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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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26

27 **ABSTRACT**

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, would move always along
146 the 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° 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°/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 (ΔMed
 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**

347 ± 6 ms, $P < 0.05$). No statistically significant change was observed in the IQR values between the
 348 two sessions (average difference = 3 ± 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 ± 10 ms, P value = 0.77; average difference of
 351 IQRs = 3 ± 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 graphs:
 364 $20^\circ/\text{s}$, rightmost graphs: $40^\circ/\text{s}$), 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 Burrellly 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 ± 4 , 17 ± 3 , 20 ± 3 , 22 ± 3 and $23 \pm 6^\circ/\text{s}$ during the “uncertain” sessions against 20 ± 3 , $18 \pm$

377 4, 18 ± 5 , 21 ± 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 either between the “certain” and “uncertain” sessions ($\Delta\text{Med} = -0.6 \pm 1.3^\circ/\text{s}$, P value = 0.15;
 383 $\Delta\text{IQR} = 0.07 \pm 0.8^\circ/\text{s}$, P value = 0.39, all quadrants and all monkeys considered, except monkey
 384 D).

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

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

390 **Figure 9 approximately here**

391 Two types of eye movements are made while a small visual target is being tracked: a
 392 slow eye movement and catchup saccades. We conjectured that tracking a target that moves
 393 always along the same path would maintain the activity conveyed by the visuomotor channels
 394 involved in the generation of slow eye movements. To test this conjecture, we checked
 395 whether the time interval elapsed from the end of the interceptive saccade to the onset of the
 396 first catch-up saccade was longer during the “certain” sessions than during the “uncertain”
 397 sessions. Figure 9A documents for each monkey, each visual quadrant and each target speed,
 398 the duration of this first intersaccadic interval. The fact that most median values are situated
 399 above the diagonal indicates that the first intersaccadic intervals were indeed longer during
 400 the “certain” sessions than during the “uncertain” ones, regardless of whether the target
 401 moved at $20^\circ/\text{s}$ or $40^\circ/\text{s}$. The paired comparison of median values confirmed longer intersaccadic
 402 intervals during the “certain” sessions than during the “uncertain” sessions when the target
 403 moved at $20^\circ/\text{s}$ ($\Delta\text{Med} = 28 \pm 27 \text{ ms}$; $P < 0.05$) and when it moved at $40^\circ/\text{s}$ ($\Delta\text{Med} = 30 \pm 13 \text{ ms}$;
 404 $P < 0.05$). The IQR values were also significantly different between the two sessions when the

405 target moved at 40°/s (Δ IQR = 20 ± 11 ms; $P < 0.05$) but not when it moved at 20°/s (Δ IQR = 16
406 ± 23 ms; P value = 0.12).

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

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

423 To test whether the post-saccadic pursuit velocity was changed during the “certain”
424 sessions, we calculated for each monkey and each visual quadrant, the ratio between the
425 amplitude of the post-saccadic eye displacement and its duration (Figure 9C). In the majority
426 of cases, the median values were smaller than the target speed during both “certain” and
427 “uncertain” sessions. Most of the data points are indeed situated below the dashed lines,
428 which indicate the target velocity. For example, when we consider the session during which
429 the target moved at 20°/s in the upper right visual field, the post-saccadic pursuit velocity
430 (median \pm IQR) was 17 ± 2 , 16 ± 2 , 12 ± 3 , 12 ± 3 and 9 ± 3 °/s during the “uncertain” sessions
431 and 18 ± 2 , 17 ± 2 , 12 ± 3 , 12 ± 2 , and 8 ± 2 °/s during the “certain” sessions (values for monkey
432 Bi, C, E, F and G, respectively). The paired comparison of median values calculated for each
433 monkey and each quadrant did not reveal any change between the “uncertain” and “certain”
434 sessions, regardless of whether the target moved at 20°/s (Δ Med = -0.3 ± 1.3 °/s; P value = 0.26)

435 or 40°/s ($\Delta\text{Med} = -3 \pm 3^\circ/\text{s}$; P value = 0.15). Concerning the variability of post-saccadic pursuit
 436 velocity, the IQR values were not significantly different between the “uncertain” and “certain”
 437 sessions, neither with the 20°/s target ($\Delta\text{IQR} = 0.4 \pm 0.7^\circ/\text{s}$, P value = 0.12) nor with the 40°/s
 438 target ($\Delta\text{IQR} = 2 \pm 3^\circ/\text{s}$; P value = 0.15). In summary, the longer intersaccadic intervals during
 439 the “certain” sessions were not associated with a different post-saccadic pursuit velocity.

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

442 **Figure 10 approximately here**

443 Catchup saccades being the other important component of the visual tracking, we also
 444 studied the influence of the occurrence frequency of the target path on their accuracy and
 445 precision. Figure 10A plots for each target velocity the radial landing positions of the first catch-
 446 up saccade as a function of its landing time when the target moved in upper left visual field
 447 (data collected in monkey Bi). The landing position values were scattered near the target path
 448 (dashed line) during both “uncertain” and “certain” sessions. The frequency of the target path
 449 did not seem to influence the accuracy of catch-up saccades as there is no noticeable
 450 difference in the shape or in the extent of the scatters of position values between the
 451 “uncertain” and “certain” sessions. As for the interceptive saccades, we quantified the
 452 accuracy and precision of catch-up saccades by calculating the position/time landing ratios.
 453 Figure 10B documents their value during both sessions. Looking at the graph corresponding to
 454 the 20°/s target, we see an asymmetry in the scatter of data points: the majority of values are
 455 larger than the target velocity and the majority of data points are situated below the diagonal
 456 line, suggesting an influence of the frequency of the target path. The paired comparison of
 457 median values confirmed a slightly smaller values of P/T landing ratio during the “certain”
 458 sessions ($\Delta\text{Med} = -0.6 \pm 0.8^\circ/\text{s}$, $P < 0.05$). The lower IQR values during the “certain” sessions
 459 was also statistically significant ($\Delta\text{IQR} = -0.4 \pm 0.6^\circ/\text{s}$, $P < 0.05$). These small differences between
 460 the “uncertain” and “certain” sessions were absent when the target moved at 40 °/s. The
 461 paired comparisons revealed no significant difference in the median and IQR values of
 462 position/time landing ratios ($\Delta\text{Med} = 0.8 \pm 1.1^\circ/\text{s}$, P-value= 0.15; $\Delta\text{IQR} = 0.3 \pm 1.2^\circ/\text{s}$, P-value =
 463 0.77).

464 In summary, when the target moved at $20^\circ/\text{s}$ along the same path, catch-up saccades
465 were slightly more accurate (2.8% decrease) and more precise (20% decrease) than when its
466 path changed across the trials. However, the difference between the “uncertain” and “certain”
467 sessions was absent when the target moved at $40^\circ/\text{s}$.

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

470 **Figure 11 approximately here**

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

486 To further test the consistency of this inference, we compared the median and IQR
487 values of radial position/time landing ratios of interceptive saccades to those of the radial post-
488 saccadic pursuit velocity (Figure 11B). For both “uncertain” and “certain” sessions, the values
489 of radial position/time landing ratio were scattered about the target velocity (horizontal
490 dashed lines) whereas the post saccadic pursuit velocity values were consistently smaller than
491 the target velocity (most data points are situated to the left of the vertical dashed lines).
492 Considering the trials recorded during the “uncertain” sessions when the target moved at
493 $20^\circ/\text{s}$ in the upper right visual field, the median values of radial position/time landing ratio

494 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
 495 G, respectively), much larger than the medial values of post-saccadic pursuit velocity, which
 496 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”
 497 sessions, the radial position/time landing ratios were most often larger than the post-saccadic
 498 pursuit velocities: 19 ± 4 versus $18 \pm 2^\circ/\text{s}$ in monkey Bi, 17 ± 3 versus $17 \pm 2^\circ/\text{s}$ (monkey C), 20
 499 ± 3 versus $12 \pm 3^\circ/\text{s}$ (monkey E), 22 ± 3 versus $12 \pm 2^\circ/\text{s}$ (monkey F) and 23 ± 6 versus $8 \pm 2^\circ/\text{s}$
 500 (monkey G).

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

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

522 **Figure 12 approximately here**

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

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

548 Figure 12B plots the median and IQR values of radial post saccadic pursuit velocity
 549 calculated for each quadrant of the visual field and each monkey as a function of the
 550 position/time landing ratio of catch-up saccades. The paired comparison of median values
 551 confirmed a statistically significant larger position/time landing ratio than the post-saccadic
 552 velocity for both “certain” and “uncertain” sessions, when the target moved at 20°/s
 553 (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

554 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
 555 the variability, the IQR values of position/time landing ratio of catch-up saccades were
 556 consistently smaller than the IQR values of post-saccadic pursuit velocity for both sessions,
 557 regardless of whether the target moved at 20°/s (uncertain: $\Delta\text{IQR} = 0.7 \pm 1$ °/s, $P < 0.05$; certain:
 558 $\Delta\text{IQR} = 0.7 \pm 1.1$ °/s, $P < 0.05$) or 40°/s (uncertain: $\Delta\text{IQR} = 3.7 \pm 2.3$ °/s; certain: $\Delta\text{IQR} = 2.4 \pm$
 559 1.2 °/s, $P < 0.05$).

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

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

564 **Figure 13 approximately here**

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

583 more precise than interceptive saccades. Indeed, when the path moved at 20 °/s, the average
584 differences were 1.5 ± 1 °/s ($P < 0.05$) and 1.8 ± 0.9 °/s ($P < 0.05$) for the “uncertain” and “certain”
585 sessions, respectively. Likewise, when the path moved at 40 °/s, the average differences were
586 2.5 ± 1.5 °/s ($P < 0.05$) and 2.8 ± 0.7 °/s ($P < 0.05$).

587

588 **DISCUSSION**

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

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

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

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

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

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

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

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

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

705 Several differences distinguish our study from previous studies in the monkey (22-24).
706 Firstly, we used longer and variable fixation intervals (from 500 to 1500 ms by increment of
707 500 ms versus 500 ms) and lower target velocities (20 or 40°/s versus 65°/s). It is not certain
708 that the fixed duration of the fixation interval is the critical factor explaining why we did not

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

727 Regarding the post-saccadic pursuit, we found that the catch-up saccades were made
728 later when the target moved always along the same path; the intersaccadic intervals were
729 longer during the “certain” sessions than during the “uncertain” ones (Fig. 9A). The target was
730 maintained longer within the central visual field during the “certain” sessions, an inference
731 that is consistent with previous studies showing a smoothing of tracking eye movements with
732 less frequent catch-up saccades in the monkey after 10-12 daily experimental sessions (4-5).
733 The longer inter-saccadic intervals during the “certain” sessions indicate that the repeated
734 presentation of the same moving target transforms its tracking from saltatory to smooth. The
735 primacy of smooth pursuit during visual tracking presumably results from an expansion of the
736 “mass” of neural activity linked to the representation of the central field. Such an expansion
737 involves not only motion sensitive neurons in the visual cortex but also pursuit-related neurons
738 in the rostral SC (52-53), the caudal fastigial nuclei (34, 54) and the ventral paraflocculus (55-
739 57).

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

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

760 General conclusion

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

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

773

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779

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784

785 **AUTHOR CONTRIBUTIONS**

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

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968 **FIGURE CAPTIONS**

969 **Figure 1: Experimental protocol.** Each trial started with the appearance of a target at the
 970 center of the visual display. The monkey was required to direct and maintain gaze toward its
 971 location for a fixation interval whose duration varied pseudo-randomly from 750 to 1500 ms
 972 (by increments of 250 ms). A gap interval of 300 ms followed the extinction of the fixation
 973 target, after which the target reappeared and moved along one out of four possible oblique
 974 paths. The monkey was rewarded for tracking the target until it disappeared. Each target path
 975 was tested with two frequencies of occurrence during sessions recorded on different days:
 976 25% (“uncertain” sessions) and 100% (“certain” sessions). Two target velocities (20 and
 977 40deg/s) were tested during separate sessions.

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

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

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

1000 **Figure 5: Average velocity of interceptive saccades during the “uncertain” and “certain”**
 1001 **sessions.** Different symbols correspond to different quadrants of the visual field and different
 1002 colors to different monkeys. The two leftmost graphs plot the median values for the 20 and
 1003 40°/s targets and the other graphs the interquartile range (IQR) values.

1004 **Figure 6: Latency of interceptive saccades.** Violin plots show for each monkey (x axis) and
 1005 each quadrant of the visual field the median (white dot) and interquartile range (black box) of
 1006 latency values and an estimation of their distribution (based on a probability density function)
 1007 for the “uncertain” (white) and “certain” (grey) sessions. The target moved at 20 deg/s (left
 1008 column) or 40 deg/s (right column).

1009 **Figure 7: Saccade latency during the “uncertain” and “certain” sessions.** Different symbols
 1010 correspond to different quadrants of the visual field and different colors to different monkeys.
 1011 Median (left column) and interquartile interval (IQR, right column) values are plotted for the
 1012 20°/s (top) and 40°/s target (bottom).

1013 **Figure 8: Accuracy and precision of interceptive saccades.** A: The landing position (radial
 1014 value) of saccades is plotted as a function of their landing time, when the target moved in the
 1015 upper left visual field, during the “uncertain” and “certain” sessions. Data collected in monkey
 1016 Bi. B: Median and interquartile range (IQR) of the position/time (P/T) landing ratio during the
 1017 “uncertain” (x-axis) and “certain” (y-axis) sessions. Different symbols correspond to different
 1018 quadrants of the visual field and different colors to different monkeys. The first and third
 1019 columns correspond to sessions during which the target moved at 20 deg/s, the second and
 1020 fourth columns to those in which the 40 deg/s target was used. The horizontal and vertical
 1021 dashed lines show the target velocity.

1022 **Figure 9: Post-saccadic pursuit eye movement.** A: The median and interquartile interval range
 1023 (IQR) values of the duration of the first intersaccadic interval (ISI) calculated during the
 1024 “certain” sessions (y-axis) are plotted as a function of values calculated during the “uncertain”
 1025 sessions (x-axis). Different symbols correspond to different quadrants of the visual field and
 1026 different colors to different monkeys. B: The amplitude (radial value) of the post-saccadic eye
 1027 movement is plotted as a function of the duration of the intersaccadic interval (from the end
 1028 of the interceptive saccade to the onset of the first catch-up saccade). The target moved in
 1029 the upper left visual field. Data collected in monkey Bi. C: The median and interquartile range
 1030 (IQR) values of the post-saccadic slow movement velocity are compared between the
 1031 “uncertain” (x-axis) and “certain” (y-axis) sessions. Different symbols correspond to different
 1032 quadrants of the visual field and different colors to different monkeys. From left to right, the
 1033 first and third columns correspond to movements made in response to the 20 deg/s target,
 1034 the second and fourth to movements made in response to the 40 deg/s target. The horizontal
 1035 and vertical dashed lines indicate the target velocity.

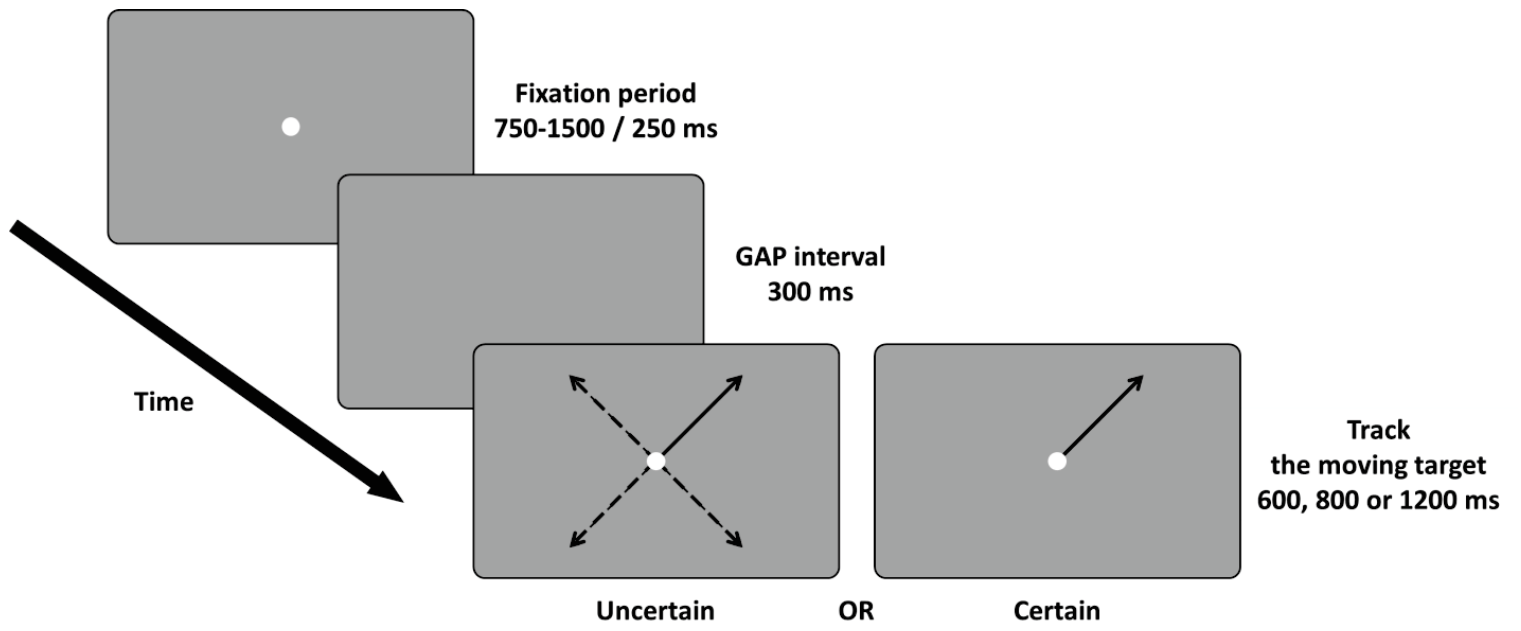
1036 **Figure 10: Landing position of catch-up saccades.** A: The landing position (radial value) of each
 1037 catch-up saccade is plotted as a function of its landing time when the target moved in the
 1038 upper left visual field, at 20 deg/s (left) or 40 deg/s (right) during the “uncertain” (first and
 1039 third columns) and “certain” (second and fourth columns) sessions. Dashed lines indicate the
 1040 target position. Data collected in monkey Bi. B: Median and interquartile range (IQR) values of
 1041 position/time landing ratio are compared between the “uncertain” (x-axis) and “certain” (y-
 1042 axis) sessions. Different symbols correspond to different quadrants of the visual field and
 1043 different colors to different monkeys. From left to right, the first and third columns correspond
 1044 to catch-up saccades made toward the 20 deg/s target, the second and fourth columns to
 1045 those made toward the 40 deg/s target. Horizontal and vertical dashed line indicate the target
 1046 velocity.

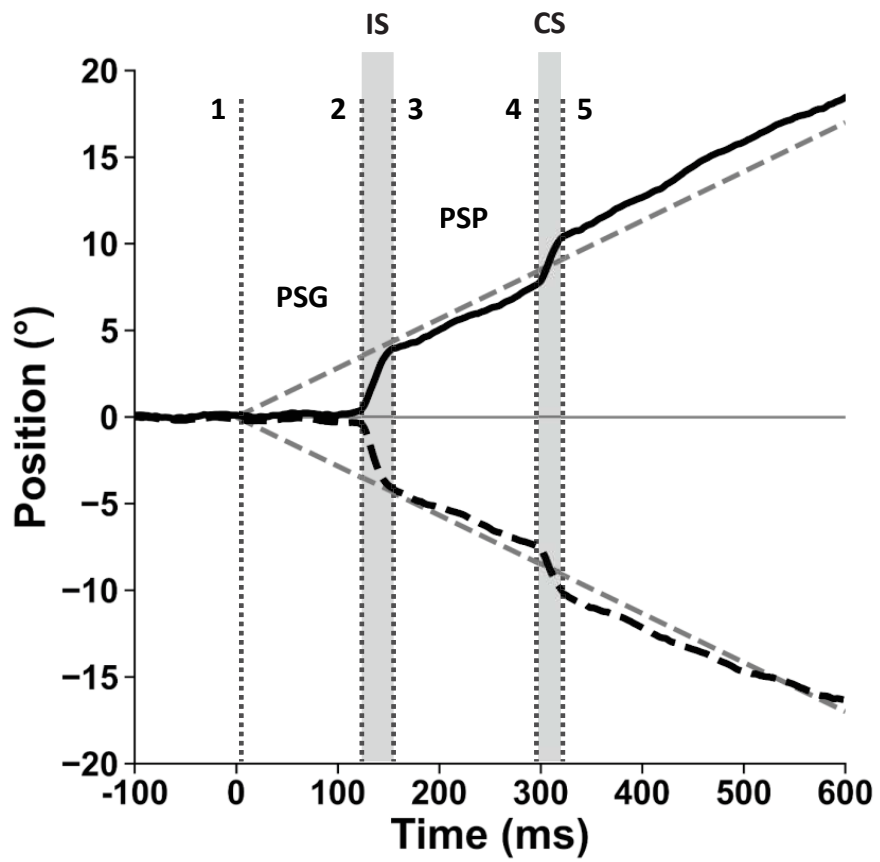
1047 **Figure 11: Position/time landing of interceptive saccades and post-saccadic pursuit velocity.**
 1048 A: The position/time (P/T) landing ratio of interceptive saccades (IS) is plotted as a function of
 1049 the post-saccadic pursuit (PSP) velocity (radial values). The data were collected in monkey Bi
 1050 when it tracked a target that moved at 20 deg/s (left half) or 40 deg/s (right half) in the upper
 1051 right quadrant of the visual field. From left to right, the first and third columns correspond to
 1052 trials recorded during the “uncertain” sessions and the second and fourth columns to trials
 1053 recorded during the “certain” sessions. Dashed lines correspond to target velocity. B: Median

1054 and interquartile range (IQR) values of position/time landing ratio of interceptive saccades (y-
1055 axis) are compared to the post saccadic pursuit eye velocity (x axis) for the uncertain (top row)
1056 and certain (bottom) sessions. Different symbols correspond to different quadrants of the
1057 visual field and different colors to different monkeys. From left to right, the first and third
1058 columns correspond to the 20 deg/s target, the second and fourth to the 40 deg/s target.
1059 Horizontal and vertical dashed lines indicate the target velocity.

1060 **Figure12: Post-saccadic pursuit velocity and position/time landing ratio of catch-up**
1061 **saccades.** A: The post-saccadic pursuit (PSP) velocity is plotted as a function of the
1062 position/time landing ratio (radial values) for the trials in which the monkey Bi tracked the
1063 target while it moved in the upper right quadrant of the visual field during the “uncertain”
1064 (first and third columns) and “certain” sessions. Dashed lines correspond to target velocity. B:
1065 The median and interquartile range (IQR) values of post saccadic pursuit velocity (y axis) are
1066 compared to the values of position/time landing ratio of catch-up saccades (x axis) made
1067 during the “uncertain” (top row) and “certain” (bottom) sessions. Different symbols
1068 correspond to different quadrants of the visual field and different colors to different monkeys.
1069 From left to right, the first and third columns correspond to the 20 deg/s target, the second
1070 and fourth to the 40 deg/s target. Horizontal and vertical dashed lines indicate the target
1071 velocity.

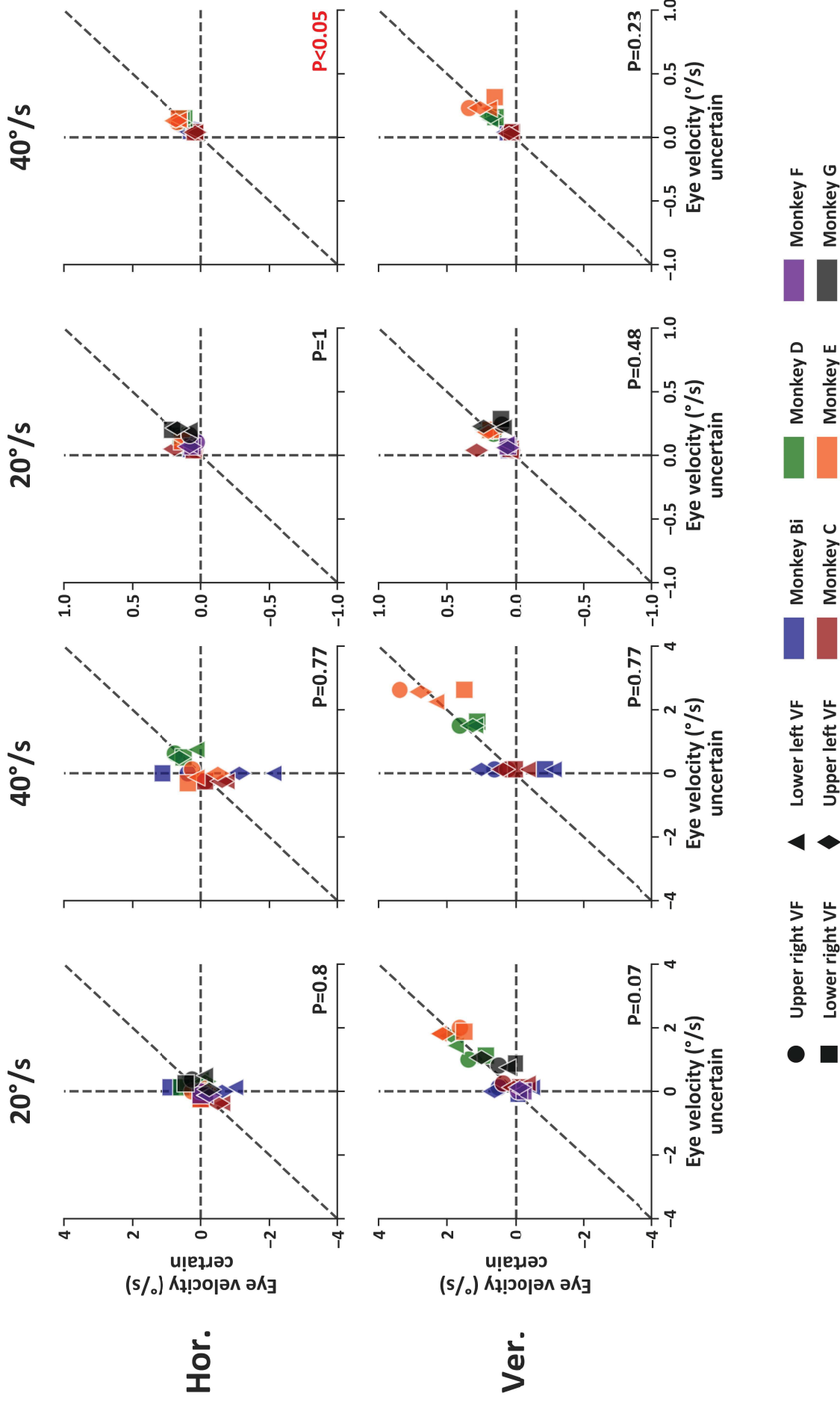
1072 **Figure 13: Accuracy and precision of interceptive and catch-up saccades.** The median and
1073 interquartile range (IQR) values of position/time landing ratio of interceptive saccades (IS, y-
1074 axis) are compared to those of catch-up saccades (CS, x-axis) made during the “uncertain” (top
1075 row) and “certain” (bottom) sessions. Different symbols correspond to different quadrants of
1076 the visual field and different colors to different monkeys. From left to right, the first and third
1077 columns correspond to the 20 deg/s target, the other columns to the 40 deg/s target.
1078 Horizontal and vertical dashed lines indicate the target velocity.

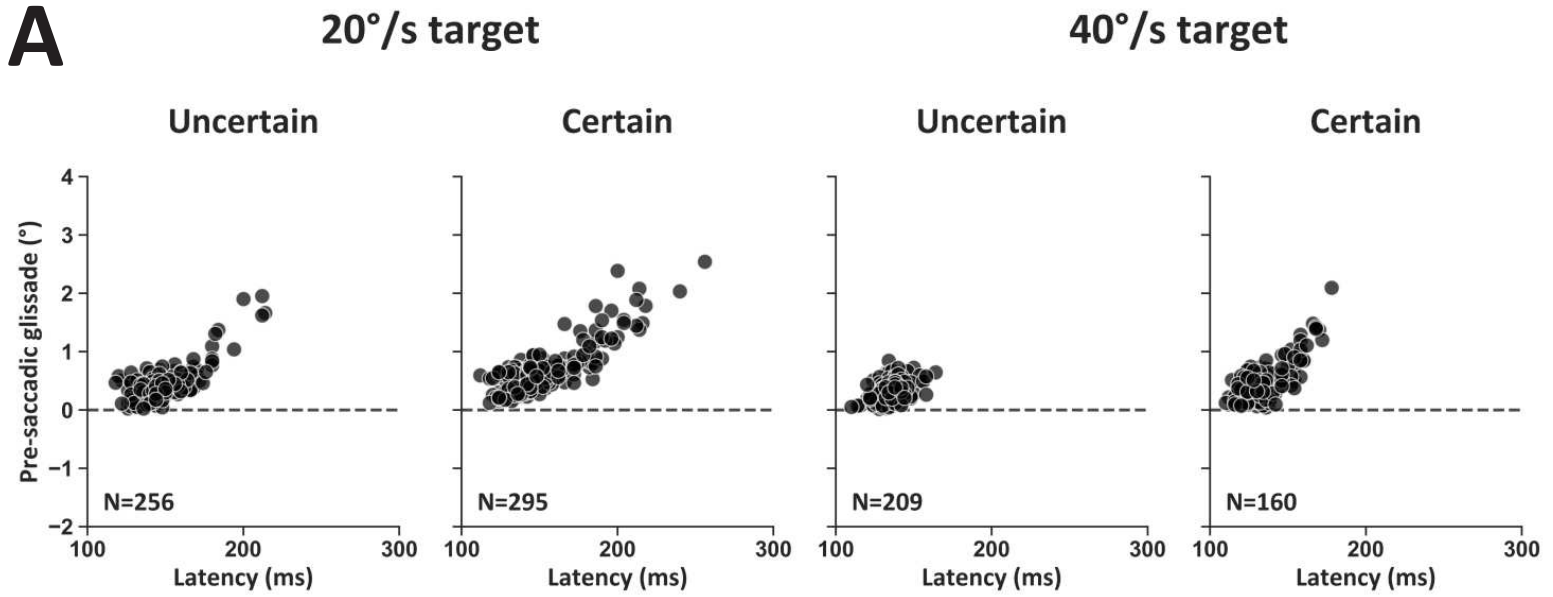
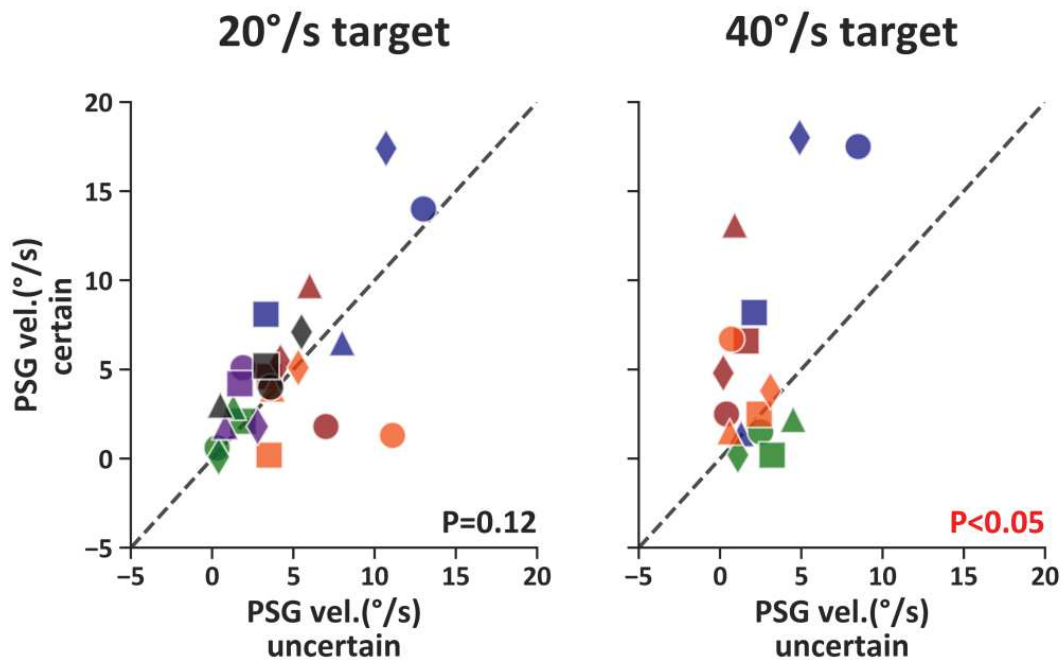




Median

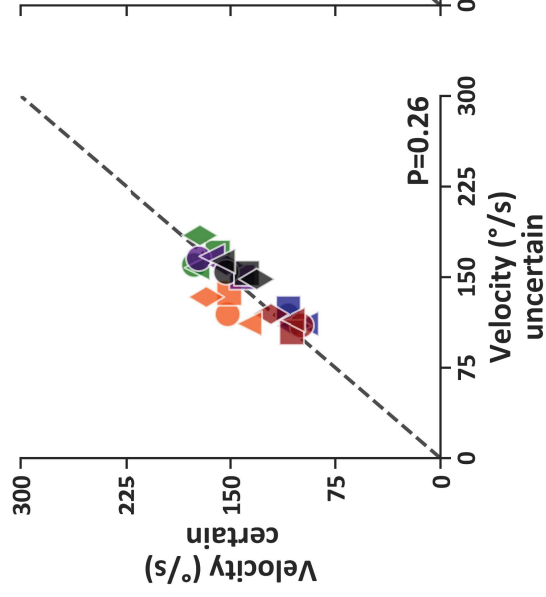
IQR



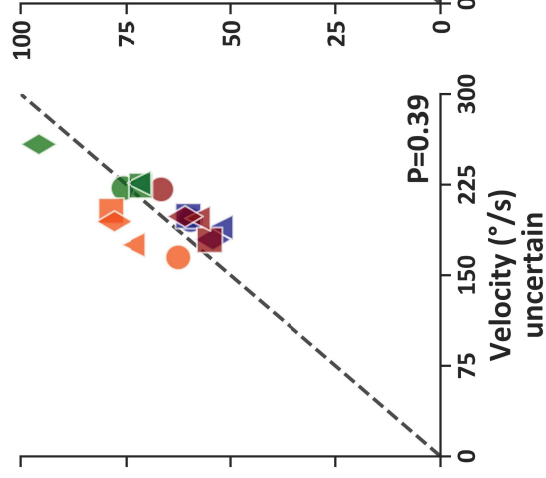
A**B**

Median

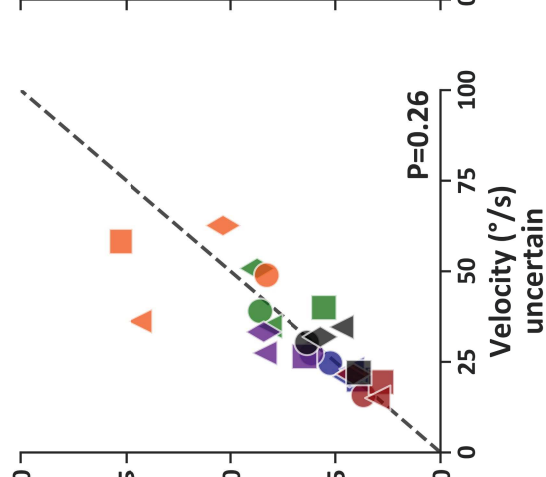
20°/s



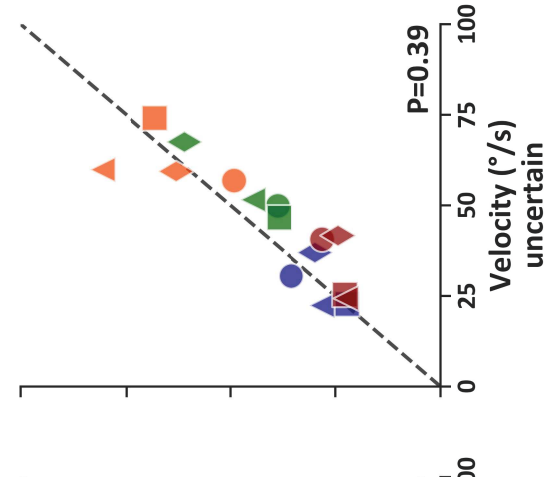
40°/s



20°/s

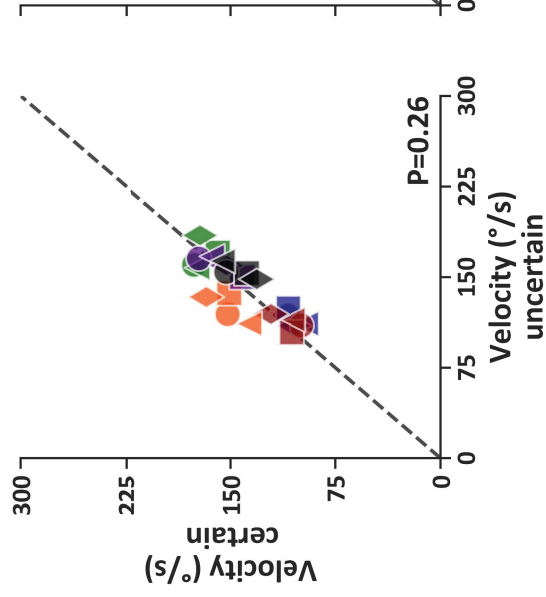


40°/s

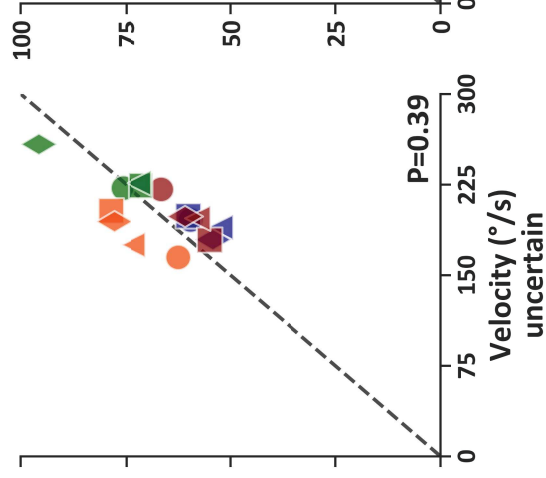


IQR

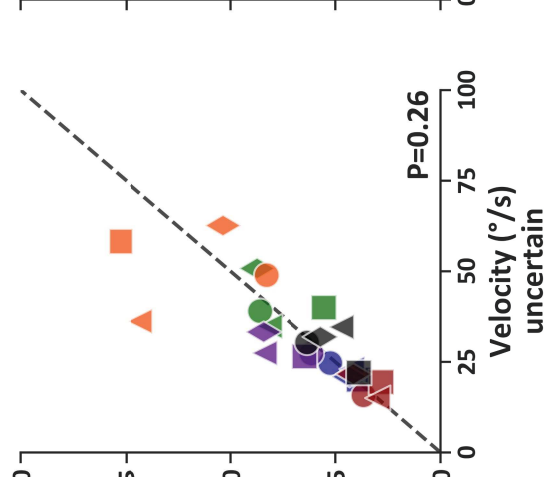
20°/s



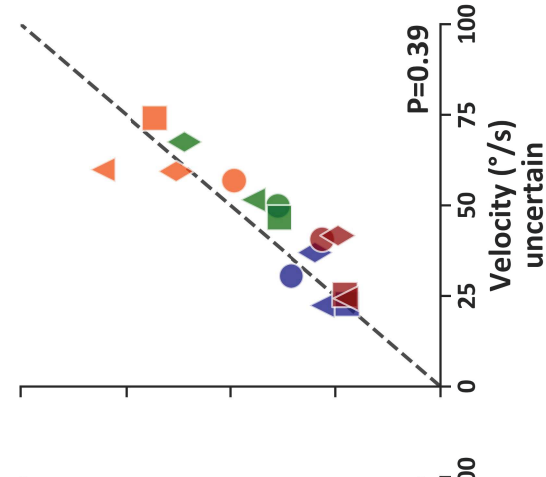
40°/s



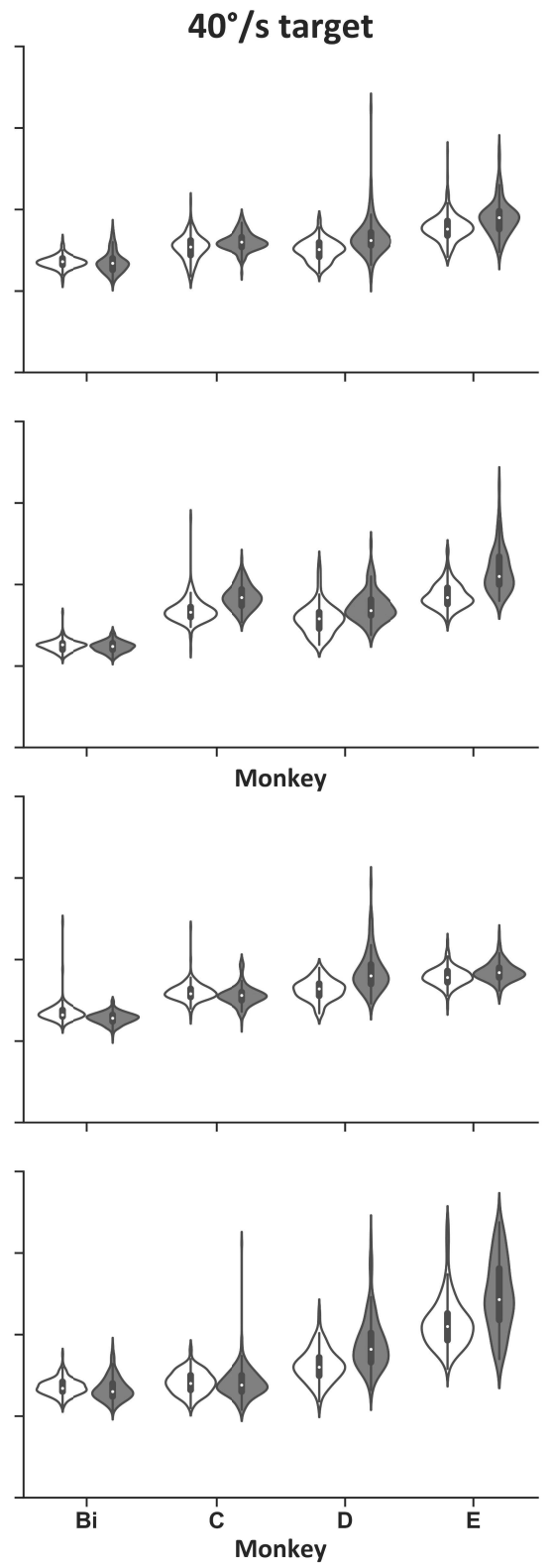
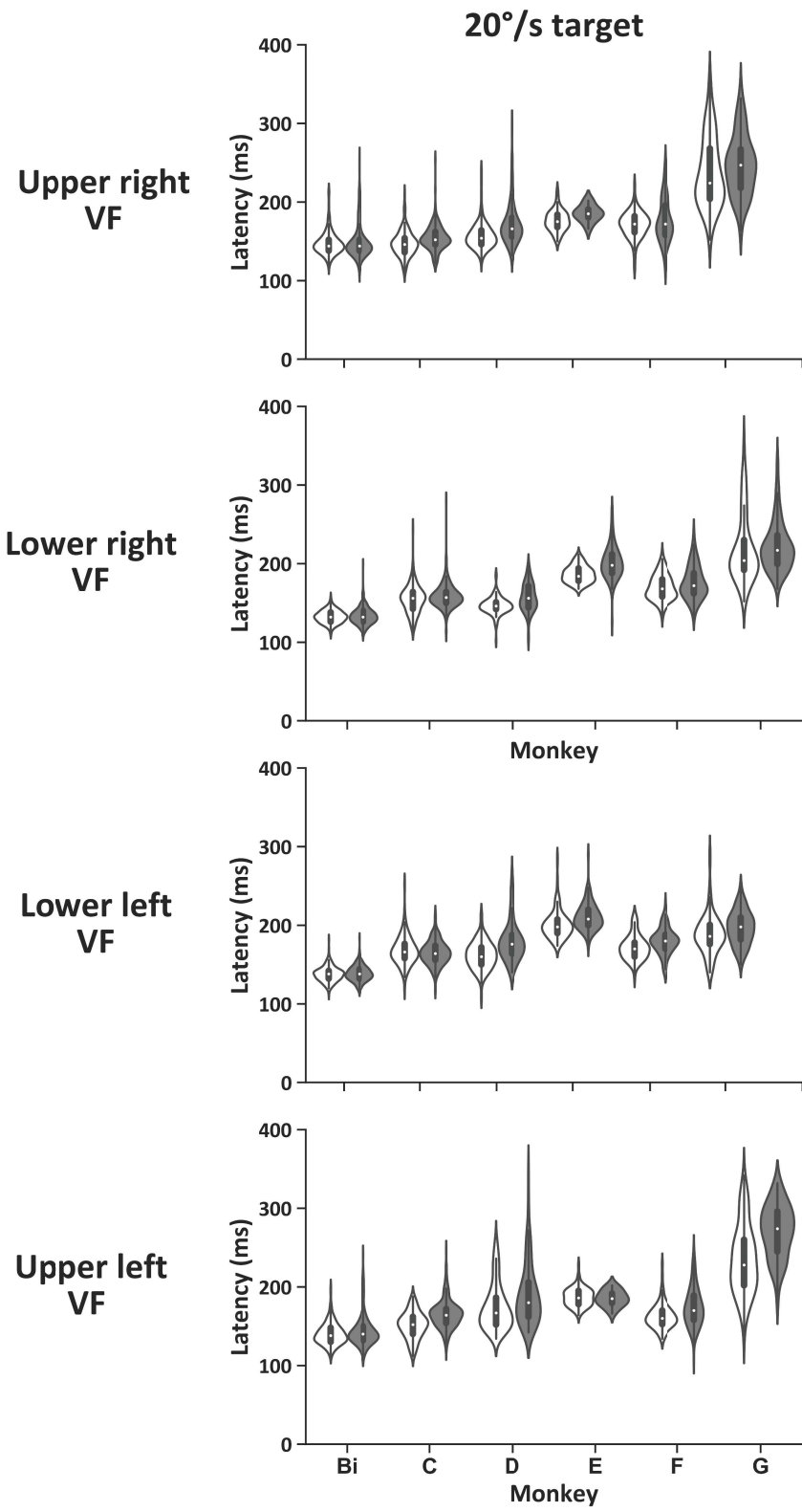
20°/s



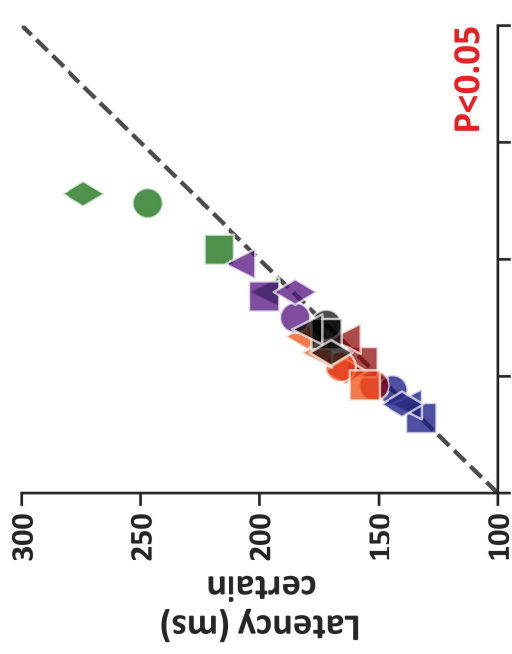
40°/s



- Upper right VF
- ▲ Lower left VF
- Lower right VF
- ◆ Lower right VF
- Monkey Bi
- Monkey C
- Monkey D
- Monkey E
- Monkey F
- Monkey G

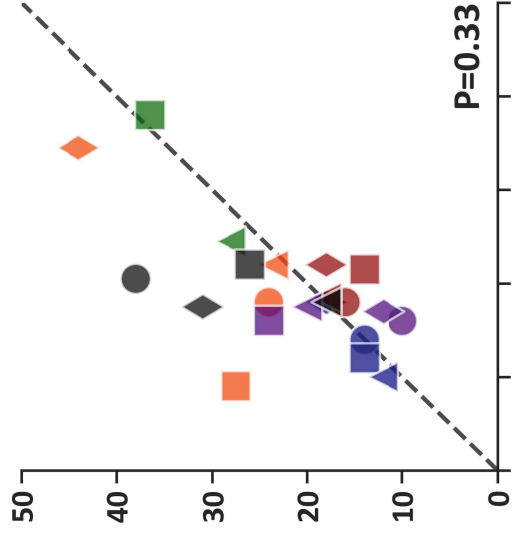


Median

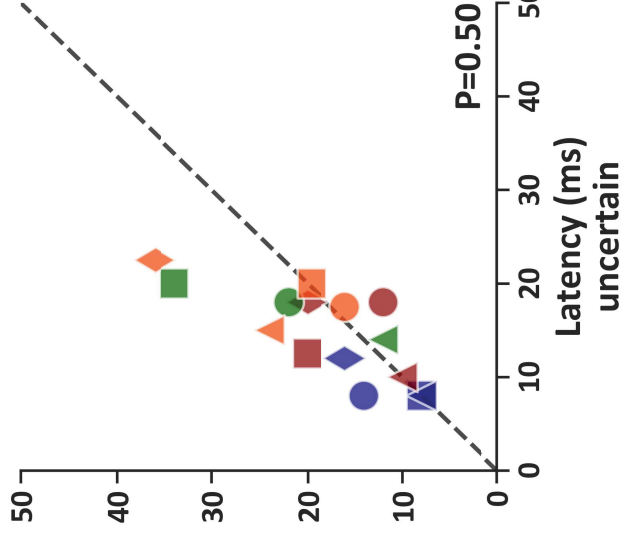
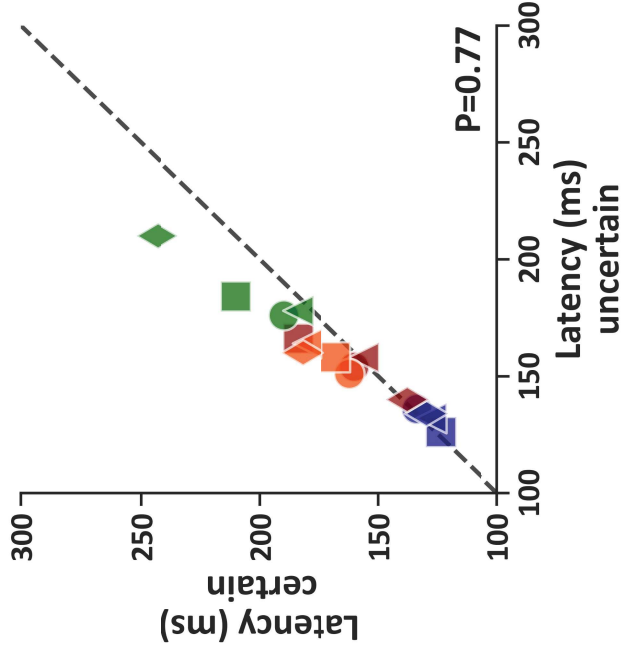


20°/s
target

IQR

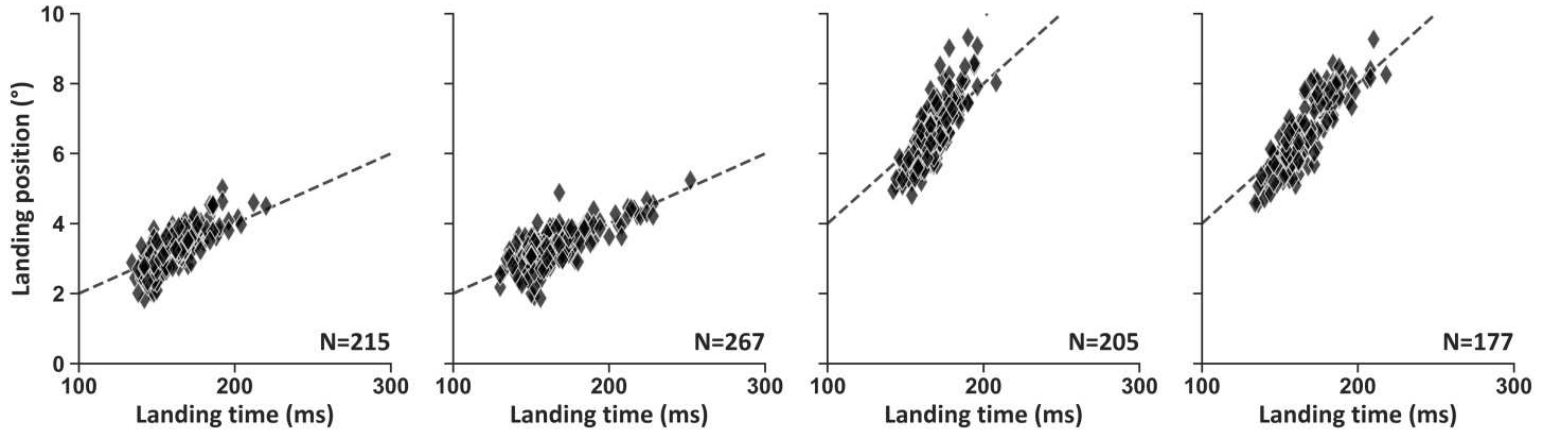
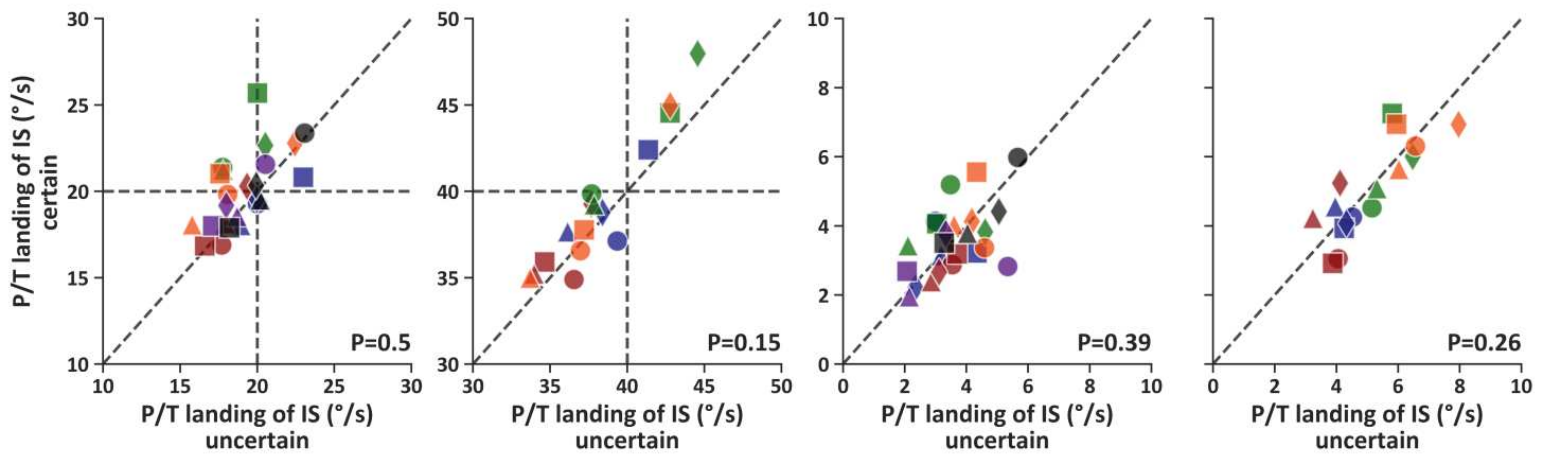


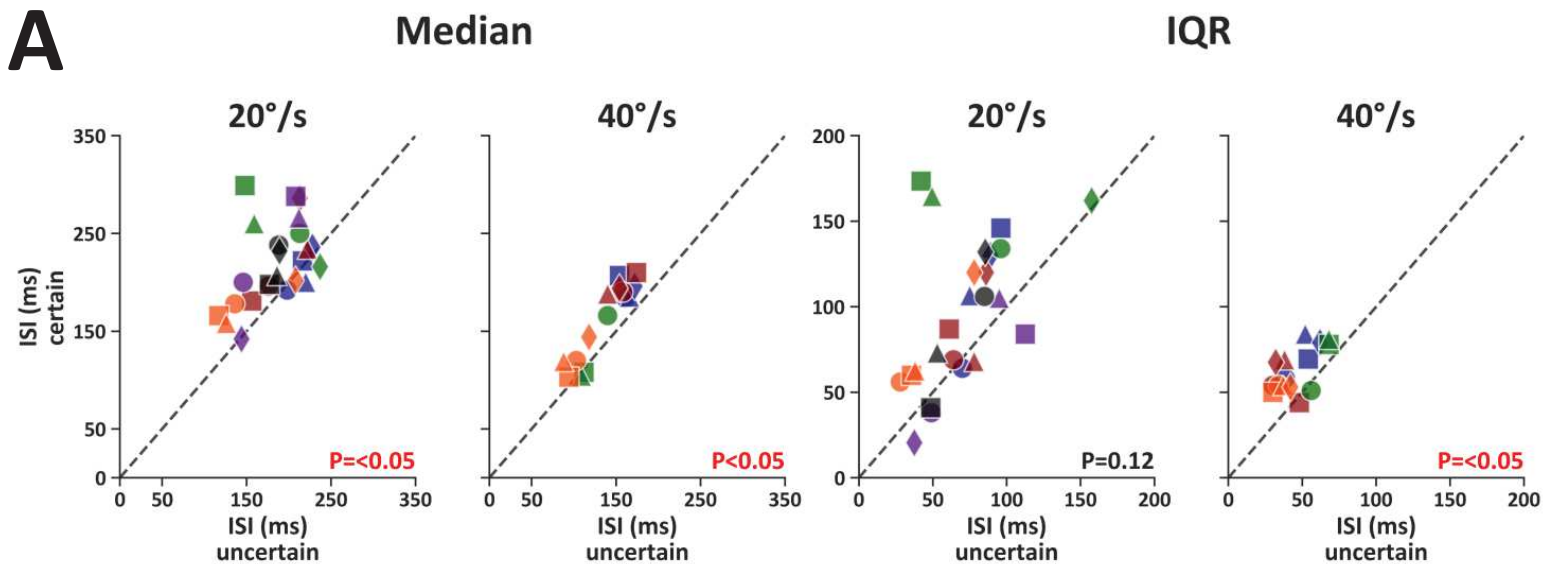
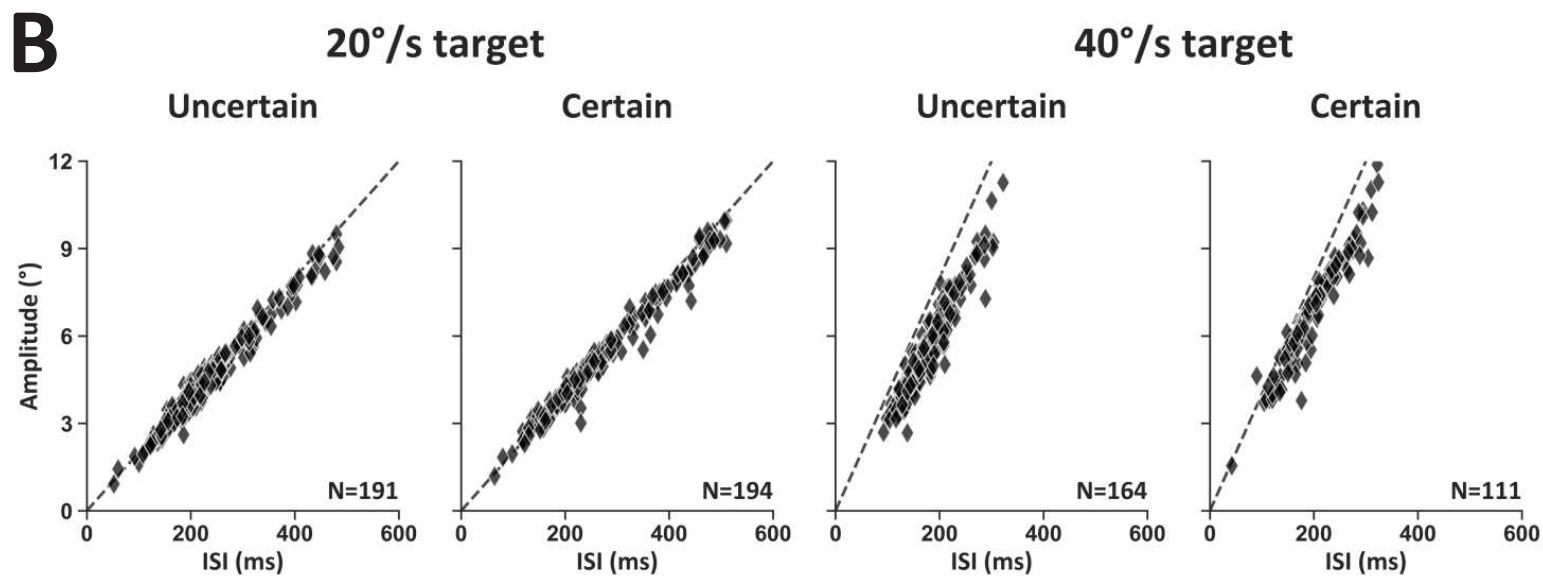
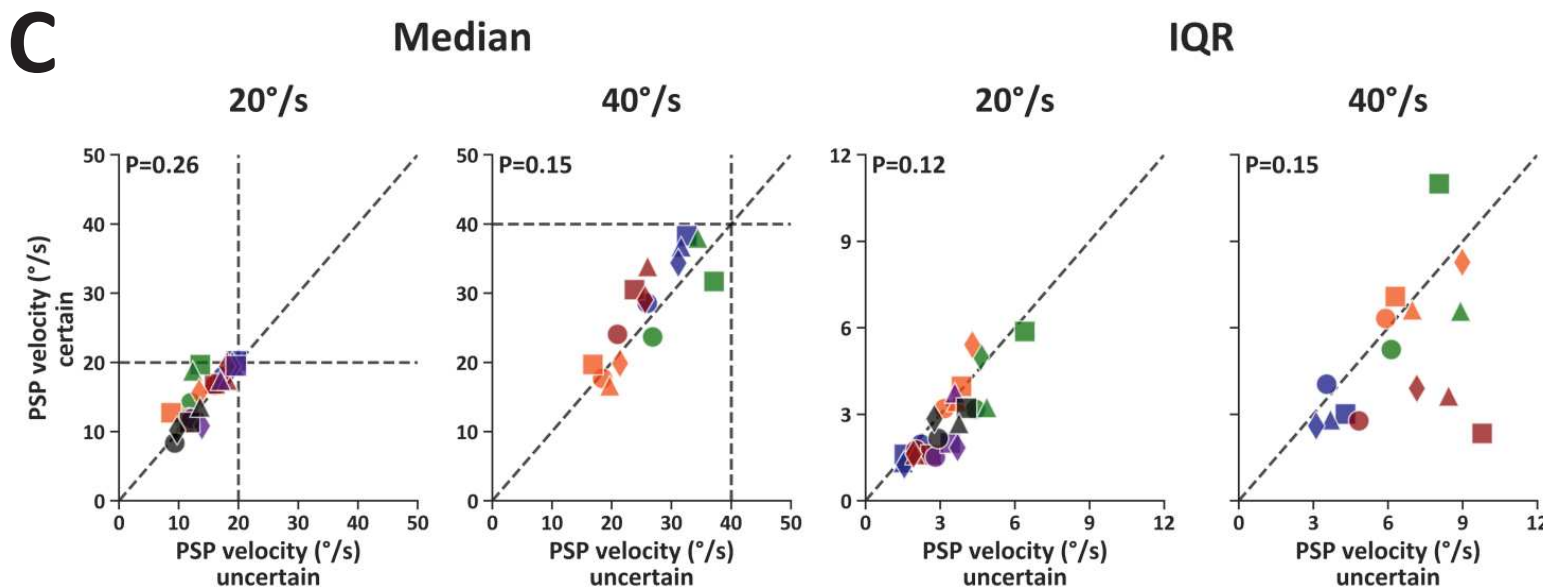
40°/s
target

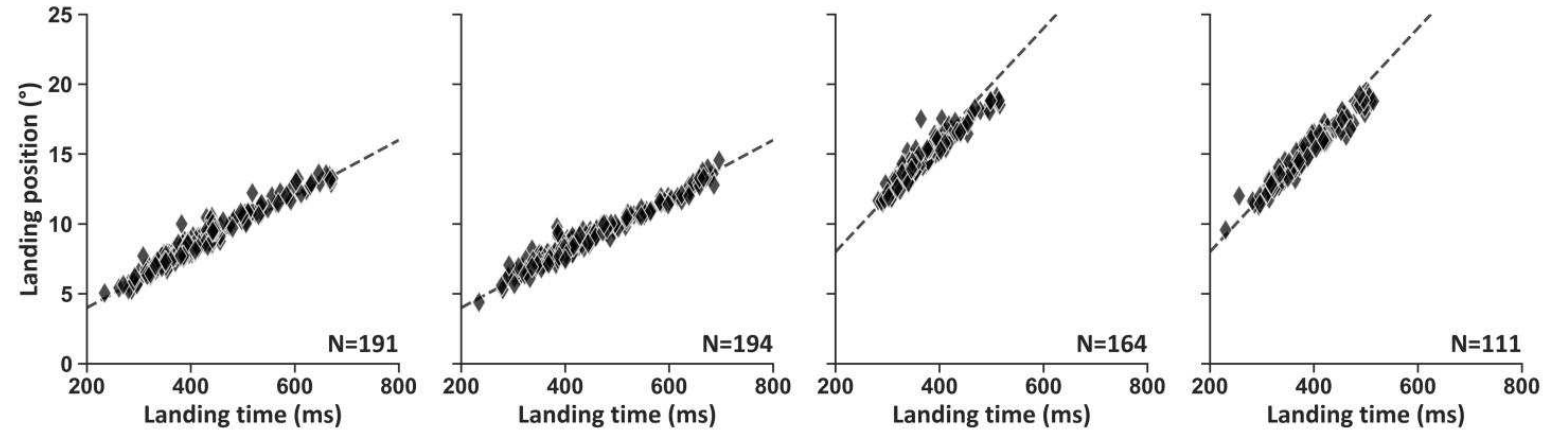
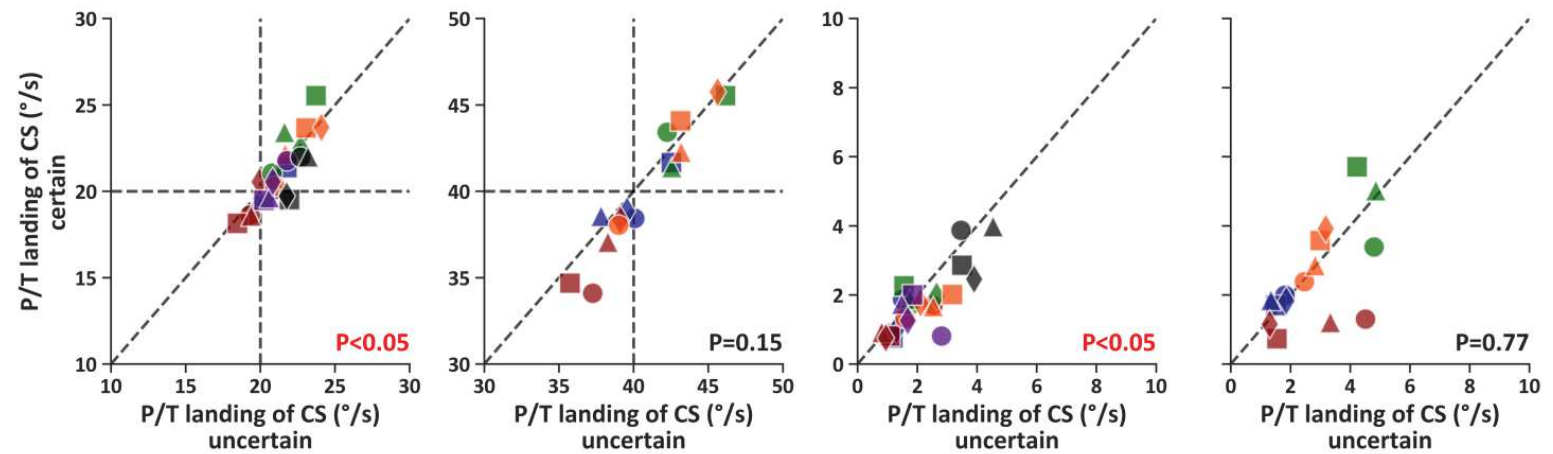


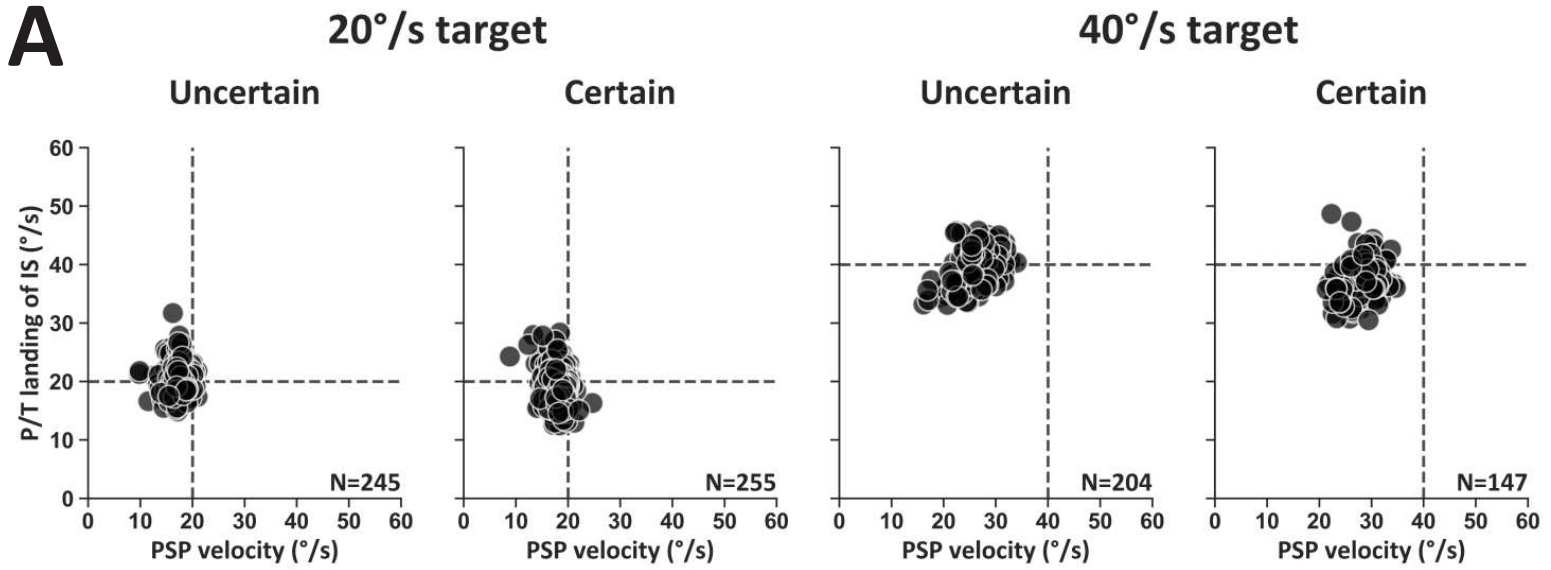
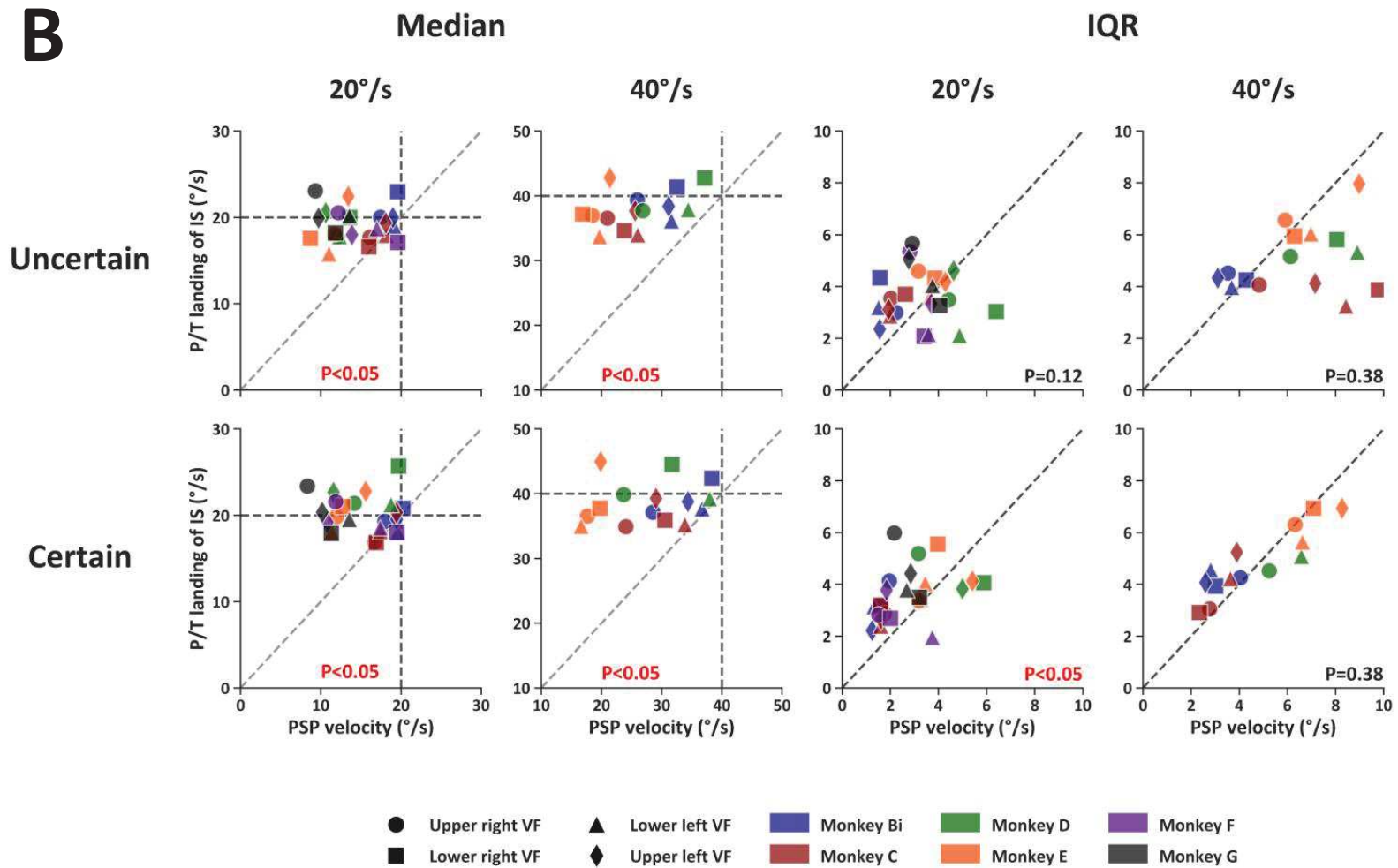
- Upper right VF
- Lower right VF
- ▲ Lower left VF
- ◆ Upper left VF

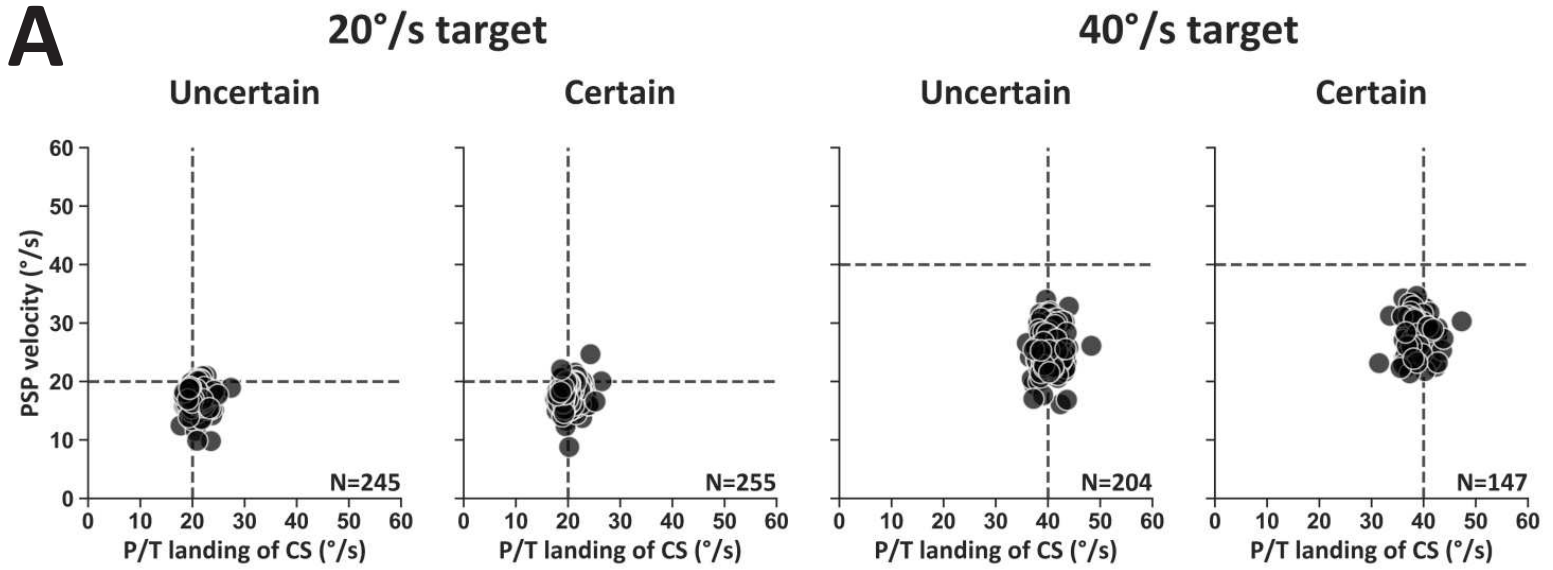
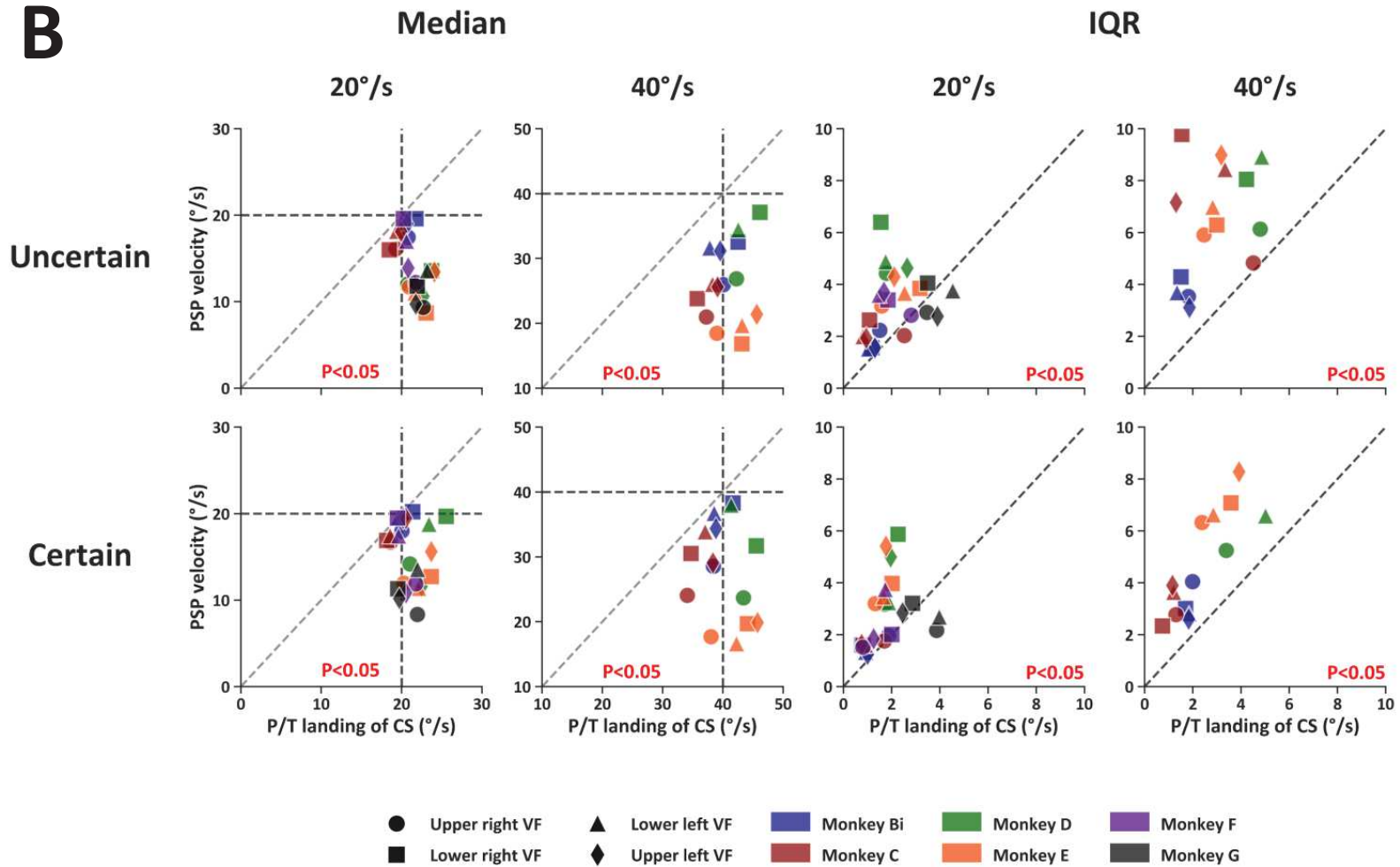
- Monkey Bi
- Monkey C
- Monkey D
- Monkey E
- Monkey F
- Monkey G

A**20°/s target****40°/s target****Uncertain****Certain****Uncertain****Certain****B****Median****IQR****20°/s****40°/s****20°/s****40°/s**

A**B****C**

A**20°/s target****40°/s target****Uncertain****Certain****Uncertain****Certain****B****Median****IQR****20°/s****40°/s****20°/s****40°/s**

A**B**

A**B**

Median

IQR

