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Motion extrapolation for eye movements predicts perceived motion-induced position shifts

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16

17 **Abstract**

18 Transmission delays in the nervous system pose challenges for the accurate localisation of moving
19 objects as the brain must rely on outdated information to determine their position in space. Acting
20 effectively in the present requires that the brain compensates not only for the time lost in the
21 transmission and processing of sensory information, but also for the expected time that will be spent
22 preparing and executing motor programs. Failure to account for these delays will result in the
23 mislocalization and mistargeting of moving objects. In the visuomotor system, where sensory and
24 motor processes are tightly coupled, this predicts that the perceived position of an object should be
25 related to the latency of saccadic eye movements aimed at it. Here we use the flash-grab effect—a
26 mislocalization of briefly flashed stimuli in the direction of a reversing moving background—to
27 induce shifts of perceived visual position in human observers (male and female). We find a linear
28 relationship between saccade latency and perceived position shift, challenging the classic dissociation
29 between “vision for action” and “vision for perception” for tasks of this kind and showing that
30 oculomotor position representations are either shared with or tightly coupled to perceptual position
31 representations. Altogether, we show that the visual system uses both the spatial and temporal
32 characteristics of an upcoming saccade to localize visual objects for both action and perception.

33

34

35 **Significance Statement:**

36

37 Accurately localizing moving objects is a computational challenge for the brain due to the inevitable
38 delays that result from neural transmission. To solve this, the brain might implement motion
39 extrapolation, predicting where an object ought to be at the present moment. Here, we use the flash-
40 grab effect to induce perceptual position shifts and show that the latency of imminent saccades
41 predicts the perceived position of the objects they target. This counterintuitive finding is important
42 because it not only shows that motion extrapolation mechanisms indeed work to reduce the
43 behavioural impact of neural transmission delays in the human brain, but also that these mechanisms
44 are closely matched in the perceptual and oculomotor systems.

45

46

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53 Discovery Projects funding scheme (project DP180102268).

54 **Introduction**

55

56 When we open our eyes, we experience seeing and acting in the present. However, due to the delays
57 inherent in neuronal transmission, the brain needs time to process what we see. Our awareness of
58 visual events therefore lags behind the occurrence of those events in the world. Nevertheless, we are
59 usually unaware of this delay, and are able to interact with even rapidly moving objects with
60 surprising accuracy (Smeets et al., 1998). One explanation for how the brain might achieve this is that
61 it overcomes its own delays through prediction. By using what it knows about how objects move in
62 the world, the brain can work ahead to compensate for known delays, essentially predicting the
63 present. In visual motion, for example, the future position of a moving object can be extrapolated
64 based on previous samples (Nijhawan, 1994), and we have recently demonstrated that such neural
65 mechanisms do indeed reduce the lag with which the brain represents the position of a moving object
66 (Hogendoorn and Burkitt, 2018). A rapidly moving ball, which would be mislocalized if the brain did
67 not compensate for processing delays, can be caught because its future location can be extrapolated
68 given enough information about its past trajectory. Accurately catching the moving ball further
69 requires that the brain compensates not only for the delays inherent in the processing of the incoming
70 visual information, but also for the additional delays incurred by the planning and execution of the
71 hand and arm movement. Effectively functioning in the present therefore requires that a predictive
72 mechanism accurately encodes the time lost in the transmission and processing of sensory
73 information, as well as the *expected time* that will be lost in preparing the next motor program,
74 transmitting the associated motor commands, and actually moving the corresponding effectors.

75

76 That the brain is able to solve this computational challenge is readily apparent in the saccadic eye-
77 movement system. Short duration, saccadic eye movements in the healthy observer are effectively
78 open-loop, ballistic motor acts that can bring moving objects into foveal vision with remarkable
79 precision (Becker, 1989; van Beers, 2007). Although the saccadic system is thought to program
80 upcoming saccades based on target locations defined by retinal input, our ability to make saccades to
81 moving objects reveals that target encoding in the saccadic system incorporates additional information
82 about the target's anticipated position (Robinson, 1965; Barmack, 1970; Keller and Johnsen, 1990;
83 Cassanello et al., 2008). Even when the moving object is only very briefly presented, monkeys trained
84 to make an eye-movement to the target make saccades that land at or close to the location where the
85 target would have been, had it still been visible (Quinet and Goffart, 2015). This shows that the
86 additional information used by the saccadic system is predictive, and that the brain is capable of using
87 that information to direct the eyes towards a moving object's future location.

88

89 Of course, the execution of eye movements has consequences for the visual information that lands on
90 the retina and accordingly for what we see – that is their primary purpose. Nevertheless, our visual

91 experience is stable across eye movements, and one of the neural mechanism responsible for
92 integrating successive fixations is saccadic remapping (Duhamel et al., 1992). In saccadic remapping,
93 directly before a saccade, visual cells start responding to stimuli that will soon fall in their receptive
94 fields, anticipating the future positions of objects on the retina. Essentially, these cells respond as if
95 the eyes had already moved. An efference copy signal that encodes the magnitude and direction of the
96 intended eye movement allows the visual system to predict the spatial consequences of the saccade
97 (Sommer and Wurtz, 2002, 2006, 2008). Similarly, just before a saccade, visual attention shifts to
98 those locations on the retina that attended objects will occupy after the movement (Rolfs et al., 2011;
99 Jonikaitis et al., 2013), a process that might give rise to a continuous visual experience.

100

101 Importantly, the study of saccadic remapping has focused on the spatial parameters of the eye
102 movement and the consequences for static stimuli. However, when executing a saccade to a *moving*
103 object, the direction of an accurate saccade necessarily depends on its timing: a saccade made with a
104 long latency must be directed further along the anticipated trajectory than a saccade made with a short
105 latency. The fact that we are generally very good at making saccades to rapidly moving objects
106 suggests that the efference copy signal that informs the visual system about imminent saccades
107 encodes not only the direction and amplitude of those eye movements, but also their anticipated
108 timing. The oculomotor system could then use the expected timing and duration of an imminent
109 saccade to extrapolate the locations of moving objects at saccade landing.

110

111 Like the oculomotor system, perception also acts as if it extrapolates the position of moving objects,
112 possibly to keep perception aligned with eye movements, or perhaps because perception depends on
113 the eye movement system for target locations. Indeed, there is a whole class of motion-induced
114 position illusions that has been argued to be a direct or indirect consequence of motion extrapolation,
115 including the flash-lag (Nijhawan, 1994), flash-drag (Krekelberg et al., 2000; Whitney and Cavanagh,
116 2000), flash-jump (Cai and Schlag, 2001), and flash-grab (Cavanagh and Anstis, 2013) effects, as well
117 as the Fröhlich effect (reviewed in (Kerzel, 2010)). We recently investigated the neural basis of the
118 flash-grab effect, and reported a strikingly early locus of interaction between visual motion and
119 position information (Hogendoorn et al., 2015). In the flash-grab effect, an object is briefly flashed on
120 a moving background that abruptly reverses direction. When the object is flashed concurrently with
121 the motion reversal of the background, the result is a large shift of the flashed object's perceived
122 position in the direction of the background's new direction of motion (Cavanagh and Anstis, 2013).
123 One interpretation of this illusion is that the unexpected reversal of the background violates its
124 predicted trajectory, necessitating a corrective signal of some kind. Because the object is flashed
125 concurrently with the reversal, the object is also shifted by this corrective signal (Cavanagh and
126 Anstis, 2013; Hogendoorn et al., 2015). We have previously postulated that this prediction-correction
127 might occur in the Superior Colliculus (SC), because SC is known to play a crucial role in the

128 preparation and execution of saccadic eye movements (Lee et al., 1988), and is specifically involved
129 in extrapolating the future positions of moving saccade targets (Fleuriet and Goffart, 2012; Goffart et
130 al., 2017). Although the cortical frontal eye fields have also been implicated in extrapolation
131 (Cassanello et al., 2008) we observed the neural signature of extrapolation at posterior, rather than
132 frontal electrodes in our EEG study (Hogendoorn et al., 2015). The hypothesis is therefore that this
133 perceptual illusion (in which no actual eye movements are made) recruits the same neural
134 mechanisms that are responsible for extrapolating the future positions of saccade targets.

135

136 This hypothesis makes the intriguing prediction that the timing of an imminent saccade can affect the
137 perceived position of a moving object that the saccade is targeting. Although this prediction might
138 seem to violate intuitive causality (i.e., we know where to move our eyes because we see where the
139 object is), it is a logical consequence of a shared neural extrapolation mechanism that compensates for
140 both sensory and motor delays: we perceive a moving object in the position that it will occupy by the
141 time we have made an eye movement to it.

142

143 In support of this hypothesis, it has been reported that when observers execute saccades to objects that
144 are perceptually shifted due to the flash-drag illusion (Whitney and Cavanagh, 2000), the degree of
145 shift depends on the latency of the saccade (de Sperati and Baud-Bovy, 2008). Although the authors
146 interpret the results in terms of a perception-action dissociation (Goodale and Milner, 1992; Goodale
147 and Westwood, 2004), with early saccades driven by an accurate dorsal “vision for action” system,
148 and later saccades drawing on ventral “vision for perception” representations that are fooled by the
149 illusion, the results are also consistent with a predictive signal that compensates for anticipated
150 saccade latency.

151

152 Here, we test the hypothesis that the perceived position of an object is correlated with the latency of
153 saccades aimed at it. Using the flash-grab effect, we first replicate the relationship between saccade
154 latency and saccade landing previously reported for the flash-drag illusion (de Sperati and Baud-
155 Bovy, 2008). We show that the pattern of results is explained equally well, and with fewer free
156 parameters, by a direct, linear relationship between shift in the landing position and saccade latency
157 than by a gradual transition from an accurate “vision for action” system to a “vision for perception”
158 system that is susceptible to the motion-induced position shift. Altogether, we show that the
159 visuomotor system uses both the spatial and temporal characteristics of the upcoming saccade to
160 localize visual objects.

161

162 **Methods**

163

164 *Observers* – Eight healthy human observers participated in the experiment (age: 20-24, 3 male). All
165 observers had normal or corrected-to-normal vision and gave informed consent prior to participation.
166 Observers received either monetary reward or course credit.

167

168 *Materials* – Stimuli were presented using a 27” ASUS ROG Swift LCD monitor running at 100 Hz
169 with a resolution of 1440x2560 pixels, controlled by a Dell Precision T3610 computer. The
170 experiment was presented using MATLAB (Mathworks inc., Natick MA) and Psychtoolbox
171 (Brainard, 1997; Pelli, 1997). Distance from the screen was kept constant at 55 cm with observers’
172 heads stabilized in a chinrest. Eye movements were recorded using an Eyelink 1000 eyetracker (SR
173 Research, Mississauga, Canada) with a sampling rate of 1000 Hz. The eyetracker was calibrated
174 before each block using the standard 9-point Eyelink calibration procedure. We also recorded 64-
175 channel EEG data during the experiment, but this dataset was not analyzed here.

176

177 *Stimuli* – The stimulus used in this experiment was an annulus comprised of 16 alternating black
178 (0.34 cd/m^2) and white (309 cd/m^2) segments (**Figure 1**). The annulus had an inner radius of 8.5° and
179 an outer radius of 12.5° and rotated at an angular velocity of 200 degrees per second. After 1000,
180 1100, 1200, 1300, 1400 or 1500 ms, the motion direction of the annulus reversed. On 90% of the
181 trials, a target stimulus was presented at reversal. On the remaining 10% of trials, no target was
182 presented. These trials served as catch-trials. The target was a red (62.6 cd/m^2) disk with a diameter of
183 2.85° and was presented for 10 ms (i.e. one frame). The target was always presented 10.5° from
184 fixation, at either 160, 180 or 200 degrees of polar angle offset from the top of the annulus. The target
185 always appeared at the border between two segments, with equal probability that the right segment
186 was black or white. To give the observers some reference as to where they observed the target, eight
187 blue lines (6.1 cd/m^2 , width: 0.23° , height: 2.3°) were drawn around the annulus (at 0, 45, 90, 135,
188 180, 225, 270, and 315 polar offset from the top of the annulus). Two smaller black lines were
189 presented between every two blue lines (width: 0.19° , height: 1.37°). All stimuli were presented on a
190 gray background (76.2 cd/m^2), with a white (309 cd/m^2) fixation dot in the center (diameter: 0.46°).

191

192 *Procedure* - The experiment consisted of 35 blocks, that were of two types. First, in the *Perception*
193 blocks (20 blocks of 120 trials each), at the end of each trial observers were asked to indicate the
194 perceived position of the target using the computer mouse, whilst maintaining fixation. On these
195 trials, the annulus of black and white segments continued moving but changed gradually to uniform
196 dark-gray (26.1 cd/m^2) starting at 400 ms after reversal and becoming fully gray 100 ms later. This
197 was done to ensure that the moving segments did not distract the observers in their answer. Observers
198 were told that they could start to move the mouse as soon as the annulus was fully gray. The image of
199 the target was drawn at the cursor location and moved with it across the screen. Observers had
200 unlimited time to respond. A new trial started as soon as a response was given. Observers were

201 instructed to click at the location of the fixation dot if they did not perceive the target. A *Perception*
202 block lasted approximately 6 minutes. Second, in the *Saccade* blocks (15 blocks of 160 trials each)
203 observers were asked to make an eye-movement to the target. On these trials, the fixation dot
204 disappeared at the time of reversal. All stimuli disappeared from the screen 500 ms after reversal, and
205 the screen remained blank for 1000 ms before a new trial started. A *Saccade* block lasted
206 approximately 8 minutes. The order in which the blocks were presented was randomized across
207 observers. At the start of each block either the word ‘mouse’ or ‘eyes’ was presented, to inform the
208 observers of an upcoming *Perception* or *Saccade* block respectively. The 35 blocks were divided over
209 multiple sessions spanning 3-5 separate days.

210

211 *Experimental Design and Statistical Analysis* – The experiment consisted of a 3x2x2 factorial design,
212 with location (160°, 180°, and 200°), reversal direction (clockwise or counter-clockwise) and
213 response (perceptual report or saccade) as factors. Differences between means in each combination of
214 condition were tested using a repeated measures ANOVA, and individual comparisons were tested
215 using two-tailed paired-sample t-tests. In subsequent analyses of saccade latency, bivariate
216 correlations were tested using Pearson’s *r*.

217

218 **Results**

219

220 Data was analyzed offline using MATLAB (The Mathworks, Natick, MA). During *Perception* blocks,
221 observers were instructed to maintain fixation at all times. Trials on which observers’ gaze direction
222 deviated more than 2.85° from fixation (i.e. size of the target) were discarded (15.3%). During
223 *Saccade* blocks, observers were instructed to make an eye-movement towards the target. Trials on
224 which participants failed to do so (28.0%) or on which eye-tracking data was missing (17.7%) were
225 discarded from the analysis. On every trial, epochs of 500 ms (starting at target onset) were extracted
226 for analysis.

227

228 Saccades were detected by calculating a 2-dimensional velocity space (Engbert and Kliegl, 2003;
229 Engbert and Mergenthaler, 2006). Data points were marked as a saccade if their velocity exceeded the
230 2 SD threshold for at least five consecutive samples (i.e. 5 ms) and the total shift in gaze exceeded 1.0
231 degree of visual angle. 9.7% and 11.2% of catch- trials were wrongfully detected in the *Perception*
232 and *Saccade* blocks respectively. In *Perception* blocks, the polar angle between the real position of
233 the target and the position reported by the observer was taken as the position shift measure. In
234 *Saccade* blocks, the polar angle between the real position of the target and the position of the saccade
235 landing was taken as the position shift measure, with saccade landing defined as the last sample of the
236 saccade.

237

238 In both trial types, we observed large shifts in the perceived position of the target contingent on the
239 reversal direction of the annulus: the flash-grab effect (Cavanagh & Anstis, 2013). **Figure 2** shows
240 distributions of perceived position across all observers for both *Perception* and *Saccade* blocks.
241 Separate one-sample t-tests revealed the absolute magnitude of the shift away from veridical to be
242 significantly different from zero for both the *Perception* ($M=23.6$, $SD=7.9$, $t(7) = 8.5$, $p<0.001$) and
243 the *Saccade* blocks ($M = 18.8$, $SD = 10.0$, $t(7) = 5.3$, $p<0.005$). Furthermore, a 2 (reversal direction) x
244 3 (target location) x 2 (block type) repeated-measures ANOVA revealed a significant main effect of
245 target location on absolute shift (loc 160° $M = 20.2$, $SD = 9.0$, loc 180°: $M = 22.5$ $SD = 11.0$, loc 200°:
246 $M = 20.7$ $SD = 9.6$, $F(2)=3.77$, $p < 0.05$). Individual post-hoc t-tests revealed that absolute shift of the
247 target at 180° was significantly greater than the absolute shift of the target that was presented at 160°
248 ($t = 2.85$, $p < 0.01$). Furthermore, the ANOVA revealed a significant three way interaction effect of
249 reversal direction, block type and target location ($F(2) = 13.63$, $p < 0.001$). This interaction is best
250 understood as the difference between *Perception* and *Saccade* blocks being largest for the off-center
251 locations with illusory shifts towards the midline, and smallest for off-center locations with illusory
252 shifts away from the midline.

253

254 To further investigate the relation between performance on the *Perception* and *Saccade* blocks, we
255 analyzed variance in both measures across observers (**Figure 3**). This showed that although the
256 strength of the illusion varied considerably across observers, the two shift measures were highly
257 correlated. The larger a participant's perceptual shift, the further their saccades land in the direction of
258 the reversal (or, vice versa). Moreover, the shifts were not only strongly correlated in magnitude, they
259 were virtually identical in size: the slopes relating *Perception* and *Saccade* shifts across participants at
260 the three locations did not differ significantly from 1.00 (means and 95% confidence intervals for
261 each condition: 1.13 (0.89-1.36), 1.03 (0.77-1.29), 1.15 (0.92-1.38)).

262

263 Subsequently, we analyzed how trial-by-trial variation in saccade latency related to shifts in target
264 landing location (deviation of saccade endpoint from location of flashed target) in the *Saccade* blocks.
265 **Figure 4** shows a plot of landing shifts as a function of saccadic onset for individual observers. The
266 figure reveals a significant positive correlation for each individual observer: shift in the saccade
267 landing increases with saccadic latency. Absolute correlations are small, but this can be attributed to
268 large variability in the signal caused by visual uncertainty, motor noise, and other factors (van Beers,
269 2007). **Figure 5** shows the relationship between mean saccadic latency and mean shift in saccade
270 landing across observers. Again, we observe a positive correlation: The observers with the fastest
271 saccades have the lowest shift in saccade landing and vice versa.

272

273 De Sperati and Baud-Bovy (2008) carried out a similar experiment and performed a similar analysis
274 procedure in which logistic functions were fitted to the data, consistent with their dual pathway

275 hypothesis. These logistic functions related saccade latency to saccadic mislocalization and had four
276 parameters: one asymptote for the mislocalisation evident for each pathway, the latency at which the
277 visuomotor system shifts from relying on one pathway to relying on the other, and the slope or
278 sharpness of the transition. Here, we provide an alternative explanation: a linear relationship between
279 saccadic onset and shift in the saccade landing, reflecting predictive compensation. To evaluate both
280 hypotheses, we fitted both linear and logistic functions to the data (plotted as solid and dashed lines
281 respectively in **Figure 4** and **Figure 5**). Subsequently, we evaluated the explanatory performance of
282 these fits using 10-fold cross validation. In doing so, we divided each dataset presented in **Figure 4**
283 and **Figure 5C** into ten subsets (with a random assignment of trials), after which nine subsets were
284 used to calculate both linear and logistic fits. Then, we calculated their ability to explain the variance
285 in the remaining subset. This process was performed ten times, so that every subset of data was tested
286 once. This showed that, even though the logistic function included two additional free parameters (4
287 rather than 2), it did not explain significantly more variance than the linear fit, either at the level of
288 individual observers (all $p > 0.29$) or with all trials collapsed across observers ($t = 0.993$, $p = 0.33$).

289

290 To directly compare the linear model and the logistic model, we subsequently compared the Bayes
291 Information Criterion (BIC) for the two models (Schwarz, 1978). The BIC weighs explained variance
292 against the number of parameters, with a lower BIC representing a better model. We evaluated BIC
293 for cross-validated model fits for individual observers (as plotted in **Figure 4**). The linear model had a
294 lower BIC for each individual observer (mean difference 10.9, range 0.7 – 24.2). A BIC difference of
295 10 or more represents “very strong evidence” in favour of the model with the lower BIC (Kass and
296 Raftery, 1995), indicating that our data strongly support a linear, rather than logistic model.

297

298 **Discussion**

299

300 In localizing moving objects, the brain must somehow anticipate the delays incurred during
301 transmission and processing of visual information. One way it might do so is through motion
302 extrapolation, and such mechanisms have been argued to underlie a range of motion-position
303 illusions. Here, we used the flash-grab illusion (Cavanagh and Anstis, 2013) to test the hypothesis that
304 these perceptual extrapolation mechanisms are shared with the oculomotor system, such that the
305 timing of imminent saccades is linearly related to the perceived position of the objects they target.

306

307 We show that when observers make saccades to objects that are extrapolated along the motion path
308 due to the flash-grab illusion, the degree of shift is directly proportional to the latency with which
309 saccades are made. We subsequently compared this interpretation against a previously-presented
310 alternative interpretation (de Sperati and Baud-Bovy, 2008) in terms of dissociable dorsal “vision for
311 action” and ventral “vision for perception” mechanisms (Goodale and Milner, 1992). De Sperati &

312 Baud-Bovy presented a model in which the relationship between saccade latency and mislocalization
313 was characterized by an S-shape, representing the premise that rapid saccades depend on an accurate
314 “vision for action” mechanism, whereas later saccades depend on “vision for perception” mechanisms
315 that are (more) susceptible to mislocalisation illusions. Because the rationale is a transition between
316 two discrete mechanisms, the function relating saccade latency and mislocalization flattens out for
317 both very early and very late saccades. Whereas our data could in principle be accounted for by a
318 transition from one mode of vision to another, we show that the relationship between saccade latency
319 and saccade landing is equally well explained, and more parsimoniously, by a direct linear
320 relationship consistent with a shared extrapolation mechanism. Furthermore, the characteristic S-
321 shape with asymptotic plateaus that de’Sperati & Baud-Bovy (2008) used to describe the shift from
322 one mode to the other was not evident in the present data (**Figure 5C**).

323

324 Irrespective of the precise mechanism, the link between saccade latency and saccade landing position
325 is clear. What is the case then for perception? Here we could not measure saccade latency prior to
326 each perceptual decision as no saccades were made in the perceptual report blocks. Nevertheless,
327 there were very strong links between perceptual judgments and saccade landings: the average size of
328 the two shifts was virtually identical across participants (**Figure 3**) and the average saccade latency
329 for each participant in *Saccade* blocks was a good predictor of their perceived shifts in the *Perception*
330 blocks (**Figure 5a**). As such, we believe that the prediction of the position of the target in this illusion
331 uses either the same neural mechanism that is responsible for the planning and execution of a saccade
332 that is aimed at it, or a similar mechanism that is calibrated to give approximately the same amount of
333 shift (for purposes of keeping perception and saccades in alignment).

334

335 Because perceptual reports and saccadic responses were obtained in separate trials, we could not
336 correlate saccade latency and perceptual position shift across trials, but only across conditions and
337 across observers. If observers had made both responses in the same trial, any resulting correlation
338 could be attributed to shared processes at the level of response, rather than reflecting a shared
339 underlying mechanism for extracting the position of a moving stimulus. That is, if asked to make a
340 saccade to the target, and subsequently report the perceived position of the target using a mouse click,
341 observers might simply report the position they fixate at the end of the trial. Such a tendency to align
342 responses would yield a correlation between saccade latency and perceptual position shift without
343 necessarily requiring a shared mechanism for location. By acquiring measures in separate blocks, we
344 eliminated this alternative explanation. The fact that correlations were evident on measures acquired
345 on different trials therefore strengthens the evidence that the two response types draw on the same
346 neural mechanisms.

347

348 The idea that the mechanisms subserving extrapolative localization are shared by the perceptual and
349 visuomotor systems closely parallels a similar proposal in the domain of saccadic adaptation (the
350 progressive correction of systematic saccade targeting errors). A number of studies have shown that
351 saccadic adaptation influences the perceptual localization of objects presented near the saccade target
352 (e.g. Awater et al., 2004; Georg and Lappe, 2009). This has prompted the proposal that saccade
353 metrics involved in shaping motor space also contribute to the metric used for the organization of
354 perceptual space (Collins et al., 2007). Our findings clearly align with that proposal.

355

356 More broadly, our findings contribute to an ongoing discussion about the degree to which action and
357 perception systems are shared c.q. dissociable (Goodale and Milner, 1992). Two decades ago, Aglioti
358 and colleagues reported that the Ebbinghaus (or Titchener) illusion, in which the size of a central
359 circle is perceived as larger or smaller depending on the size of circles surrounding it, affects
360 perceptual judgments without affecting the hand aperture of grasping movements aimed at that circle
361 (Aglioti et al., 1995). This finding has since been challenged on the basis of methodological
362 differences between perceptual and grasping tasks (Pavani et al., 1999; Franz et al., 2000; Franz and
363 Gegenfurtner, 2008). Comparable studies using other size illusions, such as the Muller-Lyer illusion
364 (Elliott and Lee, 1995) and the size-weight illusion (Brenner and Smeets, 1996) have similarly yielded
365 contradictory results. To date, the degree to which action and perception systems are differentially
366 affected by illusions of size (and related object properties) remains contentious.

367

368 Conversely, evidence with regard to the localization of objects shows several examples where the
369 perception and action systems are closely linked. For example, illusions of perceived speed affect
370 both perception and action (Smeets and Brenner, 1995). Illusions of motion direction also affect both
371 perception and action, although the effects on saccadic eye movements and smooth pursuit were
372 subtly different (Zivotofsky et al., 1996, 1998). Factors affecting motion perception, including
373 direction (Beutter and Stone, 1998; Krukowski et al., 2003), occlusion (Stone et al., 2000), motion
374 coherence (Beutter and Stone, 2000), and trial-by-trial variability (Stone and Krauzlis, 2003) similarly
375 affect smooth pursuit eye movements. Although dissociations have been reported (Zivotofsky, 2005;
376 Spering and Carrasco, 2015), Spering and Montagnini (2011) conclude in a review that the majority
377 of results points to similarities between perception and pursuit. Our findings align and extend this
378 literature, showing that motion extrapolation mechanisms are shared not only with smooth pursuit eye
379 movements, but also with ballistic saccades.

380

381 There is one motion-induced position shift (double drift; (Lisi and Cavanagh, 2015)) that does show a
382 large dissociation: there is a large effect on perception, but no effect on immediate saccades.
383 However, it is not a simple perception-action dissociation, because the illusion is present for ballistic
384 pointing (Lisi and Cavanagh, 2017) as well as for memory-based saccades (Massendari et al., 2018).

385 This double-drift illusion differs from other motion-induced position illusions in a number of ways.
386 Firstly, the position deviations are orthogonal to the motion path, not along it as in the effects studied
387 by De Sperati & Baud-Bovy (2008) and in the present study. Furthermore, the integration period is at
388 least a second, as opposed to about 100 ms for extrapolation along the motion path (Cavanagh and
389 Anstis, 2013; Lisi and Cavanagh, 2015), and the position deviations are several times larger.

390

391 It is evident from **Figure 4** and **Figure 5** that saccades never actually landed where the target would
392 have been, had it continued to rotate with the annulus. The perceptual shift similarly falls short of
393 perfect compensation. There are many reasons why the gain of this system might be low, including
394 how the oculomotor system might adjust to the target being systematically absent when the saccade
395 lands. Importantly, the size of the illusion is stable across *Perception* and *Saccade* modalities despite
396 this low gain, consistent with a shared or linked extrapolation mechanism.

397

398 Finally, we return to the alternative explanation for the results described above wherein extrapolation
399 for saccades and perception are computed independently, but that their estimates are kept similar so
400 that perception and action are always in agreement (see also (Greenwood et al., 2017)). To
401 differentiate between these hypotheses of common vs aligned but independent mechanisms, future
402 research will need to specifically alter motion-induced perceptual shifts and monitor the consequences
403 for saccadic targeting, or vice versa.

404

405

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407

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- 518
- 519

520 **Figure Captions**

521

522 *Figure 1. Experimental procedure. (i) the annulus rotates in the clock-wise (CW) or counter-clock-wise (CCW)*
523 *direction for either 1000, 1100, 1200, 1300, 1400 or 1500 ms. (ii) Reversal and target onset. The annulus*
524 *reverses its motion direction and the target is presented for 10 ms (i.e. one frame). Here, the target is presented*
525 *at the central position (i.e. at 180°). The two other possible target locations are depicted as the two transparent*
526 *disks at 160° and 200°. Targets are always presented at the border of two adjacent segments. (iii) Perception*
527 *trials: The annulus continues rotating for another 400 ms, after which it gradually starts to turn dark gray. It is*
528 *fully gray 100 ms later. The annulus is displayed until the observer gives a response. Saccade trials: The*
529 *fixation dot is removed from the screen. The annulus continues rotating, dimming to invisibility after 500 ms as*
530 *in the perception trials. A blank screen is presented for 1000 ms, after which a new trial starts.*

531

532 *Figure 2. Shifts in perceived target location (Perception blocks; red) and saccade landing position (Saccade*
533 *blocks; blue) Plots show means for each condition across all eight observers. Filled and open bars represent*
534 *clockwise and counter-clockwise reversals, respectively, with error bars indicating the standard error of the*
535 *mean (SEM). Dashed lines indicate the physical location of the target.*

536

537 *Figure 3. Target shifts for both Perception and Saccade blocks. Each circle denotes an individual observer's*
538 *mean \pm SEM. Filled circles indicate clockwise reversals while open circles indicate counter-clockwise*
539 *reversals. Equality lines are plotted as dotted lines. The black line shows a linear best-fit function.*

540

541 *Figure 4. Shift in saccade landing from target location as a function of saccade onset for eight observers. Data*
542 *is collapsed across all conditions (i.e. target location, reversal direction). Note that here, positive values*
543 *indicate a perceived position shifted in the reversal direction while negative values indicate a perceived position*
544 *shifted in the opposite direction. Linear and logistic fits of the data were calculated and are overlaid in as solid*
545 *and dashed lines respectively. The dotted line indicates the extrapolated position of the target: its position had it*
546 *rotated with the annulus.*

547

548 *Figure 5. Mean target shift for Perception blocks (A) and Saccade blocks (B) as a function of mean saccadic*
549 *latency, with each circle representing an individual observer. Shaded regions represent standard deviations.*
550 *Panel C shows shift in saccade landing as a function of saccadic latency across all individual Saccade trials*
551 *across all observers. In each panel, linear and logistic fits of the data were calculated and overlaid in solid and*
552 *dashed lines respectively. Correlation coefficients for the linear fit (r) are indicated in each panel, along with*
553 *corresponding p -values. The dotted line indicates the position of the target, had it rotated with the annulus.*

554









