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4 **Tracking a moving visual target in the rhesus monkey:**  
5 **Influence of the occurrence frequency of the target path**

6

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22 Running title: Tracking a moving visual target

23 Keywords: saccade, pursuit, tracking, prediction, extrapolation



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26

**27 ABSTRACT (250 <= 250 words)**

28           Following previous studies documenting the ability to generate anticipatory responses,  
29 we tested whether the repeated motion of a visual target along the same path affected its  
30 oculomotor tracking. In six rhesus monkeys, we evaluated how the frequency of a target path  
31 influenced the onset, the accuracy and velocity of eye movements. Three hundred  
32 milliseconds after its extinction, a central target reappeared and immediately moved toward  
33 the periphery in four possible (oblique) directions and at constant speed (20 or 40°/s). During  
34 each daily sessions, the frequency of one motion direction was either uncertain (25% of trials)  
35 or certain (100% of trials). Our results show no reduction of saccade latency between the two  
36 sessions. No express saccades were observed in either session. A slow eye movement started  
37 after target onset (pre-saccadic glissade) and its velocity was larger during the “certain”  
38 sessions only with the 40°/s target. No anticipatory eye movement was observed. Longer  
39 intersaccadic intervals were found during the “certain” sessions but the post-saccadic pursuit  
40 velocity exhibited no change. No correlation was found between the accuracy and precision of  
41 saccades (interceptive or catch-up) and the post-saccadic pursuit velocity. Repeatedly tracking  
42 a target that moves always along the same path does not favor the generation of anticipatory  
43 eye movements, saccadic or slow. Their occurrence is not spontaneous but seems to require a  
44 preliminary training. Finally, for both sessions, the lack of correlation between the saccade-  
45 related and pursuit-related kinematic parameters is consistent with separate control of  
46 saccadic and slow eye movements.

47

**48 NEW & NOTEWORTHY (70<=75 words)**

49 Following previous studies documenting anticipatory movements, we investigated how the  
50 frequency of occurrence of a target path influenced the generation of tracking eye  
51 movements. When present, the effects were small. The limited performance that we found  
52 suggests that anticipatory responses requires preliminary training, in which case, they should  
53 not be considered as a behavioral marker of the primates' ability to extrapolate but the  
54 outcome of learning and remembering past experience.

55

## 56 INTRODUCTION

57           When a small target moves across the visual field, its motion evokes a trace on the  
58 retina that initiates a cascade of parallel and intertwined neural activations, which lead to the  
59 production of a saccade and brings the target image within the central visual field. Then, a  
60 sequence of slow eye movements and small catch-up saccades maintains the visual centration  
61 (1-3). In some cases, the gaze moves smoothly as if it were locked onto the current physical  
62 location of the target. Such a spatiotemporal accuracy is quite remarkable with regard to the  
63 delays for transmitting the retinal signals to the extraocular motor nuclei. Recent works in the  
64 monkey showed that practice is required to acquire this ability to track a moving target  
65 continuously and smoothly, i.e., with no catchup saccade (4-6). Behavioral studies in human  
66 subjects also report that gaze direction can be continuously maintained toward a moving  
67 target when its path is “predictable” (7-8). By contrast, the oculomotor tracking is saltatory  
68 and composed of catchup saccades when the path is “unpredictable” (9).

69           From now on, we will avoid using the notion of “predictability” as much as possible  
70 because it is not a physical property of the target but a psychological attribute, which depends  
71 upon the subject’s ability to memorize and remember past events. When the set of possible  
72 paths taken by a moving target is limited, the so-called “predictability” of one path results from  
73 the frequency of its occurrence (physical factor) but also from the ability to remember prior  
74 experience (psychological factor). Behavioral experiments with human subjects reported that,  
75 when a target always moves along the same path, their eyes can sometimes move in the same  
76 direction as the target before its appearance (10-14). Such anticipatory slow eye movements  
77 are mostly observed when the disappearance of the fixation target is followed by a display  
78 devoid of targets (15). Small static deviations of gaze direction have also been reported in  
79 human subjects when a blank interval (gap) separates the disappearance of a central fixation  
80 target from the appearance of a second target always at the same location in the peripheral  
81 visual field (16). Thus, when there is no target left to fixate, the repeated experience of a visual  
82 event causes a deviation of the eyes toward the visual field in which an target is about to  
83 appear. The direction of gaze can either drift or shift. It is noteworthy that in the experiments  
84 cited above, the visual events were brief and constant and the cadence of their occurrence  
85 was relatively constant, raising the possibility that the ocular responses were merely  
86 conditioned automatic responses, i.e., akin to those observed during a Pavlovian conditioning

87 procedure. If it is so, then it is not certain that the drift or shift of eye position indicate a process  
88 belonging to the domain of “higher” cognitive functions.

89 In 1967, Dr Albert Fuchs, one of the founders of the modern neurophysiology of eye  
90 movements studied the performance of human subjects and monkeys while they tracked  
91 repetitive and periodic target motions (17). He showed that the monkeys did not produce  
92 anticipatory eye movements, contrary to human subjects. According to him, the monkeys were  
93 not as motivated as were their human counterparts to perform the task. Later, another  
94 founder, Dr Edward Keller, investigated with colleagues how macaque monkeys tracked a 2D  
95 circular moving target with or without a repetitive and periodic motion (18). They proposed  
96 that the reduction of the pursuit delay while tracking a rhythmically moving target was due to  
97 a “predictive mechanism” compensating for the visuomotor delays and bringing gaze direction  
98 nearby to the current physical target location. However, the periodic stimuli employed were  
99 repetitive and the eye movements could still be viewed as sequential conditioned responses  
100 that the monkeys learned in order to be rewarded.

101 Freyberg & Ilg (2008) avoided the problems caused by periodic target motions (19).  
102 When after variable fixation interval, a target moves exclusively to the right at a constant speed  
103 and when, in 50% of the trials, the early part of its motion is initially invisible during 500 ms,  
104 both the human subjects and monkeys make, sometimes, an anticipatory slow eye movement  
105 during this blank interval. Its velocity was very low but scaled to the target speed. Likewise, de  
106 Brouwer et al. (2001) studied head-restrained cats tracking a target moving at various constant  
107 speeds (20). In some cases (10-50% of trials), the target disappeared after a variable time  
108 interval. They proposed that the slow eye movements made during the target extinction were  
109 driven by a so-called “prediction”, i.e., by a process estimating the future target location.  
110 However, these slow movements could as well be driven by residual target-motion related  
111 signals that persisted after target disappearance as suggested by results reported by Mitrani  
112 and Dimitrov (21). Using a more sophisticated experimental protocol, De Hemptinne et al.  
113 (2006) showed that monkeys made 10-30 % more anticipatory slow eye movements when the  
114 target motion direction was cued by a colored fixation target (22). By co-varying the duration  
115 of the fixation and gap intervals and keeping constant the delay between the onsets of the  
116 fixation and moving targets, Badler and Heinen (2006) showed also that the anticipatory slow  
117 eye movements were timed to the disappearance of a fixation target, suggesting a temporal

118 learning (23). Finally, De Hemptinne et al. (2007) found that longer gaps were associated with  
119 a larger width of the latency distribution of anticipatory eye movements (24). In all these  
120 experiments, the monkeys' performance required a long preliminary training.

121         The frequency of a target location and its timing also influence the velocity of saccades.  
122 In human subjects, Bronstein and Kennard (1987) showed that when the target appeared at  
123 regular time intervals at the same location, the peak velocity of short latency saccades (latency  
124 < 100 ms) was 16% lower than saccades to targets whose location and timing were randomly  
125 selected among a set of values (25). A comparable slowing was observed in eye-head gaze  
126 shifts made by cats orienting toward a food target that was repeatedly presented on either  
127 side of a barrier placed in front of the animal (26). The peak velocity of gaze shifts was 26 %  
128 lower and their duration 14% higher during the "predictive target" condition than during the  
129 "visible target" condition. In the monkey, Schiller et al. (2004a) explored the effect of the  
130 frequency of target appearance at one location on the generation of short-latency (express)  
131 saccades (27). Their occurrence increased with the most frequent target locations and longer  
132 gaps were associated with a greater proportion of express saccades. However, this proportion  
133 diminished when the number of possible target locations was increased (28) or when the  
134 targets were displayed upon a heterogeneous visual background or under natural viewing  
135 conditions (29). Finally, Carpenter and Williams (1995) reported that as the frequency of  
136 occurrence of a static target increased, the latencies became shorter, their distribution  
137 shallower and the number of express saccades increased, even though the duration of the  
138 fixation interval was randomized and no gap interval separated the target onset from the  
139 extinction of the fixation target (30).

140         In this study, we completed these previous studies by testing in the monkey whether  
141 the repeated presentation of a target moving along the same path 1) produced anticipatory  
142 eye movements before its appearance and/or 2) affected its oculomotor tracking. More  
143 specifically, we evaluated how the frequency of the target path influenced the onset, the  
144 velocity and the accuracy of eye movements. On the basis of previous studies, we conjectured  
145 that repeatedly tracking a target, which after a constant gap interval, moves always along the  
146 same path would favor the occurrence of anticipatory slow eye movement and express  
147 saccades. We also conjectured that reducing the uncertainty about the target path would  
148 make the interceptive saccades and the post-saccadic velocity less variable, and thus more

149 precise. Finally, after showing in naive monkeys that saccadic and pursuit eye movements do  
150 not share common motion signals (4), we tested whether this conclusion also holds in monkeys  
151 who were overtrained to track a target moving at constant velocity.

152



## 153 MATERIAL AND METHODS

### 154 Subjects and surgical procedures

155 Six adult male rhesus monkeys (*Bi, C, D, E, F and G* ; age: 5-12 yr old; weights: 8–14 kg)  
156 were used in this study. A head restraint fixture was positioned on the top front center of the  
157 skull and secured with bone cement (Palacos) and stainless screws attached to the skull, under  
158 general anesthesia (with isoflurane or sevoflurane) and aseptic conditions. For four of these  
159 monkeys (monkeys *Bi, C, F and G*), the monitoring of their eye movements was made with the  
160 electromagnetic induction technique. A three-turn search coil was sutured with silk to the  
161 sclera under the conjunctiva of one eye after local anesthesia (with oxybuprocaine). Lead wires  
162 were passed under the skin to a connector located on the top of the skull and secured with  
163 bone cement. The scleral coil and head restrain fixture was implanted during the same surgery  
164 for the monkeys *Bi, C, D, F and G*. In monkey *D*, a persistent mydriasis after the surgery in the  
165 implanted eye led us to remove the coil.

166 The surgical procedure and experiments were performed in accordance with the  
167 guidelines from the French Ministry of Agriculture and the European Community, as well as  
168 the Regional Ethics Committee (approvals A13/01/13 and 13889-2018030211578026). The  
169 health and the maintenance of the monkeys' housing were monitored daily by a dedicated  
170 zoo-technical staff supervised by a full-time veterinarian.

### 171 Eye movement recording and visual stimulation

172 During the experimental sessions, the monkeys were seated in a chair with the head  
173 restrained, facing a LCD video monitor (Samsung SyncMaster, P227f; 1,280 × 1,024 pixels, 100-  
174 Hz refresh rate, 39 × 29 cm) located at a viewing distance of 38 cm. The visual target was a  
175 Gaussian blurred white disk of 0.4° diameter displayed over a gray background.

176 For monkey *Bi, C, F and G*, the eye movements were recorded with a phase-angle  
177 detection system (CNC Engineering, 3-ft. coil frame) and voltage signals encoding separately  
178 the horizontal and vertical positions of the eye were sampled at 500 Hz. For monkeys *D and E*,  
179 the eye movements were recorded with an IR eye tracking system (Eyelink 1000, SR Research  
180 Ltd).

181 The data acquisition, the online control of the oculomotor performance and the  
182 triggering of stimuli were controlled by a PC using the Beethoven software package (Ryklin

183 Software). Eye position signals were calibrated by having the animal fixate stationary targets  
184 located at  $\pm 16^\circ$  along the horizontal or vertical meridians.

## 185 Behavioral tasks

186 **Figure 1 approximately here**

187 In this study, we describe how the frequency of occurrence of a target path influenced  
188 the tracking eye movements. The sessions started several weeks after the monkeys were  
189 trained to make saccades to static targets located at various eccentricities, ranging from 0 to  
190  $\pm 16^\circ$  horizontally at vertical eccentricity of  $\pm 16^\circ$ . Each experimental session (lasting 1–2 h) was  
191 composed of trials whose number depended upon the monkey's motivation. Water-deprived  
192 in its home cage, each monkey received its hydration needs during daily sessions that ended  
193 when it stopped working, i.e., fixating the central target for approximately 10 successive trials.  
194 Each trial started with a warning tone (300 ms) that preceded the appearance of a target at  
195 the center of visual display (Figure 1). After the monkey directed its gaze toward its location  
196 within a surrounding fixation window ( $8^\circ$  radius centered on the target) and for a variable  
197 fixation interval (750, 1,000, 1,250 or 1,500 ms), the central target disappeared. Then, a gap  
198 interval of 300 ms started during which no target was presented on the visual display. The  
199 monkeys were no more required to maintain their gaze within the fixation window during this  
200 gap interval. Then, the target re-appeared at the center of the visual display and immediately  
201 moved with a constant speed for 800 or 1200 ms ( $20^\circ/\text{s}$ ) or 600 ms ( $40^\circ/\text{s}$ ), along one out of  
202 four possible oblique paths. The monkeys spontaneously tracked the moving target and were  
203 rewarded with a small volume of water after the target disappeared at the end of its path. All  
204 of them performed the experiment with the lowest target speed ( $20^\circ/\text{s}$ ), and only four  
205 monkeys (Bi, C, D and E) were tested with the highest target speed ( $40^\circ/\text{s}$ ). We divided the  
206 visual field into four quadrants: when the target moved rightward and upward, when it moved  
207 rightward and downward, when it moved downward and leftward and when it moved leftward  
208 and upward. Considering each target path among four possible ones, two frequencies of  
209 occurrence were tested during separate sessions, which were recorded during different days:  
210 25% ("uncertain" sessions) or 100% ("certain" sessions). During the "uncertain" sessions, the  
211 direction of the target path was pseudo-randomly selected from one trial to the next. To avoid  
212 oculomotor biases resulting from prior experience, these sessions always preceded the  
213 recordings of tracking eye movements during the "certain" sessions. During the latter, the

214 monotony of the task caused the monkeys to stop tracking the target before obtaining the  
215 same volume of water as that obtained during the “uncertain” sessions. In that case, we  
216 managed to reach their hydric satiation by proposing them other visual tracking tasks that  
217 were less monotonous.

## 218 **Data analysis**

### 219 **Figure 2 approximately here**

220 The recordings of eye movements were digitized on-line and analyzed off-line using a  
221 software program (Eyemove, designed by Kathy Pearson and Dr David L. Sparks) that detected  
222 the onset and offset of the horizontal and vertical saccade components based on a velocity  
223 threshold ( $30^\circ/s$ ). The results of this automatic detection were checked by inspecting each trial  
224 individually and adjusted manually when necessary. Several other parameters were calculated  
225 to quantify the evolution of the oculomotor responses (Figure 2). From the measurement of  
226 eye position at different times (onset and end of saccades) relative to target motion onset  
227 (dashed vertical line labeled 1), we calculated the amplitude and velocity of the interceptive  
228 (IS, grey zone delimited by the lines labeled 2 and 3) and the catch-up saccade (CS, grey zone  
229 delimited by the lines labeled 4 and 5). The latter is defined as the first correction saccade that  
230 follows the interceptive saccade. We also studied the pre-saccadic glissade (PSG, delimited by  
231 the lines labeled 1 and 2), which is the slow eye movement that was eventually made before  
232 the interceptive saccade, and the post-saccadic pursuit (PSP), which is the slow eye movement  
233 made from the end of the interceptive saccade (line 3) to the onset of the catch-up saccade  
234 (line 4). By convention, positive values correspond to upward and rightward eye positions,  
235 negative values to downward and leftward eye positions.

236 Data analysis was performed with the Statistica Software (Statsoft) and Python (Python  
237 Software Foundation, Python Language Reference, version 3.1). We performed non-  
238 parametric Wilcoxon Test for the pairwise comparison of median and interquartile range (IQR)  
239 values of each variable, except for monkey D. Indeed, because of his permanent monocular  
240 mydriasis, we preferred to examine the data collected in this monkey separately from the  
241 others. The comparison of IQR values of a given parameter between the “uncertain” and  
242 “certain” sessions enabled us to estimate whether the tracking of a target that moved in the  
243 same direction and at the same velocity during the entire session was associated with a

244 reduction of the variability of that parameter. Statistical significance threshold was set to  $P <$   
245 0.05. When the median and interquartile range (IQR) values were negative, we multiplied  
246 them by -1 in order to facilitate the comparison with the other values.

247 In some trials, most often in the monkeys Bi, D and E, gaze was deviated upward at the  
248 time when the moving target appeared because these monkeys made a spontaneous saccade  
249 during the gap interval. Therefore, for making valid comparisons between saccades  
250 (comparable retinal stimulations), we focused only on trials in which the starting eye position  
251 at target motion onset ranged from -5 to 5 degrees (horizontally and vertically). In addition to  
252 this criterion, the saccades had to land in the visual quadrant in which the target moved, within  
253 in a fixation window ranging from -5 to 5 degrees (horizontally and vertically) with respect to  
254 the target location at the time of saccade landing. In the following, we firstly report the  
255 influence of the target path frequency on the interceptive saccades. Then we describe the pre-  
256 and post-saccadic slow eye movements and the catch-up saccades. We excluded the catch-up  
257 saccades whose onset occurred 100 ms before the end of the trial. We only considered the  
258 catch-up saccades that landed within a window ranging from -5 to 5 degrees (horizontally and  
259 vertically) with respect to the target location at the time of their landing.

260

## 261 RESULTS

262 The report of results follows the temporal order of measured parameters during the  
 263 course of a trial (as illustrated in Fig. 2). After examining whether gaze was moving at target  
 264 appearance during the “certain” sessions, we will study whether the frequency of the target  
 265 path changed the pre-saccadic glissade (slow eye movement from target onset to saccade  
 266 onset), the interceptive saccade (its latency, velocity, accuracy and precision), the post-  
 267 saccadic pursuit eye movement and the catch-up saccade.

### 268 Repeatedly tracking the same target did not lead to anticipatory slow eye movement

269 **Figure 3 approximately here**

270 As previous studies reported anticipatory movements before the appearance of the  
 271 target, we examined whether gaze was moving at target onset by calculating the horizontal  
 272 and vertical velocities of the eye displacement during a temporal interval of 80 ms centered  
 273 on target motion onset. We did not study the radial velocity because its calculation leads to  
 274 positive value regardless of the direction of target motion. Figure 3 plots the statistics (median  
 275 and IQR) for each monkey, each quadrant and each target velocity. With the 20°/s target, the  
 276 paired comparison of median and IQR values failed to reveal any statistically significant  
 277 difference of eye velocity at target onset between the two sessions for the horizontal ( $\Delta\text{Med}$   
 278  $= 0.07 \pm 0.4$  °/s, P value = 0.8;  $\Delta\text{IQR} = 0.01 \pm 0.05$  °/s, P value = 1) and vertical ( $\Delta\text{Med} = 0.14 \pm$   
 279  $0.4$ , P value = 0.07;  $\Delta\text{IQR} = 0.01 \pm 0.08$  °/s, P value = 0.48) components. With the 40°/s target,  
 280 no significant difference was found either between the “certain” and “uncertain” sessions, and  
 281 this, for each component as well (horizontal:  $\Delta\text{Med} = 0.1 \pm 0.9$ °/s; vertical:  $\Delta\text{Med} = 0.1 \pm 0.7$ °/s,  
 282 P value = 0.77). The horizontal velocity was significantly more variable during the “certain”  
 283 sessions than during the “uncertain” sessions ( $\Delta\text{IQR} = 0.02 \pm 0.03$ °/s,  $P < 0.05$ ) but not the  
 284 vertical velocity ( $\Delta\text{IQR} = 0.01 \pm 0.06$ °/s, P value = 0.23). In summary, at the time of target onset  
 285 and in comparison to the “uncertain” sessions, we found no evidence of eye movement  
 286 anticipating the appearance of the target when it always moved along the same path.

### 287 Repeatedly tracking the same target did not enhance the pre-saccadic slow eye movement

288 **Figure 4 approximately here**

289 After checking whether the eyes were moving at the time of target appearance, we  
 290 then studied the eye displacement during the time interval elapsed from the target motion  
 291 onset to the saccade onset. Figure 4A shows the amplitude of the eye movement that  
 292 preceded the interceptive saccade as a function of the saccade latency when the target moved  
 293 in the upper right visual quadrant (data collected in monkey Bi). The scatter of data points  
 294 shows that later saccades were associated with larger pre-saccadic changes in eye position.  
 295 We call this change pre-saccadic glissade because its small value radically differs from the post-  
 296 saccadic smooth pursuit. To estimate its velocity, we calculated the slope of the relation  
 297 between its amplitude and the delay from target motion onset to saccade onset (which is  
 298 saccade latency). Considering for example the cases during which the 20°/s target moved in  
 299 the upper right visual field, the slopes were 13 versus 14 °/s (monkey Bi), 7 versus 2 °/s (monkey  
 300 C), 11 versus 1 °/s (monkey E), 2 versus 5 °/s (monkey F) and 4 versus 4 °/s (monkey G) during  
 301 the “uncertain” and “certain” sessions, respectively. Figure 4B plots the slope values calculated  
 302 for each visual quadrant, each monkey and each target speed. Their paired comparison  
 303 revealed no statistically significant difference between the “certain” and “uncertain” sessions  
 304 ( $\Delta$ slope =  $-0.5 \pm 3.6^\circ/\text{s}$ ,  $P$  value = 0.12). A small but significant change was observed during the  
 305 “certain” sessions when the target moved at 40°/s ( $\Delta$ slope =  $4.3 \pm 5.1^\circ/\text{s}$ ,  $P < 0.05$ ).

306 In summary, during both “uncertain” and “certain” sessions, a pre-saccadic glissade  
 307 started after the target started its motion. In comparison to the sessions in which the target  
 308 path varied across the trials, its radial velocity was increased (135% increase) during the  
 309 “certain” sessions when the target moved at 40°/s. However, no difference was observed with  
 310 the 20°/s target.

311 **Repeatedly tracking the same target reduced neither the latency nor the velocity of**  
 312 **interceptive saccades.**

313 Following the suggestions that the latency and velocity of saccades could be used as  
 314 behavioral markers of the motivation (31) and alertness (32), we checked whether the  
 315 monotony of tracking a target that repeatedly moved along the same path for a large number  
 316 of trials was associated with a decline in either the motivation or the vigilance of our monkeys.

317 **Figure 5 approximately here**



347  $\pm 6$  ms,  $P < 0.05$ ). No statistically significant change was observed in the IQR values between the  
 348 two sessions (average difference =  $3 \pm 7$  ms,  $P$  value = 0.33). With the  $40^\circ/\text{s}$  target, the paired  
 349 comparison of median and IQR values failed to reveal any significant difference between the  
 350 two sessions (average difference of medians =  $6 \pm 10$  ms,  $P$  value = 0.77; average difference of  
 351 IQRs =  $3 \pm 5$  ms;  $P$  value = 0.5).

352 In summary, within our experimental conditions, the monkeys did not exhibit any sign  
 353 of reduced motivation or reduced alertness while they repeatedly performed the same task  
 354 from one trial to the next. Between the “certain” and “uncertain” sessions, we found no  
 355 difference in the average velocity of interceptive saccades. A negligible increase (4%) of latency  
 356 was observed in the saccades toward the  $20^\circ/\text{s}$  target only. These observations contrast with  
 357 the reduced latency and velocity of “predictive” saccades as reported in previous studies  
 358 (Bronstein and Kennard 1987; Carpenter and Williams 1995)

359 **Repeatedly tracking the same target changed neither the accuracy nor the precision of**  
 360 **interceptive saccades.**

361 **Figure 8 approximately here**

362 Then, we investigated the effect of the target path frequency on the accuracy and  
 363 precision of interceptive saccades. Figure 8A plots for each target speed (leftmost columns:  
 364  $20^\circ/\text{s}$ , rightmost columns:  $40^\circ/\text{s}$ ), the landing position (radial value) of interceptive saccades as  
 365 a function of their landing time when the target moved in the upper left visual field (data from  
 366 monkey Bi). The landing positions were scattered near the target (dashed line) during both  
 367 sessions. The frequency of the target path did not seem to influence the accuracy of saccades:  
 368 the scatters of position values did not show any noticeable difference between the “uncertain”  
 369 and “certain” sessions. To quantify the accuracy and precision of saccades, we calculated the  
 370 ratio of their landing position over their landing time, a parameter that Groh et al. (1997) called  
 371 “saccadic velocity compensation” (32) and that Burrelly et al. (2018a) called “position/time  
 372 landing ratio” (P/T ratio) (33). If the interceptive saccade lands accurately on the location of  
 373 the moving target, its value should be equal to the target velocity. A ratio larger indicates  
 374 hypermetria (overshoot) and a smaller ratio hypometria (undershoot). When the  $20^\circ/\text{s}$  target  
 375 always moved in the upper right visual field, the P/T ratios were close to the target velocity:  
 376  $19 \pm 4$ ,  $17 \pm 3$ ,  $20 \pm 3$ ,  $22 \pm 3$  and  $23 \pm 6^\circ/\text{s}$  during the “uncertain” sessions against  $20 \pm 3$ ,  $18 \pm$



377 4,  $18 \pm 5$ ,  $21 \pm 5$  and  $23 \pm 6^\circ/\text{s}$  during the “uncertain” sessions (values for monkey Bi, C, E, F  
 378 and G respectively). Figure 8B plots the median and IQR values of the position/time (P/T)  
 379 landing ratio for each visual quadrant and each monkey. Their paired comparison revealed no  
 380 statistically significant difference between the two sessions ( $\Delta\text{Med} = 3 \pm 1^\circ/\text{s}$ , P value = 0.5;  
 381  $\Delta\text{IQR} = 0.2 \pm 0.85^\circ/\text{s}$ ; P value = 0.26). With the  $40^\circ/\text{s}$  target, no significant difference was found  
 382 between the “certain” and “uncertain” sessions ( $\Delta\text{Med} = -0.6 \pm 1.3^\circ/\text{s}$ , P value = 0.15;  $\Delta\text{IQR} =$   
 383  $0.07 \pm 0.8^\circ/\text{s}$ , P value = 0.39, all quadrants and all monkeys considered, except monkey D).

384 In summary, the frequency of a target path did not influence the accuracy and precision  
 385 of interceptive saccades. The saccades were neither more accurate nor more precise when  
 386 they were aimed at a target whose path and velocity were the same from one trial to the next.

387 **Repeatedly tracking the same target did not enhance the post-saccadic slow eye movement**

388 **Figure 9 approximately here**

389 Two types of eye movements are made while a small visual target is being tracked: a  
 390 slow eye movement and catchup saccades. We conjectured that tracking a target that moves  
 391 always along the same path would maintain the activity conveyed by the visuomotor channels  
 392 involved in the generation of slow eye movements. To test this conjecture, we checked  
 393 whether the time interval elapsed from the end of the interceptive saccade to the onset of the  
 394 first catch-up saccade was longer during the “certain” sessions than during the “uncertain”  
 395 sessions. Figure 9A documents for each monkey, each visual quadrant and each target speed,  
 396 the duration of this first intersaccadic interval. The fact that most median values are situated  
 397 above the diagonal indicates that the first intersaccadic intervals were indeed longer during  
 398 the “certain” sessions than during the “uncertain” ones, regardless of whether the target  
 399 moved at  $20$  or  $40^\circ/\text{s}$ . The paired comparison of median values confirmed longer intersaccadic  
 400 intervals during the “certain” sessions than during the “uncertain” sessions when the target  
 401 moved at  $20^\circ/\text{s}$  ( $\Delta\text{Med} = 28 \pm 27$  ms;  $P < 0.05$ ) and when it moved at  $40^\circ/\text{s}$  ( $\Delta\text{Med} = 30 \pm 13$  ms;  
 402  $P < 0.05$ ). The IQR values were also significantly different between the two sessions when the  
 403 target moved at  $40^\circ/\text{s}$  ( $\Delta\text{IQR} = 20 \pm 11$  ms;  $P < 0.05$ ) but not when it moved at  $20^\circ/\text{s}$  ( $\Delta\text{IQR} = 16$   
 404  $\pm 23$  ms; P value = 0.12).

405 In summary, there was a tendency for the catch-up saccades being made later when  
 406 the target moved always in the same path (15% and 21% longer intersaccadic intervals for  
 407 20°/s and 40°/s target respectively), suggesting that visual tracking is smoother (more  
 408 continuous with less frequent saccades) during the “certain” sessions during the “uncertain”  
 409 ones. For the 40°/s target, the duration of intersaccadic intervals was also more variable during  
 410 the “certain” sessions.

411 The longer intersaccadic intervals during the “certain” sessions could result from less  
 412 variable post-saccadic velocity and/or from less variable distances between gaze and target  
 413 positions. To test these possibilities, we examined the relation between the amplitude of the  
 414 post-saccadic pursuit eye movement and its duration (average post-saccadic pursuit velocity).  
 415 This relation is documented in Fig. 9B for all the trials during which monkey Bi tracked the  
 416 target moving in the upper left visual field. The data points are slightly below or close to the  
 417 diagonal dashed line, indicating that the eye moved either slower or as fast as the target when  
 418 it moved at 20°/s, regardless of whether the session was “certain” or “uncertain”. When the  
 419 target moved at 40°/s, most data points are below the dashed line during both sessions: the  
 420 eye moved slower than the target.

421 To test whether the post-saccadic pursuit velocity was changed during the “certain”  
 422 sessions, we calculated for each monkey and each visual quadrant, the ratio between the  
 423 amplitude of the post-saccadic eye displacement and its duration (Figure 9C). In the majority  
 424 of cases, the median values were smaller than the target speed during both “certain” and  
 425 “uncertain” sessions. Most of the data points are indeed situated below the dashed lines,  
 426 which indicate the target velocity. For example, when we consider the session during which  
 427 the target moved at 20°/s in the upper right visual field, the post-saccadic pursuit velocity  
 428 (median  $\pm$  IQR) was  $17 \pm 2$ ,  $16 \pm 2$ ,  $7.7 \pm 3$ ,  $12 \pm 3$  and  $9 \pm 3$  °/s during the “uncertain” sessions  
 429 and  $18 \pm 2$ ,  $17 \pm 2$ ,  $12 \pm 3$ ,  $12 \pm 2$ , and  $8 \pm 2$  °/s during the “certain” sessions (values for monkey  
 430 Bi, C, E, F and G, respectively). The paired comparison of median values calculated for each  
 431 monkey and each quadrant did not reveal any change between the “uncertain” and “certain”  
 432 sessions, regardless of whether the target moved at 20°/s ( $\Delta$ Med =  $-0.3 \pm 1.3$ °/s; P value = 0.26)  
 433 or 40°/s ( $\Delta$ Med =  $-3 \pm 3$ °/s; P value = 0.15). Concerning the variability of post-saccadic pursuit  
 434 velocity, the IQR values were not significantly different between the “uncertain” and “certain”  
 435 sessions, neither with the 20°/s target ( $\Delta$ IQR =  $0.4 \pm 0.7$ °/s, P value = 0.12) nor with the 40°/s

436 target ( $\Delta\text{IQR} = 2 \pm 3^\circ/\text{s}$ ;  $P$  value = 0.15). In summary, the longer intersaccadic intervals during  
437 the “certain” sessions were not associated with a different post-saccadic pursuit velocity.

438 **Repeatedly tracking the same target did not change the accuracy or precision of catch-up**  
439 **saccades**

440 **Figure 10 approximately here**

441 Catchup saccades being the other important component of the visual tracking, we also  
442 studied the influence of the occurrence frequency of the target path on their accuracy and  
443 precision. Figure 10A plots for each target velocity the radial landing positions of the first catch-  
444 up saccade as a function of its landing time when the target moved in upper left visual field  
445 (data collected in monkey Bi). The landing position values were scattered near the target path  
446 (dashed line) during both “uncertain” and “certain” sessions. The frequency of the target path  
447 did not seem to influence the accuracy of catch-up saccades as there is no noticeable  
448 difference in the shape or in the extent of the scatters of position values between the  
449 “uncertain” and “certain” sessions. As for the interceptive saccades, we quantified the  
450 accuracy and precision of catch-up saccades by calculating the position/time landing ratios.  
451 Figure 10B documents their value during both sessions. Looking at the graph corresponding to  
452 the  $20^\circ/\text{s}$  target, we see an asymmetry in the scatter of data points: the majority of values are  
453 larger than the target velocity and the majority of data points are situated below the diagonal  
454 line, suggesting an influence of the frequency of the target path. The paired comparison of  
455 median values confirmed a slightly smaller values of P/T landing ratio during the “certain”  
456 sessions ( $\Delta\text{Med} = -0.6 \pm 0.8^\circ/\text{s}$ ,  $P < 0.05$ ). The lower IQR values during the “certain” sessions  
457 was also statistically significant ( $\Delta\text{IQR} = -0.4 \pm 0.6^\circ/\text{s}$ ,  $P < 0.05$ ). These small differences between  
458 the “uncertain” and “certain” sessions were absent when the target moved at  $40^\circ/\text{s}$ . The  
459 paired comparisons revealed no significant difference in the median and IQR values of  
460 position/time landing ratios ( $\Delta\text{Med} = 0.8 \pm 1.1^\circ/\text{s}$ ,  $P\text{-value} = 0.15$ ;  $\Delta\text{IQR} = 0.3 \pm 1.2^\circ/\text{s}$ ,  $P\text{-value} =$   
461  $0.77$ ).

462 In summary, when the target moved at  $20^\circ/\text{s}$  along the same path, catch-up saccades  
463 was slightly more accurate (2.8% decrease) and more precise (20% decrease) than when its

464 path changed across the trials. However, the difference between the uncertain and certain  
465 sessions was absent when the target moved at 40°/s.

466 **Comparing the position/time landing ratio of interceptive saccades with the post-saccadic**  
467 **pursuit velocity**

468 **Figure 11 approximately here**

469 Anatomical, neurophysiological and clinical evidence indicate that saccadic and pursuit  
470 eye movements are not driven by common command signals (34). Studies with naive and  
471 healthy monkeys also show a clear dissociation between the saccade and pursuit  
472 performances when they track for the first time a moving target (4-5). We further investigated  
473 this dissociation in our over-trained monkeys. More specifically, we compared the radial  
474 position/time landing ratio of interceptive saccades to the radial post-saccadic pursuit velocity.  
475 Figure 11A shows the values calculated from movements made by monkey Bi when the target  
476 moved at 20°/s (leftmost two columns) and 40°/s (rightmost columns) in the upper right visual  
477 field. The values of position/time landing ratio were scattered about the target velocity  
478 (dashed lines) during both “uncertain” and “certain” sessions, illustrating the accuracy of  
479 interceptive saccades (as reported above). By contrast, the post-saccadic pursuit (PSP) velocity  
480 values were consistently smaller than the target velocity (values are situated on the left with  
481 respect to the vertical dashed lines) for both sessions. No correlation was noticeable between  
482 these two parameters, suggesting that interceptive saccades and pursuit eye movements are  
483 driven by different motion signals.

484 To further test the consistency of this inference, we compared the median and IQR  
485 values of radial position/time landing ratios of interceptive saccades to those of the radial post-  
486 saccadic pursuit velocity (Figure 11B). For both “uncertain” and “certain” sessions, the values  
487 of radial position/time landing were scattered about the target velocity (horizontal dashed  
488 lines) whereas the post saccadic pursuit velocity values were consistently smaller than the  
489 target velocity (most data points are situated to the left of the vertical dashed lines).  
490 Considering the trials recorded during the “uncertain” sessions when the target moved at  
491 20°/s in the upper right visual field, the median values of radial position/time landing ratio  
492 were  $20 \pm 3^\circ/\text{s}$ ,  $18 \pm 4^\circ/\text{s}$ ,  $18 \pm 5^\circ/\text{s}$ ,  $21 \pm 5^\circ/\text{s}$  and  $23 \pm 6^\circ/\text{s}$  (values for monkey Bi, C, E, F and  
493 G, respectively), much larger than the medial values of post-saccadic pursuit velocity, which

494 were  $17 \pm 2^\circ/\text{s}$ ,  $16 \pm 2^\circ/\text{s}$ ,  $12 \pm 3^\circ/\text{s}$ ,  $12 \pm 3^\circ/\text{s}$  and  $9 \pm 3^\circ/\text{s}$ . Likewise, during the “certain”  
 495 sessions, the radial position/time landing ratios were most often larger than the post-saccadic  
 496 pursuit velocities:  $19 \pm 4$  versus  $18 \pm 2^\circ/\text{s}$  in monkey Bi,  $17 \pm 3$  versus  $17 \pm 2^\circ/\text{s}$  (monkey C),  $20$   
 497  $\pm 3$  versus  $12 \pm 3^\circ/\text{s}$  (monkey E),  $22 \pm 3$  versus  $12 \pm 2^\circ/\text{s}$  (monkey F) and  $23 \pm 6$  versus  $8 \pm 2^\circ/\text{s}$   
 498 (monkey G).

499 The paired comparison of median values calculated for all visual quadrants and all  
 500 monkeys (except D) confirmed position/time landing ratios that were consistently larger than  
 501 the post-saccadic velocity values, during both sessions (uncertain:  $\Delta\text{Med} = 4.4 \pm 4.2^\circ/\text{s}$ ; certain:  
 502  $\Delta\text{Med} = 4.4 \pm 4.7^\circ/\text{s}$ ,  $P < 0.05$ ). With the  $40^\circ/\text{s}$  target, the position/time landing ratios was again  
 503 significantly larger than the post-saccadic velocities during both sessions (uncertain:  $\Delta\text{Med} =$   
 504  $12.9 \pm 5.4^\circ/\text{s}$ ; certain:  $\Delta\text{Med} = 10.5 \pm 7.9^\circ/\text{s}$ ,  $P < 0.05$ ). Regarding the variability, the IQR values  
 505 of position/time landing ratio of interceptive saccades were larger than the IQR values of post-  
 506 saccadic pursuit velocities, only during the “certain” sessions and when the target moved at  
 507  $20^\circ/\text{s}$  (certain:  $\Delta\text{IQR} = 1.1 \pm 1.2^\circ/\text{s}$ ,  $P < 0.05$ ; uncertain:  $\Delta\text{IQR} = 0.8 \pm 1.2^\circ/\text{s}$ ,  $P\text{-value} = 0.12$ ). This  
 508 difference is another indication that interceptive saccades and post-saccadic pursuit are driven  
 509 by different motion signals. However, this difference was absent with the  $40^\circ/\text{s}$  target  
 510 (uncertain:  $\Delta\text{IQR} = -1.1 \pm 2.3^\circ/\text{s}$ ; certain:  $\Delta\text{IQR} = 0.4 \pm 0.9^\circ/\text{s}$ ,  $P\text{-value} = 0.38$ ). The absence of  
 511 difference can result either from the small size of our sample or from the high velocity of the  
 512 target motion. In any case, with regard to their ability to match the target velocity, interceptive  
 513 saccades were more accurate than the post-saccadic pursuit eye movements. The significant  
 514 difference between the position/time landing ratios of interceptive saccades and the post-  
 515 saccadic pursuit velocity and the absence of correlation is consistent with the thesis that  
 516 interceptive saccades and post-saccadic pursuit are driven by different sets of motion signals.

517 **Comparing the post-saccadic pursuit velocity with the position/time landing ratio of catch-**  
 518 **up saccades**

519 **Figure 12 approximately here**

520 One possible cause for the difference between the position/time landing ratio of  
 521 interceptive saccades and the post-saccadic pursuit velocity is the different retinal origins of  
 522 motion signals, in the visual periphery for the former, in the central visual field for the latter.

523 Therefore, we also compared the radial post-saccadic pursuit velocity to the radial  
 524 position/time landing ratio of catch-up saccades. Figure 12A shows values obtained with the  
 525 monkeys Bi when the target moved in the upper right quadrant of the visual field. During both  
 526 “uncertain” and “certain” sessions, the radial position/time landing ratios were still scattered  
 527 about the target velocity (vertical dashed lines) with a tendency however of being slightly  
 528 faster than the target. By contrast, most of the post-saccadic pursuit velocity values were  
 529 scattered below the target velocity (horizontal dashed lines). There is no sign of correlation  
 530 between these two parameters.

531 Then, we compared the median and IQR values of the radial position/time landing  
 532 ratios of catch-up saccades to those of radial post saccadic pursuit velocity (Figure 12B). As for  
 533 the interceptive saccades, the position/time landing ratio of catch-up saccades was more  
 534 accurate than the post saccadic pursuit velocity. For instance, when the target moved at 20 °/s  
 535 in the upper right quadrant of the visual field, the median values of radial position/time  
 536 landing ratio of catch-up saccades during the “uncertain” sessions were  $21 \pm 2$ ,  $19 \pm 3$ ,  $21 \pm 2$ ,  
 537  $22 \pm 3$  and  $23 \pm 4$ °/s whereas the post-saccadic pursuit velocity values were consistently  
 538 smaller:  $17 \pm 2$ ,  $16 \pm 2$ ,  $12 \pm 3$ ,  $12 \pm 3$  and  $9 \pm 3$ °/s (values for the monkeys Bi, C, E, F and G,  
 539 respectively).. Likewise, during the “certain” sessions, the radial position/time landing ratios  
 540 were consistently larger than the post-saccadic pursuit velocity:  $20 \pm 2$  versus  $18 \pm 2$ °/s in  
 541 monkey Bi,  $19 \pm 2$  versus  $17 \pm 2$ °/s in monkey C,  $20 \pm 1$  versus  $12 \pm 3$ °/s in monkey E,  $22 \pm 1$   
 542 versus  $12 \pm 2$ °/s in monkey F and  $22 \pm 4$  versus  $8 \pm 2$ °/s in monkey G. When the target moved  
 543 at 40°/s, the radial position/time landing ratio was smaller than the target velocity but still  
 544 larger than the post-saccadic pursuit velocities.

545 Figure 12B plots the median and IQR values of radial post saccadic pursuit velocity  
 546 calculated for each quadrant of the visual field and each monkey as a function of the  
 547 position/time landing ratio of catch-up saccades. The paired comparison of median values  
 548 confirmed a statistically significant larger position/time landing ratio than the post-saccadic  
 549 velocity for both “certain” and “uncertain” sessions, when the target moved at 20°/s  
 550 (uncertain:  $\Delta\text{Med} = 6.4 \pm 4.7$ °/s; certain:  $\Delta\text{Med} = 5.5 \pm 4.6$  °/s,  $P < 0.05$ ) as well as when it moved  
 551 at 40°/s (uncertain:  $\Delta\text{Med} = 15.6 \pm 6.6$  °/s; certain:  $\Delta\text{Med} = 11.9 \pm 9.5$ °/s,  $P < 0.05$ ). Regarding  
 552 the variability, the IQR values of position/time landing ratio of catch-up saccades were  
 553 consistently smaller than the IQR values of post-saccadic pursuit velocity for both sessions,

554 regardless of whether the target moved at 20°/s (uncertain:  $\Delta\text{IQR} = 0.7 \pm 1 \text{ }^\circ/\text{s}$ , P-value = 0.004;  
 555 certain:  $\Delta\text{IQR} = 0.7 \pm 1.1 \text{ }^\circ/\text{s}$ , P<0.05) or 40°/s (uncertain:  $\Delta\text{IQR} = 3.7 \pm 2.3 \text{ }^\circ/\text{s}$ ; certain:  $\Delta\text{IQR} =$   
 556  $2.4 \pm 1.2 \text{ }^\circ/\text{s}$ , P<0.05).

557 In summary, with regard to their ability to match target velocity, the catch-up saccades  
 558 were more accurate and more precise (smaller IQR) than the post-saccadic pursuit eye  
 559 movements, during both “uncertain” and “certain” sessions and for both target velocities.

## 560 **Comparison of P/T landing ratio of interceptive and catch-up saccades**

561 **Figure 13 approximately here**

562 Finally, the different retinal origins of interceptive and catchup saccades led us to  
 563 compare their accuracy and precision (Figure 22). For both “uncertain” (top row) and “certain”  
 564 (bottom row) conditions, the position/time landing ratio of catch-up saccades seemed to be  
 565 more accurate and more precise than interceptive ones. For instance, during the “uncertain”  
 566 sessions, when the target moved at 20 °/s in the upper right visual field, the median values of  
 567 position/time landing ratio of interceptive saccades were  $20 \pm 3$ ,  $18 \pm 4$ ,  $18 \pm 5$ ,  $21 \pm 5$  and  $23$   
 568  $\pm 6 \text{ }^\circ/\text{s}$  versus  $21 \pm 2$ ,  $19 \pm 3$ ,  $21 \pm 2$ ,  $22 \pm 3$  and  $22 \pm 4 \text{ }^\circ/\text{s}$  for the catch-up saccades (monkey Bi,  
 569 C, E, F and G respectively). During the “certain” sessions, the values were  $19 \pm 4$ ,  $17 \pm 3$ ,  $20 \pm$   
 570  $3$ ,  $22 \pm 3$ ,  $26 \pm 6 \text{ }^\circ/\text{s}$  (interceptive saccades) versus  $20 \pm 2$ ,  $19 \pm 2$ ,  $20 \pm 1$ ,  $22 \pm 1$  and  $22 \pm 4 \text{ }^\circ/\text{s}$   
 571 (catch-up saccades). For the sessions in which the target moved at 20°/s, the paired  
 572 comparison confirmed significantly larger values of position/time landing ratio for the catch-  
 573 up saccades than for the interceptive saccades, regardless of whether the target path was  
 574 certain ( $\Delta\text{Med} = 1.1 \pm 1.2 \text{ }^\circ/\text{s}$ , P<0.05) or uncertain (average difference =  $2 \pm 1.7 \text{ }^\circ/\text{s}$ , P<0.05).  
 575 With the 40 °/s target, the position/time landing ratio of catch-up saccades were still larger  
 576 during the “uncertain” sessions ( $\Delta\text{Med} = 2.7 \pm 2.7 \text{ }^\circ/\text{s}$ , P<0.05). However, the difference  
 577 disappeared during the “certain” sessions ( $\Delta\text{Med} = 1.4 \pm 2.7 \text{ }^\circ/\text{s}$ , P value = 0.39). Regarding the  
 578 precision of saccades, the IQR values of position/time landing ratio were larger for the  
 579 interceptive saccades than for the catch-up saccades, indicating that catch-up saccades were  
 580 more precise than interceptive saccades. Indeed, when the path moved at 20 °/s, the average  
 581 differences were  $1.5 \pm 1 \text{ }^\circ/\text{s}$  (P<0.05) and  $1.8 \pm 0.9 \text{ }^\circ/\text{s}$  (P<0.05) for the “uncertain” and “certain”

582 sessions, respectively. Likewise, when the path moved at 40 °/s, the average differences were  
583  $2.5 \pm 1.5$  °/s (P value = 0.04) and  $2.8 \pm 0.7$  °/s (P<0.05).

584



## 585 **DISCUSSION**

586 Our study tested whether the repeated presentation of a target moving always along  
587 the same path changed its tracking in comparison with the performance during sessions in  
588 which the target could move along four possible paths. More specifically, we investigated  
589 whether a recurrent target motion was sufficient to produce anticipatory eye movements,  
590 prior to target appearance and with no preliminary training. Our results show some statistically  
591 significant differences between the two target path frequencies, at the level of interceptive  
592 saccades and at the level of post-saccadic pursuit eye movements and catch-up saccades. In  
593 particular, the latency of saccades was slightly longer (4% increase) during the “certain”  
594 sessions only when the target moved at 20°/s, not when it moved at 40°/s (Fig. 5). Intriguingly,  
595 in spite of the long gap between the extinction of the fixation target and the appearance of  
596 the moving target, no express saccades were observed in the two conditions of target  
597 frequency (Fig. 4). No difference was found between the two sessions, neither in the velocity  
598 (Fig. 3) nor in the accuracy and precision of interceptive saccades (Fig. 6). A slow eye  
599 movement started after target onset and its amplitude was larger during the “certain” sessions  
600 than during the “uncertain” ones only when the target moved at 40°/s (Fig. 8). No anticipatory  
601 slow eye movement was observed during the “certain” sessions (Fig. 7). The first intersaccadic  
602 interval (i.e. the time elapsed from the end of the interceptive saccade to the onset of the first  
603 catch-up saccade) was longer and more variable during the “certain” sessions than during the  
604 “uncertain” ones without change in the post-saccadic pursuit velocity (Fig. 9). The accuracy  
605 and precision of catch-up saccades were slightly influenced by the frequency of the target path  
606 (Fig. 10): they were more accurate and more precise during the “certain” sessions. Finally,  
607 comparisons between saccade-related and pursuit-related parameters provide additional  
608 arguments corroborating the thesis that saccadic and pursuit eye movements are driven by  
609 distinct motion signals.

### 610 **Influence of repeatedly tracking the same moving target on saccade generation.**

611 Previous studies in cats (26) and human subjects (25) showed that when a target  
612 appeared at an expected location, the peak velocity of saccades was lower than that of  
613 saccades toward a target whose location and timing were variable. In the monkey tested with  
614 the head unrestrained and looking at a target that stepped alternately and at regular intervals

615 between two fixed locations, Bizzi et al. (1972) also observed anticipatory movements. The  
616 head began to move 150 to 200 ms before the onset of the saccade, which was also slower  
617 than during trials in which the target location was varied (35). In our study, we found neither  
618 a slowing of saccades nor shorter latencies.

619 In the monkey, several studies showed that the repetitive exposure to a visual stimulus at the  
620 same location resulted in a bimodal distribution of saccade latencies (28, 36). The first mode  
621 corresponds to “express” saccades and the second mode to “regular” saccades. In the human  
622 subjects, Carpenter and Williams (1995) also reported an increasing number of express  
623 saccades as the target frequency increased (30). The observation of saccades with express  
624 latencies is not restricted to experimental conditions in which a target repeatedly appears at  
625 the same location (27-29, 37, 38). Schiller (2004b) still observed express saccades, although  
626 less frequent, when the number of possible locations was doubled (from 2 to 4). Shorter  
627 latencies were also observed when the target was always presented at the same location  
628 compared to trials in which the target could appear at two (39) or eight (40) possible locations.  
629 However, the latency does not seem to depend upon the prior knowledge of target location  
630 or the duration of the gap interval because Rohrer and Sparks (1993) did not observe reduced  
631 latencies or more express saccades when the performance during sessions with one single  
632 target and one single gap interval duration was compared to sessions in which the possible  
633 target locations were more numerous (N=10) and the gap durations more variable (N=4) (36).  
634 In in spite of a long gap interval, we did not observe a bimodal distribution signaling the  
635 presence of express saccades. This absence may lead to infer that the neural processes  
636 triggering interceptive saccades differ from those triggering saccades toward a static target but  
637 this inference would not be compatible with observations made by Krauzlis & Miles (1996).  
638 These authors reported saccades with very short latency during a task in which the monkeys  
639 were required to pursue of a centripetal target (41). In our study, the target always started its  
640 motion from the central visual field. This centrality might explain the absence of express  
641 saccades if a saccade is not triggered as long as the flows of bilateral activity propagating from  
642 the fovea to the bilateral pre-oculomotor networks stay within a mode in which opposing  
643 commands counterbalance with each other (42-44). Prior to generating a saccadic or slow eye  
644 movement, the maintenance of gaze direction involves sustained activities within different  
645 groups of neurons in the left and right parts of the reticular formation, the cerebellum and the

646 deep superior colliculi (45). Concerning the latter, the activity is not restricted to their rostral  
647 pole: it extends more caudally, even during steady fixation. Sparks et al. (2000) showed  
648 bilateral activity during the gap interval at sites sensitive to target eccentricities of 8 degrees  
649 (see their Fig. 4) (46). Dorris and Munoz (1998) also showed that the firing rate before target  
650 presentation increased when the target repeatedly appeared into the neuron's response field  
651 and that its level was negatively correlated with the saccade latency (39). The higher the rate,  
652 the shorter the latency. Likewise, Basso and Wurtz (1998) showed that increasing the number  
653 of possible locations was associated with a decrease of firing rate preceding the target  
654 presentation (40). These two observations suggest a link between the prelude activity and  
655 saccade latency. However, the persistence of the prelude activity for a long time without  
656 saccade initiation argue against its causal role in triggering saccades (see the panels G and I in  
657 Fig. 4 of Sparks et al. 2000; 46). The level of firing rate likely plays a secondary role in  
658 comparison with the bilaterality of activity and the number of active neurons during fixation.

659       Regarding the accuracy and precision of interceptive saccades, our result showed no  
660 influence of the target path frequency. The position/time landing ratio reached values that  
661 were close to the target velocity (see Fig. 6). The observation of some values slightly exceeding  
662 the target velocity does not entail that the monkeys programmed a saccade toward a future  
663 location of the target. As explained by Goffart et al. (2017), the amplitude of interceptive  
664 saccades is variable like the amplitude of saccades toward a static target, and the variability of  
665 final errors increases more toward values corresponding to past locations of the target than  
666 toward values corresponding to its future locations (see their Figure 3; 47). Furthermore, it is  
667 quite remarkable that our monkeys never performed saccades toward future locations of the  
668 target, neither during the pre-saccadic interval (Fig. 4A) nor during the intersaccadic interval  
669 (Fig. 10A), even during the sessions in which the target moved always along the same path.  
670 Consistent with reservations expressed elsewhere (43, 47), the absence of "predictive"  
671 saccades during the "certain" sessions contradicts the claim that "in [their] programming [...],  
672 target motion is used to predict the future target position so as to assure a spatial lead of the  
673 gaze at the saccade end, instead of attempting a precise capture of the target" (48-49).

674 **Influence of repeatedly tracking the same moving target on smooth pursuit.**

675           Several studies reported that human and monkeys can make anticipatory eye  
676 movements (references in the introduction). In the monkey, Freyberg and Ilg (2008) observed  
677 eye movements in the absence of a moving target during sessions in which a monkey tracked  
678 a target that moved at a constant speed and always to the right in half of the trials. In the other  
679 half, the initial portion of the target motion was invisible for 500 ms and the monkeys  
680 sometimes made a slow eye movement followed by a saccade in the same direction as the  
681 target. Their observations seemingly contradict the conclusion that macaque monkeys are not  
682 capable of predictive tracking, contrary to human subjects (17). However, their explanation  
683 that an inappropriate training was responsible for the absence of predictive tracking in the  
684 study of Dr Fuchs is unfounded because both studies used a small window to control gaze  
685 accuracy and comparable duration of conditioning procedure (10 versus 8 weeks). In fact, the  
686 tasks were quite different between the two studies. In Fuchs (1967), the monkeys were trained  
687 to follow a target that periodically moved back and forth between two symmetrical locations  
688 with respect to straight ahead. Contrary to the human performance, which exhibited a phase  
689 lead or anticipation of target motion, the monkeys lagged more and more behind the target  
690 as the frequency increased. In our study, although the disappearance of the fixation target was  
691 a signal of the target onset 300 ms later, none of our six monkeys exhibited any eye movement  
692 during the gap interval. One difference between the study of Freyberg and Ilg (2008) and ours  
693 is that our monkeys were not trained to track the same target for several weeks. Only one or  
694 two blocks of trials were recorded for each target path during the “certain” sessions. A second  
695 difference is the absence of trials in which the motion was invisible in our sessions. Other  
696 studies did not indicate how long their monkeys were trained (22-24). This is regrettable  
697 because overtraining monkeys to direct their gaze within a small window in order to be  
698 rewarded can lead to situations in which the eye movements do not belong to the natural  
699 animal's behavioral repertoire. For instance, monkeys can learn to make antisaccades by  
700 merely inverting the electrical polarity of the cables that connect the eye coil to the phase  
701 detector (David L. Sparks, personal communication).

702           Several differences distinguish our study from previous studies in the monkey (22-24).  
703 Firstly, we used longer and variable fixation intervals (from 500 to 1500 ms by increment of  
704 500 ms versus 500 ms) and lower target velocities (20 or 40°/s versus 65°/s). It is not certain  
705 that the fixed duration of the fixation interval is the critical factor explaining why we did not

706 observe anticipatory responses. Indeed, in other studies, variable fixation intervals did not  
707 prevent the occurrence of anticipatory eye movements (19) or the occurrence of express  
708 saccades and the reduction of saccade latencies (30). Secondly, those previous studies used  
709 horizontal target motions whereas we used oblique target motions. Horizontal and vertical eye  
710 movements are under the control of different neuronal populations located in different nuclei  
711 in the brainstem (45). The generation of oblique movements involves a coordination of  
712 anatomically separate groups of neurons. The absence of anticipatory eye movement may  
713 result from the fact that they involve more than one neural network. Our observations of  
714 changes in one component (horizontal or vertical) but not in the other are compatible with  
715 this explanation (50). Finally, in previous studies, the anticipatory eye movements were  
716 obtained during a specific experimental paradigm, after intense training. By contrast, we did  
717 not train our monkeys until they produced anticipatory responses. We merely wanted to know  
718 whether these movements could be rapidly observed with almost no training. Our results  
719 indicate that the generation of anticipatory movements requires training and thus, that  
720 prediction or anticipation are merely reproduction of learned responses instead of the  
721 signature of higher cognitive functions. As Ashby (1963) explained: “to predict the future is to  
722 perform an operation on the past. The essential point is that the agent in the act of prediction  
723 depends wholly on the actual past and not in the least on the actual future” (51).

724         Regarding the post-saccadic pursuit, we found that the catch-up saccades were made  
725 later when the target moved always along the same path; the intersaccadic intervals were  
726 longer during the “certain” sessions than during the “uncertain” ones (Fig. 9A). The target was  
727 maintained longer within the central visual field during the “certain” sessions, an inference  
728 that is consistent with previous studies showing a smoothing of tracking eye movements with  
729 less frequent catch-up saccades in the monkey after 10-12 daily experimental sessions (4-5).  
730 The longer inter-saccadic intervals during the “certain” sessions indicate that the repeated  
731 presentation of the same moving target transforms its tracking from saltatory to smooth. The  
732 primacy of smooth pursuit during visual tracking presumably results from an expansion of the  
733 “mass” of neural activity linked to the representation of the central field. Such an expansion  
734 involves not only motion sensitive neurons in the visual cortex but also pursuit-related neurons  
735 in the rostral SC (52-53), the caudal fastigial nuclei (34, 54) and the ventral paraflocculus (55-  
736 57).

**737 Comparison of interceptive saccades, catch-up saccades and post saccadic pursuit.**

738 Several evidence indicate that saccadic and pursuit eye movements are not driven by  
739 common motion signals. Behavioral studies with naive and healthy monkeys show a clear  
740 dissociation between the saccade and pursuit performances when they track for the first time  
741 a moving target (4-5). The present study provides additional arguments corroborating this  
742 dissociation. . The relation between the position/time landing ratio of saccades (interceptive  
743 or catchup) and the post-saccadic pursuit velocity does not reveal any tendency for a  
744 correlation (see Figs. 11A and 12A) that would suggest common signals. Lesional studies also  
745 support the segregation of processes underlying the generation of saccadic and pursuit eye  
746 movements. Unilateral pharmacological inactivation of the caudal fastigial nucleus leads to  
747 uncorrelated impairments of saccadic and pursuit eye movements (34). Helmchen et al. (2022)  
748 reported a patient suffering from bilateral fastigial lesion who exhibited a bilateral saccade  
749 hypermetria with a lower (although not statistically significant) initial pursuit acceleration (58).  
750 Several other studies report cases of patients suffering from saccade disorders with no pursuit  
751 deficit (59) or inversely, subjects exhibiting difficulties in pursuit with no saccade alteration  
752 (60-62). The observations reported in our study add to the set of arguments supporting the  
753 thesis that the neural control of saccadic and pursuit eye movements involves separate  
754 processes. This separation does not entail a lack of coordination, which has been shown to  
755 change with practice (4-5) and to involve the caudal fastigial nucleus (34) and the frontal eye  
756 field (60).

**757 General conclusion**

758 In this study, we thoroughly described in the rhesus macaque monkey how the  
759 occurrence frequency of a target path influenced the tracking eye movements. When they  
760 were present, the effects were very small. In spite of of a gap interval before the target motion  
761 onset, our monkeys did not generate anticipatory eye movements when the target kept  
762 moving along the same path. We observed neither premature saccades nor express saccades.  
763 In line with other works performed by our group (63-64), our results are compatible with a  
764 short horizon of predictability during oculomotor tracking in the macaque monkey, in  
765 accordance with the conclusion that the predictive abilities are quite limited in the macaque  
766 monkey (17). An alternative explanation is that our monkeys were not trained to make

767 anticipatory responses, in which case, they should not be considered as a behavioral marker  
768 of the primates' ability to extrapolate but the outcome of learning and remembering past  
769 experience.

770

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776

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781

782 **AUTHOR CONTRIBUTIONS**

783 L.G. conceived and designed research; N.O.D. and L.G. performed the experiments; N.O.D.  
784 and L.G. analyzed the data; N.O.D. and L.G. interpreted the results of experiments; N.O.D.  
785 and L.G. prepared the figures; L.G. drafted the manuscript; N.O.D. and L.G. edited and revised  
786 the manuscript; N.O.D. and L.G. approved the final version of manuscript.

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- 962
- 963

964 **FIGURE CAPTIONS**

965 **Figure 1: Experimental protocol.** Each trial started with the appearance of a target at the  
 966 center of the visual display. The monkey was required to direct and maintain gaze toward its  
 967 location for a fixation interval whose duration varied pseudo-randomly from 750 to 1500 ms  
 968 (by increments of 250 ms). A gap interval of 300 ms followed the extinction of the fixation  
 969 target, after which the target reappeared and moved along one out of four possible oblique  
 970 paths. The monkey was rewarded for tracking the target until it disappeared. Each target path  
 971 was tested with two frequencies of occurrence during sessions recorded on different days:  
 972 25% (“uncertain” sessions) and 100% (“certain” sessions). Two target velocities (20 and  
 973 40deg/s) were tested during separate sessions.

974 **Figure 2: Definition of parameters.** The presaccadic glissade (PSG) is the change of eye  
 975 position during time interval elapsed from target motion onset (black vertical dashed line  
 976 labeled 1) to the onset (vertical line labeled 2) of the interceptive saccade (IS). A post-saccadic  
 977 pursuit eye movement (PSP, delimited by the lines labeled 3 and 4) follows the interceptive  
 978 saccade until a catchup saccade (CS) is launched. The grey dashed lines represent the target  
 979 moving at 40°/s. The black continuous and dashed curves represent respectively the  
 980 horizontal and vertical components of the visual tracking response. Data collected in monkey  
 981 Bi.

982 **Figure 3: Eye velocity at target motion onset.** The eye velocity of each component (top:  
 983 horizontal, bottom: vertical) during the “certain” sessions is plotted as a function of the  
 984 velocity during the certain (x-axis) sessions. They were calculated during the interval elapsed  
 985 from 40 ms before target motion onset to 40 ms after. Different symbols correspond to  
 986 different quadrant of the visual field and different colors to different monkeys. From left to  
 987 right, the first and third columns correspond to the median and IQR values obtained with the  
 988 20 deg/s target, the second and fourth columns to values with the 40 deg/s target.

989 **Figure 4: Pre-saccadic glissade.** A: The amplitude (radial value) of the pre-saccadic slow eye  
 990 movement is plotted as a function of saccade latency. The target moved at 20 or 40°/s in the  
 991 upper right quadrant of the visual field (left: uncertain sessions; right: certain session). Data  
 992 collected in monkey Bi. B: Median and interquartile range (IQR) values of the pre-saccadic  
 993 displacement amplitude (from target motion onset to saccade onset) during the “uncertain”  
 994 (x axis) and “certain” (y axis) sessions. Different symbols correspond to different quadrants of  
 995 the visual field and different colors to different monkeys.

996 **Figure 5: Latency of interceptive saccades.** Violin plots show for each monkey (x axis) and  
 997 each quadrant of the visual field the median (white dot) and interquartile range (black box) of  
 998 latency values and an estimation of their distribution (based on a probability density function)  
 999 for the “uncertain” (white) and “certain” (grey) sessions. The target moved at 20 deg/s (left  
 1000 column) or 40 deg/s (right column).

1001 **Figure 6: Saccade latency.** Different symbols correspond to different quadrants of the visual  
 1002 field and different colors to different monkeys. Median (left column) and interquartile interval  
 1003 (IQR, right column) values are plotted for the 20°/s (top) and 40°/s target (bottom).

1004 **Figure 7: Average velocity of interceptive saccades.** Different symbols correspond to different  
 1005 quadrants of the visual field and different colors to different monkeys. The two leftmost

1006 graphs plot the median values for the 20 and 40°/s targets and the other graphs the  
1007 interquartile range (IQR) values.

1008 **Figure 8: Accuracy and precision of interceptive saccades.** A: The landing position (radial  
1009 value) of saccades is plotted as a function of their landing time, when the target moved in the  
1010 upper left visual field, during the “uncertain” and “certain” sessions. Data collected in monkey  
1011 Bi. B: Median and interquartile range (IQR) of the position/time (P/T) landing ratio during the  
1012 “uncertain” (x-axis) and “certain” (y-axis) sessions. Different symbols correspond to different  
1013 quadrant of the visual field and different colors to different monkeys. The first and third  
1014 columns correspond to sessions during which the target moved at 20 deg/s, the second and  
1015 fourth columns to those in which the 40 deg/s target was used. The horizontal and vertical  
1016 dashed lines show the target velocity.

1017 **Figure 9: Post-saccadic pursuit eye movement.** A: The median and interquartile interval range  
1018 (IQR) values of the duration of the first intersaccadic interval (ISI) calculated during the  
1019 “certain” sessions (y-axis) are plotted as a function of values calculated during the “uncertain”  
1020 sessions (x-axis). Different symbols correspond to different quadrants of the visual field and  
1021 different colors to different monkeys. Top row: the target moved at 20 deg/s; bottom:  
1022 40deg/s. B: The amplitude (radial value) of the post-saccadic eye movement is plotted as a  
1023 function of the duration of the intersaccadic interval (from the end of the interceptive saccade  
1024 to the onset of the first catch-up saccade). The target moved in the upper left visual field. Data  
1025 collected in monkey Bi. C: The median and interquartile range (IQR) values of the post-saccadic  
1026 slow movement velocity are compared between the “uncertain” (x-axis) and “certain” (y-axis)  
1027 sessions. Different symbols correspond to different quadrants of the visual field and different  
1028 colors to different monkeys. From left to right, the first and third columns correspond to  
1029 movements made in response to the 20 deg/s target, the second and fourth to movements  
1030 made in response to the 40 deg/s target. The horizontal and vertical dashed lines indicate the  
1031 target velocity.

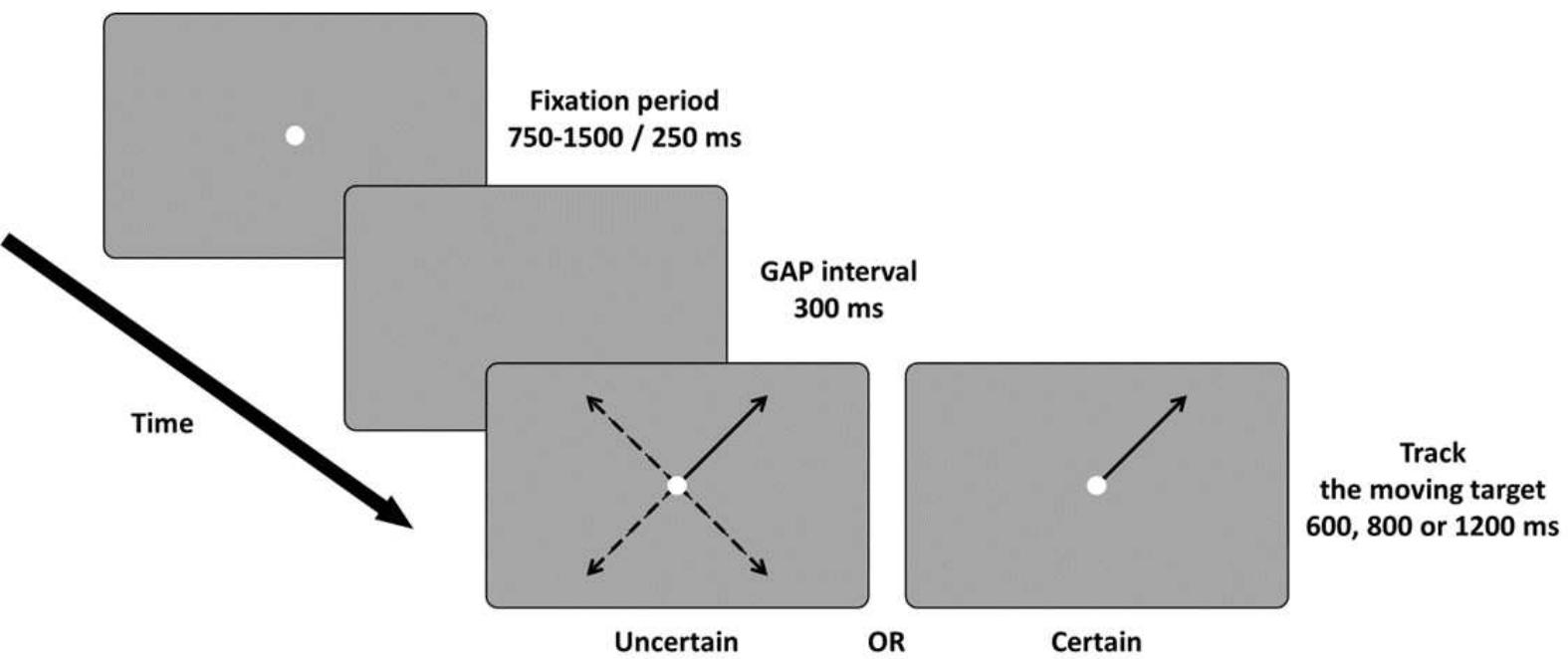
1032 **Figure 10: Landing position of catch-up saccades.** A: The landing position (radial value) of each  
1033 catch-up saccade is plotted as a function of its landing time when the target moved in the  
1034 upper left visual field, at 20 deg/s (left) or 40 deg/s (right) during the “uncertain” (first and  
1035 third columns) and “certain” (second and fourth columns) sessions. Dashed lines indicate the  
1036 target position. Data collected in monkey Bi. B: Median and interquartile range (IQR) values of  
1037 position/time landing ratio are compared between the “uncertain” (x-axis) and “certain” (y-  
1038 axis) sessions. Different symbols correspond to different quadrants of the visual field and  
1039 different colors to different monkeys. From left to right, the first and third columns correspond  
1040 to catch-up saccades made toward the 20 deg/s target, the second and fourth columns to  
1041 those made toward the 40 deg/s target. Horizontal and vertical dashed line indicate the target  
1042 velocity.

1043 **Figure 11: Position/time landing of interceptive saccades and post-saccadic pursuit velocity.**  
1044 A: The position/time (P/T) landing ratio of interceptive saccades (IS) is plotted as a function of  
1045 the post-saccadic pursuit (PSP) velocity (radial values). The data were collected in monkey Bi  
1046 when it tracked a target that moved at 20 deg/s (left half) or 40 deg/s (right half) in the upper  
1047 right quadrant of the visual field. From left to right, the first and third columns correspond to  
1048 trials recorded during the “uncertain” sessions and the second and fourth columns to trials  
1049 recorded during the “certain” sessions. Dashed lines correspond to target velocity. B: Median  
1050 and interquartile range (IQR) values of position/time landing ratio of interceptive saccades (y-

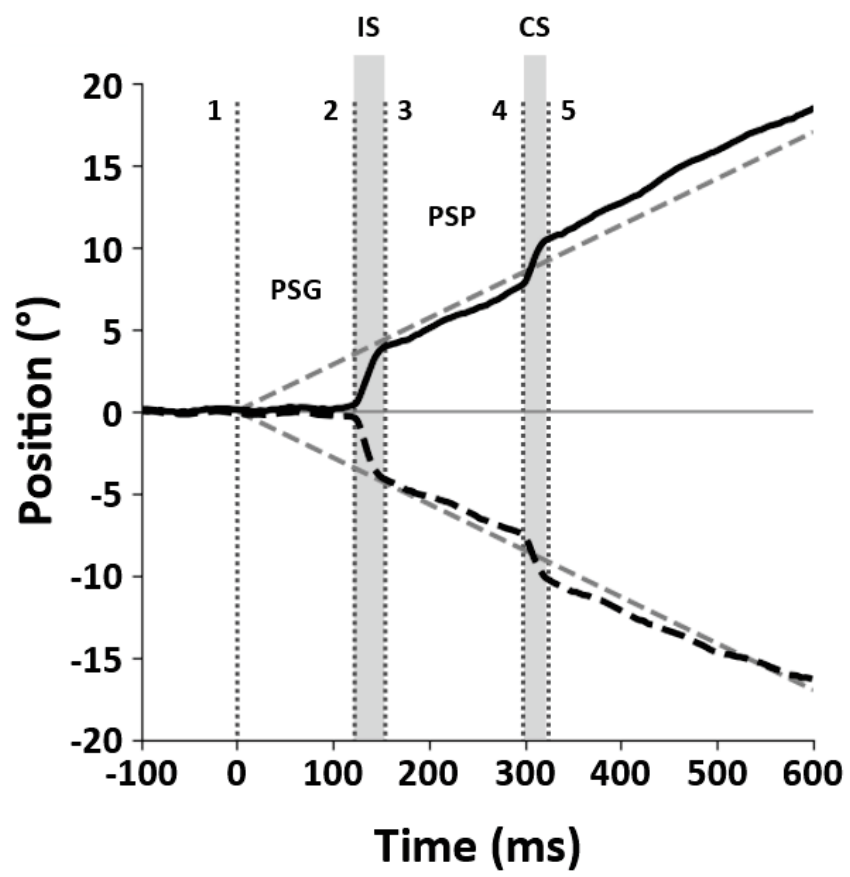
1051 axis) are compared to the post saccadic pursuit eye velocity (x axis) for the uncertain (top row)  
1052 and certain (bottom) sessions. Different symbols correspond to different quadrants of the  
1053 visual field and different colors to different monkeys. From left to right, the first and third  
1054 columns correspond to the 20 deg/s target, the second and fourth to the 40 deg/s target.  
1055 Horizontal and vertical dashed lines indicate the target velocity.

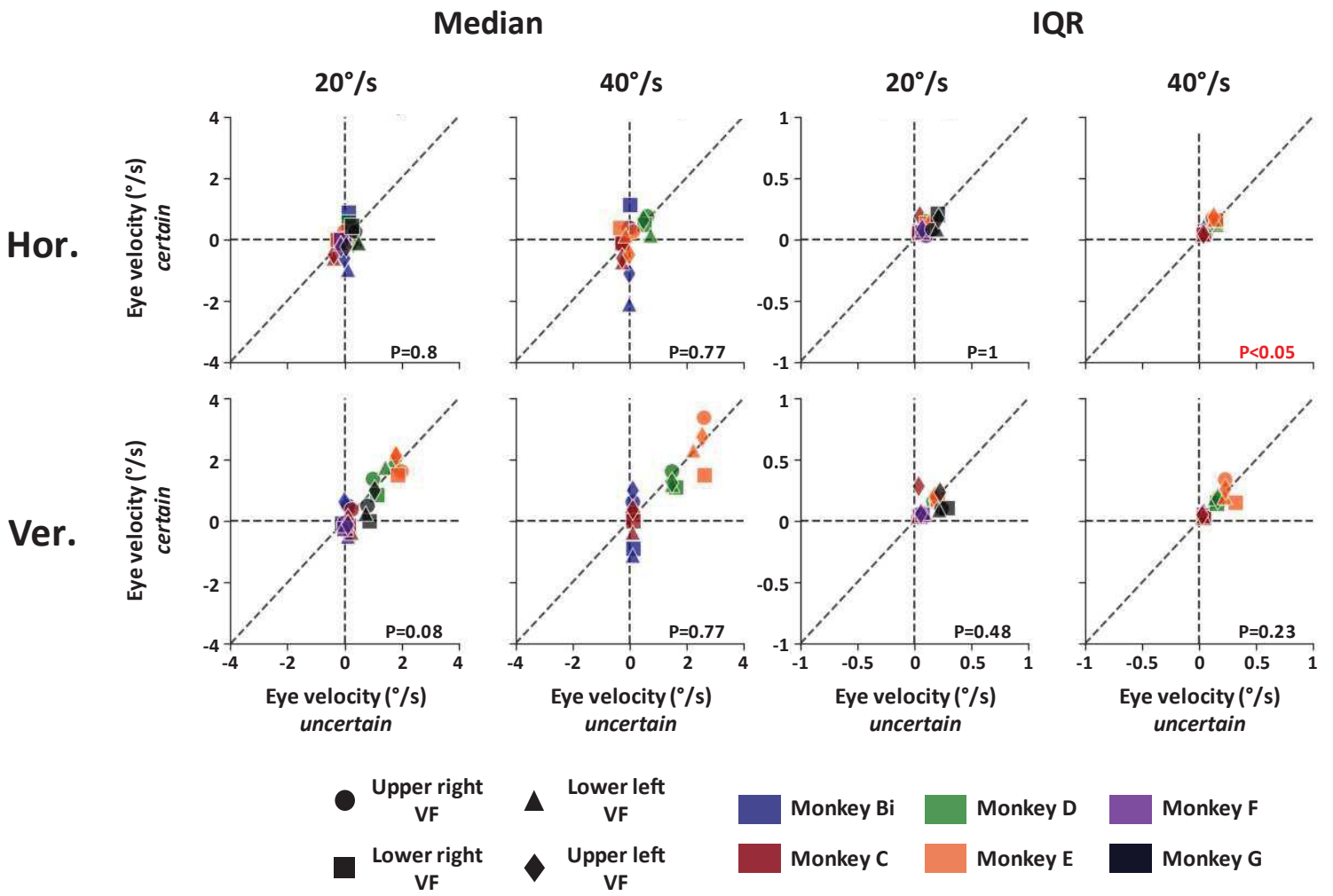
1056 **Figure12: Post-saccadic pursuit velocity and position/time landing ratio of catch-up**  
1057 **saccades.** A: The post-saccadic pursuit (PSP) velocity is plotted as a function of the  
1058 position/time landing ratio (radial values) for the trials in which the monkey Bi tracked the  
1059 target while it moved in the upper right quadrant of the visual field during the “uncertain”  
1060 (first and third columns) and “certain” sessions. Dashed lines correspond to target velocity. B:  
1061 The median and interquartile range (IQR) values of post saccadic pursuit velocity (y axis) are  
1062 compared to the values of position/time landing ratio of catch-up saccades (x axis) made  
1063 during the “uncertain” (top row) and “certain” (bottom) sessions. Different symbols  
1064 correspond to different quadrants of the visual field and different colors to different monkeys.  
1065 From left to right, the first and third columns correspond to the 20 deg/s target, the second  
1066 and fourth to the 40 deg/s target. Horizontal and vertical dashed lines indicate the target  
1067 velocity.

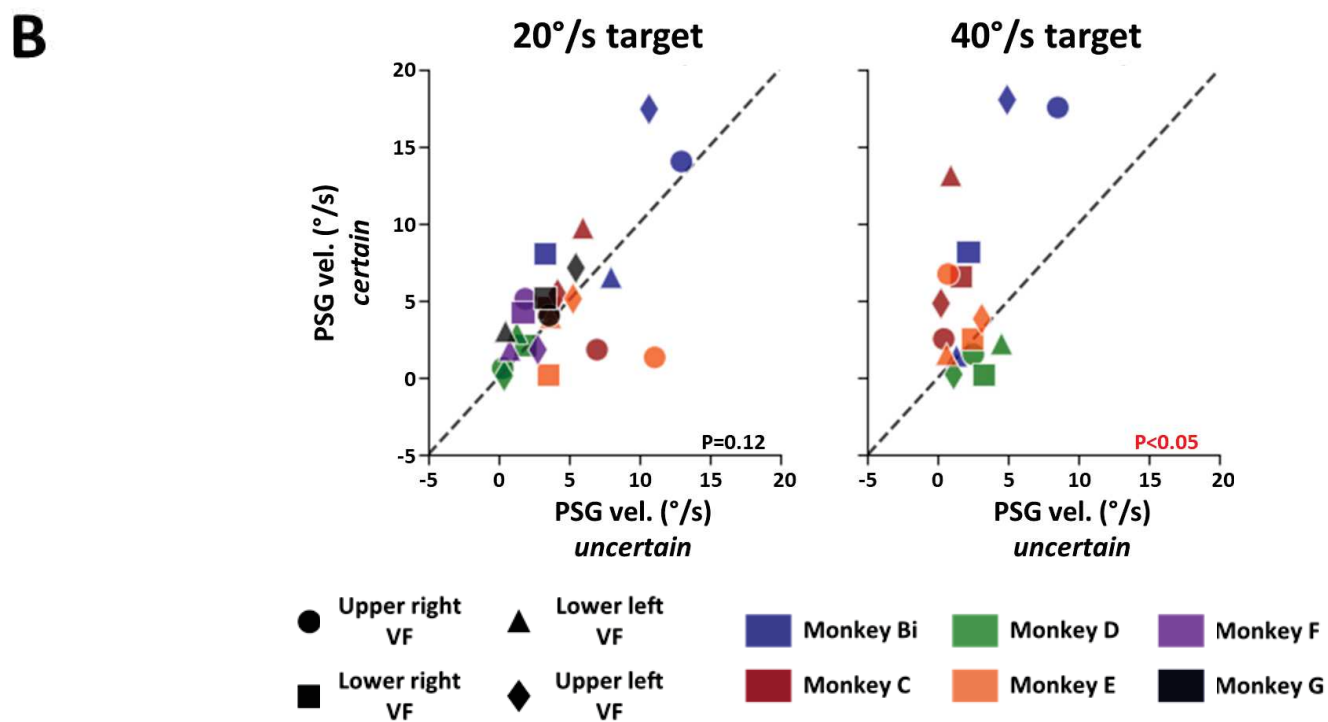
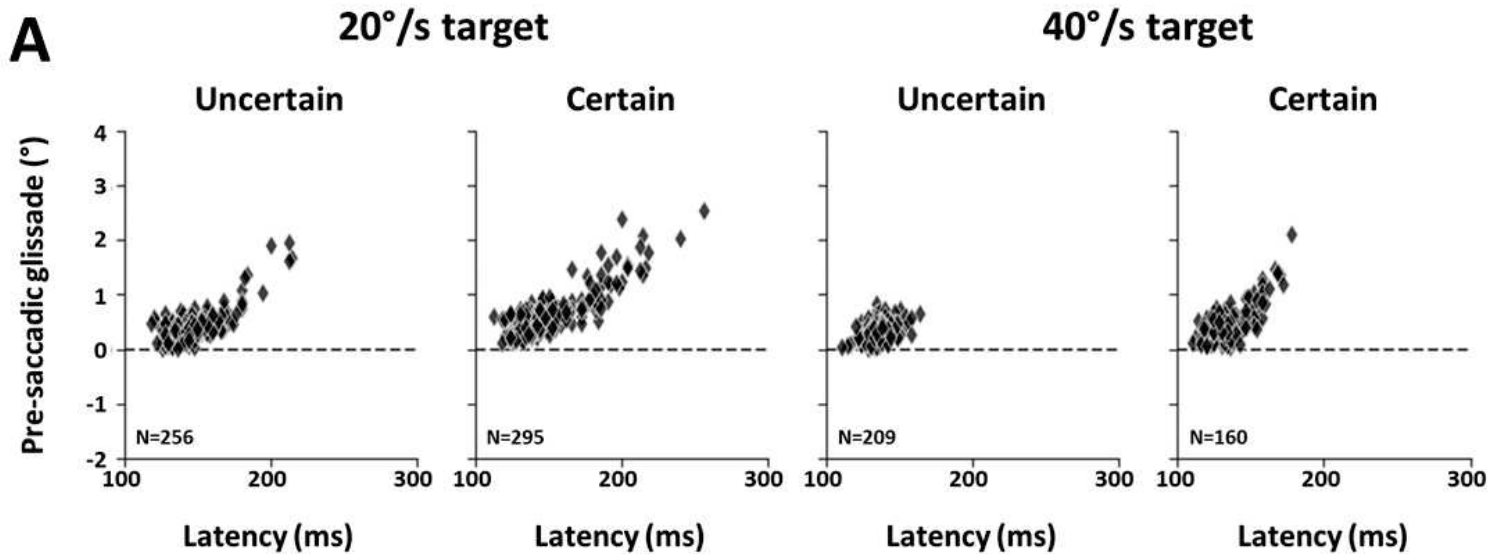
1068 **Figure 13: Accuracy and precision of interceptive and catch-up saccades.** The median and  
1069 interquartile range (IQR) values of position/time landing ratio of interceptive saccades (IS, y-  
1070 axis) are compared to those of catch-up saccades (CS, x-axis) made during the “uncertain” (top  
1071 row) and “certain” (bottom) sessions. Different symbols correspond to different quadrants of  
1072 the visual field and different colors to different monkeys. From left to right, the first and third  
1073 columns correspond to the 20 deg/s target, the other columns to the 40 deg/s target.  
1074 Horizontal and vertical dashed lines indicate the target velocity.

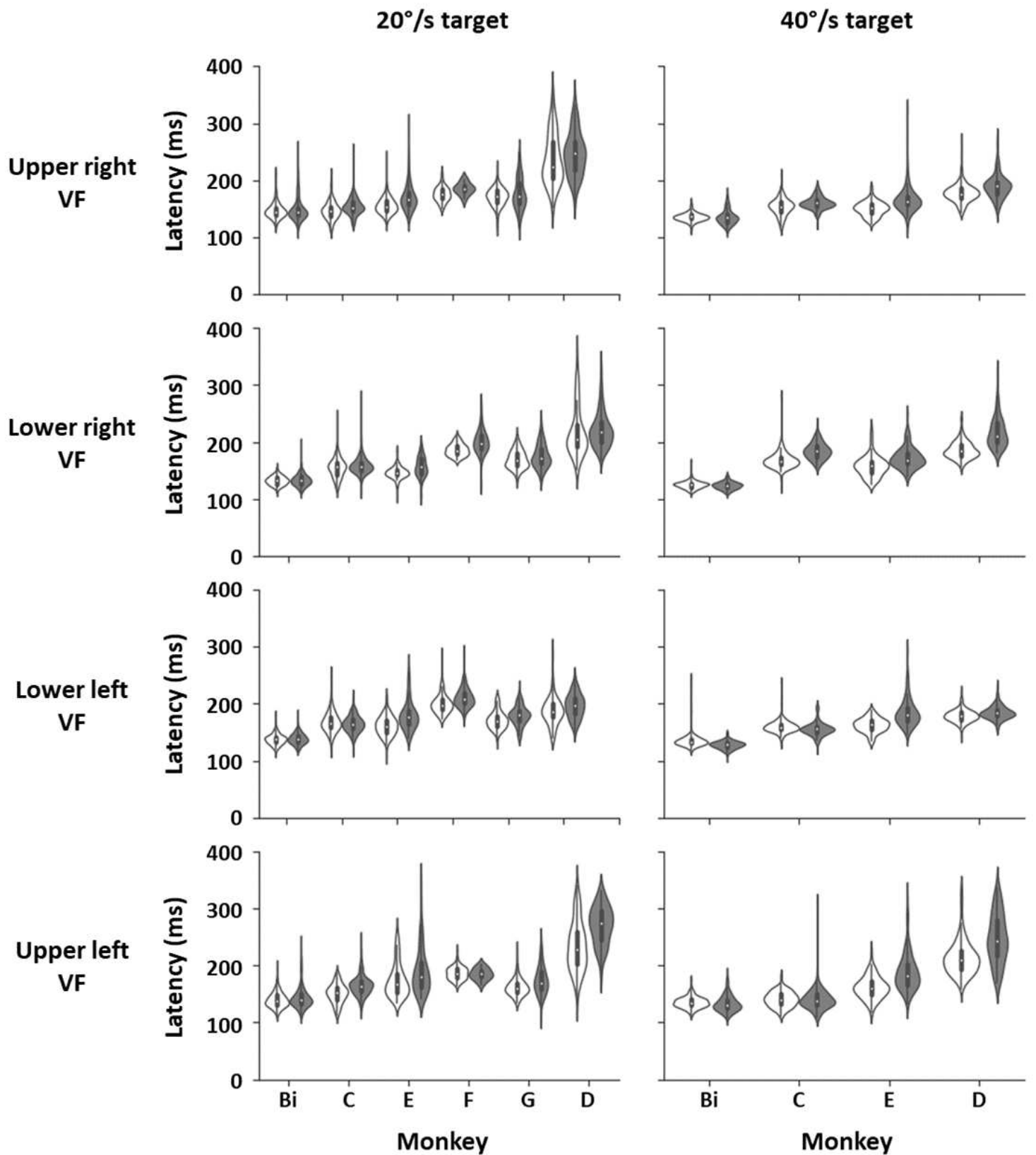




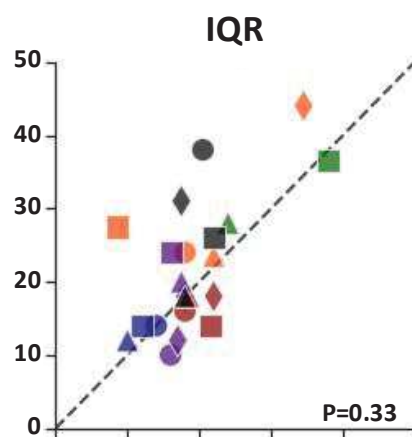
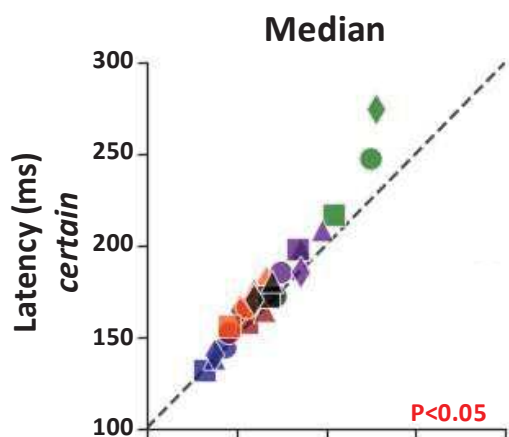






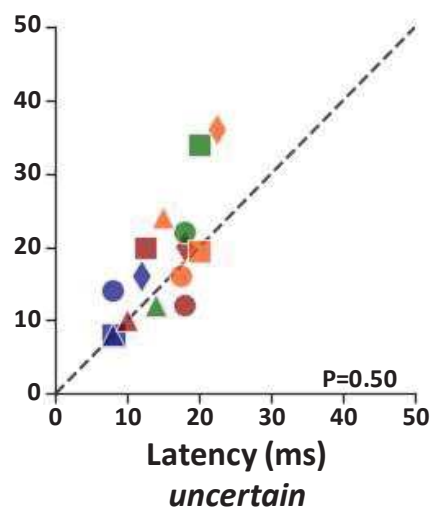
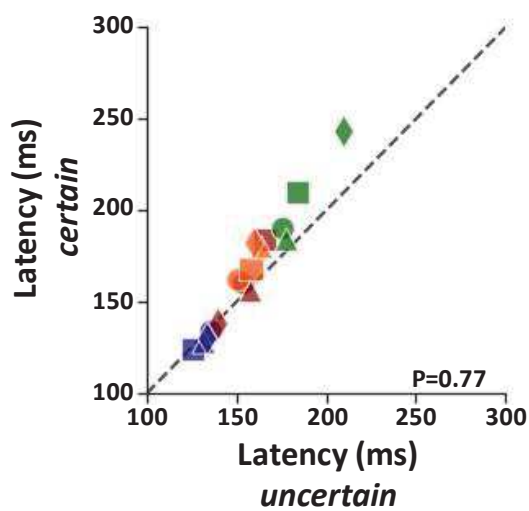


20°/s  
target

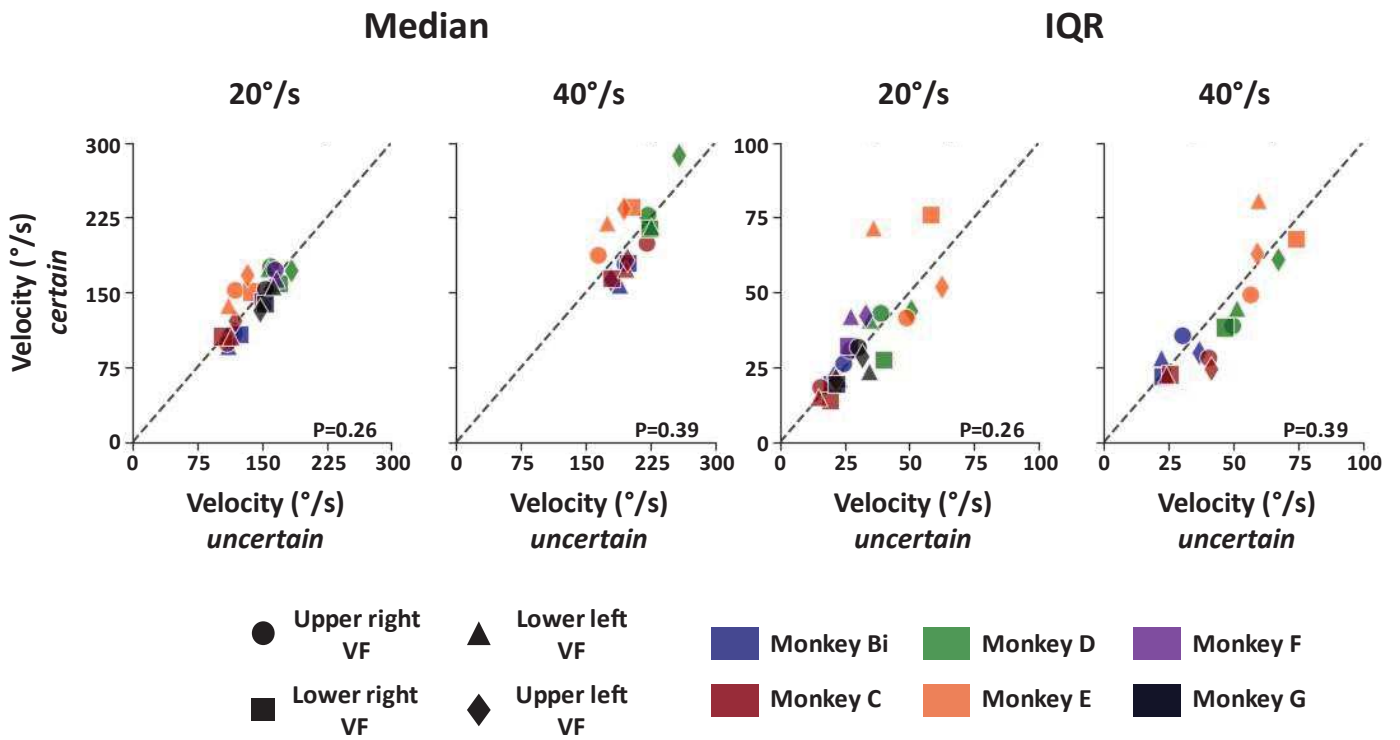


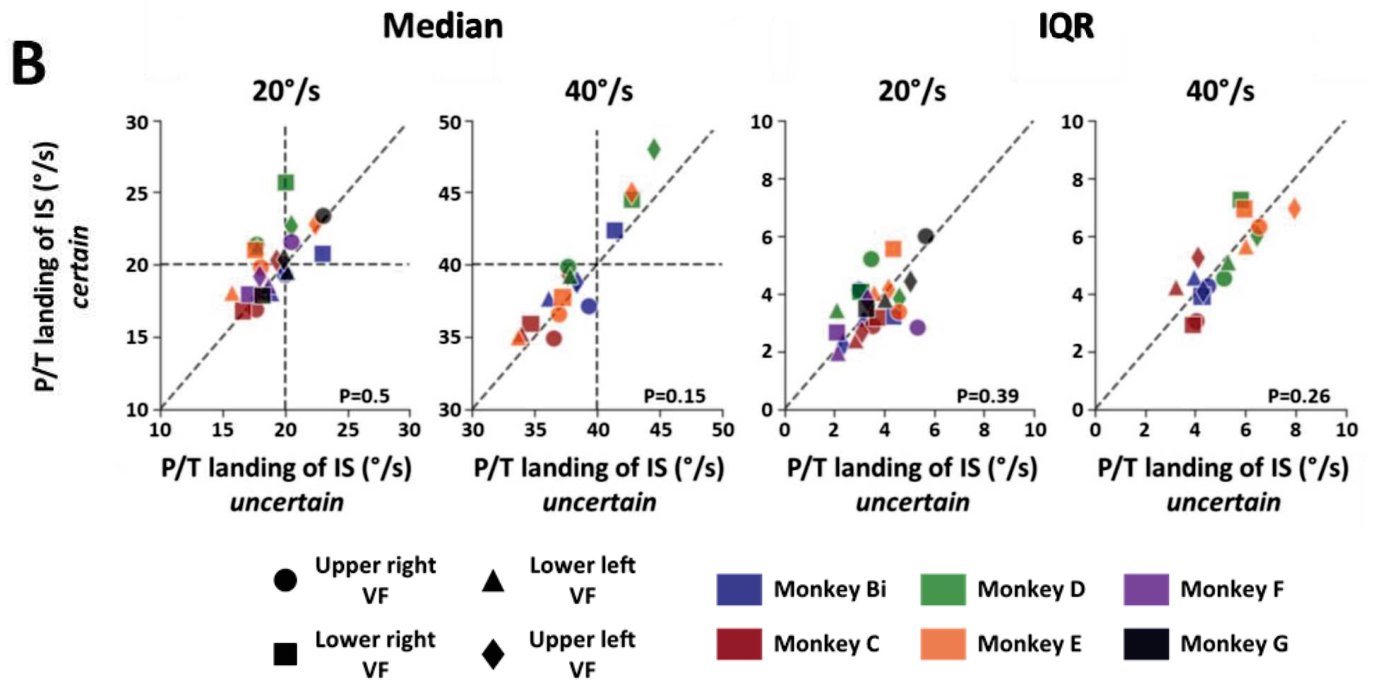
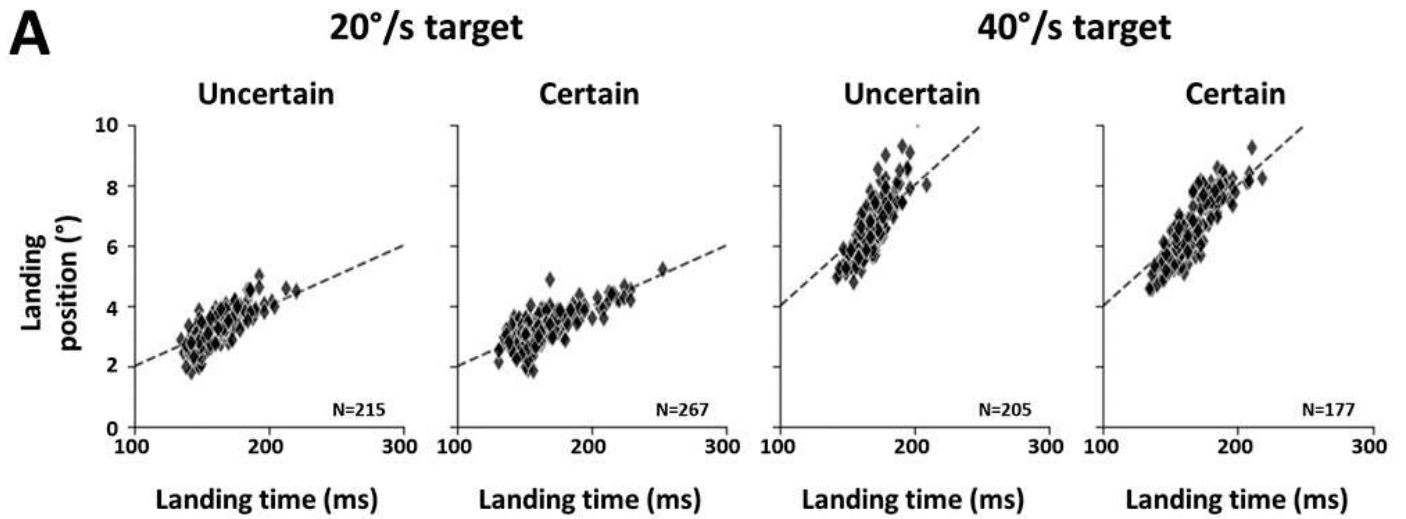
- Upper right VF
- Lower right VF
- ▲ Lower left VF
- ◆ Upper left VF

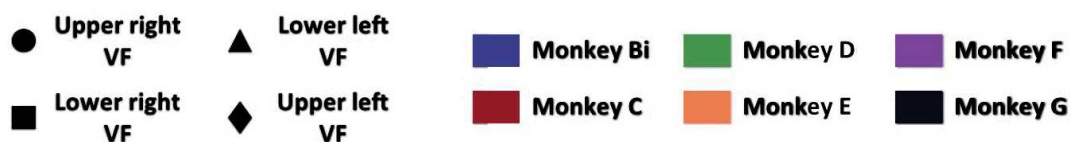
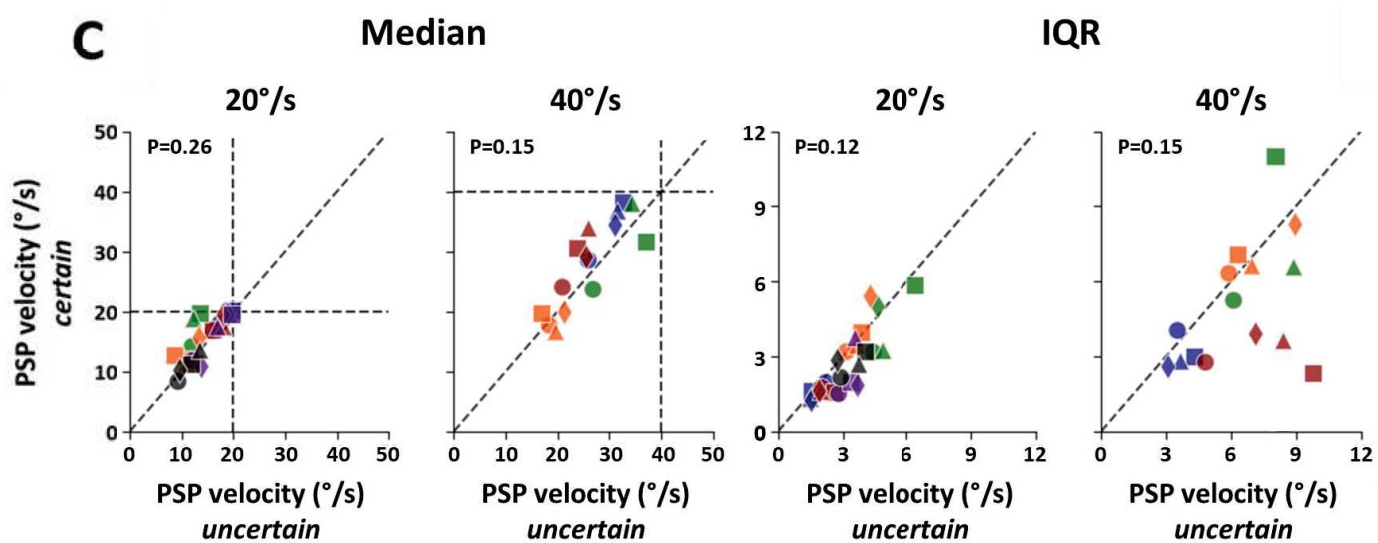
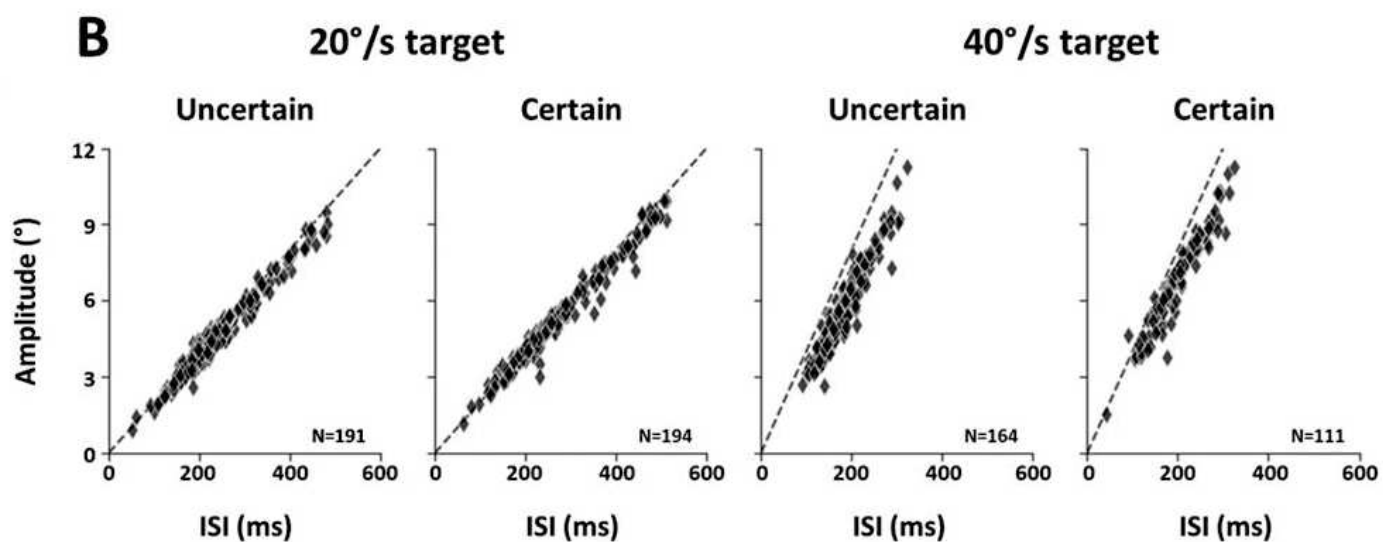
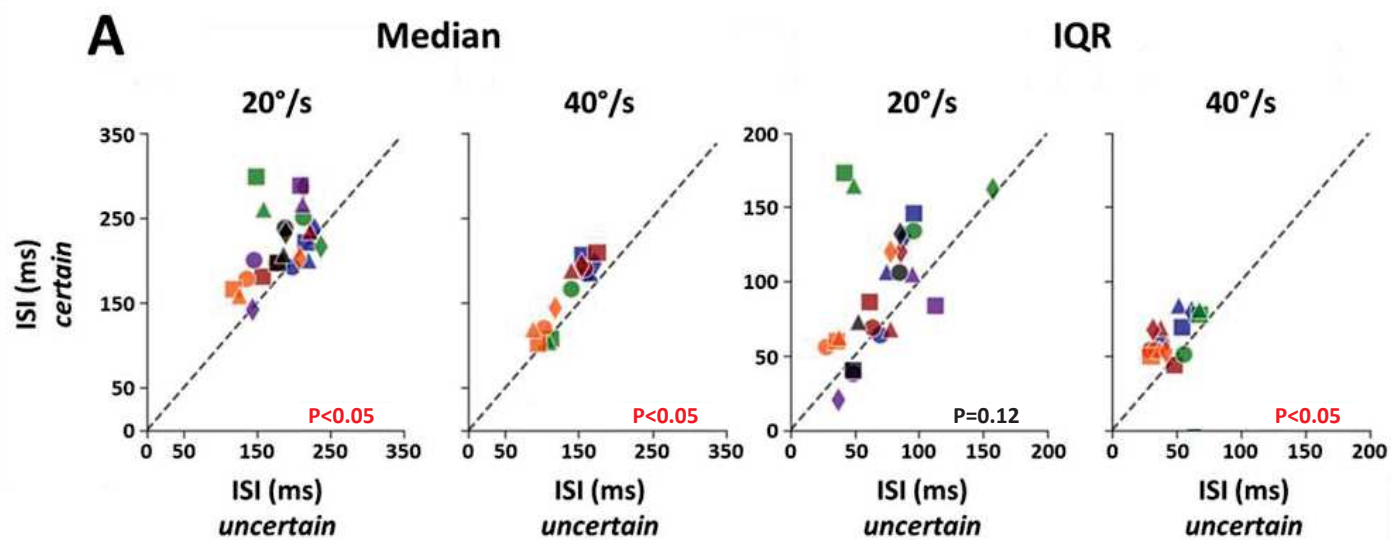
40°/s  
target



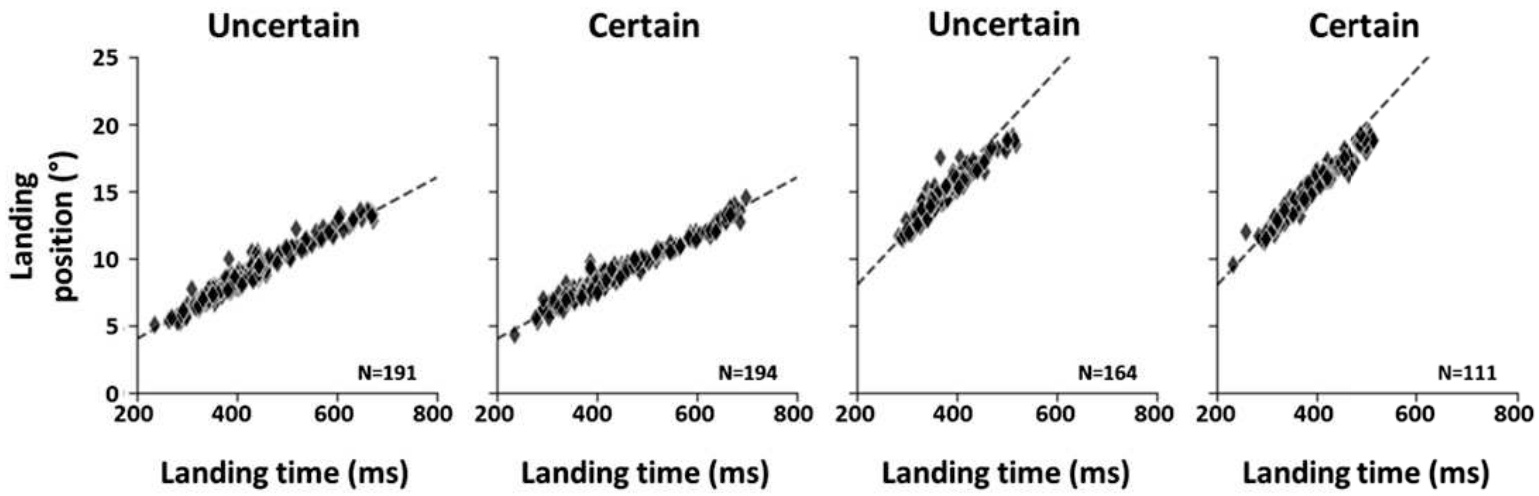
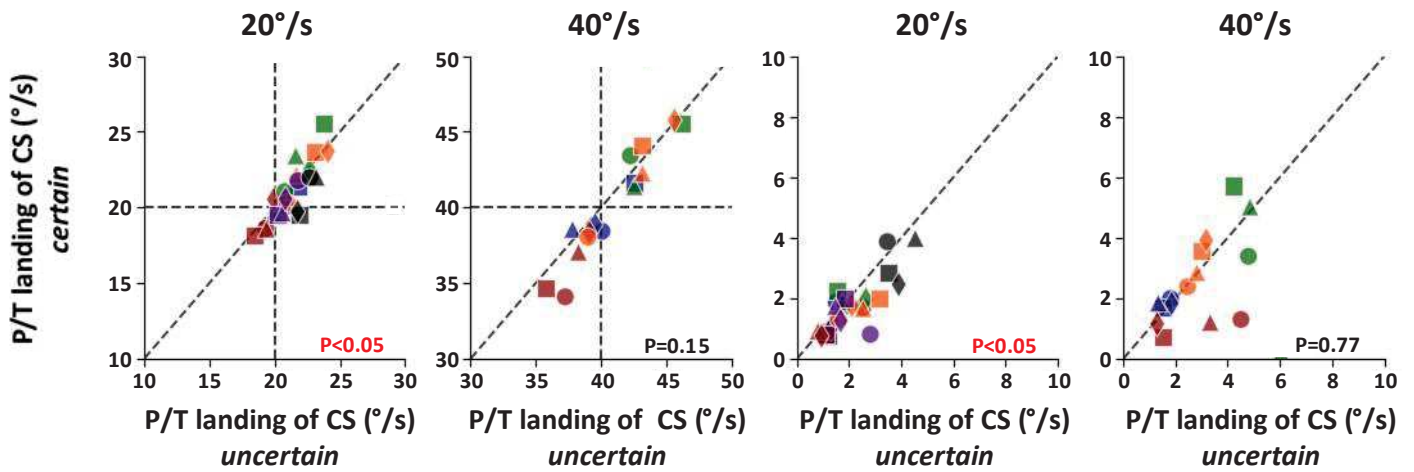
- Monkey Bi
- Monkey C
- Monkey D
- Monkey E
- Monkey F
- Monkey G









**A****20°/s target****40°/s target****B****Median****IQR**● Upper right  
VF▲ Lower left  
VF

■ Monkey Bi

■ Monkey D

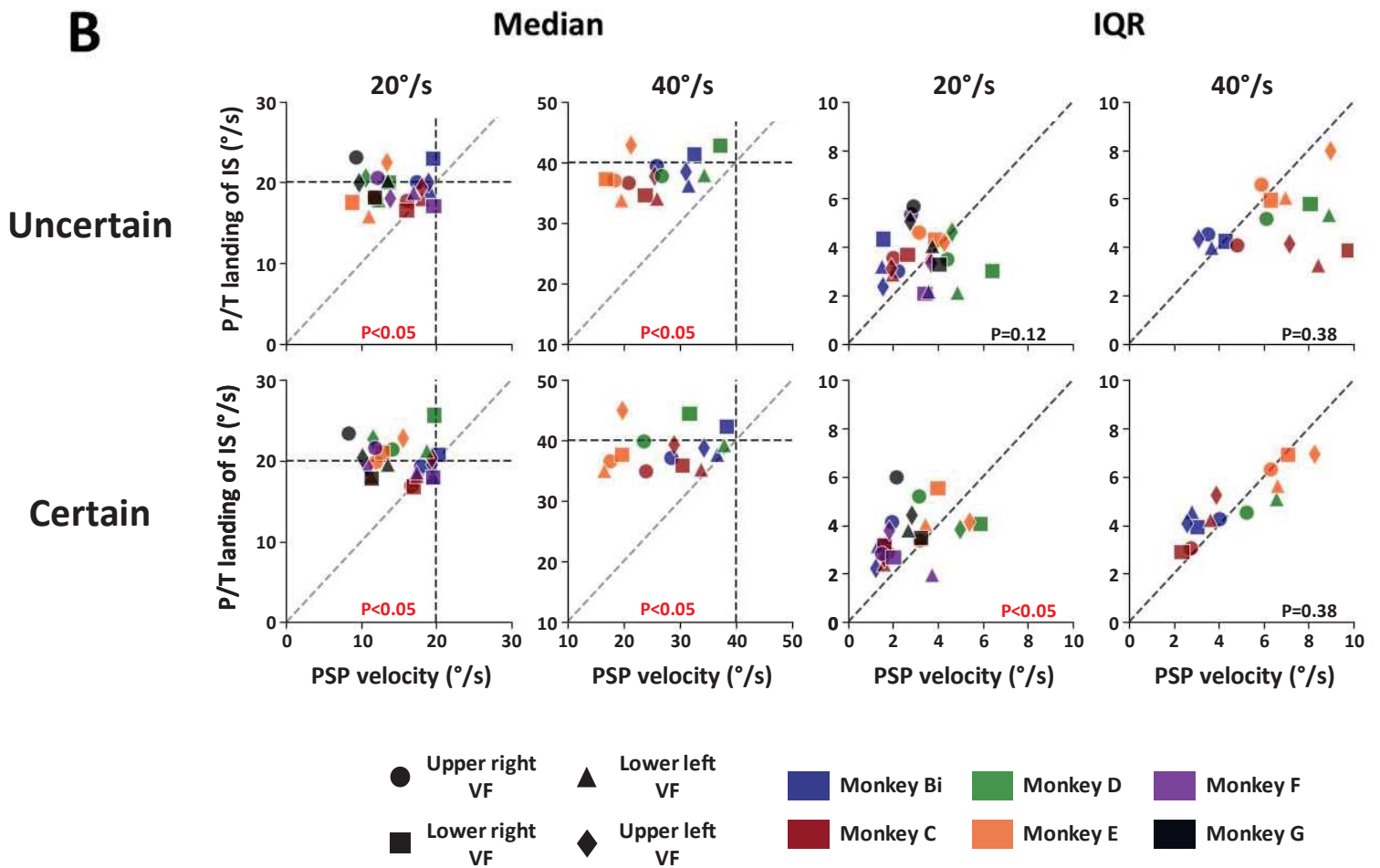
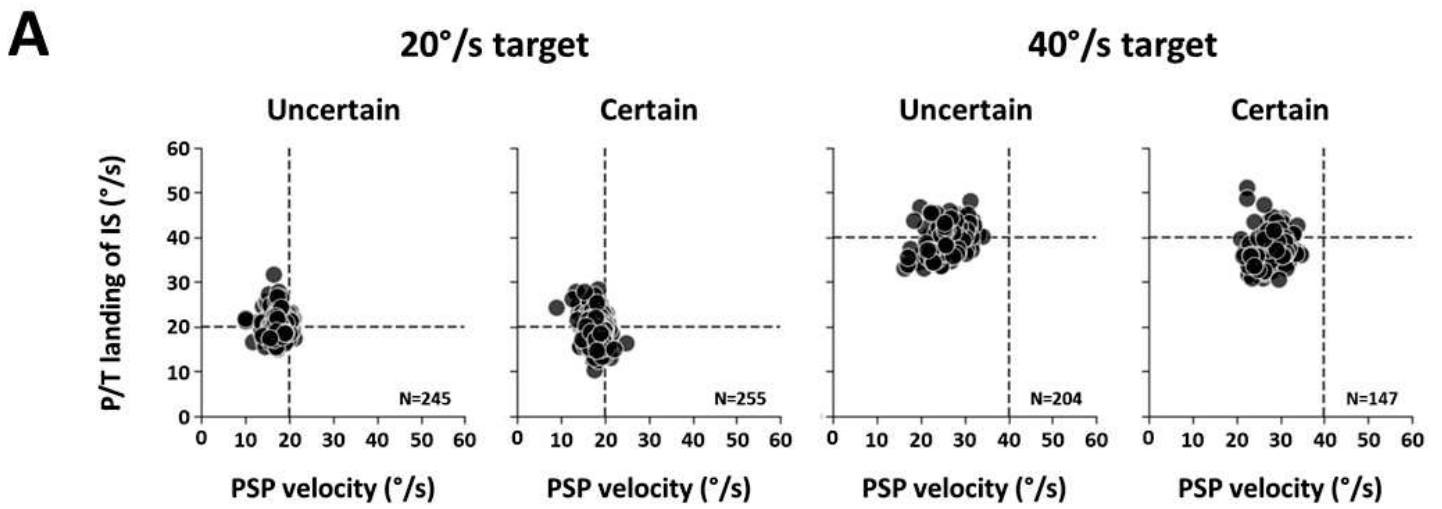
■ Monkey F

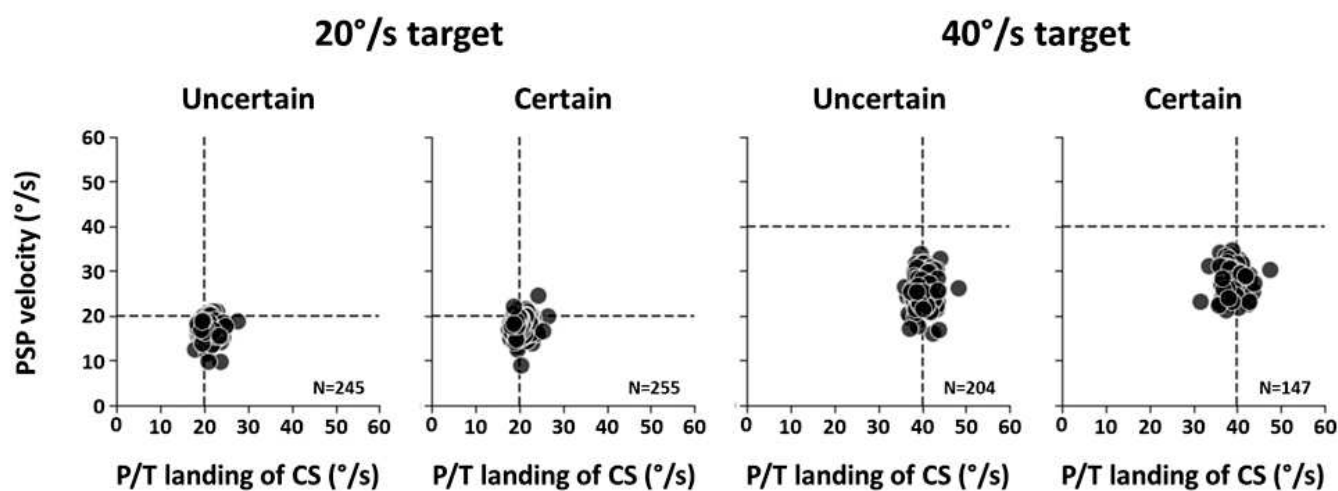
■ Lower right  
VF◆ Upper left  
VF

■ Monkey C

■ Monkey E

■ Monkey G



**A****B**