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

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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

68
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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**

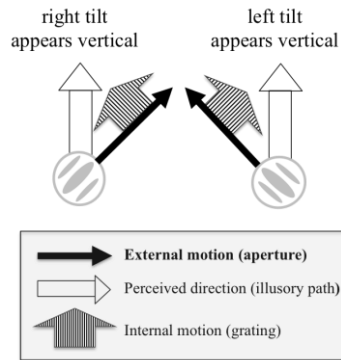
177 Participants sat in a quiet, dark room. We recorded the right-eye gaze position
178 with an SR Research Eyelink 1000 desktop mounted eye tracker, at a sampling rate of
179 1 kHz. Participant's head was positioned on a chin rest, with an adjustable forehead
180 rest, 54 cm in front of a gamma linearized 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 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.

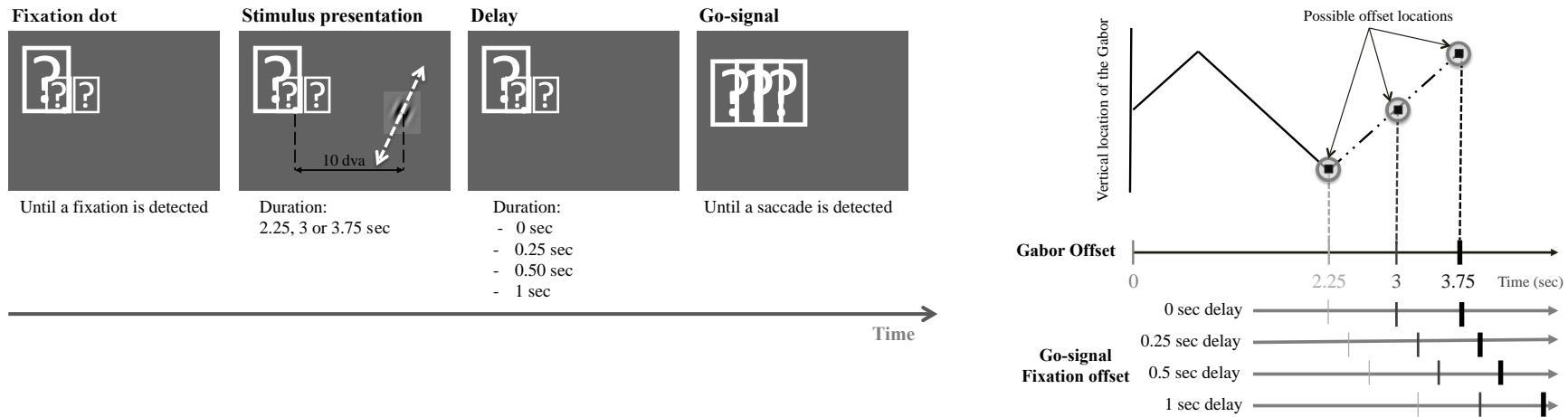
260 **Memory trials:** In the 4 blocks of memory-guided saccade trials, each trial started
261 when the participant fixated on a black dot (a circle of 0.2 dva diameter). The position
262 of the fixation dot was jittered horizontally and vertically from trial to trial according
263 to two Gaussian distributions ($SD = 0.2$ 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.

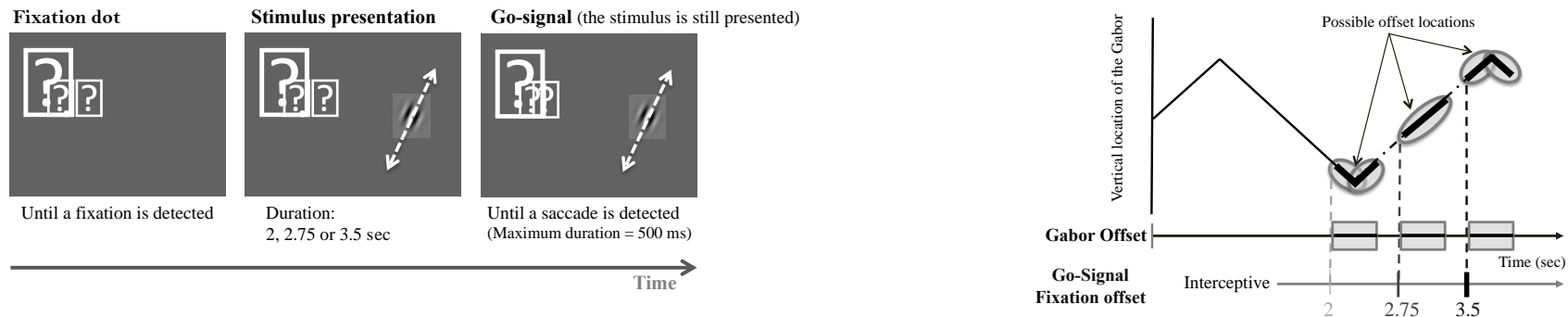
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279 **Interceptive trials:** The procedure (summarized in Figure 2B) was almost identical to
280 the memory-guided saccade trials, except that the Gabor did not disappear before or
281 concurrently with the go-signal. Instead, the go-signal was given 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° , 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° [range from 38° to 58°] and the
376 mean left tilt that was perceived as vertical was -57.6° [range from -70° to -42°],
377 revealing a dramatic influence of the internal motion on the perceived orientation of
378 the trajectory.

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

381 **3.2.1. Saccade latency**

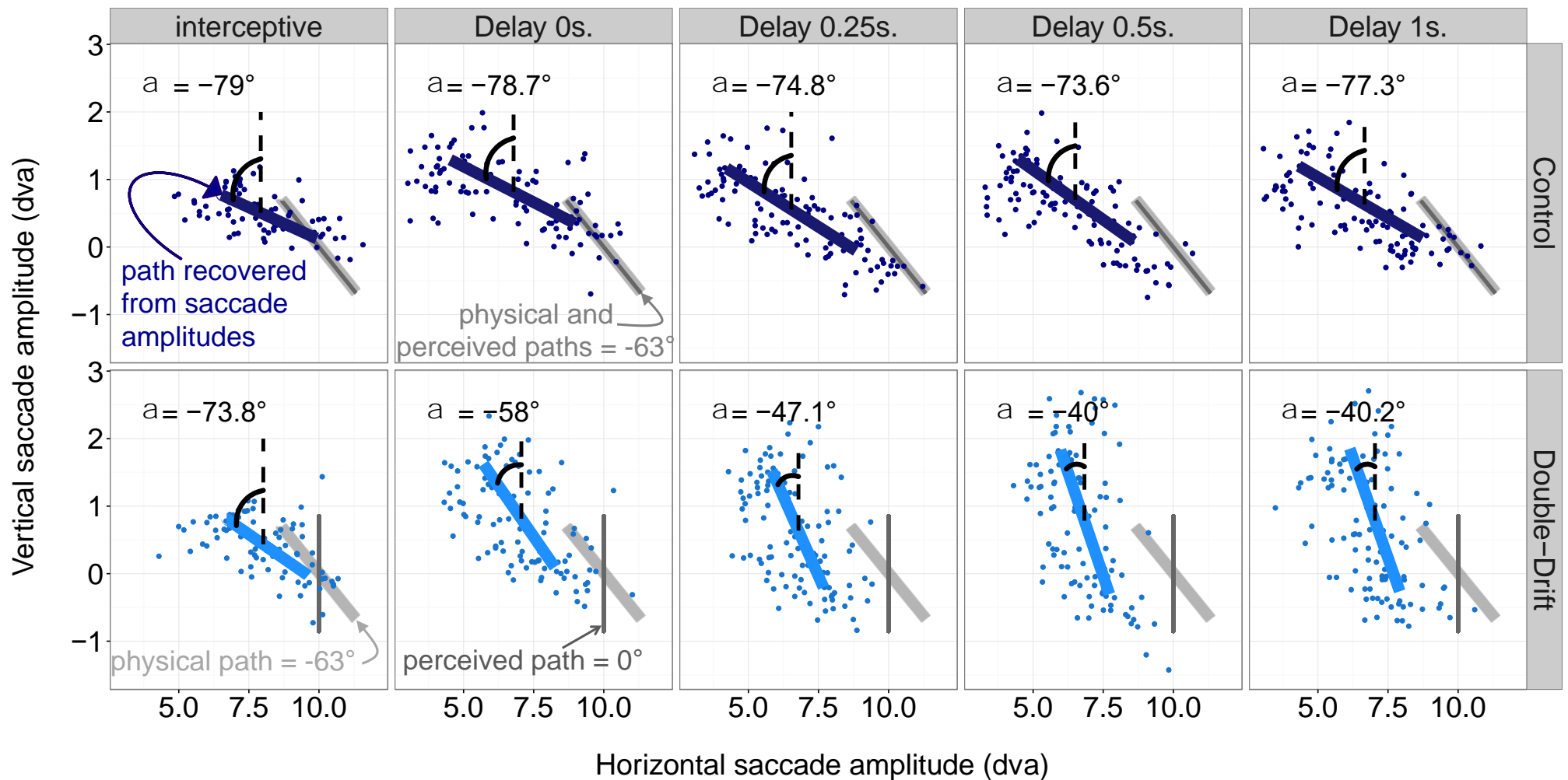
382 The ANOVA revealed an effect of the delay ($F(4,36) = 14.23; p < .001$). This
383 indicates that there were some differences in saccade latency across the memory delay.
384 In particular, we found that saccade latencies were longer in the interceptive ($m = 249$;
385 $se = 7.57$) and the 0 delay 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

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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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 (α) is indicated in each graph. For this participant, the orientation of the double-drift path that appeared vertical in the perceptual test was -63° . 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° to -79°) and is relatively close to the real angle of the physical path (-63°). 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°) is also close to the angle of the physical path (-63°) while in the memory conditions, the angle of the recovered path (varying from -58° to -40°) is closer to vertical.

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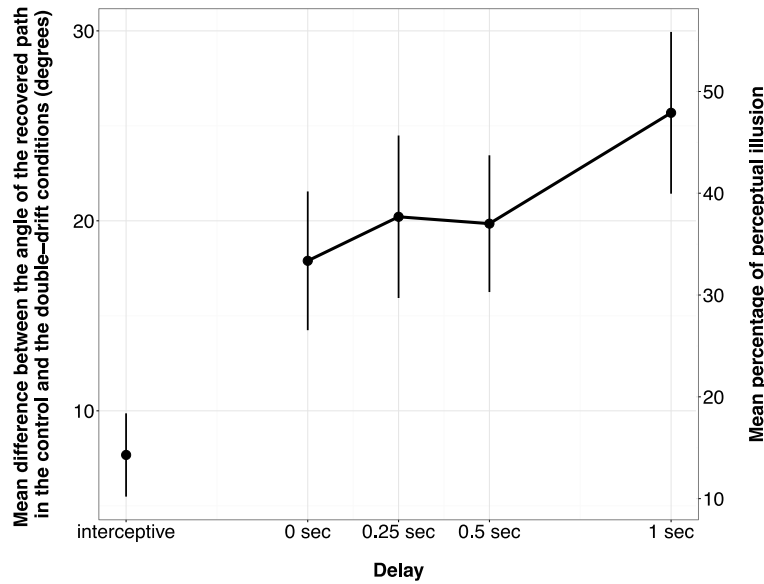


Figure 4. Mean difference between the angle of the recovered path in the control and the double-drift conditions as a function of the delay. The right hand y-axis shows the result as a percentage of the angular difference between the perceived path and the physical path. A full perceptual illusion would 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

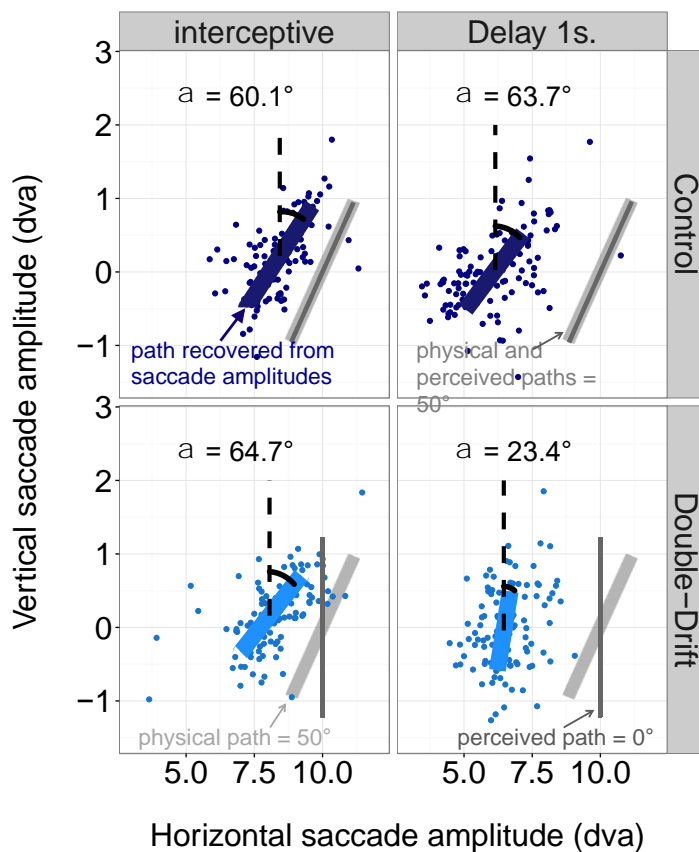
712 path differed with the delay in the two motion conditions: control (without internal
 713 motion) vs. double-drift (with internal motion). Figure 6 presents the mean difference
 714 across participants between the angle of the recovered path in the control and the double-
 715 drift conditions for 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° , se = 1.65) than in the 1-sec delay condition (mean
 720 = 33.74° , 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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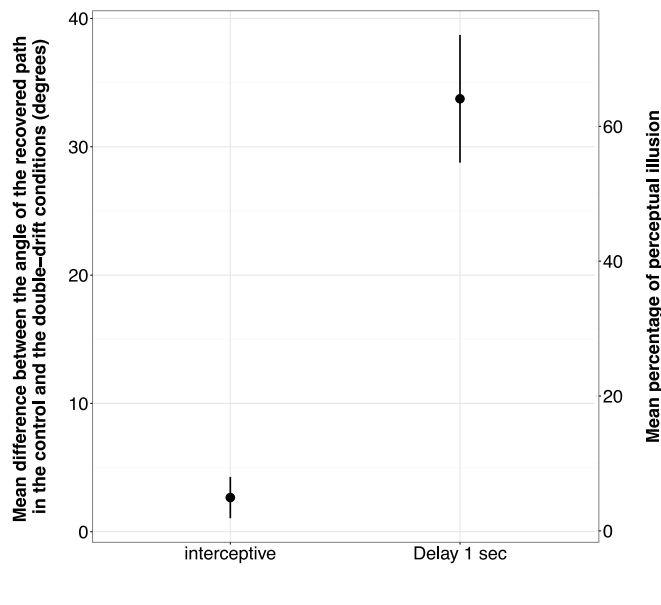
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Figure 5. Results for one representative participant in the supplemental experiment that used a mixed design. Horizontal and vertical saccade amplitudes for one participant are plotted along with the fitted value of the multivariate linear model (blue 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 (α) 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° . 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° and
 741 63.7° respectively) and is relatively close to the real angle of the physical path (50°). 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°) is also close to the angle of the physical path (50°) while in the
 745 memory conditions, the angle of the recovered path (23.4°) is closer to vertical.
 746
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 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° . Error bars
 756 represent the standard error.

757
 758
 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

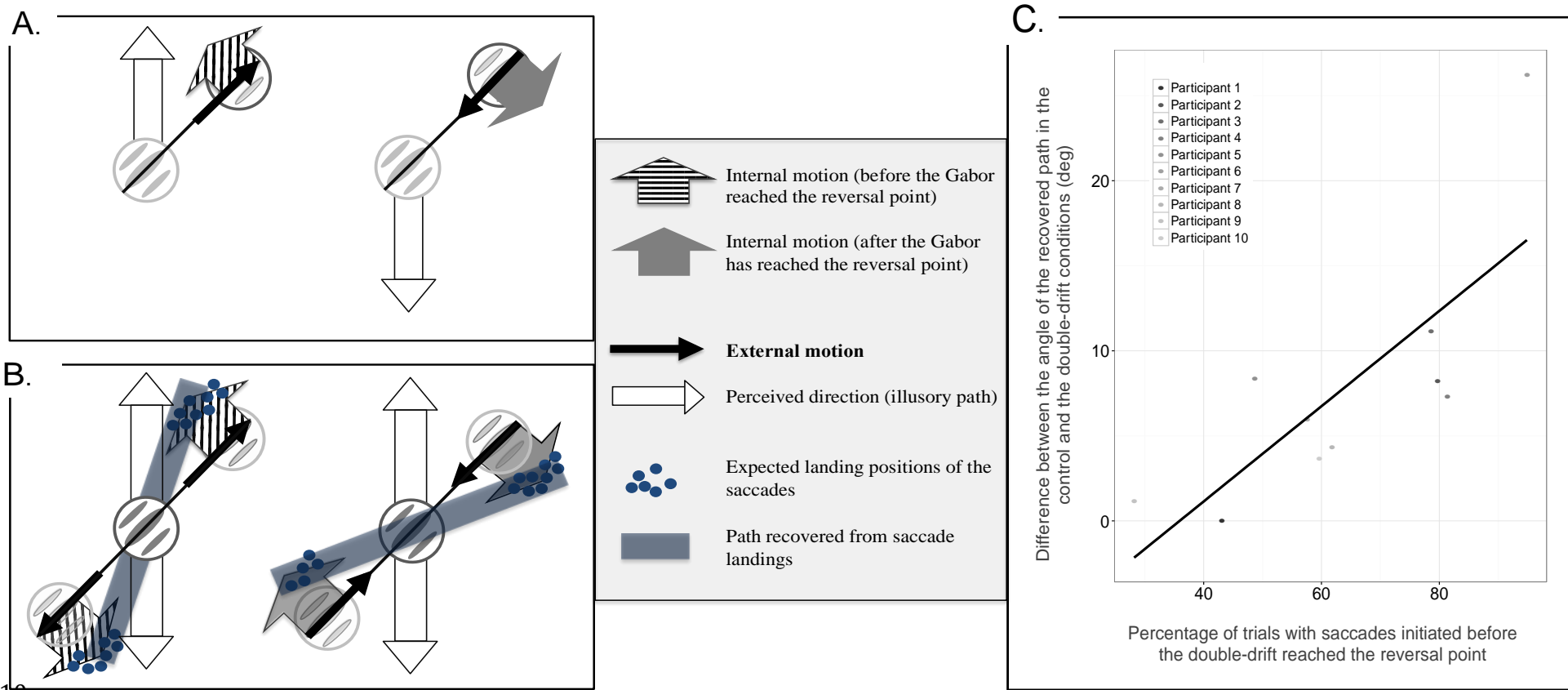
769 The finding of a small but significant difference between visually-guided saccades
770 targeting control and double-drift stimuli contrasts with the absence of a significant
771 difference in Lisi and Cavanagh (2015). Here, we will illustrate how a difference in the
772 experimental paradigm may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



810

811

812 **Figure 7.**

813

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
 815 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
 816 reached the reversal point (right side of the figure), the internal motion is in the opposite direction, i.e. away from the illusory path.

817

818 **Illustration of the bias that occurred in our experiment.** Depending on when the saccades were initiated (before or after the Gabor has reached
 819 reversal point; left side and right side of the figure respectively), the internal motion was in two possible directions. Saccades landings (blue points)
 820 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
 821 participants initiated more often their saccades before the Gabor reached the reversal point (left side), it biased the orientation toward the perceived path
 822 when triggering saccades only before the upper and lower end points.

823

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

827 ***Acknowledgments***

828 The research leading to these results received funding from the European Research Council
829 under the European Union's Seventh Framework Program (FP7/ 2007-2013)/ERC Grant
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831

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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 (α) 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° . 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° to -79°) and is relatively close to the real angle of the physical path
990 (-63°). 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°) is also close to the angle of the
993 physical path (-63°) while in the memory conditions, the angle of the recovered path
994 (varying from -58° to -40°) 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° . 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 (α) 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° . 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° and 63.7° respectively) and is relatively close to the real angle of the
1015 physical path (50°). 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°) is also close to the angle
1018 of the physical path (50°) while in the memory conditions, the angle of the recovered
1019 path (23.4°) 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.

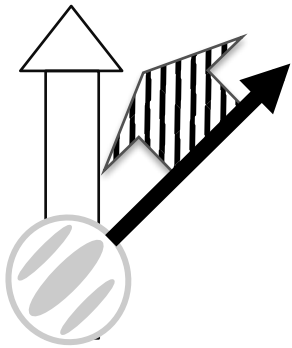
1035 **B. Illustration of the bias that occurred in our experiment.** Depending on when
1036 the saccades were initiated (before or after the Gabor has reached the reversal point; left
1037 side and right side of the figure respectively), the internal motion was in two possible
1038 directions. Saccades 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.

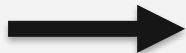
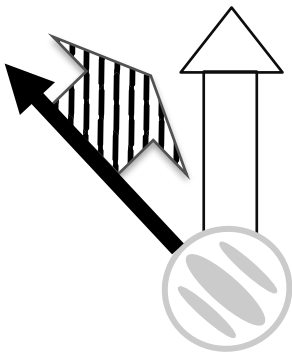
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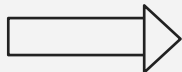
right tilt
appears vertical



left tilt
appears vertical



External motion (aperture)

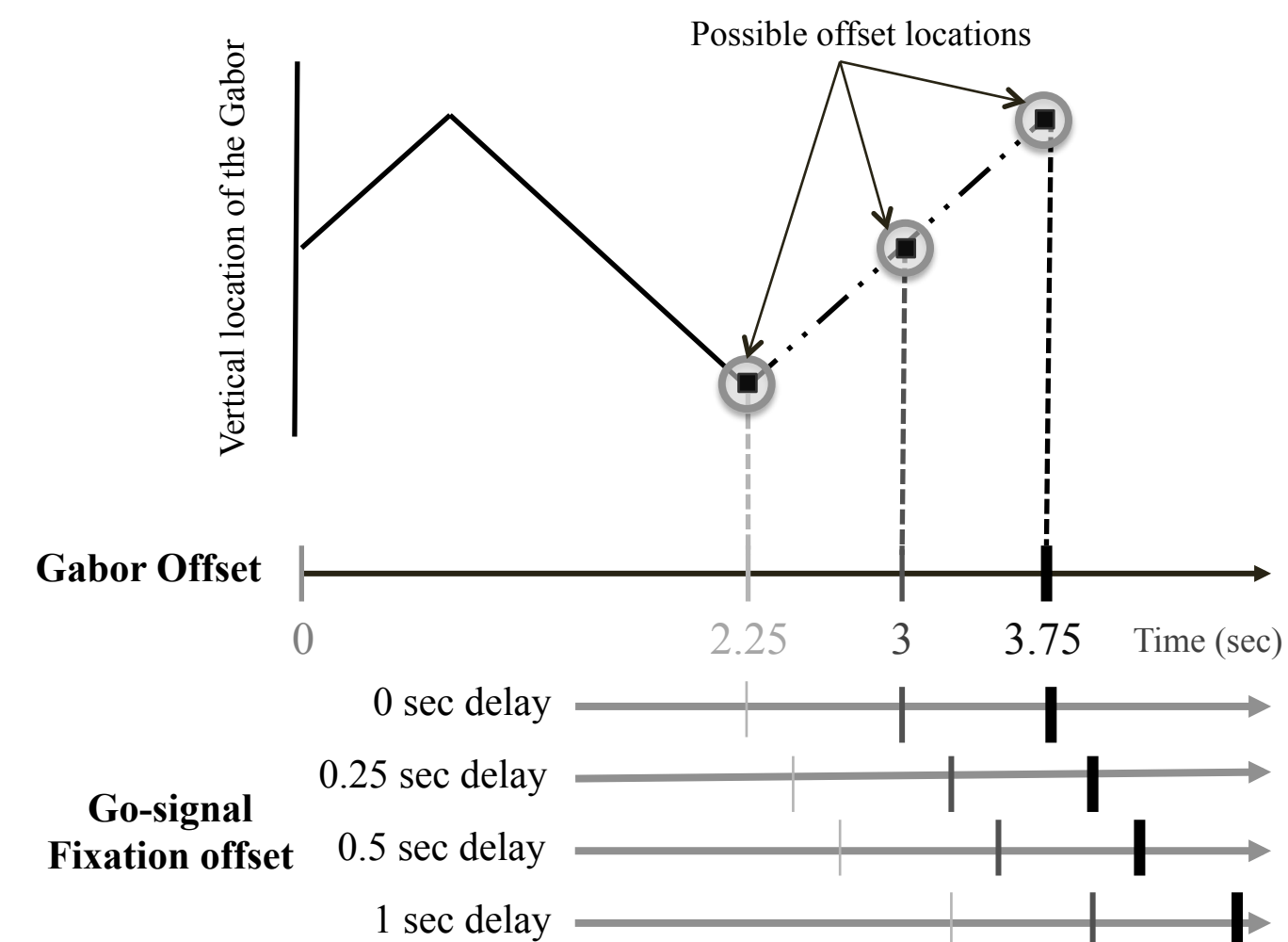
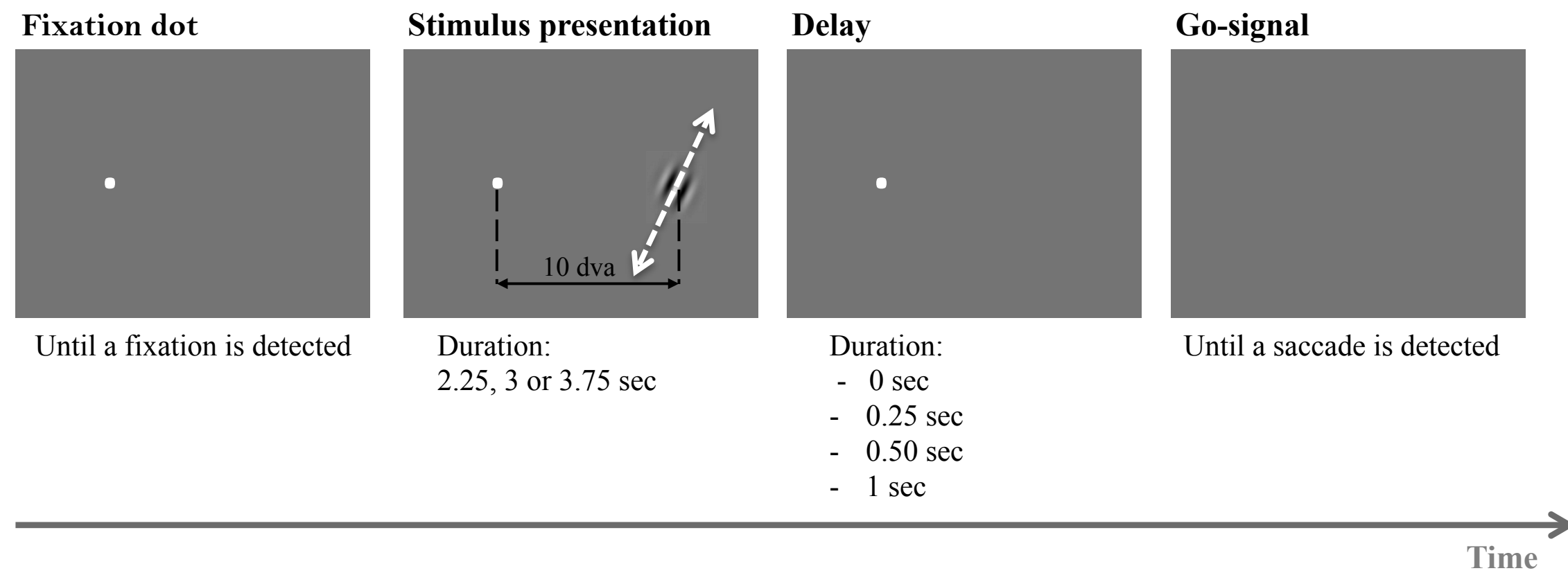


Perceived direction (illusory path)

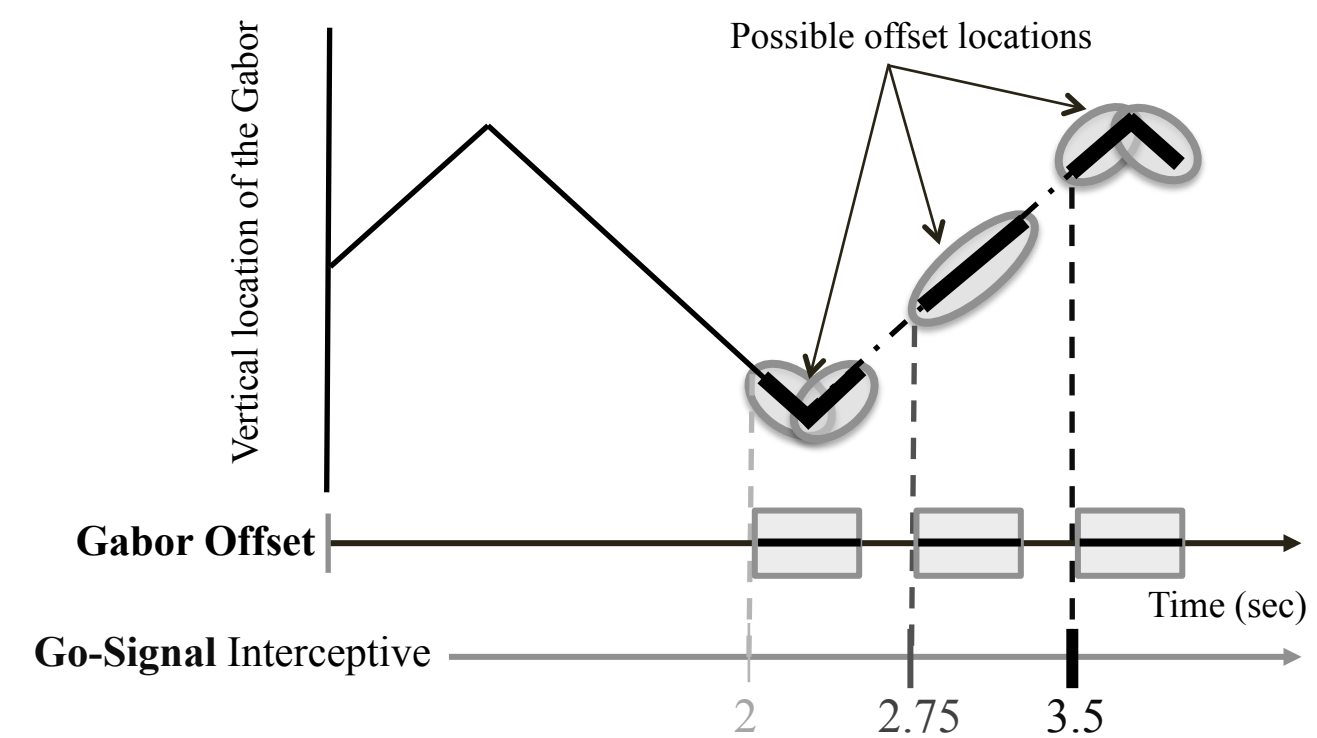
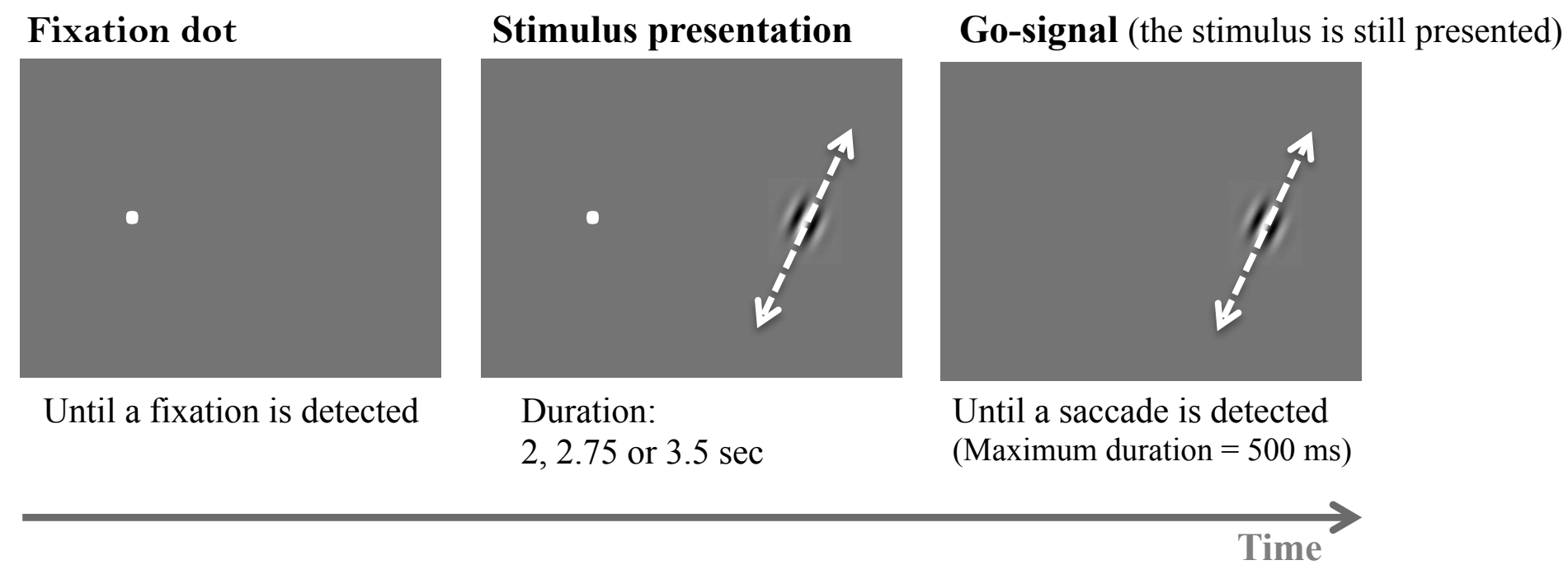


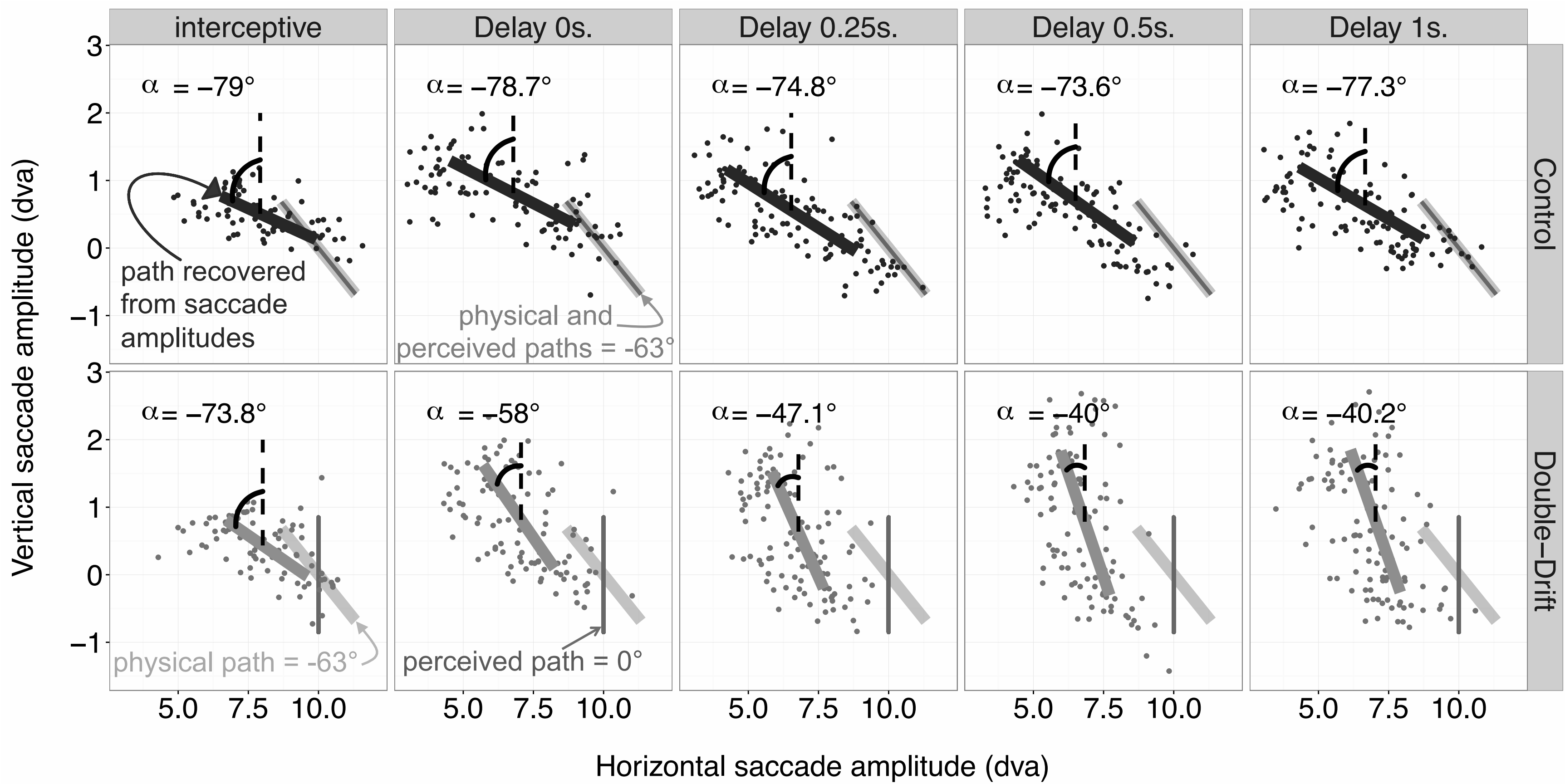
Internal motion (grating)

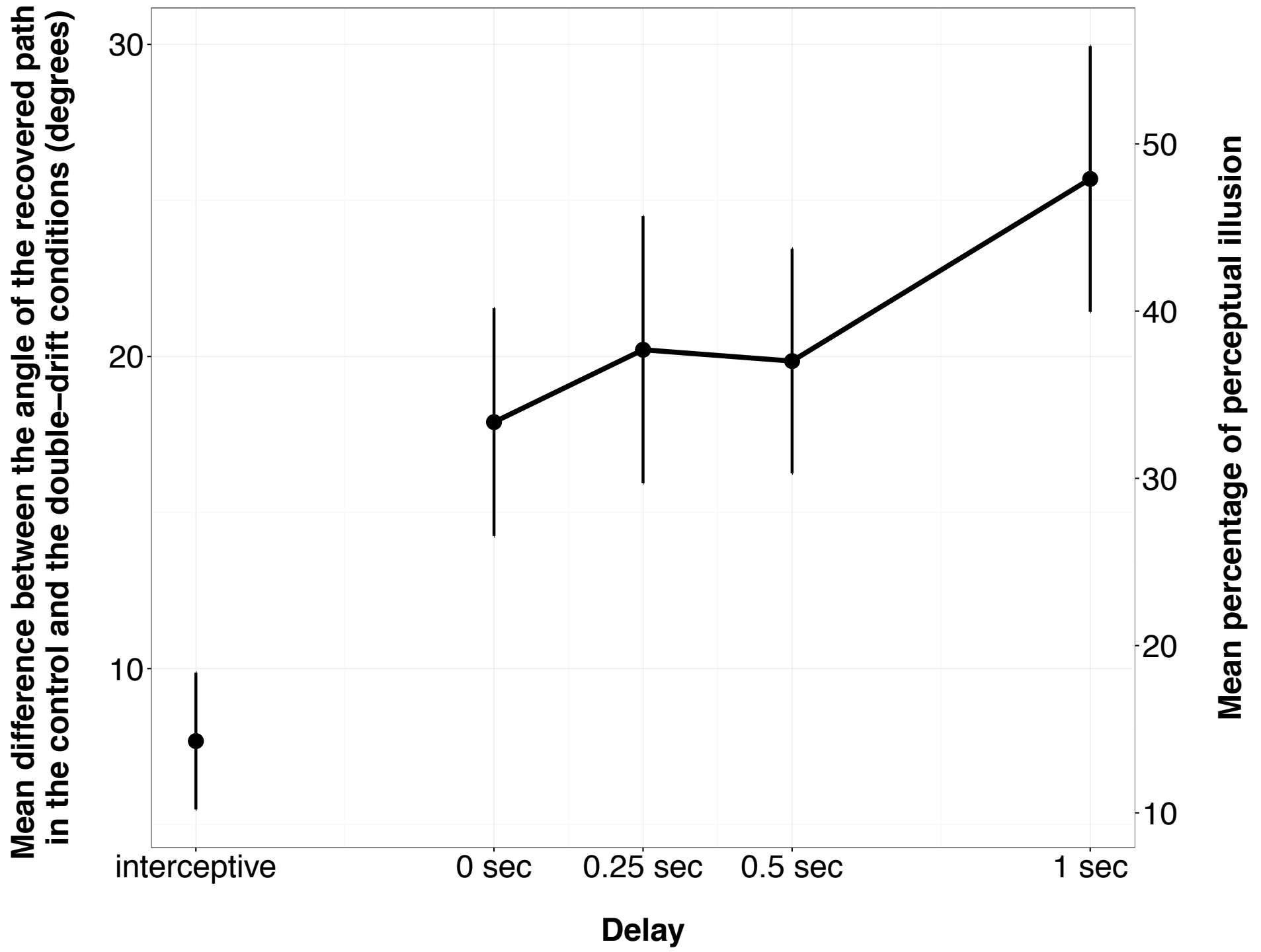
A. Memory trials



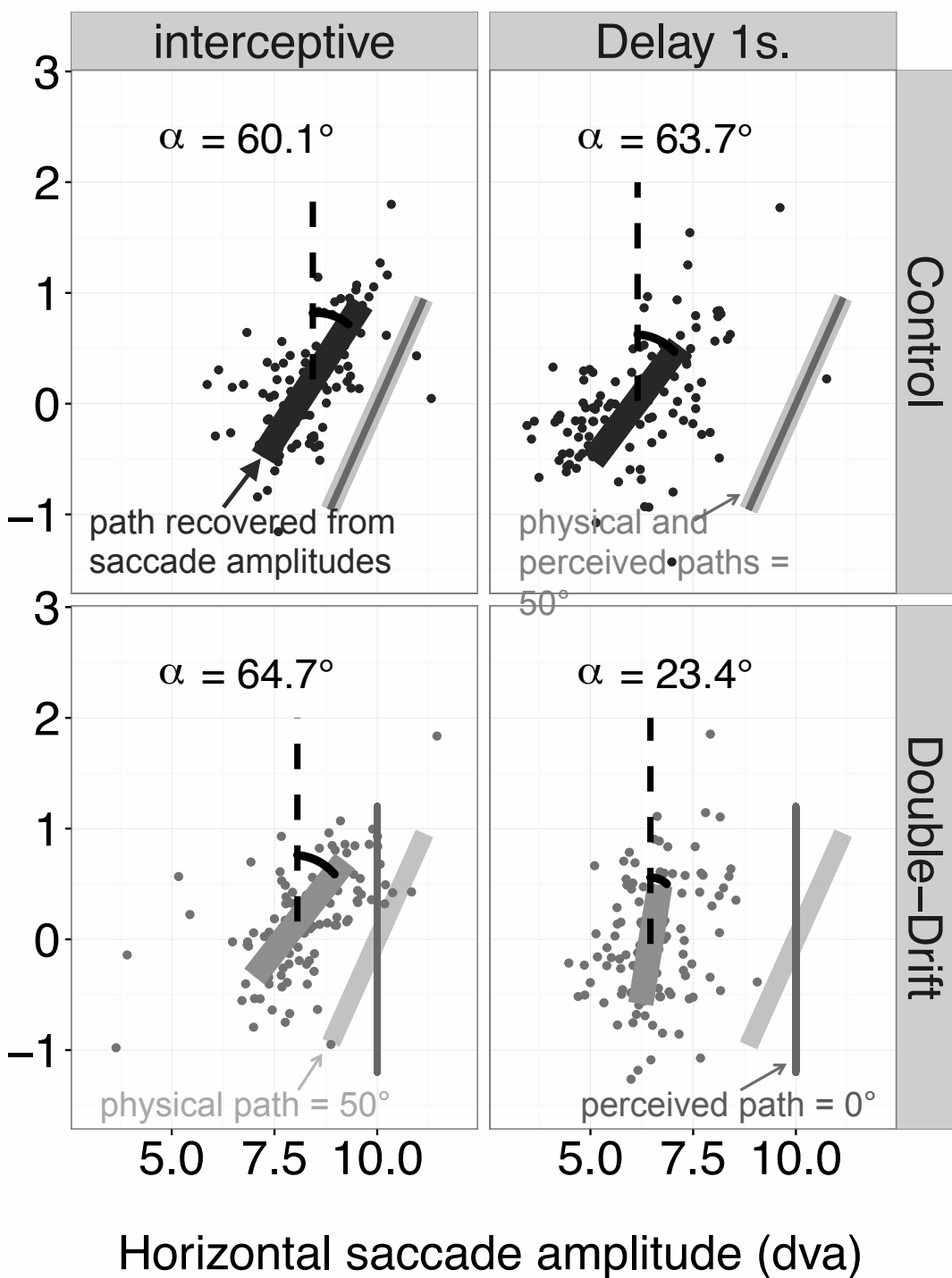
B. Interceptive trials



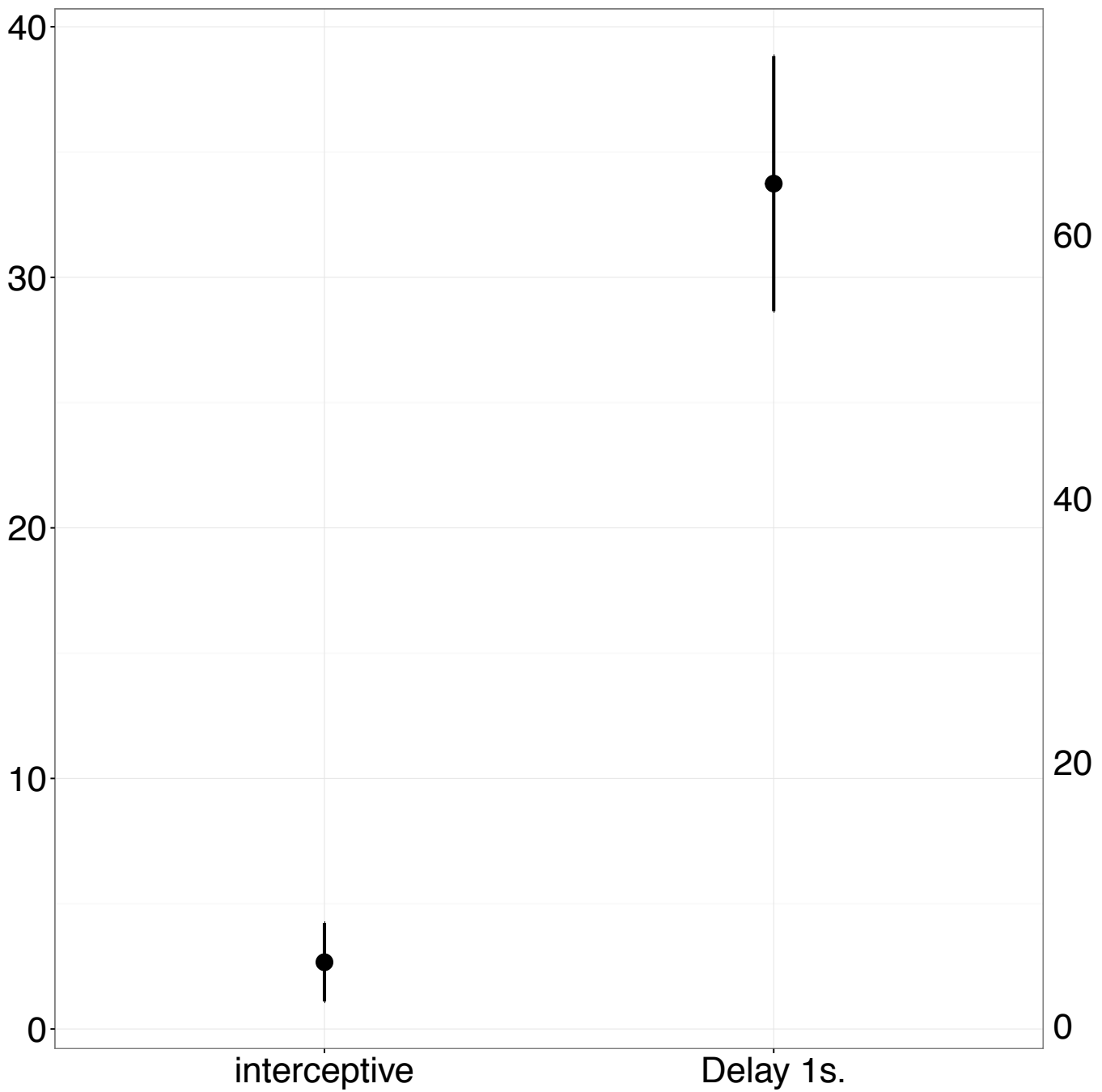




Vertical saccade amplitude (dva)



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



Mean percentage of perceptual illusion

