance of the hand from the tap position.  
323 Unlike for the finger, there was no specified starting position for the head and gaze. To obtain  
324 somewhat comparable normalised distances for the head and gaze we assumed that subjects  
325 started each trial with their head approximately in front of the position at which the targets  
326 appeared and with their gaze directed at where the targets appeared. We divided the distances of  
327 the head and gaze from the tap position by the distance from the position at which the target  
328 appeared to where it was tapped. The latter distance was always approximately 25 cm, but not  
329 precisely so on each trial because the tap was not always exactly at the centre of the hitting  
330 zone. With these assumptions the initial normalized distance will be one unless subjects respond

331 before the target appears. Gaze and the head are not required to end at any particular place, so  
332 they do not have to end at zero as the hand does, although we do expect gaze to end near the tap  
333 irrespective of whether subjects pursue the target or fixate where they tap. To compare how  
334 subjects moved in the different conditions we plotted the normalised distances of gaze, head and  
335 hand across time for each experiment and condition. To be able to evaluate the consistency of  
336 any visible differences the plots include the standard error across subjects at each moment.

337         The number of saccades per trial and whether the saccades were towards the target or  
338 towards the interception location provided additional measures of gaze behaviour. Determining  
339 the number of saccades towards the target can help evaluate to what extent differences in gaze  
340 behaviour result from being unable to predict how the target will move. We identified saccades  
341 using a similar method to that described in de la Malla et al. (2017). We considered the eyes to  
342 be making a saccade if the gaze speed remained above a threshold of three times the target's  
343 speed for more than 10 ms. Since the target did not move at a constant speed, this threshold  
344 differs slightly at different moments. Once we had detected a saccade we determined when it  
345 ended by first localizing the maximal deceleration of gaze and then finding the moment at  
346 which gaze no longer decelerated by more than  $5 \text{ cm/s}^2$ . We used the gaze position at the end of  
347 the saccade to distinguish between saccades that contribute to keeping gaze on the target and  
348 ones that direct gaze towards the hitting zone. If a saccade ended closer to the centre of the  
349 target than to the centre of the disk or to the midline of the ring (both at 25 cm from the screen  
350 centre), we considered it to be a saccade that served to keep gaze on the target. Otherwise, we  
351 considered it to be a saccade towards the hitting zone. We do not expect subjects to be able to  
352 pursue an unpredictably moving target very precisely, so we expect them to make more  
353 saccades when tracking the target in the Ring condition in which the precise position at which  
354 one would be able to hit the target was not known in advance. We tested whether this is the case  
355 using a one-sided paired t-test.

356         We also compared hand movements in the Disk and Ring conditions on a number of  
357 measures using one-sided t-tests on subject means. We compared (i) the proportion of targets  
358 hit, (ii) timing precision for hitting the target, (iii) peak speed of movement of the finger, (iv)  
359 time to peak speed (how rapidly subjects responded), and (v) the directness of the movement  
360 (the distance travelled: the sum of displacements across consecutive measurements until the  
361 time of the tap). In Experiment 1, knowing in advance where the finger's movement will need  
362 to end, as one did in the Disk condition, makes it possible to plan the movement as soon as the  
363 target appears, rather than having to track the target's meandering trajectory. We predicted that  
364 this might lead to (i) more targets being hit; (ii) timing being more precise; (iii) the mean peak  
365 speed being higher and (iv) occurring earlier; and (v) the movements being more direct in the  
366 Disk condition. As the subjects were the same in both conditions we used paired t-tests.

In Experiments 2 and 3 the position at which the finger's movement will end is still known earlier in the Disk condition, but the straight trajectories allow one to infer where the target is to be hit as soon as it starts moving (i.e. immediately after it appears) in the Ring condition. Thus, although the direction of any differences between the conditions would be expected to be the same as for Experiment 1, we expect all the differences between conditions to be smaller. We expect the behaviour of the finger in both conditions to be similar to that in the Disk condition of Experiment 1. The peak speed might still occur slightly later in the Ring condition because the interception point is only revealed by the target's motion, rather than being revealed even before the target appears (by the position of the Disk). Since the target trajectories were simpler in Experiment 2 than in Experiment 1, and were even more predictable in Experiment 3, we expected performance to become better in consecutive experiments (more targets hit and better timing) and the movements to possibly also become faster and occur earlier. We used one-sided paired tests when comparing Experiments 2 and 3, but tests were not paired when comparing those experiments with Experiment 1 because the subjects were not all the same.

## Results

### Experiment 1: unpredictable trajectories

The subjects' goal was to tap on the screen in such a manner that their fingertip was within both the target and the hitting zone at the time of the tap. Subjects successfully hit more targets in the Disk condition than in the Ring condition (Table 1). On average subjects tapped at the correct place (25 cm from the screen centre) and time (1.2 s after the target appeared) in both conditions, but the variability (standard deviation) in the time at which individual subjects tapped was smaller in the Disk condition than in the Ring condition (Table 2). Thus, their timing was more precise in the Disk condition.

Experiment	Disk	Ring	One-sided paired t-tests
1	72.2	57.4	$t_7=3.36$ , $p=0.006$
2	83.8	85.4	$t_4=2.02$ , $p=0.94$
3	86.0	94.0	$t_4=1.73$ , $p=0.92$

**Table 1.** Percentage of targets hit. A target is considered to have been hit if the finger, as calibrated, was within the bounds of both the target and the hitting zone at the time of the tap. Performance only differed significantly between the Disk and Ring condition in Experiment 1. Performance in Experiments 2 and 3 differed significantly from that in Experiment 1 (Experiment 2, Disk:  $t_{4,7}=2.3$ ,  $p=0.03$ ; Ring:  $t_{4,7}=5.12$ ,  $p=0.0003$ ; Experiment 3, Disk:  $t_{4,7}=2.34$ ,

398  $p=0.03$ ; Ring:  $t_{4,7}=7.02$ ,  $p<0.001$ ) but not from each other (Disk:  $t_{4,4}=0.33$ ,  $p=0.38$ ; Ring:  
 399  $t_{4,4}=1.46$ ,  $p=0.09$ ).

400

Experiment	Disk	Ring	One-sided paired t-tests
1	36	48	$t_7=2.72$ , $p=0.015$
2	33	44	$t_4=1.48$ , $p=0.11$
3	26	28	$t_4=0.71$ , $p=0.26$

401 **Table 2.** Variability in the timing of the hits (standard deviation in ms). Performance only  
 402 differed significantly between the Disk and Ring condition in Experiment 1. Performance in  
 403 Experiment 3 differed significantly from that in Experiment 1 (Disk:  $t_{7,4}=1.92$ ,  $p=0.04$ ; Ring:  
 404  $t_{7,4}=3.05$ ,  $p=0.008$ ), but the other differences between experiments were not significant.

405

406

407 Figure 2 shows two example trials from a representative subject for Experiment 1.  
 408 There are clear differences between how the subject moved to intercept the targets in the two  
 409 conditions. When the position at which to hit the target was not known in advance (Ring  
 410 condition, left panel), the gaze (blue) more or less followed the target's movement (grey) until  
 411 the moment of the tap. It did so in quite a jerky manner, presumably because the eyes made  
 412 many saccades to correct for errors in predicting how the target would proceed. Therefore, these  
 413 saccades are not really to catch up with the target position, but anticipating where the target will  
 414 be next and thus often anticipating incorrect positions because the target moves unpredictably.  
 415 When the position at which to hit the target was known in advance (Disk condition, right panel),  
 416 gaze was immediately directed towards this position: the blue curve starts and remains close to  
 417 the disk rather than following the target. Both the head and the hand also moved sooner in the  
 418 direction of the hitting zone in the Disk condition than in the Ring condition: a smaller part of  
 419 the trajectory is clearly red or green. One can also see that the hand moves along a straighter  
 420 path in the Disk than in the Ring condition.

421

422

423 **Figure 2 here**

424

425 **Figure 2.** Example of gaze, head and hand movements on single trials for a representative  
 426 subject in the two conditions of Experiment 1. Data of two trials with the same target trajectory  
 427 from the moment the target appeared until the time of the tap. The colours of the curves change  
 428 with the remaining time to tap: from black to either grey, blue, red or green (for the target, gaze,  
 429 head and hand, respectively).

430

431 The differences between the two example trials of Figure 2 are characteristic of the  
432 differences between the two conditions for this subject (Figure 3) as well as for other subjects.  
433 Due to the time period between the subject placing his or her finger at the starting position and  
434 the target appearing, gaze was usually no longer directed at the starting position by the time the  
435 target appeared. In the Ring condition gaze was usually directed at the centre of the screen,  
436 where the targets appeared, and then tracked the target. In the Disk condition gaze was often  
437 already directed towards the hitting zone by the time the target appeared, as is the case in the  
438 trial shown in Figure 2 (the hitting zone was visible well before the target appeared). On some  
439 other trials of this condition gaze was directed at the centre of the screen until the target  
440 appeared, but when the target appeared a saccade was made to the disk rather than gaze tracking  
441 the target.

442

443

444 **Figure 3 here**

445

446 **Figure 3.** Gaze, head and hand movements of all trials of the same representative subject in  
447 Experiment 1 shown in Figure 2. Colours change from black to blue (gaze), red (head) and  
448 green (hand) across time from when the target appears to the moment of the tap (as in Figure 2).

449

450

451 To illustrate the time-course of the gaze movements we plotted the average normalized  
452 distance of gaze from the tap position as a function of the time to hit the target (Figure 4A).  
453 There is a clear difference between the Ring and the Disk condition. In the Ring condition the  
454 distance between the gaze and the tap position decreases constantly across time at a similar pace  
455 as the target approaches the tap position (thin black dotted line). This is consistent with subjects  
456 trying to track the target with their eyes. As could be expected on the basis of Figures 2 and 3,  
457 on average subjects were already looking closer to the hitting zone when the target appeared in  
458 the Disk condition (dashed blue curve lower than solid blue curve from the start in Figure 4A).  
459 Consequently, the distance between gaze and the tap position changed much less across time.  
460 The average normalized distance between gaze and tap position only decreased to about 0.2 in  
461 both conditions (Figure 4A). This corresponds to a distance of about 5 cm at the moment of the  
462 tap. This could mean that gaze was not directed at the position that was tapped, but it could also  
463 arise from measurement errors (see Discussion). We never required subjects to fixate a specific  
464 position during the experiment, to avoid biasing where they looked, so we did not try to correct  
465 for systematic shifts (such as the overall shift to the upper right in the left panels of Figure 3),  
466 for instance by assuming that on average subjects were looking at the disks when they hit the  
467 targets, because we cannot be sure that this was the case. Importantly, the differences that we

find between the two conditions cannot be due to eye-tracker shifts because the trials of the two conditions were interleaved.

A closer look at the tracking strategy (inset in Figure 4A) reveals that subjects made more than twice as many saccades in the Ring than in the Disk condition ( $t_7=8.9$ ,  $p<0.001$ ). In accordance with subjects trying to keep their eyes on the unpredictably moving target in the Ring condition, we see that the increase in the number of saccades is caused by an increase in the number of saccades directed to the target ( $t_7=11.4$ ,  $p<0.001$ ).

The movements of the head and the hand also differed between the two conditions (Figure 4B and 4C). The head was closer to the hitting zone in the Disk condition than in the Ring condition from the moment the target appeared (dashed red curve lower than solid red curve). At least part of this difference in head position is probably related to the above-mentioned difference in gaze: one can orient one's head towards the position at which the target is to be hit before the target appears in the Disk condition, but not in the Ring condition. The hand was not allowed to start moving before the target appeared, so it always started at a normalized distance of 1. It took some time for the hand to start moving when the target appeared. Once the hand did start moving it approached the tap position sooner in the Disk condition than in the Ring condition.

#### Figure 4 here

**Figure 4.** Analysis of the average gaze, head and hand movements of all eight subjects in Experiment 1 (A-C) and of all five subjects in Experiments 2 (D-F) and 3 (G-I). Normalized distance to the tap position as a function of the time until the target is hit for the gaze, head and hand. The lines (continuous for the Ring condition, dashed for the Disk condition) and shaded areas are the means and standard errors of the subjects' individual mean values. A normalized distance of zero corresponds to being at the tap position. A normalized distance of one corresponds to being where the target appeared for the gaze and the head, and corresponds to being at the finger's starting position for the hand. In the gaze panels, we also show the mean normalised distance of the target from the tap position (black dotted curve). The inset in A shows the number of saccades per trial in Experiment 1, split by whether saccades ended closer to the target (black bars) or closer to the tap position (white bars). Error bars are standard errors across the subjects' mean numbers of saccades.

In accordance with the impression one gets from the gaze panels of figures 2, 3 and 4A, the distance travelled by gaze while the target was present was longer in the Ring condition than

505 in the Disk condition ( $53 \pm 4$  cm versus  $32 \pm 3$  cm; mean  $\pm$  standard error across subjects;  
506  $t_7=6.3$ ,  $p=0.0002$ ). This is consistent with subjects trying to pursue the target in the Ring  
507 condition but not in the Disk condition.

508 Unlike gaze, the head does not travel significantly less in the Disk condition ( $t_7=1.11$ ,  
509  $p=0.15$ ): it travels an average of  $8.2 \pm 0.9$  cm. The peak speed of the head was not significantly  
510 higher ( $t_7=-6.2$ ,  $p=0.99$ ) in the Disk ( $18 \pm 2$  cm/s) than in the Ring condition ( $21 \pm 2$  cm/s).  
511 However, the head did reach the peak speed earlier in the Disk condition ( $t_7=4.86$ ,  $p=0.0009$ ):  
512 the peak speed occurred after  $0.71 \pm 0.05$  s in the Disk condition and after  $0.89 \pm 0.03$  s in the  
513 Ring condition. The hand trajectories were straighter (shorter) in the Disk condition ( $t_7=6.20$ ,  
514  $p=0.0002$ ): the mean distance travelled by the hand was  $43.4 \pm 0.3$  cm in the Disk condition and  
515  $51.6 \pm 1.4$  cm in the Ring condition. Despite the shorter distance, the peak speed of the hand  
516 was higher in the Disk condition: it was  $122 \pm 3$  cm/s in the Disk condition and  $112 \pm 5$  cm/s in  
517 the Ring condition ( $t_7=2.5$ ,  $p=0.02$ ). The peak speed of the hand also occurred earlier ( $t_7=3.44$ ,  
518  $p=0.005$ ) in the Disk condition ( $0.52 \pm 0.03$  s) than in the Ring condition ( $0.65 \pm 0.05$  s). These  
519 findings support the idea that knowing in advance where they will hit the target allows subjects  
520 to move sooner, more directly and faster.

521 The location at which subjects will be able to hit the target only gradually became  
522 apparent in the Ring condition. When the ring appeared and the target started to move subjects  
523 could have followed the strategy of moving their hand directly to some position within the ring  
524 and adjust their movement along the ring as the target approached it. Figure 5 shows that they  
525 did not do this. They seldom moved along the ring (left panels). Furthermore, when the target  
526 was to be hit at the closest position to the hand's starting position subjects moved their hand  
527 towards the target, within the ring, before moving it back down to the ring as the target  
528 approached the ring (bottom left panel). In the Disk condition (right panels), subjects moved  
529 their hand to the hitting zone along a much straighter path, only moving beyond the hitting zone  
530 when the hitting zone was near the hand's starting position (bottom right panel) a single time.

531

532

533 **Figure 5 here**

534

535 **Figure 5.** Hand movements of all trials of all eight subjects for the furthest (top panels) and the  
536 nearest (bottom panels) hitting zones in Experiment 1. All trajectories start at the hand's starting  
537 point near the bottom of the panel. Colour changes from black to green across time as in Figures  
538 2 and 3.

539

540

541



## 542 Experiment 2: predictable trajectories

543

544 The first experiment showed a marked difference in movement strategies between the  
545 two conditions. We attribute the difference to the predictability of the interception location. In  
546 the second experiment we kept the conditions the same, but the interception location was  
547 predictable from just after the targets appeared and started moving because the targets moved at  
548 a constant velocity along straight paths. Subjects managed to hit more targets when the targets  
549 moved more predictably, and there was no longer a significant difference between the Disk and  
550 Ring conditions (Table 1). The variability in the timing of the taps was also no longer  
551 significantly larger in the Ring than in the Disk condition (Table 2). The differences in  
552 performance between the two conditions were therefore not just due to the interception location  
553 being known before the target appeared in the Disk condition.

554 The tap accuracy and timing were similar in the Ring and Disk conditions (Table 1 and  
555 2), but there were small differences between the two conditions. On average, gaze travelled less  
556 in the Disk ( $33.2 \pm 3$  cm) than in the Ring ( $48.6 \pm 3$  cm) condition. The difference was not  
557 consistent across subjects ( $t_4 = 1.7$ ,  $p = 0.08$ ) and is easily explained by the interception location  
558 being known before the target appears in the Disk condition, while it only becomes apparent  
559 from the motion of the target in the Ring condition (it is evident as soon as the target moves  
560 because the target always moves along a straight path). Gaze was often already at the  
561 interception location by the time the target appeared in the Disk condition, whereas it could only  
562 move there after the target started moving in the Ring condition (Figure 4D). That the time at  
563 which the interception location is known is important is also evident from the difference  
564 between gaze in the Ring conditions of Experiments 1 and 2: gaze reaches the vicinity of the tap  
565 position earlier in Experiment 2 (compare Figure 4A and 4D). In Experiment 1 it took an  
566 average of 1.04 s for gaze to be within 10% of the final normalized distance to the tap position.  
567 In Experiment 2 it only took 0.79 s ( $t_{4,7} = 3.84$ ,  $p = 0.003$ ). This difference is undoubtedly the  
568 result of the predictable target motion revealing the interception location. However, the  
569 difference in performance between the Disk conditions of Experiments 1 and 2 (Table 1)  
570 suggests that there is also a direct effect of the predictability of target motion.

571 The difference in head position between the two conditions is smaller in Experiment 2  
572 (Figure 4E) than in Experiment 1 (Figure 4B) from the moment that the target appears, although  
573 there is no difference between the experiments in terms of the available information at that  
574 moment. The difference is consistent with the difference in gaze at the moment the target  
575 appears also being smaller in Experiment 2 than in Experiment 1. Thus, the differences in head  
576 movement between the conditions are probably due to differences in gaze. The differences in  
577 gaze between the two experiments might be the result of the initial target trajectory always  
578 being informative in Experiment 2.

579 The hand movements were extremely similar in the Disk and Ring conditions of  
 580 Experiment 2 (Figure 4F), with the hand traveling 42.1 cm in both cases. The small difference  
 581 in movement onset is consistent with the hitting position becoming apparent slightly later for  
 582 the Ring than for the Disk condition. The hand did not appear to move as quickly to the hitting  
 583 zone in this experiment as it had in the Disk condition of Experiment 1. The peak speed was  
 584  $110 \pm 8$  for the Disk condition and  $107 \pm 7$  cm/s for the Ring condition ( $t_4=1.92$ ,  $p=0.06$ ), which  
 585 are values close to the peak velocity of the hand for the Ring condition in Experiment 1 (113  
 586 cm/s). The peak speed occurred after 0.6 s, for both conditions, which is midway between the  
 587 values that we found for the Disk and Ring conditions in Experiment 1. The results of this  
 588 experiment support the idea that knowing that the target's initial movement will be informative  
 589 of the interception location on all trials influences how subjects approach the task.

590

591

### 592 **Experiment 3: predictable trajectories and tap positions**

593

594 In Experiment 2 we found that the predictability of the hitting position influences  
 595 interceptive actions. In Experiment 3 we investigated whether the degree of predictability was  
 596 important. To do so we made it even easier to predict where the targets will be hit in the Ring  
 597 condition. We repeated the second experiment but with only four of the 24 hitting zones (values  
 598 of  $D$  in Equation 1 of 0, 90, 180 and 270°). The percentage of targets that were hit was highest  
 599 in this experiment, though not significantly higher than in Experiment 2 (Table 1). The  
 600 percentage of targets that were hit was not lower for the Ring condition (94%) than for the Disk  
 601 condition (86%). The standard deviation in timing the hits was lowest in this experiment,  
 602 though not significantly lower than in Experiment 2 (Table 2).

603 The time course of the movements in Experiment 3 was very similar to that in  
 604 Experiment 2 (Figure 4G-I). Again, the main difference between the Ring and Disk conditions  
 605 is that gaze was directed to the hitting zone before the target appeared in the Disk condition,  
 606 whereas it obviously could not be in the Ring condition. Movements of the head hardly  
 607 contributed to this difference, and the arm movements were not affected by knowing where the  
 608 target would be hit in advance. Even the tiny delay in hand movement onset seems to have  
 609 vanished, probably because it is easier to tell in which of the four directions the target is  
 610 moving, than to distinguish between 24 directions. The peak speed of the hand ( $102 \pm 6$  cm/s)  
 611 and the time at which it occurred (0.59 s after appearing, when the target was almost half way to  
 612 the interception location) were similar to the values in Experiment 2 ( $t_{4,4}=1.51$ ,  $p=0.90$  and  $t_{4,4}=-$   
 613  $0.06$ ,  $p=0.52$ , for the peak speed and the time at which it occurred, respectively). The fact that,  
 614 again, performance was slightly different from that of the Disk condition of Experiment 1,  
 615 supports the notion that beside the target's path being relevant because it influences when one

616 knows where the target is to be hit, it is presumably also easier to determine when the target will  
617 arrive at the position at which it is to be hit when the target is moving more predictably.

618

619

## 620 **Discussion**

621

622       What options does one have to successfully intercept a target that moves unpredictably?  
623 When one tries to catch a note that is blown away by the wind, the only option is to track it with  
624 one's gaze as one adjusts one's arm movement so that the hand reaches the note. When trying to  
625 intercept a predictably moving object one could follow the same strategy, but one could also  
626 predict where one will be able to intercept the target and immediately direct one's gaze and  
627 movement towards that location. We examined how the circumstances influence what people do  
628 and how the choice influences their performance.

629       The results of Experiment 1 suggest that even if the target moves in an unpredictable  
630 manner, so that it is essential to constantly monitor its motion, pursuing the target with one's  
631 gaze is not always the best strategy for guiding the hit. In order to pursue a target smoothly with  
632 no delay one must be able to anticipate how it will continue moving (Lisberger et al., 1981;  
633 Kowler and Steinman, 1979). If a target's trajectory is completely unpredictable (Ring condition  
634 of Experiment 1), gaze must track the target (Figures 2, 3 and 4A), even if this means that  
635 pursuit of the target will be interspersed with saccades (inset of Figure 4A). Such saccades will  
636 temporarily limit what one perceives (Zuber and Stark, 1966; Bridgeman et al., 1975; Burr et  
637 al., 1999; Castet and Masson, 2000; Maij et al., 2012; Ross et al., 2001) and give rise to errors  
638 in judging the target's position and motion (Matin and Pearce, 1965; Mateeff, 1978; Honda,  
639 1989; Morrone et al., 1997; Schlag and Schlag-Rey, 2002; Maij et al., 2009; 2011; Matziridi et  
640 al., 2015; Goettker et al., 2018; 2019). If one knows where one will be able to hit the target in  
641 advance (imagine waiting for a fly to settle on a particular breadcrumb that it is clearly circling  
642 around; Disk condition), it appears to be better to quickly direct one's gaze towards that position  
643 and track its approach with peripheral vision (Figure 4A) because doing so appears to improve  
644 performance (Tables 1 and 2). That performance is better when fixating in such circumstances  
645 need not be due to the disadvantages associated with having to perform saccades to keep the  
646 target in central vision outweighing the disadvantages of relying on peripheral vision to track  
647 the target's motion, because being able to anticipate where one will be able to hit the target may  
648 be advantageous for other reasons. However, the fact that subjects did not consistently pursue  
649 the target in the Disk condition trials although they did pursue the target on the interleaved Ring  
650 condition trials suggests that fixating is advantageous under these circumstances.

651 As mentioned in the results, it seems surprising that subjects appeared not to direct their  
652 gaze exactly at the tap position at the moment of the tap (Figures 4A, 4D and 4G). In order to  
653 not bias their gaze behaviour we did not give them instructions about where to look at any time,  
654 except during the eye movement calibration during which subjects fixated a static dot (see  
655 Methods). The measured precision during calibration was about 0.7 degrees horizontally and  
656 1.2 degrees vertically for each eye (root mean square deviation). However, recorded eye  
657 orientations are known to drift, mainly due to headband slippage, giving rise to systematic  
658 shifts. Therefore, we cannot determine with certainty which part of the distance between gaze  
659 and tap position at the moment of the tap is due to measurement errors and which to the fact that  
660 subjects may not have directed their gaze precisely at the tap position when tapping.

661 Our results are largely in agreement with previous studies on how people interact with  
662 unpredictable moving targets (Danion and Flanagan, 2018; Mrotek and Soechting, 2007; Xia  
663 and Barnes, 1999). Danion and Flanagan (2018) examined subjects' gaze strategy when  
664 tracking a target that moved along an unpredictable trajectory. In one condition their subjects  
665 had to track a target with their hand, without instructions about gaze. They found that gaze  
666 always also tracked the target. This is consistent with our observation that subjects track  
667 unpredictable target motion if they do not know how the target will move. Mrotek and  
668 Soechting (2007) examined subjects' gaze strategy in an interception task. In their task, subjects  
669 were free to choose when and where to hit the targets. They observed that subjects pursued the  
670 target, but also that saccades were suppressed just before the moment of interception. This is  
671 consistent with our proposal that making saccades near the time of interception comes at a cost.  
672 However, the cost cannot be very high because people do in some circumstances make saccades  
673 to where they are required to hit a target before reaching it with the hand (rather than pursuing it  
674 smoothly until it is hit) when the target moves predictably (de la Malla et al., 2017).

675 In both the Disk and Ring condition, the target has to be hit at a specific time and place.  
676 This restricts the adjustments that subjects can make when guiding the hand to the target  
677 (Brenner and Smeets, 2015). When the target's trajectory is unpredictable, knowing where to hit  
678 it in advance might not improve the timing of the tap (Experiment 1; Table 2) through its  
679 influence on the eye movements, but by making it easier to judge when to hit the target. The  
680 targets moved quite smoothly, so knowing that they will pass a certain position probably helped  
681 estimate when that would happen. However, judging when the target will cross the ring is less  
682 reliable because a small change in the trajectory, that is constantly curving, can change the  
683 position at which the target crosses the ring, and therefore also the time at which it does so at its  
684 current speed. The hand must also reach the changed position. The hand followed the target to  
685 some extent in the Ring condition of Experiment 1. Subjects did not quickly move their hand to  
686 the ring and then adjust its position along the ring (Figure 5), but the hand did not closely track  
687 the target either (Figure 2). This may just be due to physical limitations in how the hand can be

688 moved, but subjects may intentionally avoid occluding the target with the hand, or even avoid  
689 occluding parts of the screen across which the target may move during its meanderings.

690 The predictability of the targets' trajectories also influenced head movements to some  
691 extent. Previous studies have reported that head movements contribute substantially to keeping  
692 moving targets in central vision when interacting with them (Bahill and LaRitz, 1984; Mann et  
693 al., 2013; Fogt and Zimmermann, 2014; Fogt and Persson, 2017). Most of those studies  
694 involved sports such as baseball or cricket, in which the ball's angular displacement near the  
695 time of the hit is so large that it is impossible to track the ball by moving the eyes only. In our  
696 study the distance between where the targets appeared and the hitting zone was only 25 cm  
697 (about 25 deg, depending on where the subject chose to stand), so large head movements were  
698 not necessary to keep track of the moving targets. However, head movements did contribute to  
699 the changes in gaze (Figure 4B, E and H). The contribution was modest, but the differences  
700 between the conditions were more or less consistent with the differences in gaze, although gaze  
701 changed more and more abruptly.

702 In summary, for the conditions used in the current study the preferred strategy was to  
703 quickly direct one's gaze at the position at which the target will be hit. Gaze only tracked the  
704 target when the interception point was initially unknown (Ring condition) and could not  
705 immediately be inferred from the target's motion (Experiment 1). In that case performance was  
706 relatively poor, presumably because it was impossible to keep one's eyes on the target and  
707 because the hand movement was constantly adjusted as a result of it being difficult to anticipate  
708 when and where the target could be hit. The experiments suggest that how people approach an  
709 interception task is mainly determined by how reliably they can predict the interception location  
710 rather than by how reliably they can predict the target's movement to that location, at least when  
711 an interception zone is specified.

## 714 References

- 715  
716 Bahill, A.T. and McDonald, J.D. (1983) Smooth pursuit eye movements in response to  
717 predictable target motions. *Vision Res*, **23** (12), 1573-1583  
718 Bahill, A.T. and LaRitz, T. (1984) Why can't batters keep their eyes on the ball. *American*  
719 *Scientist*, **72**(3), 249-253.  
720 Braun, D. I., Mennie, N., Rasche, C., Schutz, A. C., Hawken, M. J., & Gegenfurtner, K. R.  
721 (2008). Smooth pursuit eye movements to isoluminant targets. *J Neurophysiol*, **100** (3),  
722 1287-1300.

723 Breitmeyer, B.G. and Ogmen, H. (2000) Recent models and findings in visual backward  
 724 masking: a comparison, review, and update. *Perception and Psychophysics*, **62** (8),  
 725 1572-1595.

726 Brenner, E. and Smeets, J.B.J. (2007) Flexibility in intercepting moving objects. *J Vision*,  
 727 **7**(5):14, 1-17

728 Brenner, E. and Smeets, J.B.J. (2009) Sources of variability in interceptive movements. *Exp*  
 729 *Brain Res*, **195** (1), 117-133

730 Brenner, E. and Smeets, J.B.J. (2011) Continuous visual control of interception. *Hum Movement*  
 731 *Sci*, **30** (3), 475-494

732 Brenner, E. and Smeets, J.B.J. (2015a) How people achieve their amazing temporal precision in  
 733 interception. *J Vision*, **15**(3):8, 1-21

734 Bridgeman, B., Hendry, D., and Stark, L. (1975) Failure to detect displacement of visual world  
 735 during saccadic eye movements. *Vis. Res.* **15**, 719–722

736 Burr, D.C., Morgan, M.J. and Morrone, M.C. (1999) Saccadic suppression precedes visual  
 737 motion analysis. *Curr. Biol.* **9**, 1207–1209

738 Castet, E. and Masson, G.S. (2000) Motion perception during saccadic eye movements. *Nat.*  
 739 *Neurosci.* **3**, 177–183

740 Cesqui, B., Mezzetti, M., Lacquaniti, F., and d'Avella, A. (2015). Gaze behavior in one-handed  
 741 catching and its relation with interceptive performance: what the eyes can't tell. *PLoS*  
 742 *One*, **10**(3), e0119445.

743 Danion, F. R., and Flanagan, J. R. (2018). Different gaze strategies during eye versus hand  
 744 tracking of a moving target. *Scientific Reports*, **8**(1), 10059.

745 de la Malla, C., Smeets, J.B.J. and Brenner, E. (2017) Potential systematic interception errors  
 746 are avoided when tracking the target with one's eyes. *Scientific Reports*, **7** (1): 10793

747 de la Malla, C., Smeets, J.B.J. and Brenner, E. (2018) Errors in interception can be predicted  
 748 from errors in perception. *Cortex* **98**, 49-59.

749 de la Malla, C., Brenner, E., de Haan, E. H., and Smeets, J. B. J. (2019). A visual illusion that  
 750 influences perception and action through the dorsal pathway. *Communications*  
 751 *biology*, **2**(1), 38.

752 Diaz, G., Cooper, J., Rothkopf, C. and Hayhoe, M. (2013) Saccades to future ball location  
 753 reveal memory-based prediction in a virtual-reality interception task. *J Vision*, **13** (20),  
 754 1-14

755 Dorr, M., Martinetz, T., Gegenfurtner, K. R., and Barth, E. (2010) Variability of eye movements  
 756 when viewing dynamic natural scenes. *J Vision*, **10** (10), 1-17.

757 Fogt, N. F., and Zimmerman, A. B. (2014). A method to monitor eye and head tracking  
 758 movements in college baseball players. *Optometry and Vision Science*, **91**(2), 200-211.

759 Fogt, N., and Persson, T. W. (2017). A pilot study of horizontal head and eye rotations in  
760 baseball batting. *Optometry and vision science: official publication of the American*  
761 *Academy of Optometry*, **94**(8), 789-796.

762 Fookien, J., Yeo, S. H., Pai, D. K., & Spering, M. (2016). Eye movement accuracy determines  
763 natural interception strategies. *J Vision*, **16** (14), 1-15.

764 Goettker, A., Braun, D. I., Schütz, A. C., and Gegenfurtner, K. R. (2018). Execution of saccadic  
765 eye movements affects speed perception. *Proc Natl Acad Sci USA*, **115** (9), 2240-2245.

766 Goettker, A., Brenner, E., Gegenfurtner, K. R., and de la Malla, C. (2019). Corrective saccades  
767 influence velocity judgements and interception. *Scientific Reports* 9(1): 5395

768 Graf, E.W., Warren, P.A. and Maloney, L.T. (2005) Explicit estimation of visual uncertainty in  
769 human motion processing. *Vision Res*, **45**(24), 3050-3059.

770 Hayhoe, M. and Ballard, D. (2005) Eye movements in natural behaviour. *Trends in Cognitive*  
771 *Sciences*, **9** (4), 188-194

772 Honda H. (1989) Perceptual localization of visual stimuli flashed during saccades. *Percept*  
773 *Psychophys*. **45**,162–174

774 Johansson, R.S., Westling, G., Bäckström, A. and Flanagan, J.R. (2001) Eye-hand coordination  
775 in object manipulation. *J Neurosci*, **21** (17), 6917-6932

776 Kowler, E. and Steinman, R. M. (1979) The effect of expectations on slow oculomotor control –  
777 I. Periodic target steps. *Vision Res*, **19**, 619-632.

778 Land, M.F. (2006) Eye movements and the control of actions in everyday life. *Progress in*  
779 *Retinal and Eye Research*, **25** (3), 296-324

780 Land, M.F. and Hayhoe, M. (2001) In what ways do eye movements contribute to everyday  
781 activities? *Vision Res*, **41**, 3559-3565

782 Land, M.F. and McLeod, P. (2000) From eye movements to actions: how batsmen hit the ball.  
783 *Nat Neurosci*, **3** (12), 1340-1345

784 Lisberger, S. G., Evinger, C., Johanson, G. W. and Fuchs, A. F. (1981) Relationship between  
785 acceleration and retinal image velocity during foveal smooth pursuit in man and  
786 monkey. *J Neurophysiol*, **46**, 229-249.

787 Lisberger, S. G., Morris, E. J., & Tychsen, L. (1987). Visual motion processing and sensory-  
788 motor integration for smooth pursuit eye movements. *Annual Rev Neurosci*, **10**(1), 97-  
789 129.

790 López-Moliner, J., and Brenner, E. (2016). Flexible timing of eye movements when catching a  
791 ball. *J Vis*, **16**(5), 13-13.

792 Maij F., Brenner E. and Smeets J.B.J. (2009) Temporal information can influence spatial  
793 localization. *J Neurophysiol*. **102**, 490–495

794 Maij, F., Brenner, E. and Smeets, J.B.J. (2011) Temporal uncertainty separates flashes from  
795 their background during saccades. *J Neurosci* **31**, 3708-3711.

796 Majj, F., Matziridi, M., Smeets, J.B.J., Brenner, E. (2012) Luminance contrast in the  
 797 background makes flashes harder to detect during saccades. *Vision Res* **60**, 22-27.

798 Mann, D. L., Spratford, W., Abernethy, B. (2013). The head tracks and gaze predicts: how the  
 799 world's best batters hit a ball. *PloS one*, **8**(3), e58289.

800 Matin, L. and Pearce, D.G. (1965) Visual perception of direction for stimuli flashed during  
 801 voluntary saccadic eye movements. *Science*, **148**, 1485–1488

802 Mateeff, S. (1978) Saccadic eye movements and localization of visual stimuli. *Percept*  
 803 *Psychophys.* **24**, 215–224

804 Matziridi, M., Brenner, E. and Smeets, J. B. (2015). The role of temporal information in  
 805 perisaccadic mislocalization. *PloS one*, **10**(9), e0134081.

806 Mennie, N., Hayhoe, M. and Sullivan, B. (2007) Look-ahead fixations: anticipatory eye  
 807 movements in natural tasks. *Exp Brain Res*, **179** (3), 427-442

808 Morrone, M.C., Ross, J. and Burr, D.C. (1997) Apparent position of visual targets during real  
 809 and simulated saccadic eye movements. *J Neurosci.* **17**, 7941–7953

810 Mrotek, L.A. and Soechting, J.F. (2007) Target interception: hand-eye coordination and  
 811 strategies. *J Neurosci*, **27**, 7297-7309

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

814 Pelz, J., Hayhoe, M. and Loeber, R. (2001) The coordination of eye, head, and hand movements  
 815 in a natural task. *Exp Brain Res*, **139** (3), 266-277

816 RStudio Team (2018). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA.  
 817 URL <http://www.rstudio.com/>

818 Robinson, D. A. (1965) The mechanics of human smooth pursuit eye movements. *J Physiol*  
 819 (Lond) **180**, 569-591.

820 Ross, J., Morrone, M. C., Goldberg, M. E., and Burr, D. C. (2001) Changes in visual perception  
 821 at the time of saccades. *Trends Neurosci*, **24**(2), 113-121.

822 Schlag, J. and Schlag-Rey, M. (2002) Through the eye, slowly: delays and localization errors in  
 823 the visual system. *Nat Rev Neurosci.* **3** (3), 191-215.

824 Schütz, A.C., Braun, D.I. and Gegenfurtner, K.R. (2009) Object recognition during foveating  
 825 eye movements. *Vision Res* **49**, 2241-2253

826 Smeets, J.B.J., Hayhoe, M. and Ballard, D.H. (1996) Goal-directed arm movements change eye-  
 827 head coordination. *Exp Brain Res*, **109** (3), 434-440

828 Soechting, J.F. and Flanders, M. (2008) Extrapolation of visual motion for manual interception.  
 829 *J Neurophysiol*, **99** (6), 2956-2967

830 Spering, M., Schütz, A. C., Braun, D. I., and Gegenfurtner, K. R. (2011) Keep your eyes on the  
 831 ball: smooth pursuit eye movements enhance prediction of visual motion. *J*  
 832 *Neurophysiol*, **105** (4), 1756-1767.



833 van den Berg, A. V. (1988) Human smooth pursuit during transient perturbations of predictable  
834 and unpredictable target movement. *Exp Brain Res*, **72**, 95-108.  
835 Xia, R., & Barnes, G. (1999). Oculomanual coordination in tracking of pseudorandom target  
836 motion stimuli. *Journal of Motor Behavior*, **31**(1), 21-38.  
837 Zuber, B. L. and Stark, L. (1966). Saccadic suppression: elevation of visual threshold associated  
838 with saccadic eye movements. *Experimental Neurology*, **16**(1), 65-79.  
839

#### 840 **Author's note**

841 Experimental data will be archived in a public data repository. The link to access it will  
842 be included in a final version of the paper, if accepted. At the moment it is available on request  
843 for checking.  
844

#### 845 **ACKNOWLEDGEMENTS**

846  
847 This work was supported by grant NWO 464-13-169 from the Dutch Organization for  
848 Scientific Research to EB and by ESRC grant ES/M00001X/1 to SKR.  
849

850 **Figure legends**

851

852 **Figure 1.** Schematic representation of the task and conditions. (A) Subjects started with their  
853 index finger at the red dot and had to intercept a moving target (black dot) by tapping on it  
854 when it reached the white hitting zone. (B) In the Ring condition, the hitting zone was always  
855 the same large white ring. (C) In the Disk condition, it was a small white disk at one of 24  
856 possible positions. The white dashed lines in C indicate the other possible positions. They were  
857 not visible during the experiment. The six curves in B and C show the six possible paths that the  
858 target could take to one of the 24 hitting zones.

859

860 **Figure 2.** Example of gaze, head and hand movements on single trials for a representative  
861 subject in the two conditions of Experiment 1. Data of two trials with the same target trajectory  
862 from the moment the target appeared until the time of the tap. The colours of the curves change  
863 with the remaining time to tap: from black to either grey, blue, red or green (for the target, gaze,  
864 head and hand, respectively).

865

866 **Figure 3.** Gaze, head and hand movements of all trials of the same representative subject in  
867 Experiment 1 shown in Figure 2. Colours change from black to blue (gaze), red (head) and  
868 green (hand) across time from when the target appears to the moment of the tap (as in Figure 2).

869

870 **Figure 4.** Analysis of the average gaze, head and hand movements of all eight subjects in  
871 Experiment 1 (A-C) and of all five subjects in Experiments 2 (D-F) and 3 (G-I). Normalized  
872 distance to the tap position as a function of the time until the target is hit for the gaze, head and  
873 hand. The lines (continuous for the Ring condition, dashed for the Disk condition) and shaded  
874 areas are the means and standard errors of the subjects' individual mean values. A normalized  
875 distance of zero corresponds to being at the tap position. A normalized distance of one  
876 corresponds to being where the target appeared for the gaze and the head, and corresponds to  
877 being at the finger's starting position for the hand. In the gaze panels, we also show the mean  
878 normalised distance of the target from the tap position (black dotted curve). The inset in A  
879 shows the number of saccades per trial in Experiment 1, split by whether saccades ended closer  
880 to the target (black bars) or closer to the tap position (white bars). Error bars are standard errors  
881 across the subjects' mean numbers of saccades.

882

883 **Figure 5.** Hand movements of all trials of all eight subjects for the furthest (top panels) and the  
884 nearest (bottom panels) hitting zones in Experiment 1. All trajectories start at the hand's starting  
885 point near the bottom of the panel. Colour changes from black to green across time as in Figures  
886 2 and 3.

887 **Table legends**

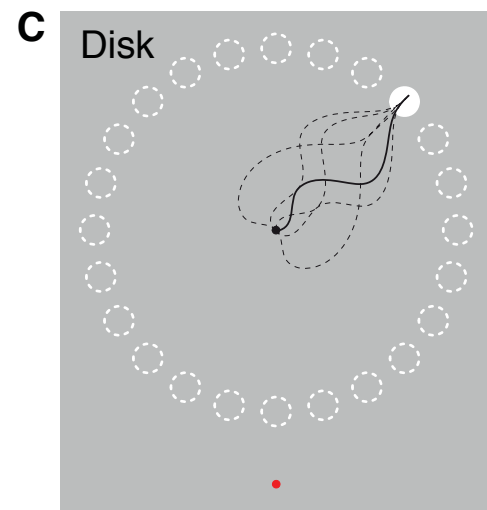
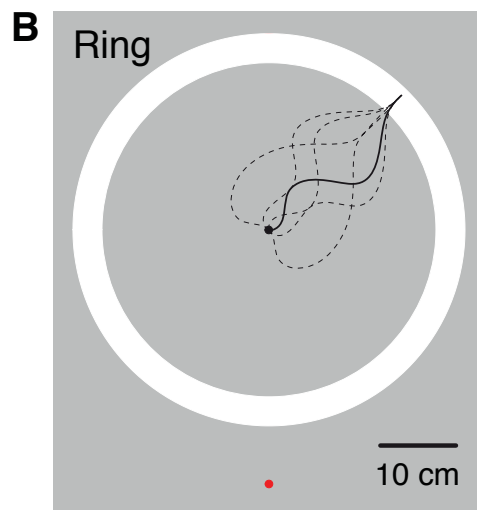
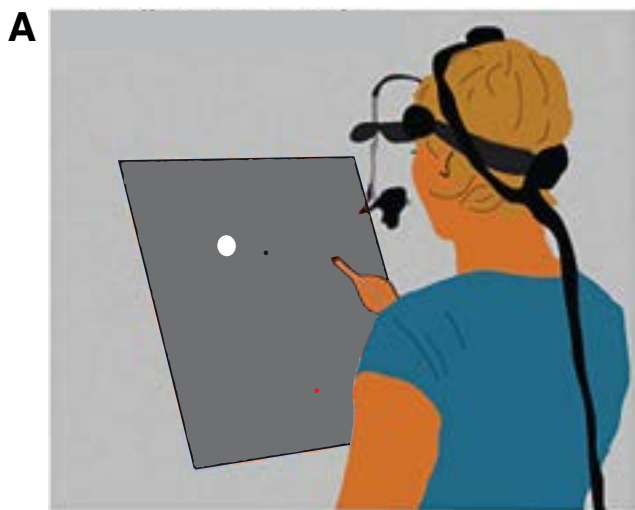
888

889 **Table 1.** Percentage of targets hit. A target is considered to have been hit if the finger, as  
890 calibrated, was within the bounds of both the target and the hitting zone at the time of the tap.  
891 Performance only differed significantly between the Disk and Ring condition in Experiment 1.  
892 Performance in Experiments 2 and 3 differed significantly from that in Experiment 1  
893 (Experiment 2, Disk:  $t_{4,7}=2.3$ ,  $p=0.03$ ; Ring:  $t_{4,7}=5.12$ ,  $p=0.0003$ ; Experiment 3, Disk:  $t_{4,7}=2.34$ ,  
894  $p=0.03$ ; Ring:  $t_{4,7}=7.02$ ,  $p<0.001$ ) but not from each other (Disk:  $t_{4,4}=0.33$ ,  $p=0.38$ ; Ring:  
895  $t_{4,4}=1.46$ ,  $p=0.09$ ).

896

897 **Table 2.** Variability in the timing of the hits (standard deviation in ms). Performance only  
898 differed significantly between the Disk and Ring condition in Experiment 1. Performance in  
899 Experiment 3 differed significantly from that in Experiment 1 (Disk:  $t_{7,4}=1.92$ ,  $p=0.04$ ; Ring:  
900  $t_{7,4}=3.05$ ,  $p=0.008$ ), but the other differences between experiments were not significant.

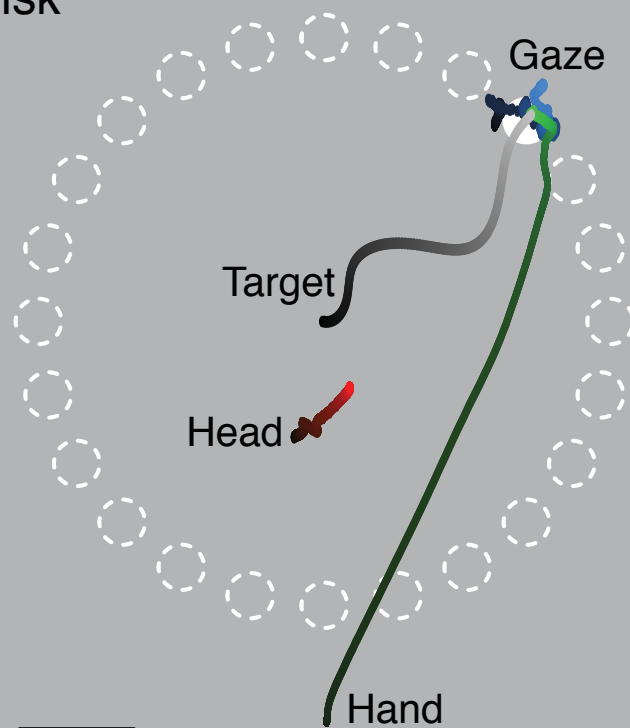
901



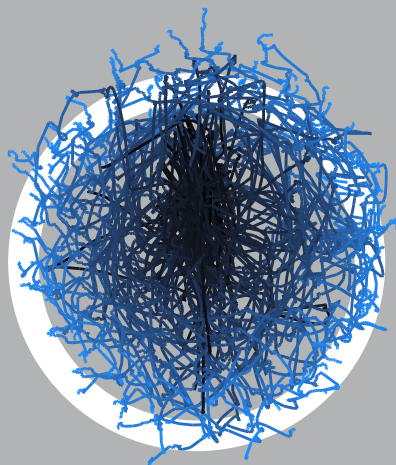
## Ring



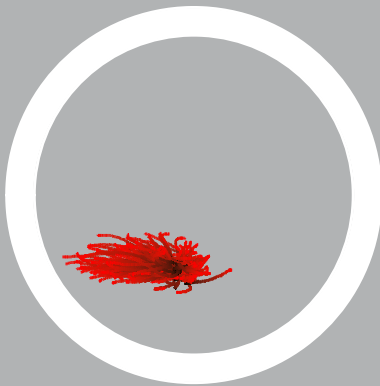
## Disk



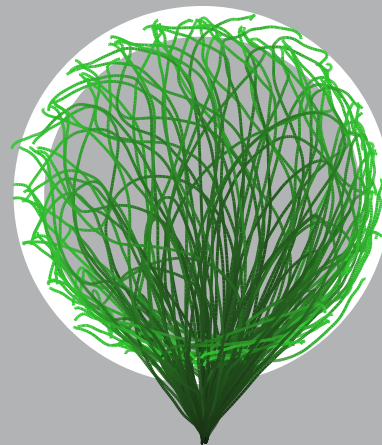
Gaze



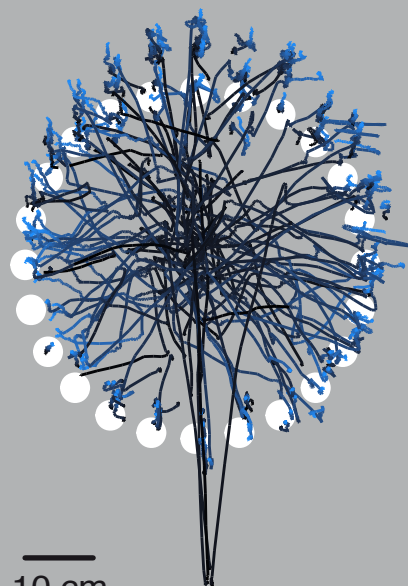
Head



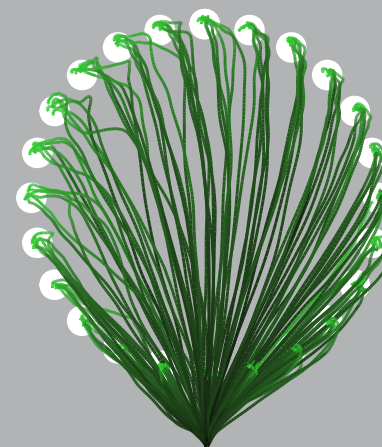
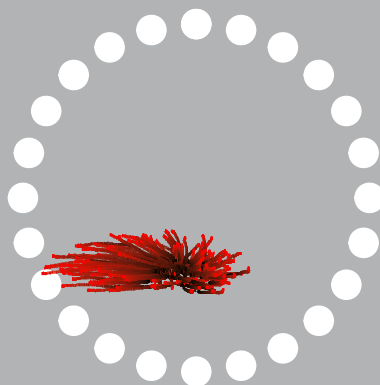
Hand



Ring



10 cm



Disk

