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# Memory-guided saccades show effect of perceptual illusion whereas visually-guided saccades do not

Delphine Massendari<sup>1</sup>, Matteo Lisi<sup>2</sup>, Thérèse Collins<sup>1</sup> & Patrick Cavanagh<sup>1,3</sup>

<sup>1</sup> Laboratoire Psychologie de la Perception, CNRS UMR 8248, Université Paris Descartes, 75006 Paris, France

<sup>2</sup> Centre for Applied Vision Research, City, University of London, London, UK

<sup>3</sup> Department Psychological and Brain Sciences, Dartmouth College, Hanover, New Hampshire, USA

Delphine.Massendari@gmail.com

Matteo.Lisi@city.ac.uk

Therese.collins@parisdescartes.fr

Patrick.Cavanagh@parisdescartes.fr

Corresponding author: Delphine Massendari, Laboratoire Psychologie de la perception, CNRS UMR 8248, Université Paris Descartes, Centre Biomédical des Saints-Pères, 45, rue des Saints-Pères, 75270 Paris Cedex 06 ; Phone : +33(0)1.42.86.42.68 ; Fax : +33(0)1.42.86.33.22 ; Email : delphine.massendari@gmail.com

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39 **Abstract**

40 The double-drift stimulus (a drifting Gabor with orthogonal internal motion)  
41 generates a large discrepancy between its physical and perceived path. Surprisingly,  
42 saccades directed to the double-drift stimulus land along the physical, and not  
43 perceived, path (Lisi & Cavanagh, 2015). Here we asked whether memory-guided  
44 saccades exhibited the same dissociation from perception. Participants were asked to  
45 keep their gaze centered on a fixation dot while the double-drift stimulus moved back  
46 and forth on a linear path in the periphery. The offset of the fixation was the go-signal  
47 to make a saccade to the target. In the visually-guided saccade condition, the Gabor  
48 kept moving on its trajectory after the go-signal but was removed once the saccade  
49 began. In the memory conditions, the Gabor disappeared before or at the same time as  
50 the go-signal (0 to 1000 ms delay) and participants made a saccade to its remembered  
51 location. The results showed that visually-guided saccades again targeted the physical  
52 rather than the perceived location. However, memory saccades, even with 0 ms delay,  
53 had landing positions shifted toward the perceived location. Our result shows that  
54 memory- and visually-guided saccades are based on different spatial information.

55

56 **New & Noteworthy**

57 We compared the effect of a perceptual illusion on two types of saccades:  
58 visually-guided vs. memory-guided saccades and found that while visually-guided  
59 saccades were almost unaffected by the perceptual illusion, memory-guided saccades  
60 exhibit a strong effect of the illusion. Our result is the first evidence in the literature to  
61 show that visually- and memory- guided saccades use different spatial representations

62

63 **Keywords**

64 Memory-guided saccades  
65 Visually-guided saccades  
66 Double-drift illusion  
67 Action-perception dissociation

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## 71 **1. INTRODUCTION**

72 When a single Gabor seen in peripheral vision moves back and forth along a  
73 linear trajectory and its internal motion drifts in an orthogonal direction (a double-drift  
74 stimulus), the perceived orientation of the path can deviate by 45° or more from its  
75 physical path (Tse & Hsieh, 2006; Shapiro, Lu, Huang, Knight & Ennis, 2010; Kwon,  
76 Tadin & Knill, 2015; Lisi & Cavanagh, 2015; see Figure 1). This double-drift illusion  
77 thus exhibits a very large distortion between the physical and perceived paths.  
78 Recently, Lisi and Cavanagh (2015) found that saccadic eye movements directed to the  
79 double-drift stimulus targeted locations along their physical rather than perceived  
80 trajectories, providing strong evidence for a dissociation between perception and  
81 saccadic eye movements. In the current study, we asked if memory-guided saccades  
82 would exhibit the same dissociation from perception.

83 Although the explanatory mechanisms of the double-drift illusion are still not  
84 completely clear, a common idea is that the two motion vectors, the external direction  
85 of the aperture and the internal direction of the sinewave carrier, combine to produce  
86 an illusory direction. The apparent location of the stimulus is then extrapolated along  
87 this illusory direction, shifting further and further away from the physical location.  
88 According to Lisi & Cavanagh (2015, 2017) the different responses of saccades and  
89 perception to the double-drift stimulus result from the differences in the temporal  
90 interval over which this motion-induced position error accumulates: while in  
91 perception it would accumulate over a long interval (possibly up to 1500ms), in the  
92 saccadic system the extrapolation is thought to cover a much shorter temporal interval,  
93 no longer than the latency of the saccade (de Brouwer, Missal, Barnes, & Lefèvre,  
94 2002; Etchells, Benton, Ludwig, & Gilchrist, 2010), resulting in a smaller position  
95 error.

96 The difference between the saccade and perceptual results might be attributed to  
97 the difference in response modes: in the initial experiment (Lisi & Cavanagh, 2015),  
98 the perceptual effect was measured as a change in motion direction whereas the  
99 saccade required an action toward a position target. However, Lisi and Cavanagh  
100 (2015) demonstrated in a second experiment that the perceptual effect was indeed  
101 based on a position shift and then also showed (Lisi & Cavanagh, 2017) that the lack  
102 of effect in the saccade case was not a general loss for any action toward the target  
103 position: pointing responses were significantly more influenced by the illusion than

104 saccades. There appears to be something specific to the rapid programming of  
105 saccades that limits the time window over which the past sensory history influences  
106 the estimate of target location.

107 The study by Lisi & Cavanagh (2015) focused on interceptive, visually-guided  
108 saccades, leaving open the question of what would happen when there is no current input  
109 available as in the case of a memory saccade (i.e., the target is removed from view before  
110 the action is initiated). Memory-guided saccades rely on information stored in memory to  
111 guide the eyes toward the remembered location when there is no visual stimulus.  
112 Movements directed to a remembered location of an object do show differences in  
113 dynamics and accuracy compared to visually-guided saccades (Becker & Fuchs, 1969;  
114 Gnadt, Bracewell & Andersen, 1991; Smit, van Gisbergen & Cools, 1987; White, Sparks &  
115 Stanford, 1994). Furthermore, the neural systems generating saccades to remembered  
116 locations are to some degree independent from those generating visually-guided saccades  
117 (e.g. Hikosaka & Wurtz, 1985; Funahashi, Bruce & Goldman-Rakic, 1989).

118 Wong and Mack (1981) were the first to hypothesize that saccade programming  
119 could be based on perceptual coordinates (which may differ from retinal coordinates in  
120 some instances) but only for position information stored in memory. The underlying  
121 assumption is that memory for visual location is encoded in perceptual coordinates and  
122 when saccades are memory-guided, the saccadic target has no simultaneous  
123 conflicting, retinal information. Wong & Mack never tested their hypothesis but there  
124 is supporting evidence from experiments with grasping movements. For example,  
125 Westwood & Goodale (2003) used a size-contrast illusion to assess the contribution of  
126 perceptual mechanisms to the control of visually guided and memory-guided grasping  
127 movements. They found that the peak grip aperture was less affected by the perceptual  
128 size illusion when the target array was visible compared to when the target array was  
129 occluded from view. They argued that perceptual mechanisms are necessary for the  
130 control of memory-guided action. According to them, this is because the dedicated  
131 visuomotor mechanisms of the dorsal stream require direct visual input and have only  
132 a brief memory. When an action is memory-guided, its control must access a stored  
133 representation of the target and this stored representation cannot be provided by the  
134 visuomotor mechanisms in the dorsal pathway. Thus, the stored representation  
135 available for the delayed grasp would be provided by the perceptual mechanisms in  
136 the ventral pathway, that is, the very mechanisms that lead to perception (see also  
137 Goodale, Jakobson & Keillor, 1994; Post & Welch, 1996; Hu, Easgleson, & Goodale,

138 1999; Westwood, Chapman & Roy, 2000; Westwood, Heath & Roy, 2000; for a review  
139 see Carey, 2001; for an alternative point of view see Franz, Gegenfurtner, Bühlhoff &  
140 Föhle, 2000).

141 Together, these results suggest visually-guided and memory-guided actions may  
142 not rely on the same sources of information. Two studies have tested this hypothesis in  
143 the context of saccadic eye movements using the Müller-Lyer illusion (de Brouwer,  
144 Brenner, Medendorp & Smeets, 2014; de Brouwer, Breener & Smeets, 2016). In these,  
145 de Brouwer and colleagues found no difference in the size of the illusion between  
146 memory-guided (0.8-s delay) and visually guided saccades to a briefly presented  
147 Müller-Lyer figure. They later confirmed this result with the duration of the delay  
148 increasing from 0 to 1.8 s. From their results they suggested that the absence of an  
149 increase in illusion effects on memory-guided saccades suggests that the same  
150 representation is used, independently of any delay. This is reasonable given that there  
151 is no proposal that the representation of the Müller-Lyer figure would be changing  
152 over time other than through the inevitable degradation of precision with delay.

153 The evidence that visually- and memory- guided saccades use the same spatial  
154 representations of the target can best be challenged using a changing stimulus, one that  
155 may reveal different extents of temporal integration for visual and memory  
156 representations. To this aim, we conducted an experiment similar to the one carried out  
157 by Lisi & Cavanagh (2015) with the addition of a memory delay between the  
158 disappearance of the stimulus and the go-signal to execute the saccade. Participants  
159 thus had to execute the saccades toward the remembered location of the double-drift  
160 stimulus. We tested different memory delay durations. As a control, our experiment  
161 also included trials without a memory delay in which saccades were visually guided.  
162 Our hypothesis was that the distribution of landing positions for visually-guided  
163 saccades would be aligned with the physical path (as shown by Lisi & Cavanagh,  
164 2015) whereas for memory-guided saccades, landing positions would be more aligned  
165 with the perceived path.

166

## 167 **2. METHOD**

### 168 **2.1. Participants**

169 Participants were 10 volunteers (6 female, including one author; mean age = 27.2,  
170 standard deviation = 6.7). All observers reported having normal or corrected-to-normal  
171 vision. Informed consent was obtained in writing in prior to participation and the

172 protocol for the study was approved by the Université Paris Descartes Review Board,  
173 CERES, in accordance with French regulations and the Declaration of Helsinki. All  
174 (except the author) were naive to the specific purpose of the experiment.

175

## 176 **2.2. Setup**

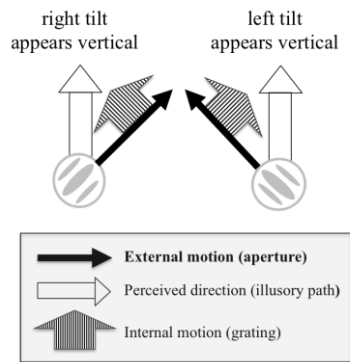
177 Participants sat in a quiet, dark room. We recorded the right-eye gaze position  
178 with an SR Research Eyelink 1000 desktop mounted eye tracker, at a sampling rate of  
179 1 kHz. Participant's head was positioned on a chin rest, with an adjustable forehead  
180 rest, 54 cm in front of a gamma linearized Compaq P1220 CRT screen (vertical  
181 refresh rate 120Hz) that was used to present stimuli. An Apple computer running  
182 MATLAB (Mathworks) with the Psychophysics and Eyelink toolboxes (Pelli, 1997;  
183 Brainard, 1997; Cornelissen, Peters & Palmer, 2002) controlled stimulus presentation  
184 and response collection.

185

## 186 **2.3. Stimuli**

187 In both the perceptual and saccade conditions, the stimulus was a Gabor pattern  
188 (sinusoidal luminance modulations within a Gaussian contrast envelope) with a spatial  
189 frequency of 2 cycles/dva (cycles per degree of visual angle) and 100% contrast. The  
190 standard deviation of the contrast envelope was 0.1 dva. The Gabor moved back and  
191 forth along a linear path 3 dva in length, with a speed of 2 dva/sec (external motion).  
192 The sinusoidal grating had the same orientation as the motion path, and drifted in an  
193 orthogonal direction with a temporal frequency of 3Hz and a speed of 1.5 dva/sec  
194 (internal motion), reversing its direction in synchrony with path reversals at the two  
195 endpoints (every 1.5 seconds). The combination of internal and external motion can  
196 make a tilted path appear vertical (see Figure 1): a right tilted path can appear vertical  
197 if the internal motion is to the left while the Gabor moves upward (and to the right  
198 when it moves downward), and vice versa for a left tilted path (see Lisi & Cavanagh,  
199 2015, [Movie S1](#)). The stimulus was presented on a uniform gray background ( $5.3$   
200  $\text{cd/m}^2$ ) and the midpoint of the trajectory was placed at 10 dva from fixation to the  
201 right on the horizontal midline (see Figure 2).

202



203

204

205 **Figure 1. The two double-drift stimuli with tilted paths that appear vertical due**  
 206 **to the addition of internal motion.**

207

## 208 **2.4. Part 1: Perceptual task**

### 209 **2.4.1. Procedure and design**

210 The aim of the perceptual task was to measure the orientation of the Gabor's  
 211 physical path that was perceived as vertical for each participant. We used the same  
 212 perceptual task as Lisi and Cavanagh (2015). We presented Gabor patterns moving  
 213 along paths with different orientations, and participants were asked to judge the  
 214 left/right tilt of the motion path. The stimulus was displayed until participants  
 215 provided a response by pressing on the left or right arrow key. Gaze position was  
 216 recorded and monitored online with the eye-tracker, and trials in which the participant  
 217 shifted gaze away from the fixation point or blinked before giving the response were  
 218 immediately aborted and repeated at the end of the block. The physical orientation of  
 219 the path was adjusted by means of multiple interleaved QUEST staircases (Watson &  
 220 Pelli, 1983) that converged to a 50% proportion of "right" tilt responses. Trials with  
 221 left and right tilt were randomly interleaved. Each participant performed two sessions  
 222 of 240 trials each, divided in six blocks.

223

### 224 **2.4.2. Data analysis**

225 For each participant and condition the point of subjective verticality of the  
 226 physical trajectory was computed as the orientation corresponding to the 0.5 level of a  
 227 cumulative Gaussian psychometric function, fitted by maximum likelihood on the  
 228 proportion of "right" tilt responses (i.e., the orientation that would yield 50% "left"  
 229 and 50% "right" tilt responses).

230 We thus obtained for each participant the physical left-tilted and right-tilted  
 231 orientations of the Gabor's physical path that were perceived as vertical.

## 232           **2.5. Part 2: Saccade task**

### 233           **2.5.1. Procedure and design**

234           The aim of the saccade task was to measure the influence of the removal of the  
235 Gabor stimulus before the execution of the saccade (memory conditions) on the  
236 landing position of the first saccade. The saccade task comprised five sessions. Among  
237 the five sessions: (i) four contained memory trials in which participants were asked to  
238 saccade to the last seen position of the target and where the Gabor disappeared at the  
239 same time as (delay 0 sec) or before (delays 0.25, 0.5 and 1 sec.) the fixation offset  
240 and (ii) one contained visually-guided (i.e. interceptive) trials in which participants  
241 were asked to saccade to the moving Gabor (i.e. to intercept it) and where the Gabor  
242 remained present and in motion after fixation offset until a saccade was detected (and  
243 for a maximum duration of 500 ms). The exact procedures used for memory and  
244 interceptive trials are detailed in the two next paragraphs and in Figure 2. Each delay  
245 was presented in a separate session. The order of the five sessions was  
246 counterbalanced across participants using a Latin square. Each session lasted one hour  
247 and included 480 trials divided into 10 blocks. However, note that we also ran a  
248 control experiment with interleaved memory and visuallyguided trials to ensure that  
249 the presentation of the different delays in separate sessions had no influence in the  
250 results obtained (see Appendix 1).

251           In the saccade task, each participant was presented only the orientations of the  
252 motion path that corresponded to perceived verticality of the motion path (as measured  
253 in the perceptual task). In each block, the orientation of the physical path could be  
254 right-tilted or left-tilted and the internal motion could be absent (control condition) or  
255 present (double-drift condition): this yielded a total of 120 repetitions per condition.  
256 The different conditions were randomly interleaved in each block. During the saccade  
257 task, gaze position was recorded at 1Khz and monitored online; trials in which  
258 participants shifted gaze or blinked before the disappearance of the fixation dot were  
259 aborted and repeated within the same block.

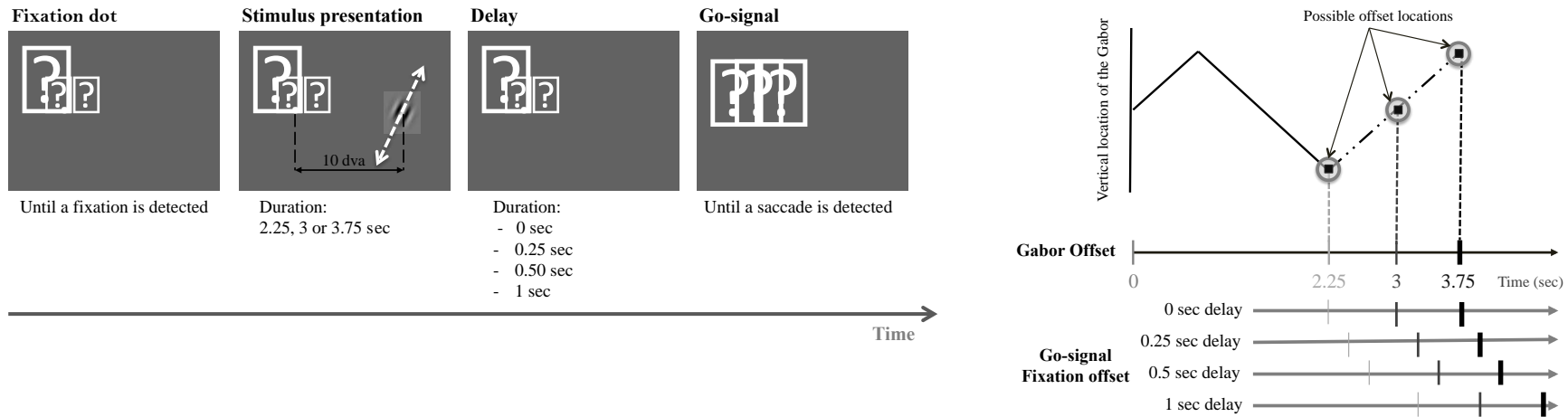
260           **Memory trials:** In the 4 blocks of memory-guided saccade trials, each trial started  
261 when the participant fixated on a black dot (a circle of 0.2 dva diameter). The position  
262 of the fixation dot was jittered horizontally and vertically from trial to trial according  
263 to two Gaussian distributions ( $SD = 0.2$  dva) centered on (-4, 0) relative to screen  
264 center. After a random interval of 400-600ms, the Gabor appeared in the central  
265 position of its motion path, 10 dva to the right of the fixation point and started moving

266 upwards or downwards. During stimulus presentation, the fixation dot remained on the  
267 screen and participants were asked to keep their eyes on it. The Gabor drifted for 2.25,  
268 3 or 3.75 seconds, leading to three possible offset locations: the two extremities or the  
269 center of the path (see right panel of Figure 2A). Participants were then asked to  
270 saccade to this offset location (i.e. to the position where the Gabor target was last seen  
271 and removed) as soon as go-signal instructed them to do so, 0, 250, 500 or 1000 ms  
272 later. The go-signal was the removal of the fixation point. Each delay was presented in  
273 a separate session. In all conditions, the actual delay between go-signal and saccade  
274 was the sum of the experimenter-defined delay and the saccade latency on that trial  
275 (mean latency in the memory trials = 215 ms, SD across participants = 46 ms). In the  
276 0-delay condition, the actual delay was therefore equal to saccade latency. The general  
277 procedure used for the memory trials is summarized in Figure 2A.

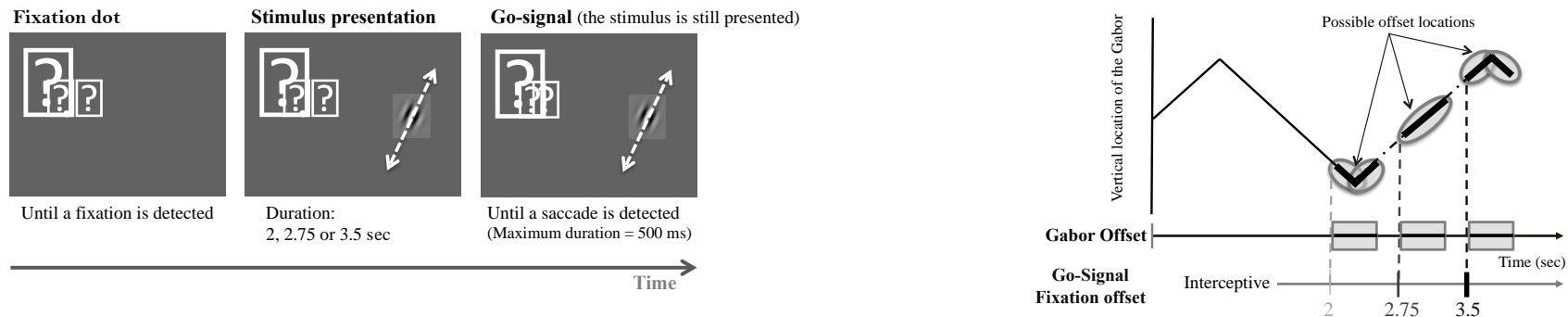
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279 **Interceptive trials:** The procedure (summarized in Figure 2B) was almost identical to  
280 the memory-guided saccade trials, except that the Gabor did not disappear before or  
281 concurrently with the go-signal. Instead, the go-signal was given and the Gabor  
282 continued drifting until gaze position was detected outside a circular area with 2 dva of  
283 the radius around the fixation and for a maximum duration of 500 ms. Participants  
284 thus had 500 ms to initiate their saccades to intercept the stimulus. As soon as the  
285 saccade was detected, the Gabor was removed and this could happen at any point in  
286 time during the 500 ms interval. The go-signal was given 250 ms before the Gabor  
287 reached one of the two endpoints of its path or the center of the path so that the Gabor  
288 was exactly at one of these three possible locations when participants initiated their  
289 saccades with a latency of 250 ms. The 250 ms value had been chosen *a priori* to  
290 approximately match the mean saccade latency of the participants in this session. We  
291 observed *a posteriori* that it was an appropriate estimation (mean across participants =  
292 249 ms; SD across participants = 35 ms). This was done in order to have a duration of  
293 presentation of the Gabor in the interceptive trials that corresponds on average to the  
294 duration of presentation in the memory condition and thus have interceptive saccades  
295 targeting approximately the same locations as in memory trials (see right panels in  
296 Figure 2). As soon as a saccade was detected, the Gabor was removed so that  
297 participants received no feedback about the accuracy of their saccades. Participants  
298 were instructed to execute a saccade as soon as the fixation point disappeared in order  
299 to intercept the moving Gabor.

## A. Memory trials



## B. Interceptive trials



300

301 **Figure 2. Procedure used in the memory (Panel A) or interceptive (Panel B) trials.**

302 The left side of the figure illustrates the general procedure. In memory trials the stimulus had already disappeared at the time when the go-  
 303 signal was given (i.e. the removal of the fixation point) whereas in the interceptive saccade trials the stimulus was still present. The right side  
 304 of the figure presents the vertical location of the target as a function of stimulus time presentation. In memory trials, the stimulus could be  
 305 presented for 2.25, 3 or 3.75 sec, leading to three possible offset locations: the two extremities or the center of the path. Following Gabor  
 306 offset, the go-signal was given after a delay varying from 0 to 1 sec. In interceptive trials, the stimulus remained presented for 500 ms after  
 307 the go-signal. Participants thus had 500 ms to initiate their saccades to intercept the stimulus. As soon as the saccade was detected, the Gabor  
 308 was removed and this could happen at any point in time during the 500 ms interval. The go-signal was given 250 ms before the Gabor  
 309 reached one of the two extremities or the center of the path. The Gabor was exactly at one of these three possible locations when participants  
 310 initiated their saccades with a latency of 250 ms.

311  
312

## 2.5.2. Data analysis

313 The eye-position signal was re-analyzed offline using a saccade-fixation algorithm  
314 based on two-dimensional eye velocity (Engbert & Mergenthaler, 2006). Only the first  
315 saccade that followed the go-signal (i.e. the disappearance of the fixation dot) was  
316 considered for analysis. Trials were excluded from the analysis when no saccade was  
317 detected after the go-signal, a blink occurred before the saccade, the first saccade had  
318 an amplitude less than  $1^\circ$ , an eye-tracker sampling error occurred, or saccade latency  
319 was shorter than 100 ms or longer than 500 ms. This resulted in a rejection of 13.3 %  
320 of the trials.

321

322

### 2.5.2.1. Saccade amplitude

323 We analyzed horizontal and vertical saccade amplitudes (the differences in the  
324 horizontal and vertical coordinates of saccade offset and onset positions) to recover the  
325 landing position of the saccades in each condition. For each participant we fitted a  
326 multivariate linear model with the horizontal and vertical saccade amplitudes as  
327 dependent variables (e.g. see Figure 3). The models included as linear predictors the  
328 horizontal and vertical coordinates of the Gabor at the moment of its disappearance  
329 (i.e. the offset location of the Gabor) together with the condition (with versus without  
330 internal motion) and the interactions between condition and Gabor coordinates. We  
331 fitted this multivariate model for each participant, each delay, and each orientation of  
332 the physical path, and then used the fitted model to generate horizontal and vertical  
333 amplitudes of saccades for all points along the path of the Gabor. Then we computed a  
334 linear regression of the vertical on the horizontal predicted saccade amplitudes, and  
335 derived the angle of deviation from vertical from the regression slope (e.g. see Figure  
336 3). We used this two-step approach because separating the noise in the vertical vs.  
337 horizontal dimensions gives a better match to the typically larger variability of saccade  
338 landings along the radial than tangential axis (Deubel, 1987; van Opstal & van  
339 Gisbergen, 1989). Finally, the difference between the angle of the recovered path in  
340 the control condition and the double-drift condition was calculated for each participant  
341 and each delay, but independently of the right versus left orientation of the tilt since,  
342 as revealed by an Analysis of Variance with a 2 (orientation of the tilt) x 5 (delay)  
343 within-subject design, there was no significant difference between the two orientations  
344 (left-tilted:  $m=16.7$ ,  $se=1.9$ ; right-tilted:  $m=18.9$   $se= 2.03$ ;  $F(1,9)=2.42$ ,  $p=.15$ ) and no  
345 interaction between the orientation of the tilt and delay ( $F(4,36)=1.47$ ;  $p=.23$ ). Thus,

346 we first calculated the mean difference between the control and double-drift condition  
347 for the left- and right-tilted paths and then averaged the two values for each participant  
348 and each delay. This difference was taken as a dependent variable in the statistical  
349 analyses; the larger the difference, the larger the effect of the internal motion on the  
350 orientation of the trajectory targeted by the saccades.  
351 We performed the following statistical analyses. We first ran a one-way ANOVA with  
352 a 5 (delay) within-subject design and then tested whether each condition (interceptive,  
353 0 s delay, 0.25 s delay, 0.5 s delay and 1 s delay) differed from 0 by using five paired-  
354 t-tests that were corrected for multiple comparisons with a Bonferroni correction (i.e.,  
355 the p value was multiplied by the number of comparison; here five). These five  
356 comparisons indicated whether or not the difference between the control and double-  
357 drift condition was significant for each delay. Second, we performed a separate  
358 analysis for the four memory saccade conditions by testing the effect of the delay. To  
359 do this, we ran an analysis of variance using a within-subject design including the  
360 delay as a continuous factor. Finally, to determine whether the absence of the stimulus  
361 during saccade programming was enough to induce a difference between the control  
362 and the double-drift condition, we tested the difference between the interceptive and  
363 the 0 delay conditions.

364

#### 365 **2.5.2.2. Saccade latency**

366 We wanted to ensure that any difference observed on saccade amplitude (and  
367 thus on the angle of the recovered path) between the two internal motion conditions  
368 (control *vs.* double-drift) was not due to a difference in latencies. To do so, we ran a  
369 two-way ANOVA with a 5 (delay) x 2 (internal motion) within-subject design.

370

### 371 **3. RESULTS**

#### 372 **3.1. Results of the perceptual task**

373 For the 10 participants, the orientations of the physical path that were perceived as  
374 vertical strongly deviated from 0 (with 0 corresponding to physical vertical). The  
375 mean right tilt that was perceived as vertical was  $49.2^\circ$  [range from  $38^\circ$  to  $58^\circ$ ] and the  
376 mean left tilt that was perceived as vertical was  $-57.6^\circ$  [range from  $-70^\circ$  to  $-42^\circ$ ],  
377 revealing a dramatic influence of the internal motion on the perceived orientation of  
378 the trajectory.

379

## 380           **3.2. Results of the saccade task**

### 381           **3.2.1. Saccade latency**

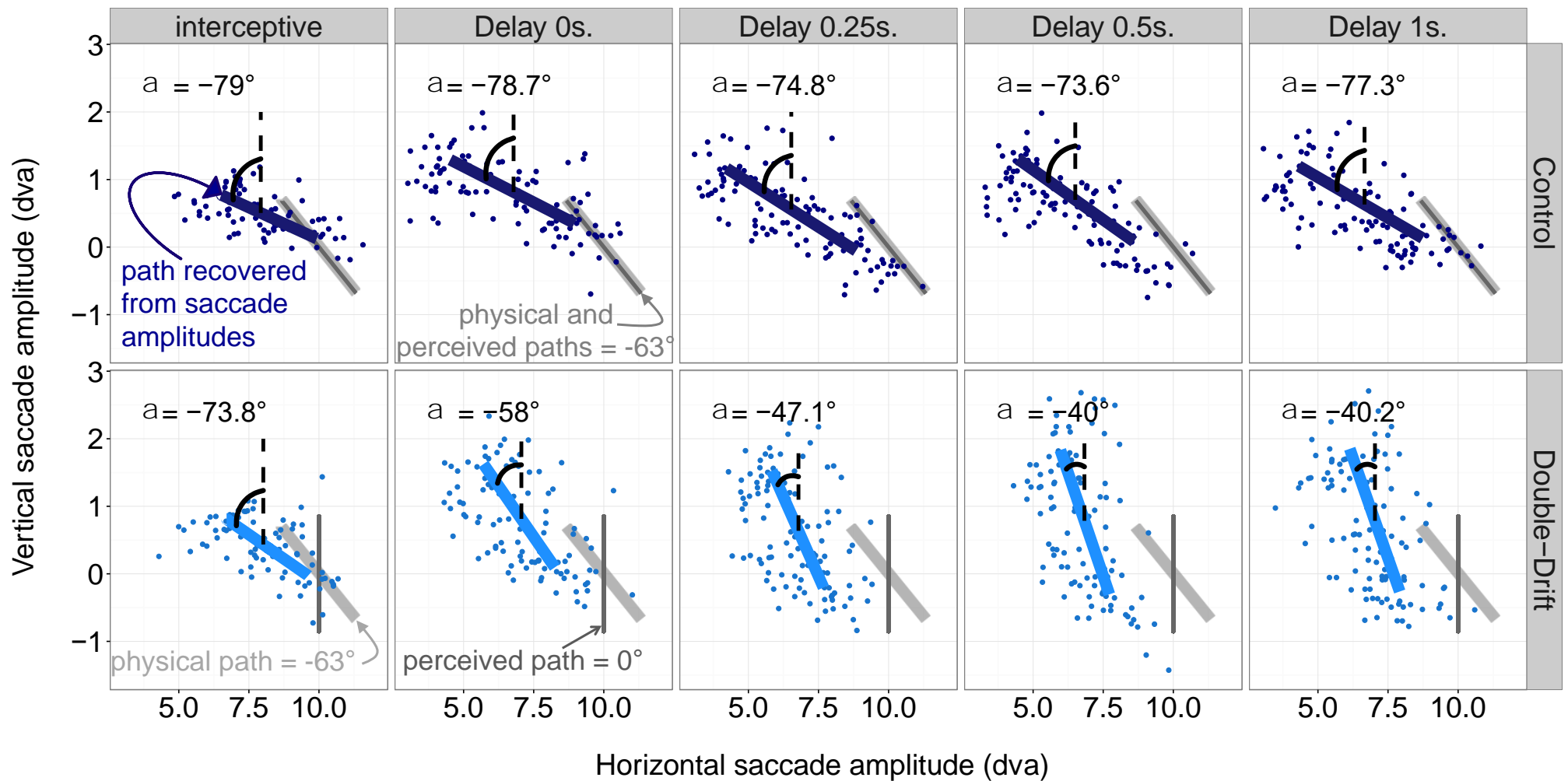
382           The ANOVA revealed an effect of the delay ( $F(4,36) = 14.23; p < .001$ ). This  
383 indicates that there were some differences in saccade latency across the memory delay.  
384 In particular, we found that saccade latencies were longer in the interceptive ( $m = 249$ ;  
385  $se = 7.57$ ) and the 0 delay conditions ( $m = 265$  ms;  $se = 11.21$ ) compared to the other  
386 delays (delay 0.25:  $m = 197$ ,  $se = 5.5$ ; delay 0.5:  $m = 188$ ,  $se = 6.5$ ; delay 1:  $m = 208$ ,  
387  $se = 6.1$ ). However, the most important result is that the ANOVA did not reveal any  
388 effect of the internal motion ( $F(1,9) = 4.7$ ,  $p = .06$ ) nor interaction between the two  
389 ( $F(4, 36) = 0.49$ ,  $p = .75$ ), thus excluding latency as a potential explanatory factor for  
390 any difference between control and double-drift conditions in the distributions of  
391 saccadic endpoints.

392

393

### **3.2.2. Angle of the path recovered from saccade amplitude**

394           Results obtained in the saccade task are presented in Figures 3 and 4. Figure 3  
395 presents the results from one representative participant for only one orientation of the  
396 tilt (left-tilted path) and shows how the angle of the recovered path evolved with the  
397 delay in the two motion conditions: control (without internal motion) vs. double-drift  
398 (with internal motion). Figure 4 presents the mean difference across participants  
399 between the angle of the recovered path in the control and the double-drift conditions  
400 for the different delays.



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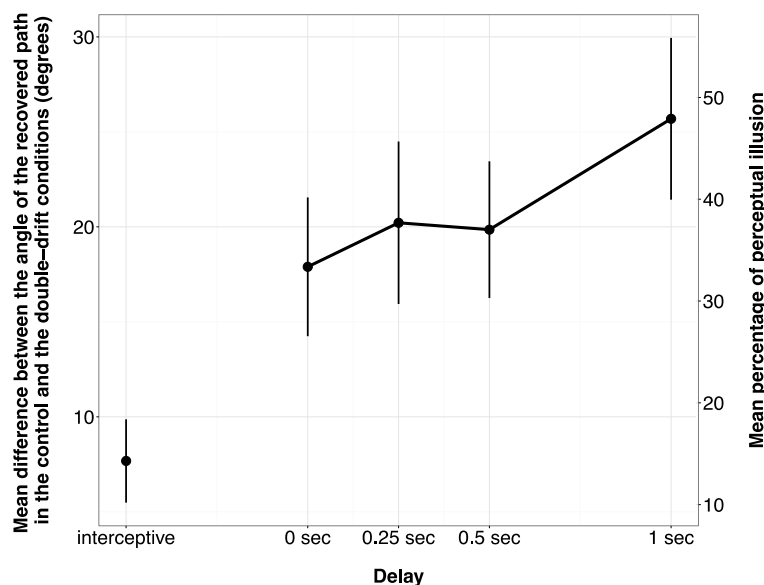
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**Figure 3.** Horizontal and vertical saccade amplitudes for one representative participant are plotted along with the fitted value of the multivariate linear model (blue lines). The results for the control condition (with no internal motion) are presented on the upper panels and those for the double-drift condition (where the physical path was tilted to the left and the perceived path was vertical) on the lower panels. The panels from left to right correspond to the different delays starting with the interceptive condition. The angle of the deviation of the recovered path from vertical ( $\alpha$ ) is indicated in each graph. For this participant, the orientation of the double-drift path that appeared vertical in the perceptual test was  $-63^\circ$ . This was then the path orientation presented in both the control and double-drift saccade conditions shown here. In the control condition, the angle of the recovered path is similar for each delay (varying from  $-73.6^\circ$  to  $-79^\circ$ ) and is relatively close to the real angle of the physical path ( $-63^\circ$ ). In the double-drift condition, there is a difference between the interceptive condition and the four other conditions with a memory delay. In the interceptive condition, the angle of the recovered path ( $-73.8^\circ$ ) is also close to the angle of the physical path ( $-63^\circ$ ) while in the memory conditions, the angle of the recovered path (varying from  $-58^\circ$  to  $-40^\circ$ ) is closer to vertical.

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**Figure 4.** Mean difference between the angle of the recovered path in the control and the double-drift conditions as a function of the delay. The right hand y-axis shows the result as a percentage of the angular difference between the perceived path and the physical path. A full perceptual illusion would correspond to an average deviation between the two paths of 52°. Error bars represent the standard error.

The one-way ANOVA with a 5 (delay) within-subject design revealed an effect of the delay ( $F(4,36)= 6.89; p<.001$ ).

The difference between the control and the double-drift condition was the smallest in the interceptive condition (7.68° on average,  $se = 2.21$ ). However, it was significant ( $t(9)=3.296$ ; *Bonferroni corrected*  $p <.05$ ), contrary to Lisi & Cavanagh (2015).

Furthermore, the four comparisons that tested whether each delay condition differed from 0 were all significant (delay 0:  $m=17.9$ ,  $se=3.78$ ,  $t(9)=4.54$ ; delay 0.25:  $m=20.22$ ,  $se=4.19$ ,  $t(9) = 4.51$ ; delay 0.5:  $m=19.85$ ,  $se=3.59$ ,  $t(9)= 5.27$ ; delay 1:  $m=25.7$ ,  $se=4.38$ ,  $t(9)=5.56$ ; *Bonferroni corrected*  $ps$  always  $< 0.01$ ) indicating that the control condition differed systematically from the double-drift condition when saccades were memory-guided, regardless of the duration of the memory-delay.

Figure 4 also shows that when a memory-delay is added before the execution of the saccade, the difference between the control and the double-drift conditions becomes bigger. The planned comparison between the interceptive (mean = 7.68;  $se = 2.21$ ) and the 0 delay ( $m=17.9$ ,  $se=3.78$ ) condition was significant ( $t(9) = 2.54$ ;  $p<.05$ ). Finally, the ANOVA that was run to assess the effect of the delay on the difference between the angle of the recovered path in the control and the double-drift conditions revealed a linear effect of the delay ( $F(1,9)=6.6$ ;  $p<.05$ ). This indicated that the difference between the

474 control and double-drift conditions, and thus, the effect of the illusion, increased with  
475 delay. Taken together, these results indicate that if the stimulus is absent while the  
476 saccade is programmed (delays 0 ms to 1 sec), the saccade landings in the double-drift  
477 condition differ from those in the interceptive condition, in the direction of the perceptual  
478 illusion. Furthermore, increasing the delay led to a greater deviation in the direction of  
479 the illusion.

480

#### 481 **4. DISCUSSION**

482 The aim of this study was to compare the effect of the double-drift illusion on two  
483 types of saccades: visually-guided saccades and memory-guided saccades. Lisi &  
484 Cavanagh (2015) have recently shown that although the double-drift stimulus leads to a  
485 very large discrepancy between its physical and its perceived path, visually-guided  
486 saccades directed toward it land along the physical, and not the perceived, path. In this  
487 study, we asked whether memory-guided saccades would exhibit the same dissociation  
488 from perception.

489 Several arguments support the prediction that whenever a visually guided action is  
490 immune from a perception illusion, the corresponding memory-guided action may be  
491 influenced by the illusion. Many authors have proposed that memory encodes the  
492 perceived location of the stimulus even when this does not correspond to its retinal  
493 location (Wong & Mack, 1981; Westwood & Goodale, 2003, Hu, Easgleson, & Goodale,  
494 1999; Goodale, Jakobson & Keillor, 1994). Thus, when the information specifying the  
495 position of a target is derived from memory, the eyes should be directed toward its  
496 perceived, and not retinal, location. However, this prediction has not been tested for  
497 saccades and this study was designed to fill this gap. We conducted an experiment similar  
498 to the one carried out by Lisi & Cavanagh (2015) with the addition of a memory delay  
499 between the disappearance of the stimulus, and the go signal to execute the saccade.  
500 Participants thus had to memorize the offset position of the double-drift during a delay  
501 varying from 0 to 1 second and then execute the saccade toward the remembered location  
502 where the double-drift stimulus disappeared. The variable delay tested whether the  
503 influence of the perceptual illusion, if any, changed with the retention interval. Our  
504 experiment also included trials without a memory delay in which participants were  
505 instructed to intercept the double-drift, i.e. saccades were visually guided. In this  
506 condition, we expected to replicate the results obtained by Lisi & Cavanagh (2015).

507 Consistent with this general hypothesis, we found a significant difference between  
508 visually-guided and memory-guided saccades such that visually-guided saccades landed  
509 closer to the physical path while memory-guided saccades were shifted toward the  
510 perceived path, showing on average as much as 48% of the perceptual illusion for the  
511 condition with the largest effect. Furthermore, increasing the duration of the delay  
512 significantly increased the effect of the illusion (from 33% to 48%). Unexpectedly,  
513 visually-guided saccades also showed a small effect of the illusion (about 13%). The  
514 finding of a significant (although small) difference between visually-guided saccades  
515 targeting control and double-drift stimuli – a 7.68° shift in the direction of the perceptual  
516 illusion – contrasts with the absence of a significant difference in Lisi and Cavanagh  
517 (2015). This effect is most likely due to the difference in our sampling of path locations.  
518 In our experiment, participants were asked to saccade to one of 3 locations, as opposed to  
519 one of 6 in the previous study, doubling the frequency of sampling points where the  
520 constant, non-accumulating effect of internal motion at saccade onset (Lisi & Cavanagh,  
521 2015) could influence the orientation recovered from saccade landings (see Appendix 2).

522 In the following, we will discuss the larger effect of the illusion for memory-guided  
523 saccades, compared with visually-guided saccades. We argue that the memory trace  
524 available to the oculomotor system is of lower accuracy and stability than that available  
525 in perceptual memory explaining why the saccade program may access both to achieve  
526 better performance.

527 The main result of this study is that visually-guided saccades differed from memory-  
528 guided saccades. While visually-guided saccades were much less sensitive to the illusory  
529 effect, memory-guided saccades showed a clear effect of the illusion, which was robust  
530 and statistically significant in all the delay conditions tested, and reached on average 48%  
531 of the perceptual effect. Our results are in agreement with the general idea that movement  
532 control may be guided by perceptual memory when the target is no longer present (Wong  
533 & Mack, 1981; Goodale, Jakobson & Keillor, 1994; Post & Welch, 1996; Hu, Easgleson,  
534 & Goodale, 1999; Westwood, Chapman & Roy, 2000; Westwood, Heath & Roy, 2000;  
535 Carey, 2001). Until now, the evidence for this hypothesis has come from experiments  
536 with grasping movements. Our results thus provide evidence that this hypothesis is also  
537 valid for saccadic eye movements. Below, we speculate about the neurophysiological  
538 mechanisms that could account for our results.

539 Brain-imaging studies on memory-guided saccades have provided evidence that  
540 some neurons show a tonic level of discharge that persists after the offset of the visual

541 target until the saccade is performed and could therefore support saccades to remembered  
542 target locations (for reviews, see e.g. Curtis, 2006; Mackey, Devinsky, Doyle, Goldinos  
543 & Curtis, 2016). More precisely, neurons that showed persistent delay period activity (i.e.  
544 activity in absence of visual stimuli falling within their receptive fields) have been found  
545 in a small subset of regions, most notably the lateral intraparietal area (LIP) and the  
546 Frontal Eye fields (FEF). All these areas would be necessary for intact spatial working  
547 memory. Furthermore, they both have projections to the Superior Colliculus (SC; for a  
548 review, see White & Munoz, 2011) so that they can send diverse delay activity signals  
549 (including ones related to memory) to the SC, where the signals may be used for saccade  
550 generation (e.g. see Sommer & Wurtz, 2000). However, the question of what is actually  
551 being remembered or coded for by this delay activity still remains unanswered (Curtis,  
552 2006). This question is particularly relevant in the case of our experiment in which the  
553 target induces a mismatch between veridical (i.e. retinal) and perceived target location.  
554 The present result, showing that memory-guided saccades exhibit an effect of the illusion,  
555 suggests that some of the remembered location originates with the perceptual  
556 representation of the target. Furthermore, as we found that the effect of the illusion was  
557 observed from the shortest delay, 0 ms, this suggests that the switch of spatial  
558 representation (between the retinal to the the perceived location) is triggered by the  
559 absence of the stimulus during saccade programming. One explanation for this transition  
560 is that the “oculomotor memory” of the veridical/retinal location may be unreliable, i.e. it  
561 might have a poor precision. Thus, saccade-targeting tasks are based on the more  
562 veridical oculomotor representation to the extent that retinal information is available —  
563 the stimulus is present — when the saccade is initiated. However, as soon as the stimulus  
564 disappears, an alternative source of information, the remembered perceptual location is  
565 accessed for movement control as it is now more reliable than the oculomotor location  
566 memory. This information appears to be rapidly accessible and ready to be used by the  
567 saccadic system in agreement with the finding of Westwood, Heath & Roy (2000) who  
568 found that illusory-size effects on peak grip aperture emerged with extremely brief  
569 retention intervals (i.e. 0-450 ms).

570 Our results also suggest that in addition to being unreliable, the oculomotor memory  
571 decays over time as seen in a greater effect of the illusion with increasing delay duration.  
572 The decrease of tonic activity seen in oculomotor structures that occurs over the course of  
573 several hundred milliseconds after target disappearance might be responsible of these  
574 changes in memory saccade accuracy (Edelman & Goldberg, 2001). Thus, as the ability

575 of the oculomotor system to keep a memory trace of the veridical target location (i.e. the  
576 retinal location) decays over time, the targeting information would rely increasingly on  
577 the perceptual memory with longer delays. The absence of a full effect of the illusion  
578 even at 1 second delay suggests that the oculomotor memory of the veridical/retinal  
579 location decays relatively slowly, which is compatible with the time constant of decaying  
580 collicular activity following target disappearance (Edelman & Goldberg, 2001). This  
581 residual oculomotor information would be combined with information stored in  
582 perceptual memory, possibly at the level of premotor areas for eye movements, which are  
583 known to be involved in the orienting of spatial attention (Moore & Fallah, 2001,  
584 Casarotti, Lisi, Umiltà & Zorzi, 2012) and consequently also in spatial working memory  
585 (Awh & Jonides, 2001).

586

## 587 **5. CONCLUSIONS**

588 Overall, these results point to a difference in the spatial representation of the target  
589 used to program visually-guided saccades as opposed to that used to program memory-  
590 guided saccades. While visually-guided saccades were almost unaffected by the internal  
591 motion of the Gabor, memory-guided saccades showed a bias consistent with the  
592 perceptual effect (although with a smaller amplitude). As recently proposed by Lisi &  
593 Cavanagh (2017), these results support the idea that there are two distinct spatial  
594 representations of the visual world. One map, used to generate visually-guided saccadic  
595 eye movements, would represent the retinal locations of potential saccadic targets using  
596 only recent sensory signals. The other map supports conscious perception and would  
597 integrate sensory signals over a much longer temporal interval, producing the  
598 accumulating shift that dramatically changes the perceived path. Our results here suggest  
599 that the information on this second “perceptual” map can be accessed for memory-guided  
600 saccades when there is no retinal input during the programming of the saccade. It is not  
601 the sole source of location information though as the deviation from the physical path  
602 showed on average about 50% of the illusion strength, a value that suggests a mixing of  
603 the two representations. We propose that there is a memory of the target location in the  
604 saccade system that gets combined with that from the perceptual system for memory-  
605 guided saccades. Although we did not directly address this question, it is evident that the  
606 saccade system represents space in a mostly retinotopic coordinate frame (Golomb, Chun  
607 & Mazer, 2008), whereas the perceptual system may use a range of reference frames  
608 (Bosco, Breveglieri, Reser, Galletti, & Fattori, 2015; Chang & Snyder, 2010). Our

609 evidence that the two systems combine for memory-guided saccades has implications for  
610 the way we conceptualize how the visual and oculomotor systems use different  
611 information for guiding actions toward a unified perceptual experience.

612

## 613 **Appendix 1. Supplemental experiment**

614

615 The supplemental experiment used the same general procedure as the main experiment  
616 but differed on two points. First, there were only two delay conditions: interceptive and  
617 1-sec delay. Second, the interceptive and memory trials were no longer presented in  
618 separate blocks during the saccade task, but were mixed within blocks.

619

## 620 **METHOD**

### 621 **Participants**

622 Participants were 5 volunteers (4 females, including one author; mean age = 28.8,  
623 standard deviation = 5.9); three of them had participated in the main experiment. All  
624 observers reported having normal or corrected-to-normal vision. Informed consent was  
625 obtained in writing in prior to participation and the protocol for the study was approved  
626 by the Université Paris Descartes Review Board, CERES, in accordance with French  
627 regulations and the Declaration of Helsinki. All (except the author) were naive to the  
628 specific purpose of the experiment.

629

### 630 **Setup and stimuli**

631 This supplemental experiment used exactly the same setup and stimuli as the main  
632 experiment (see sections 2.2 and 2.3 in the main text).

633

### 634 **Part 1: Perceptual task**

635 Only the two participants who had not participated in the main experiment performed  
636 the perceptual task. For the three other participants, we used the results of the perceptual  
637 task they ran for the main experiment to set the physical direction perceived as vertical.  
638 The procedure and the data analysis were the same as described in section 2.4.1. of the  
639 main text.

640

### 641 **Part 2: Saccade task - Mixed design**

642 **Procedure and design**

643 The saccade task comprised interceptive trials and memory trials (1-sec delay)  
644 randomly interleaved. The procedures used for the two types of trials were identical to  
645 the main experiment (for details, see section 2.5.1. of the main text). The experiment  
646 lasted two hours and included 960 trials divided in 2 sessions of 10 blocks. As in the  
647 main experiment, in the saccade task, each participant was presented only the orientations  
648 of the motion path that corresponded to perceived verticality of the motion path (as  
649 measured in the perceptual task). In each block, the orientation of the physical path could  
650 be right-tilted or left-tilted, the internal motion could be absent (control condition) or  
651 present (double-drift condition) and the fixation offset could occurs before (interceptive  
652 condition) or after (memory condition) the removal of the drifting Gabor. There were 120  
653 repetitions of each condition. The different conditions were randomly interleaved in each  
654 block.

655

## 656 **Data analysis**

### 657 *Data selection*

658 We applied the same selection criterion (see section 2.5.2) to the data. This resulted in  
659 a rejection of 8.9% of the trials.

660

### 661 *Saccade amplitude*

662 As in the main experiment, we fitted a multivariate linear model with the horizontal  
663 and vertical saccade amplitudes as dependent variables (for details see section 2.5.2.1 of  
664 the main text) and then computed a linear regression to derived the angle of the deviation  
665 from vertical from the regression slope. Finally, the difference between the angle of the  
666 recovered path in the control condition and the double-drift condition was calculated for  
667 each participant and each delay, but independently of the right versus left orientation of  
668 the tilt since, as revealed by an Analysis of Variance with a 2 (orientation of the tilt) x 2  
669 (delay) within-subject design, there was no significant difference between the two  
670 orientations (left-tilted:  $m=16.9$ ,  $se=5.25$ ; right-tilted:  $m=19.48$   $se= 6.58$ ;  $F(1,4)=0.19$ ,  
671  $p=.68$ ) and no interaction between the orientation of the tilt and delay ( $F(1,4)=0.52$ ;  
672  $p=.51$ ). Thus, we first calculated the mean difference between the control and double-  
673 drift condition for the left- and right-tilted paths and then averaged the two values for  
674 each participant and each delay. This difference was taken as a dependent variable in the  
675 statistical analyses.

676 We performed the following statistical analyses. We first ran a one-way ANOVA with

677 a 2 (delay) within-subject design and then tested whether each condition (interceptive and  
678 1-sec. delay) differed from 0 by using two paired-t-tests that were corrected for multiple  
679 comparisons with a Bonferroni correction (i.e., the p value was multiplied by the number  
680 of comparison; here two). These two comparisons indicated whether or not the difference  
681 between the control and double-drift condition was significant for each delay.

682

### 683 *Saccade latency*

684 We wanted to ensure that any difference observed on saccade amplitude (and thus  
685 on the angle of the recovered path) between the two internal motion conditions (control  
686 vs. double-drift) was not due to a difference in latencies. To do so, we ran a two-way  
687 ANOVA with a 2 (delay) x 2 (internal motion) within-subject design.

688

## 689 **RESULTS**

### 690 **Perceptual task**

691 For the 5 participants, the orientations of the physical path that were perceived as  
692 vertical strongly deviated from 0 (with 0 corresponding to physical vertical). The mean  
693 right tilt that was perceived as vertical was 56.2° [range from 50° to 60°] and the mean  
694 left tilt that was perceived as vertical was -51.9° [range from -58° to -41°].

695

### 696 **Saccade task: mixed design**

#### 697 **Saccade latency**

698 The ANOVA revealed an effect of the delay ( $F(1,4) = 47.89$ ;  $p < .01$ ). This indicates  
699 that latency differed between the two delays. In particular, we found that saccade latency  
700 was longer in the interceptive ( $m = 328$  ms;  $se = 13.6$ ) compared to the 1 sec-delay ( $m =$   
701  $216$ ,  $se = 7.8$ ). However, as in the blocked design, the ANOVA did not reveal any effect  
702 of the internal motion ( $F(1,4) = 0.5$ ,  $p = .52$ ) nor interaction between the two ( $F(1, 4) =$   
703  $0.40$ ,  $p = .55$ ), thus excluding again latency as a potential explanatory factor for any  
704 difference between control and double-drift conditions in the distributions of saccadic  
705 endpoints.

706

707

#### 708 **Angle of the path recovered from saccade amplitude**

709 Results obtained in the saccade task that used a mixed design are presented in  
710 Figures 5 and 6. Figure 5 presents the results from one representative participant for only  
711 one orientation of the tilt (right-tilted path) and shows how the angle of the recovered

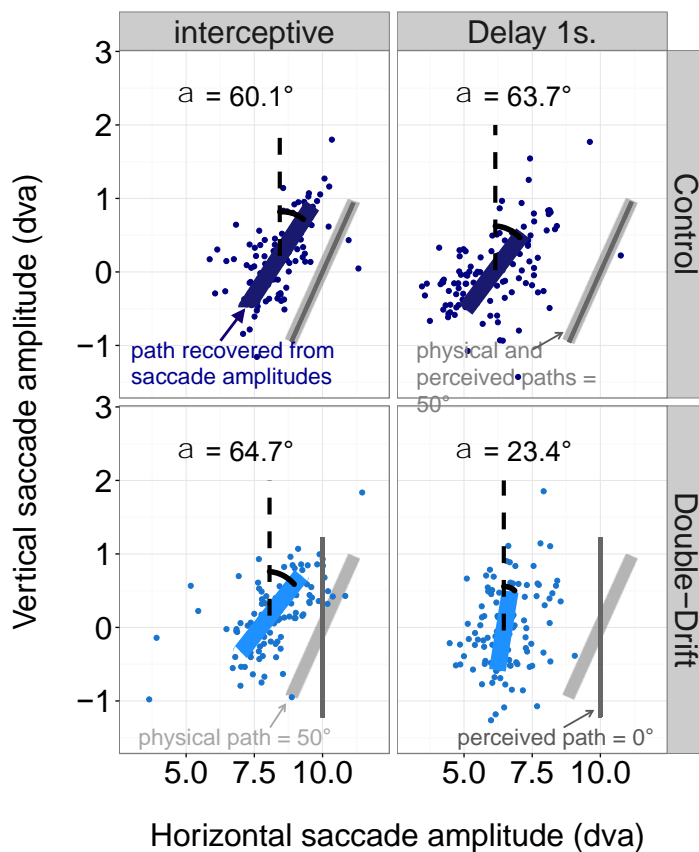
712 path differed with the delay in the two motion conditions: control (without internal  
 713 motion) vs. double-drift (with internal motion). Figure 6 presents the mean difference  
 714 across participants between the angle of the recovered path in the control and the double-  
 715 drift conditions for the two different delays.

716 The one-way ANOVA with a 2 (delay) within-subject design revealed an effect of  
 717 the delay ( $F(1,4) = 40.49; p < .01$ ).

718 The difference between the control and the double-drift condition was smaller in the  
 719 interceptive condition (mean =  $2.66^\circ$ , se = 1.65) than in the 1-sec delay condition (mean  
 720 =  $33.74^\circ$ , se = 5.11). The first comparison that tested whether the interceptive condition  
 721 differed from 0 was not significant ( $t(4) = 1.48$ ; *Bonferroni corrected*  $p = .43$ ).

722 Nevertheless, the second comparison that tested whether the memory condition (1-sec  
 723 delay) differed from 0 was strongly significant ( $t(4) = 5.99$ ; *Bonferroni corrected*  $p <$   
 724  $0.01$ ) indicating that the control condition differed from the double-drift condition when  
 725 saccades were memory-guided but not when there were visually-guided.

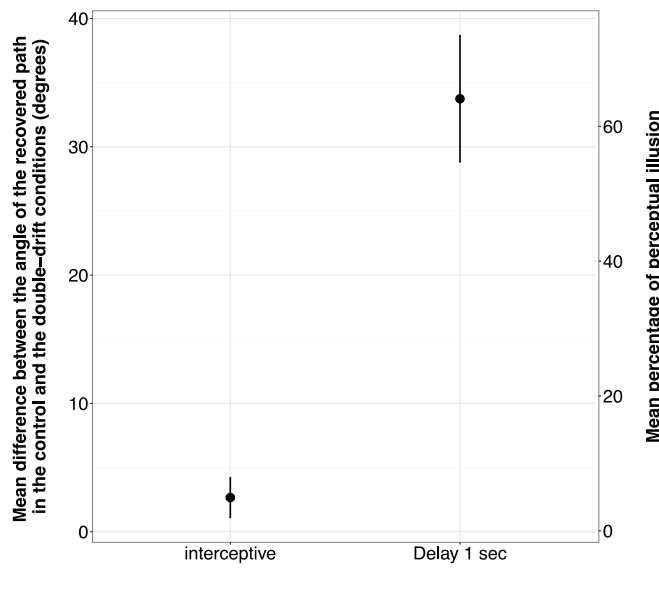
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**Figure 5. Results for one representative participant in the supplemental experiment that used a mixed design.** Horizontal and vertical saccade amplitudes for one participant are plotted along with the fitted value of the multivariate linear model (blue lines). The results for the control condition (with no internal motion) are presented

733 on the upper panels and those for the double-drift condition (where the physical path was  
 734 tilted to the left and the perceived path was vertical) on the lower panels. The left panels  
 735 correspond to the interceptive condition and the right panels correspond to the 1sec-delay.  
 736 The angle of the deviation of the recovered path from vertical ( $\alpha$ ) is indicated in each  
 737 graph. For this participant, the orientation of the double-drift path that appeared vertical  
 738 in the perceptual test was  $50^\circ$ . This was then the path orientation presented in both the  
 739 control and double-drift saccade conditions shown here. In the control condition, the  
 740 angle of the recovered path is similar for the interceptive and the 1sec. delay ( $60.1^\circ$  and  
 741  $63.7^\circ$  respectively) and is relatively close to the real angle of the physical path ( $50^\circ$ ). In  
 742 the double-drift condition, there is a difference between the interceptive condition and the  
 743 four other conditions with a memory delay. In the interceptive condition, the angle of the  
 744 recovered path ( $64.7^\circ$ ) is also close to the angle of the physical path ( $50^\circ$ ) while in the  
 745 memory conditions, the angle of the recovered path ( $23.4^\circ$ ) is closer to vertical.  
 746  
 747  
 748



749  
 750  
 751 **Figure 6. Mean difference between the angle of the recovered path in the control**  
 752 **and the double-drift conditions as a function of the delay in the supplemental**  
 753 **experience.** The right hand y-axis shows the result as a percentage of the angular  
 754 difference between the perceived path and the physical path. A full perceptual illusion  
 755 would correspond to an average deviation between the two paths of  $54^\circ$ . Error bars  
 756 represent the standard error.

757  
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### 759 Conclusion

760 The results obtained in the main experiment using a blocked design were confirmed  
 761 in this supplementary experiment using a mixed design.

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## 767 **Appendix 2. About the effect of the illusion on visually-guided saccades**

768

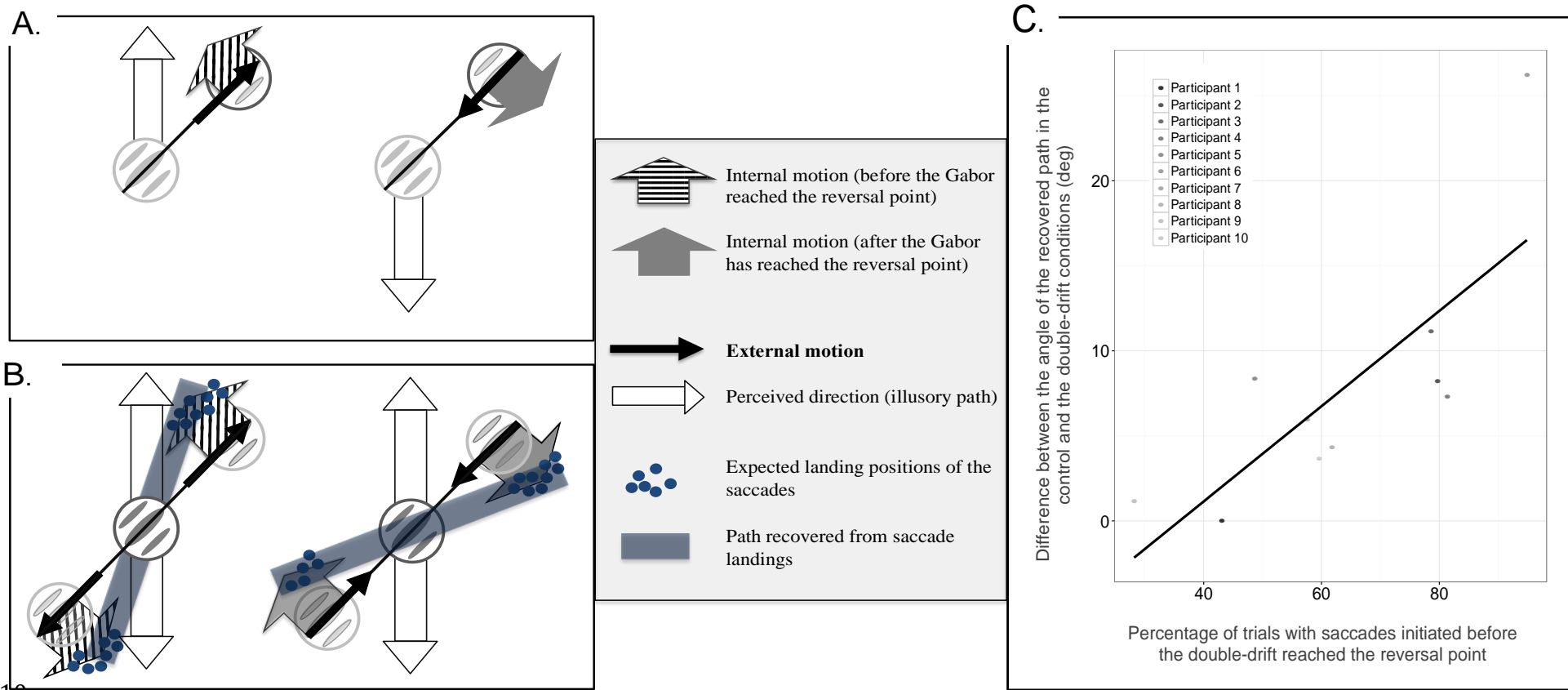
769           The finding of a small but significant difference between visually-guided saccades  
770 targeting control and double-drift stimuli contrasts with the absence of a significant  
771 difference in Lisi and Cavanagh (2015). Here, we will illustrate how a difference in the  
772 experimental paradigm may account for this difference in outcomes.

773           While Lisi & Cavanagh (2015) found no differences in the orientation of the  
774 trajectories recovered from saccades made in the control and double-drift conditions, they  
775 also found that the landing positions were slightly shifted in the direction of the internal  
776 motion but that this local shift did not change or accumulate over time (see Supplemental  
777 Material in Lisi & Cavanagh, 2015, see also Kerzel & Gegenfurtner, 2005). This shift  
778 induced by the internal motion is a constant offset but can be in one direction when the  
779 Gabor is, say, moving up, and in the opposite direction when it is moving down. If the  
780 path is sampled at the ends of the path, this constant offset can bias the orientation of the  
781 path. These upper and lower endpoints of the trajectory correspond to the reversal points  
782 where the Gabor and its internal motion reversed their directions. Depending on when the  
783 participants initiate their saccades (i.e. before or after the Gabor reached the reversal  
784 point), the internal motion can be in two different directions, shifting the landing further  
785 or closer from the physical path (see Figure 7-A for an illustration). This shift can thus be  
786 in the same or opposite direction of the illusion depending on the timing of the saccade.  
787 More precisely, saccade landing positions should be shifted toward the perceived/illusory  
788 path when they were initiated before the Gabor reached the reversal point, and in the  
789 opposite direction when saccade were initiated after the Gabor has reached the reversal  
790 point (see Figure 7-B).

791           In the present experiment, the majority of trials to one or the other of the two end  
792 points (66%) were initiated before the Gabor reached the reversal point, biasing the  
793 orientation toward the perceived path. If this imbalance is the cause of the small effect  
794 found here for visually-guided saccades, then the size of this effect should increase across  
795 participants with the proportion of saccades that were initiated before the Gabor reached  
796 the reversal point. This is what we found (see Figure 7-C): participants who had the  
797 stronger effect of the illusion in the visually-guided saccades condition were also the  
798 participants who executed saccades more often before the Gabor reached the reversal  
799 point.

800           In Lisi & Cavanagh (2015), this issue concerning the reversal points was limited  
801 by sampling a larger number of offset locations, so that only two out of six corresponded  
802 to target locations close to the reversal points. In our experiment, two out of three  
803 sampled locations were at the end points. The bias was thus two times more evident in  
804 our experiment than in Lisi & Cavanagh (2015). This could explain why we found a  
805 small effect of the illusion for visually-guided saccades that was not reported in the  
806 previous experiment.

807           To conclude, the small effect of internal motion on the orientation of the saccade  
808 landings is more likely due to our sampling of path locations rather than a change in the  
809 representation of the target path for saccades in the direction of the perceptual illusion.



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**Figure 7.**

**814 Illustration of the direction of the internal motion as a function of the external motion of the Gabor.** Before the Gabor reached the reversal point (left side of the figure), the internal motion is in direction of the perceived path, i.e. in direction of the illusion. To the contrary, after the Gabor has reached the reversal point (right side of the figure), the internal motion is in the opposite direction, i.e. away from the illusory path.

**818 Illustration of the bias that occurred in our experiment.** Depending on when the saccades were initiated (before or after the Gabor has reached reversal point; left side and right side of the figure respectively), the internal motion was in two possible directions. Saccades landings (blue points) are thus shifted in direction of the internal motion. This affects in turn the orientation of the path recovered from saccade landings. In our experiment, as participants initiated more often their saccades before the Gabor reached the reversal point (left side), it biased the orientation toward the perceived path when triggering saccades only before the upper and lower end points.

**824 Scatter plot representing the difference between the angle of the recovered path in the control and the double-drift conditions as a function of the percentage of trials with saccades initiated before the double-drift reached the reversal point in the visually-guided saccades condition.** Each point corresponds to one participant. The black line corresponds to the regression line.

827        ***Acknowledgments***

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830 Agreement No. AG324070 to PC.

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832        **References**

- 833 Awh, E., Armstrong, K. M., & Moore, T. (2006). Visual and oculomotor selection:  
834 links, causes and implications for spatial attention. *Trends in Cognitive*  
835 *Sciences*, 10(3), 124–130.
- 836 Becker, W., & Fuchs, A. F. (1969). Further properties of the human saccadic system:  
837 eye movements and correction saccades with and without visual fixation  
838 points. *Vision Research*, 9(10), 1247–1258.
- 839 Bruno, N., Knox, P. C., & de Grave, D. D. (2010). A metaanalysis of the effect of the  
840 Müller-Lyer illusion on saccadic eye movements: no general support for a  
841 dissociation of perception and oculomotor action. *Vision research*, 50(24), 2671-  
842 2682.
- 843 Bosco, A., Breveglieri, R., Reser, D., Galletti, C., & Fattori, P. (2014). Multiple  
844 representation of reaching space in the medial posterior parietal area  
845 V6A. *Cerebral Cortex*. 25(6), 1654–1667
- 846 Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10, 433–436.
- 847 de Brouwer, A. J., Brenner, E., Medendorp, W. P., & Smeets, J. B. (2014). Time  
848 course of the effect of the Müller-Lyer illusion on saccades and perceptual  
849 judgments. *Journal of vision*, 14(1), 4-4.
- 850 de Brouwer, A. J., Brenner, E., Medendorp, W. P., & Smeets, J. B. (2014). Time course  
851 of the effect of the Müller-Lyer illusion on saccades and perceptual  
852 judgments. *Journal of vision*, 14(1), 4-4.
- 853 de Brouwer, A. J., Brenner, E., & Smeets, J. B. (2016). Keeping a target in memory  
854 does not increase the effect of the Müller-Lyer illusion on saccades. *Experimental*  
855 *brain research*, 234(4), 977-983.
- 856

857 de Brouwer, S., Missal, M., Barnes, G., & Lefèvre, P. (2002). Quantitative analysis of  
858 catch-up saccades during sustained pursuit. *Journal of Neurophysiology*, *87*(4),  
859 1772–1780.

860 Carey, D. P. (2001). Do action systems resist visual illusions? *Trends in Cognitive*  
861 *Sciences*, *5*(3), 109–113.

862 Casarotti, M., Lisi, M., Umiltà, C., & Zorzi, M. (2012). Paying attention through eye  
863 movements: A computational investigation of the premotor theory of spatial  
864 attention. *Journal of Cognitive Neuroscience*, *24*(7), 1519–1531.

865 Chang, S. W., & Snyder, L. H. (2010). Idiosyncratic and systematic aspects of spatial  
866 representations in the macaque parietal cortex. *Proceedings of the National*  
867 *Academy of Sciences*, *107*(17), 7951–7956.

868 Cornelissen, F. W., Peters, E. M., & Palmer, J. (2002). The EyeLink Toolbox: eye  
869 tracking with MATLAB and the Psychophysics Toolbox. *Behavior Research*  
870 *Methods, Instruments, & Computers*, *34*(4), 613–617.

871 Curtis, C. E. (2006). Prefrontal and parietal contributions to spatial working  
872 memory. *Neuroscience*, *139*(1), 173–180.

873 Deubel, H. (1987). Adaptivity of gain and direction in oblique saccades. *Eye*  
874 *Movements; from Physiology to Cognition*.

875 Edelman, J. A., & Goldberg, M. E. (2001). Dependence of saccade-related activity in  
876 the primate superior colliculus on visual target presence. *Journal of*  
877 *Neurophysiology*, *86*(2), 676–691.

878 Engbert, R., & Mergenthaler, K. (2006). Microsaccades are triggered by low retinal  
879 image slip. *Proceedings of the National Academy of Sciences*, *103*(18), 7192–  
880 7197.

881 Etchells, P. J., Benton, C. P., Ludwig, C. J., & Gilchrist, I. D. (2010). The target  
882 velocity integration function for saccades. *Journal of Vision*, *10*(6), 7–7.

883 Franz, V. H., Gegenfurtner, K. R., Bühlhoff, H. H., & Fahle, M. (2000). Grasping visual  
884 illusions: No evidence for a dissociation between perception and  
885 action. *Psychological Science*, *11*(1), 20–25.

886 Funahashi, S., Bruce, C. J., & Goldman-Rakic, P. S. (1989). Mnemonic coding of visual  
887 space in the monkey's dorsolateral prefrontal cortex. *Journal of*  
888 *Neurophysiology*, *61*(2), 331–349.

889 Gilster, R., & Kuhtz-Buschbeck, J. P. (2009). The Müller-Lyer illusion: Investigation of  
890 a center of gravity effect on the amplitudes of saccades. *Journal of vision*, 10(1),  
891 11-11.

892 Gnadt, J. W., Bracewell, R. M., & Andersen, R. A. (1991). Sensorimotor  
893 transformation during eye movements to remembered visual targets. *Vision*  
894 *Research*, 31(4), 693–715.

895 Golomb, J. D., Chun, M. M., & Mazer, J. A. (2008). The native coordinate system of  
896 spatial attention is retinotopic. *Journal of Neuroscience*, 28(42), 10654–10662.

897 Goodale, M. A., Jakobson, L. S., & Keillor, J. M. (1994). Differences in the visual  
898 control of pantomimed and natural grasping  
899 movements. *Neuropsychologia*, 32(10), 1159–1178.

900 Herwig, A., Beisert, M., & Schneider, W. X. (2010). On the spatial interaction of visual  
901 working memory and attention: evidence for a global effect from memory-guided  
902 saccades. *Journal of vision*, 10(5), 8-8.

903 Hikosaka, O., & Wurtz, R. H. (1985). Modification of saccadic eye movements by  
904 GABA-related substances. I. Effect of muscimol and bicuculline in monkey  
905 superior colliculus. *Journal of Neurophysiology*, 53(1), 266–291.

906 Hu, Y., Eagleson, R., & Goodale, M. A. (1999). The effects of delay on the kinematics  
907 of grasping. *Experimental Brain Research*, 126(1), 109–116.

908 Kerzel, D., & Gegenfurtner, K. R. (2005). Motion-induced illusory displacement  
909 reexamined: differences between perception and action?. *Experimental brain*  
910 *research*, 162(2), 191-201.

911 Kwon, O.-S., Tadin, D., & Knill, D. C. (2015). Unifying account of visual motion and  
912 position perception. *Proceedings of the National Academy of Sciences*, 112(26),  
913 8142–8147.

914 Lisi, M., & Cavanagh, P. (2015). Dissociation between the perceptual and saccadic  
915 localization of moving objects. *Current Biology*, 25(19), 2535–2540.

916 Lisi, M., & Cavanagh, P. (2017). Different spatial representations guide eye and hand  
917 movements. *Journal of Vision*, 17(2), 12–12.

918 Mackey, W. E., Devinsky, O., Doyle, W. K., Meager, M. R., & Curtis, C. E. (2016).  
919 Human dorsolateral prefrontal cortex is not necessary for spatial working  
920 memory. *Journal of Neuroscience*, 36(10), 2847–2856.

921 Moore, T., & Fallah, M. (2001). Control of eye movements and spatial  
922 attention. *Proceedings of the National Academy of Sciences*, 98(3), 1273–1276.

923 Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics:  
924 Transforming numbers into movies. *Spatial Vision*, 10(4), 437–442.

925 Post, R. B., & Welch, R. B. (1996). Is there dissociation of perceptual and motor  
926 responses to figural illusions? *Perception*, 25(5), 569–581.

927 Shapiro, A., Lu, Z.-L., Huang, C.-B., Knight, E., & Ennis, R. (2010). Transitions  
928 between central and peripheral vision create spatial/temporal distortions: a  
929 hypothesis concerning the perceived break of the curveball. *PLoS One*, 5(10).

930 Smit, A. C., Van Gisbergen, J. A. M., & Cools, A. R. (1987). A parametric analysis of  
931 human saccades in different experimental paradigms. *Vision Research*, 27(10),  
932 1745–1762.

933 Sommer, M. A., & Wurtz, R. H. (2000). Composition and topographic organization of  
934 signals sent from the frontal eye field to the superior colliculus. *Journal of*  
935 *Neurophysiology*, 83(4), 1979–2001.

936 Tse, P. U., & Hsieh, P.-J. (2006). The infinite regress illusion reveals faulty integration  
937 of local and global motion signals. *Vision Research*, 46(22), 3881–3885.

938 Van Opstal, A. J., & Van Gisbergen, J. A. M. (1989). Scatter in the metrics of saccades  
939 and properties of the collicular motor map. *Vision Research*, 29(9), 1183–1196.

940 Watson, A. B., & Pelli, D. G. (1983). QUEST: A Bayesian adaptive psychometric  
941 method. *Attention, Perception, & Psychophysics*, 33(2), 113–120.

942 Westwood, D. A., Chapman, C. D., & Roy, E. A. (2000). Pantomimed actions may be  
943 controlled by the ventral visual stream. *Experimental Brain Research*, 130(4),  
944 545–548.

945 Westwood, D. A., & Goodale, M. A. (2003). Perceptual illusion and the real-time  
946 control of action. *Spatial Vision*, 16(3), 243–254.

947 Westwood, D. A., Heath, M., & Roy, E. A. (2000). The effect of a pictorial illusion on  
948 closed-loop and open-loop prehension. *Experimental Brain Research*, 134(4),  
949 456–463.

950 White, J. M., Sparks, D. L., & Stanford, T. R. (1994). Saccades to remembered target  
951 locations: an analysis of systematic and variable errors. *Vision Research*, 34(1),  
952 79–92.

953 Wong, E., & Mack, A. (1981). Saccadic programming and perceived location. *Acta*  
954 *Psychologica*, 48(1), 123–131.

955

956 **Figure Captions**

957

958 **Figure 1. The two double-drift stimuli with tilted paths that appear vertical**  
959 **due to the addition of internal motion.**

960

961 **Figure 2. Procedure used in the memory (Panel A) or interceptive (Panel B)**  
962 **trials.** The left side of the figure illustrates the general procedure. In memory trials the  
963 stimulus had already disappeared at the time when the go-signal was given (i.e. the  
964 removal of the fixation point) whereas in the interceptive saccade trials the stimulus was  
965 still present.

966 The right side of the figure presents the vertical location of the target as a function  
967 of stimulus time presentation. In memory trials, the stimulus could be presented for  
968 2.25, 3 or 3.75 sec, leading to three possible offset locations: the two extremities or the  
969 center of the path. Following Gabor offset, the go-signal was given after a delay varying  
970 from 0 to 1 sec. In interceptive trials, the stimulus remained presented for 500 ms after  
971 the go-signal. Participants thus had 500 ms to initiate their saccades to intercept the  
972 stimulus. As soon as the saccade was detected, the Gabor was removed and this could  
973 happen at any point in time during the 500 ms interval. The go-signal was given 250 ms  
974 before the Gabor reached one of the two extremities or the center of the path. The Gabor  
975 was exactly at one of these three possible locations when participants initiated their  
976 saccades with a latency of 250 ms.

977

978 **Figure 3. Horizontal and vertical saccade amplitudes for one representative**  
979 **participant are plotted along with the fitted value of the multivariate linear model**  
980 **(blue lines).** The results for the control condition (with no internal motion) are  
981 presented on the upper panels and those for the double-drift condition (where the  
982 physical path was tilted to the left and the perceived path was vertical) on the lower  
983 panels. The panels from left to right correspond to the different delays starting with the  
984 interceptive condition. The angle of the deviation of the recovered path from vertical  
985 ( $\alpha$ ) is indicated in each graph. For this participant, the orientation of the double-drift  
986 path that appeared vertical in the perceptual test was  $-63^\circ$ . This was then the path  
987 orientation presented in both the control and double-drift saccade conditions shown  
988 here. In the control condition, the angle of the recovered path is similar for each delay

989 (varying from  $-73.6^\circ$  to  $-79^\circ$ ) and is relatively close to the real angle of the physical path  
990 ( $-63^\circ$ ). In the double-drift condition, there is a difference between the interceptive  
991 condition and the four other conditions with a memory delay. In the interceptive  
992 condition, the angle of the recovered path ( $-73.8^\circ$ ) is also close to the angle of the  
993 physical path ( $-63^\circ$ ) while in the memory conditions, the angle of the recovered path  
994 (varying from  $-58^\circ$  to  $-40^\circ$ ) is closer to vertical.

995

996 **Figure 4. Mean difference between the angle of the recovered path in the**  
997 **control and the double-drift conditions as a function of the delay.** The right hand y-  
998 axis shows the result as a percentage of the angular difference between the perceived  
999 path and the physical path. A full perceptual illusion would correspond to an average  
1000 deviation between the two paths of  $52^\circ$ . Error bars represent the standard error.

1001

1002 **Figure 5. Results for one representative participant in the supplemental**  
1003 **experiment that used a mixed design.** Horizontal and vertical saccade amplitudes for  
1004 one participant are plotted along with the fitted value of the multivariate linear model  
1005 (blue lines). The results for the control condition (with no internal motion) are presented  
1006 on the upper panels and those for the double-drift condition (where the physical path  
1007 was tilted to the left and the perceived path was vertical) on the lower panels. The left  
1008 panels correspond to the interceptive condition and the right panels correspond to the  
1009 1sec-delay. The angle of the deviation of the recovered path from vertical ( $\alpha$ ) is  
1010 indicated in each graph. For this participant, the orientation of the double-drift path that  
1011 appeared vertical in the perceptual test was  $50^\circ$ . This was then the path orientation  
1012 presented in both the control and double-drift saccade conditions shown here. In the  
1013 control condition, the angle of the recovered path is similar for the interceptive and the  
1014 1sec. delay ( $60.1^\circ$  and  $63.7^\circ$  respectively) and is relatively close to the real angle of the  
1015 physical path ( $50^\circ$ ). In the double-drift condition, there is a difference between the  
1016 interceptive condition and the four other conditions with a memory delay. In the  
1017 interceptive condition, the angle of the recovered path ( $64.7^\circ$ ) is also close to the angle  
1018 of the physical path ( $50^\circ$ ) while in the memory conditions, the angle of the recovered  
1019 path ( $23.4^\circ$ ) is closer to vertical.

1020

1021 **Figure 6. Mean difference between the angle of the recovered path in the**  
1022 **control and the double-drift conditions as a function of the delay in the**

1023 **supplemental experience (that used a mixed design).** The right hand y-axis shows the  
1024 result as a percentage of the angular difference between the perceived path and the  
1025 physical path. A full perceptual illusion would correspond to an average deviation  
1026 between the two paths of 54°. Error bars represent the standard error.

1027

1028 **Figure 7.**

1029 **A. Illustration of the direction of the internal motion as a function of the**  
1030 **external motion of the Gabor.** Before the Gabor reached the reversal point (left side of  
1031 the figure), the internal motion is in direction of the perceived path, i.e. in direction of  
1032 the illusion. To the contrary, after the Gabor has reached the reversal point (right side of  
1033 the figure), the internal motion is in the opposite direction, i.e. away from the illusory  
1034 path.

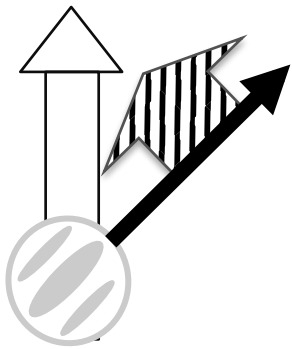
1035 **B. Illustration of the bias that occurred in our experiment.** Depending on when  
1036 the saccades were initiated (before or after the Gabor has reached the reversal point; left  
1037 side and right side of the figure respectively), the internal motion was in two possible  
1038 directions. Saccades landings (blue points) were thus shifted in direction of the internal  
1039 motion. This affects in turn the orientation of the path recovered from saccade landings.  
1040 In our experiment, as participants initiated more often their saccades before the Gabor  
1041 reached the reversal point (left side), it biased the orientation toward the perceived path  
1042 when triggering saccades only before the upper and lower end points.

1043 **C. Scatter plot representing the difference between the angle of the recovered**  
1044 **path in the control and the double-drift conditions as a function of the percentage**  
1045 **of trials with saccades initiated before the double-drift reached the reversal point**  
1046 **in the visually-guided saccades condition.** Each dot corresponds to one participant.  
1047 The black line corresponds to the regression line.

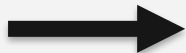
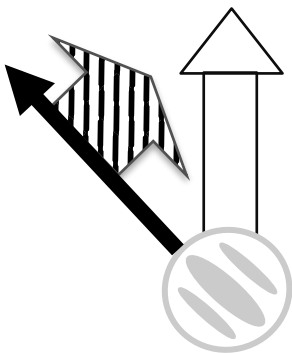
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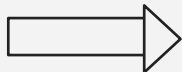
right tilt  
appears vertical



left tilt  
appears vertical



**External motion (aperture)**

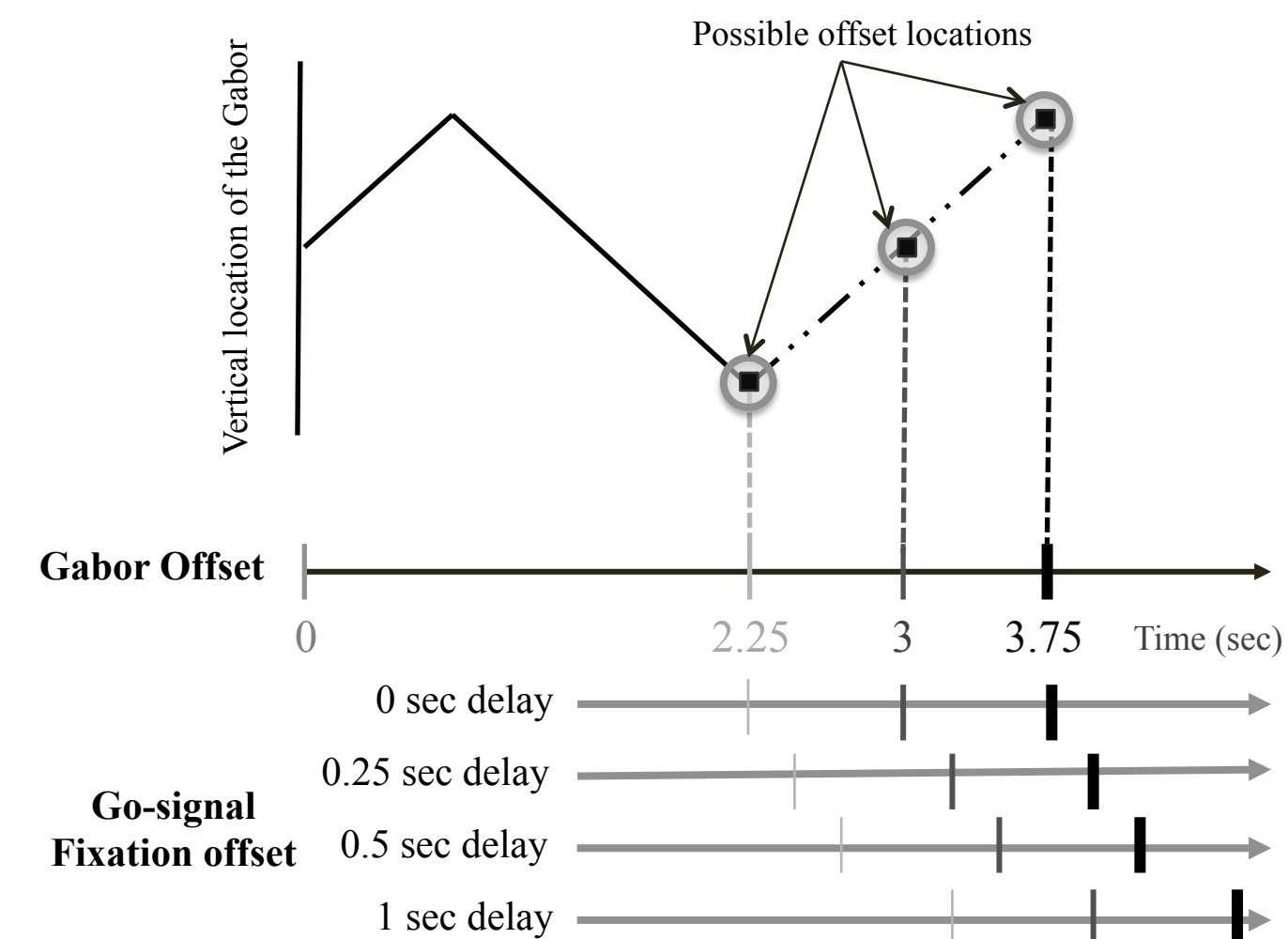
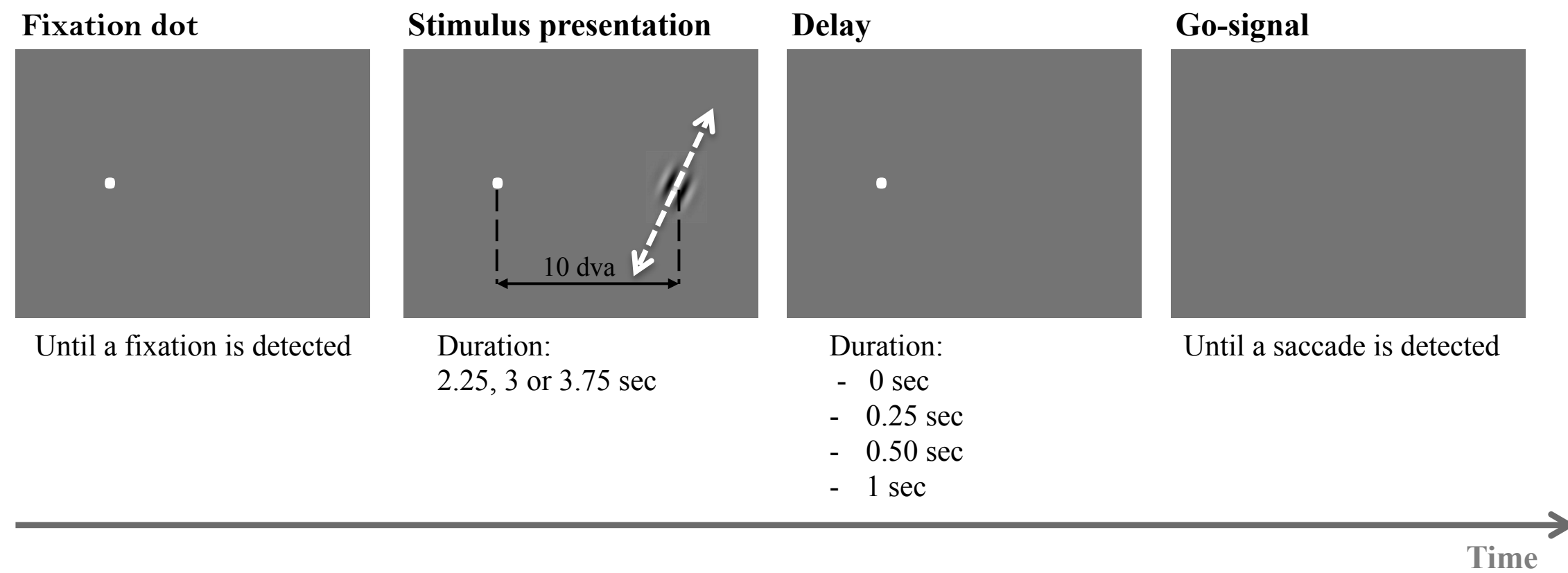


Perceived direction (illusory path)

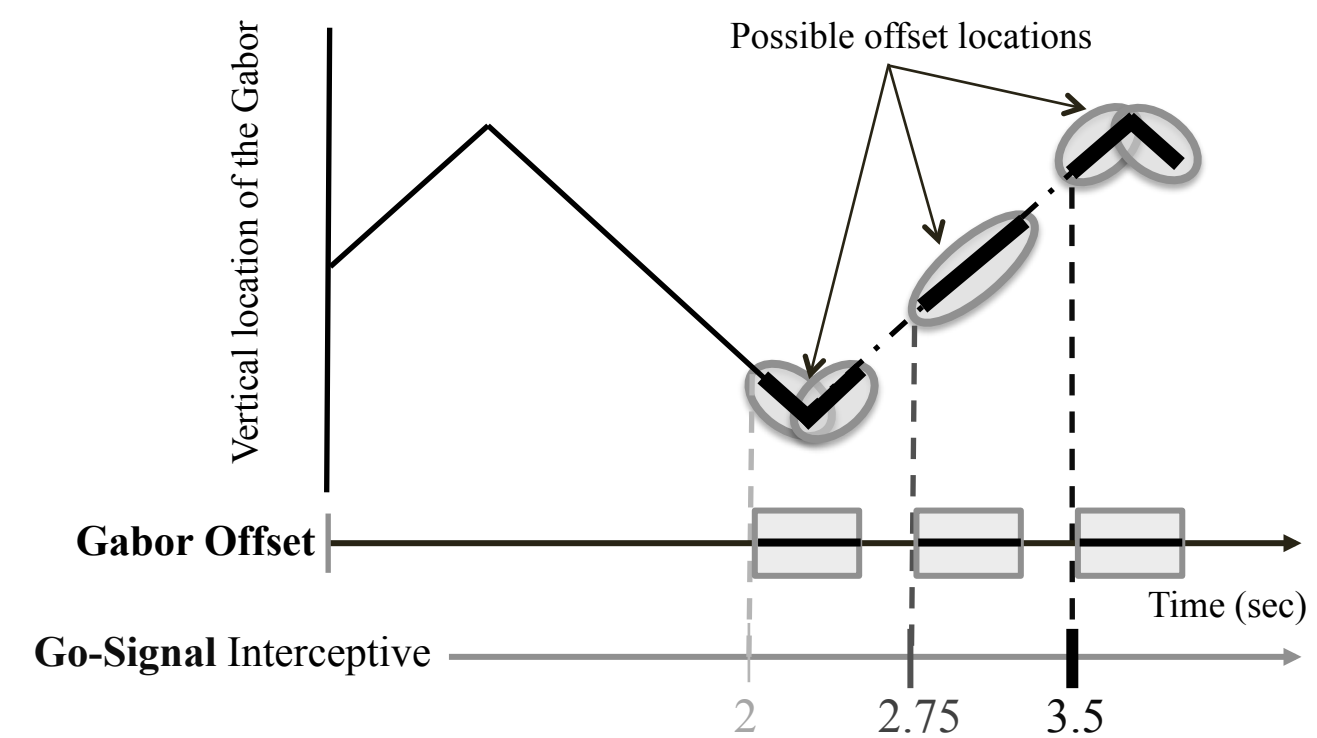
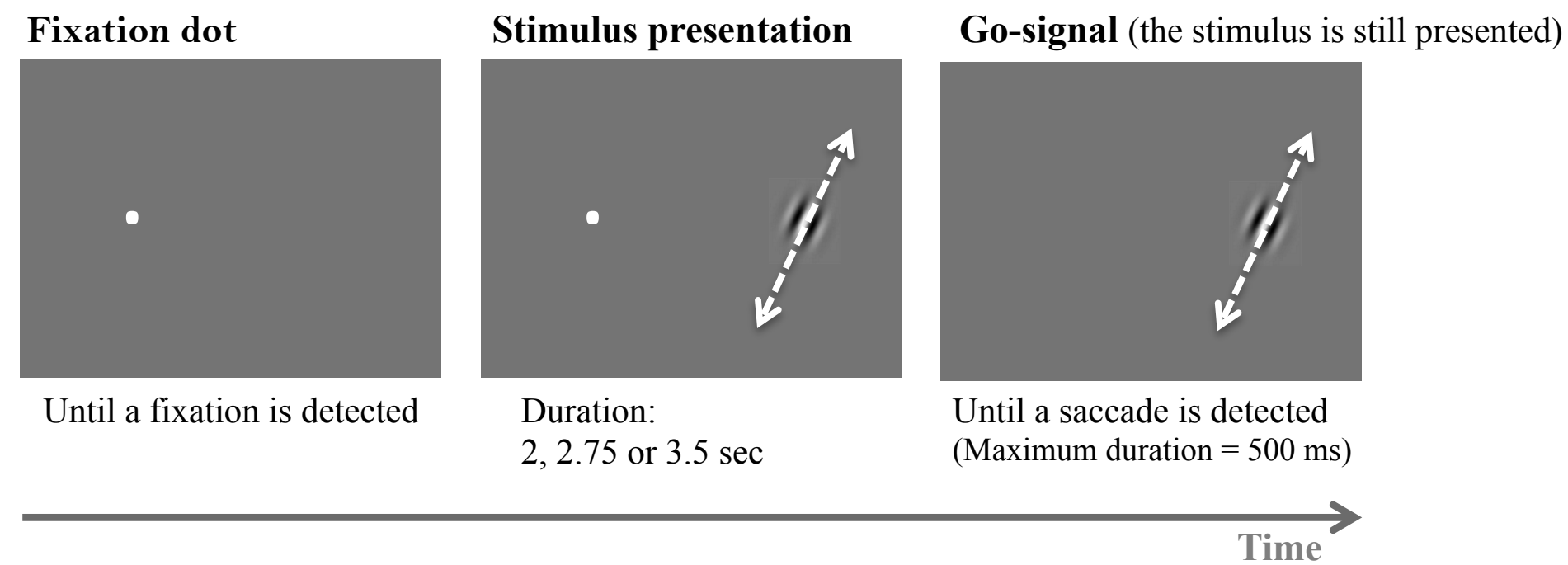


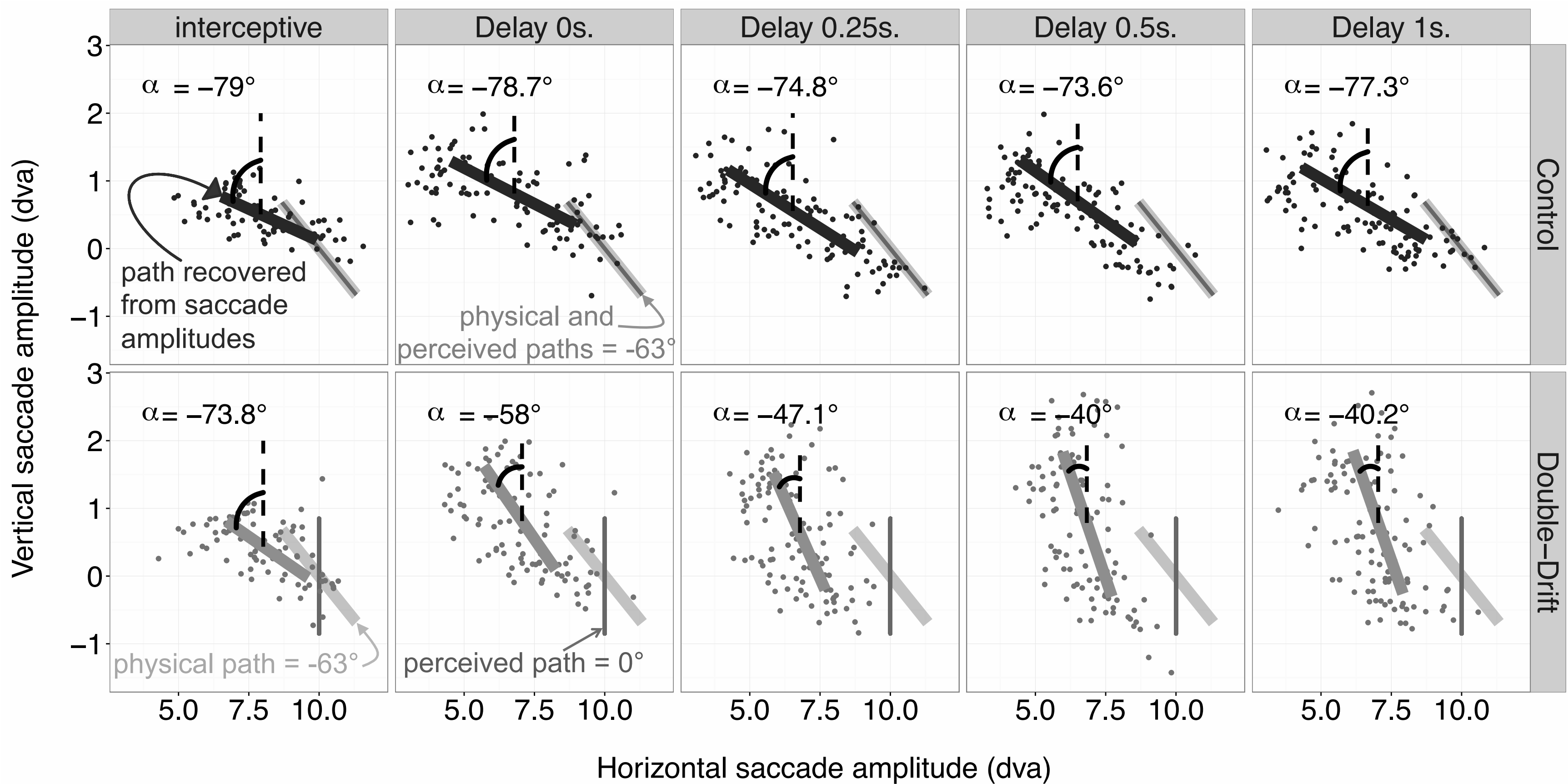
Internal motion (grating)

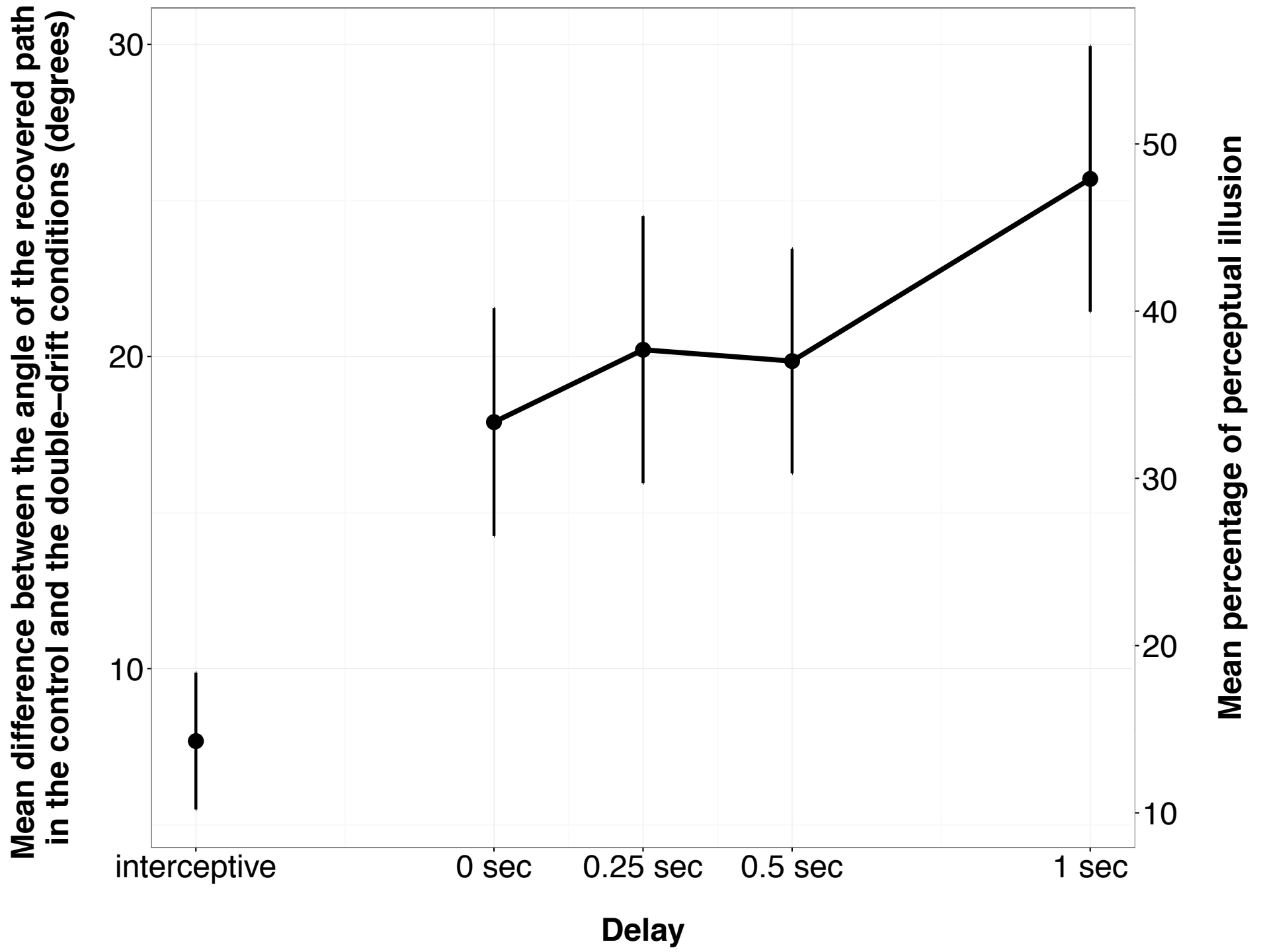
## A. Memory trials



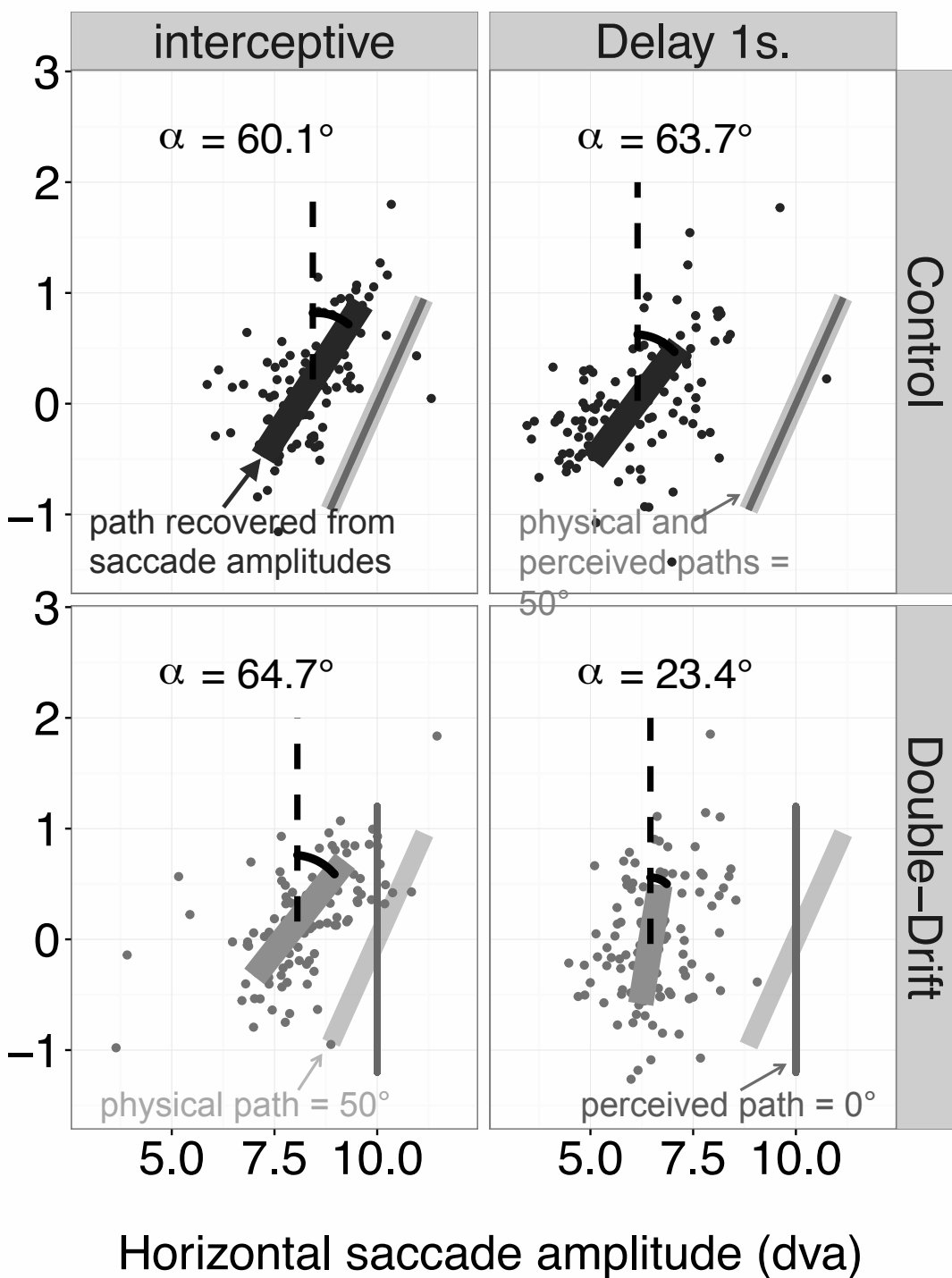
## B. Interceptive trials



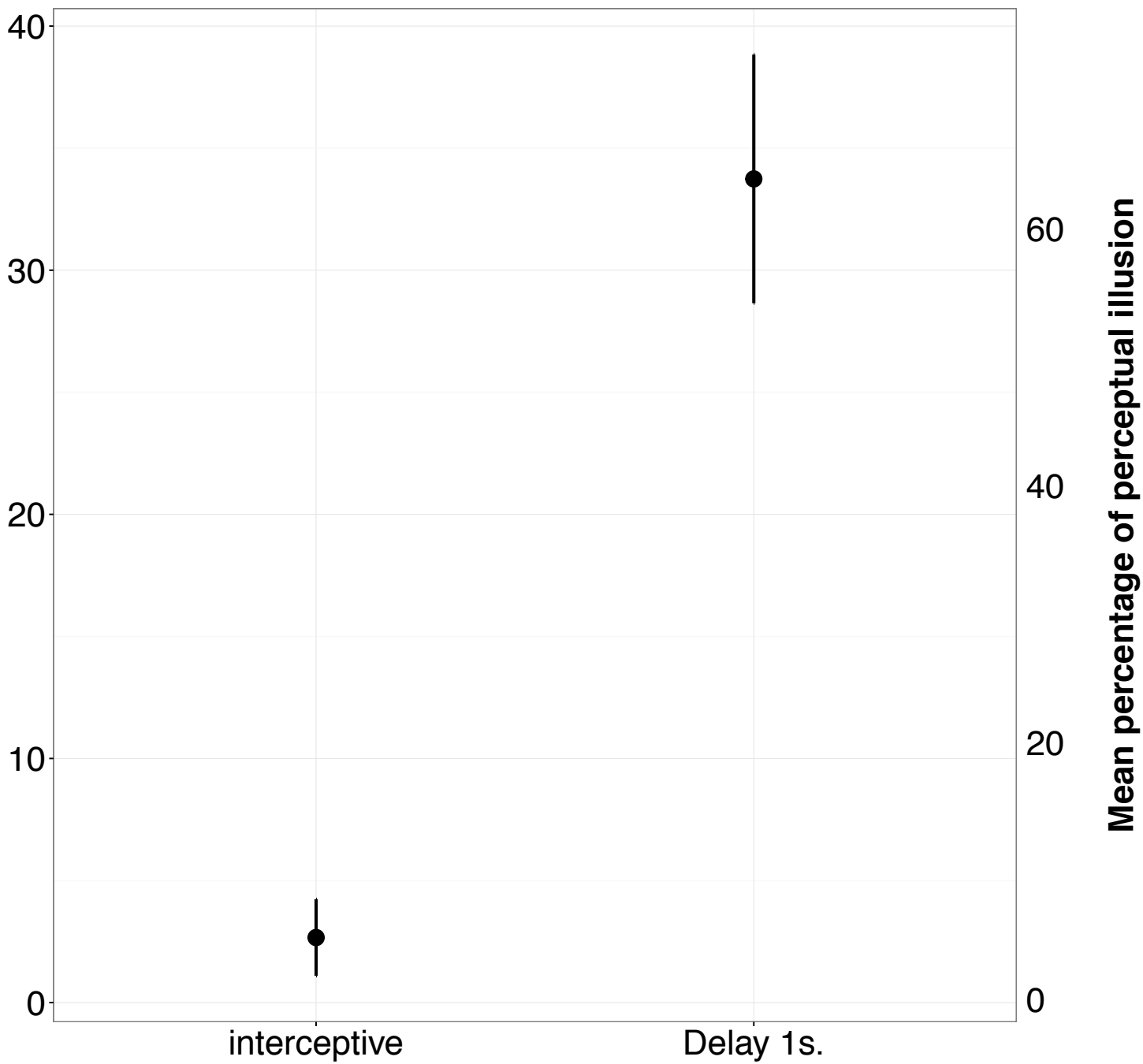




Vertical saccade amplitude (dva)



**Mean difference between the angle of the recovered path  
in the control and the double-drift conditions (degrees)**



**Mean percentage of perceptual illusion**

