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## Tracking a moving visual target in the rhesus monkey: Influence of the occurrence frequency of the target path

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## ABSTRACT

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

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

## INTRODUCTION

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

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

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

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

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

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

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

In this study, we completed these previous studies by testing in the monkey whether the repeated presentation of a target moving along the same path 1) produced anticipatory eye movements before its appearance and/or 2) affected its oculomotor tracking. More specifically, we evaluated how the frequency of the target path influenced the onset, the velocity and the accuracy of eye movements. On the basis of previous studies, we conjectured that repeatedly tracking a target, which after a constant gap interval, would move always along the same path would favor the occurrence of anticipatory slow eye movement and express saccades. We also conjectured that reducing the uncertainty about the target path would 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



## MATERIAL AND METHODS

### Subjects and surgical procedures

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

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

### Eye movement recording and visual stimulation

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

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

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

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

## Behavioral tasks

### Figure 1 approximately here

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

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

## Data analysis

### Figure 2 approximately here

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

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

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

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

## RESULTS

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

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

Figure 3 approximately here

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

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

Figure 4 approximately here

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

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

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

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

**Figure 5 approximately here**

Regarding the velocity, we calculated for each visual quadrant and each monkey, the ratio between the radial amplitude of saccades and their duration, i.e. their average velocity. The comparison of median and interquartile range (IQR) values (Figure 5) revealed no consistent difference between the “certain” and “uncertain” sessions (mean  $\pm$  std of differences of median values  $\Delta\text{Med} = 0.3 \pm 15$  and  $2 \pm 28^\circ/\text{s}$  for the  $20^\circ/\text{s}$  and  $40^\circ/\text{s}$  target, respectively, Wilcoxon non parametric tests, P value = 0.26 and 0.39). The variability of average velocities was not changed either as the IQR values were not significantly different between the “certain” and “uncertain” sessions (mean  $\pm$  std of differences of interquartile range values:  $\Delta\text{IQR} = 0.3 \pm 15.5$  and  $2 \pm 28^\circ/\text{s}$  for the  $20^\circ/\text{s}$  and  $40^\circ/\text{s}$  target, respectively, P values = 0.26 and 0.39).

#### Figure 6 approximately here

Regarding the latency of interceptive saccades, figure 6 shows the distribution of its values for each quadrant of the visual field during the “uncertain” (white) and “certain” (grey) sessions (left column:  $20^\circ/\text{s}$ ; right column:  $40^\circ/\text{s}$ ). Although an interval (gap) separated the target motion onset from the offset of the fixation target, the distributions of latency values do not exhibit a double peak suggestive of the presence of express saccades. In our study, we found no saccade with a latency smaller than 102 ms. When we consider for example the saccades toward the  $20^\circ/\text{s}$  target moving in the upper right quadrant, the statistics of latency values were identical between the “uncertain” and “certain” sessions in monkey Bi (both medians  $\pm$  IQRs =  $144 \pm 14$  ms) and in monkey G ( $172 \pm 21$  versus  $172 \pm 38$  ms). Very small differences were observed in the other monkeys:  $146 \pm 18$  versus  $152 \pm 16$  ms (monkey C; 6 ms difference),  $154 \pm 18$  versus  $166 \pm 24$  ms (monkey E; 12 ms difference),  $175 \pm 16$  versus  $185 \pm 10$  ms (monkey F; 10 ms difference).

#### Figure 7 approximately here

To test whether these small differences were reproducible and statistically significant, we performed a paired comparison (Wilcoxon non-parametric test) of median values between the “uncertain” and “certain” sessions for all visual quadrants and all monkeys, except monkey D (values plotted in Fig. 7). With the  $20^\circ/\text{s}$  target, a very small but significant latency increase (4%) was then detected during the “certain” sessions (average difference of median values= 6

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

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

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

### Figure 8 approximately here

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



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

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

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

**Figure 9 approximately here**

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

target moved at 40°/s ( $\Delta\text{IQR} = 20 \pm 11$  ms;  $P < 0.05$ ) but not when it moved at 20°/s ( $\Delta\text{IQR} = 16 \pm 23$  ms;  $P$  value = 0.12).

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

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

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

or 40°/s ( $\Delta\text{Med} = -3 \pm 3^\circ/\text{s}$ ; P value = 0.15). Concerning the variability of post-saccadic pursuit velocity, the IQR values were not significantly different between the “uncertain” and “certain” 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 target ( $\Delta\text{IQR} = 2 \pm 3^\circ/\text{s}$ ; P value = 0.15). In summary, the longer intersaccadic intervals during the “certain” sessions were not associated with a different post-saccadic pursuit velocity.

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

#### **Figure 10 approximately here**

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

In summary, when the target moved at 20°/s along the same path, catch-up saccades were slightly more accurate (2.8% decrease) and more precise (20% decrease) than when its path changed across the trials. However, the difference between the “uncertain” and “certain” sessions was absent when the target moved at 40°/s.

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

#### **Figure 11 approximately here**

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

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

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 G, respectively), much larger than the medial values of post-saccadic pursuit velocity, which 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” sessions, the radial position/time landing ratios were most often larger than the post-saccadic 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),  $20 \pm 3$  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  $8 \pm 2^\circ/\text{s}$  (monkey G).

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

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

**Figure 12 approximately here**

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

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

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

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

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

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

**Figure 13 approximately here**

Finally, the different retinal origins of interceptive and catchup saccades led us to compare their accuracy and precision (Figure 22). For both “uncertain” (top row) and “certain” (bottom row) conditions, the position/time landing ratio of catch-up saccades seemed to be more accurate and more precise than interceptive ones. For instance, during the “uncertain” sessions, when the target moved at 20 °/s in the upper right visual field, the median values of position/time landing ratio of interceptive saccades were  $20 \pm 3$ ,  $18 \pm 4$ ,  $18 \pm 5$ ,  $21 \pm 5$  and  $23 \pm 6$  °/s versus  $21 \pm 2$ ,  $19 \pm 3$ ,  $21 \pm 2$ ,  $22 \pm 3$  and  $22 \pm 4$  °/s for the catch-up saccades (monkey Bi, C, E, F and G respectively). During the “certain” sessions, the values were  $19 \pm 4$ ,  $17 \pm 3$ ,  $20 \pm 3$ ,  $22 \pm 3$ ,  $26 \pm 6$  °/s (interceptive saccades) versus  $20 \pm 2$ ,  $19 \pm 2$ ,  $20 \pm 1$ ,  $22 \pm 1$  and  $22 \pm 4$  °/s (catch-up saccades). For the sessions in which the target moved at 20°/s, the paired comparison confirmed significantly larger values of position/time landing ratio for the catch-up saccades than for the interceptive saccades, regardless of whether the target path was certain ( $\Delta\text{Med} = 1.1 \pm 1.2$  °/s,  $P < 0.05$ ) or uncertain (average difference =  $2 \pm 1.7$  °/s,  $P < 0.05$ ). With the 40 °/s target, the position/time landing ratio of catch-up saccades were still larger during the “uncertain” sessions ( $\Delta\text{Med} = 2.7 \pm 2.7$  °/s,  $P < 0.05$ ). However, the difference disappeared during the “certain” sessions ( $\Delta\text{Med} = 1.4 \pm 2.7$  °/s,  $P \text{ value} = 0.39$ ). Regarding the precision of saccades, the IQR values of position/time landing ratio were larger for the 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  $1.5 \pm 1$  °/s ( $P < 0.05$ ) and  $1.8 \pm 0.9$  °/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  $2.5 \pm 1.5$  °/s ( $P < 0.05$ ) and  $2.8 \pm 0.7$  °/s ( $P < 0.05$ ).

587



## DISCUSSION

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

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

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

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

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

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

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

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

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

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

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

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

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

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

## **General conclusion**

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

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## **AUTHOR CONTRIBUTIONS**

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



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## FIGURE CAPTIONS

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

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

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

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

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

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



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

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

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

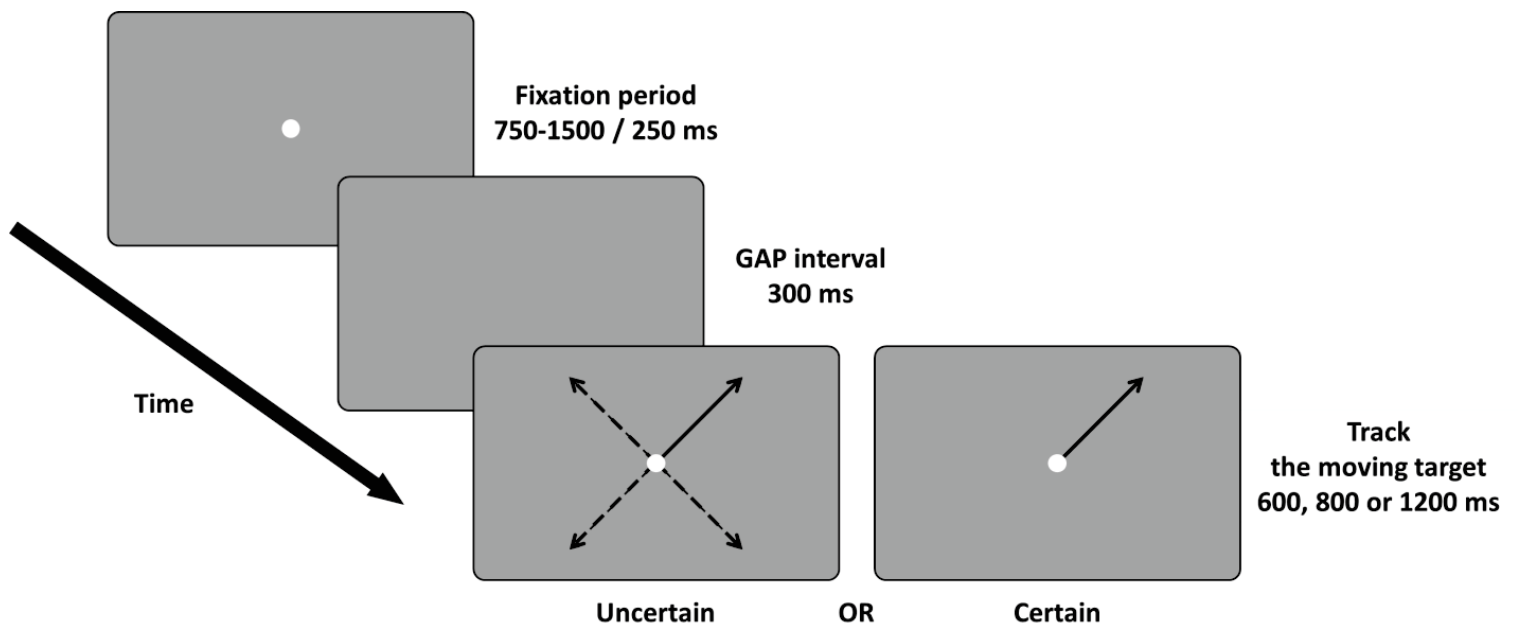
**Figure 10: Landing position of catch-up saccades.** A: The landing position (radial value) of each catch-up saccade is plotted as a function of its landing time when the target moved in the upper left visual field, at 20 deg/s (left) or 40 deg/s (right) during the “uncertain” (first and third columns)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

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

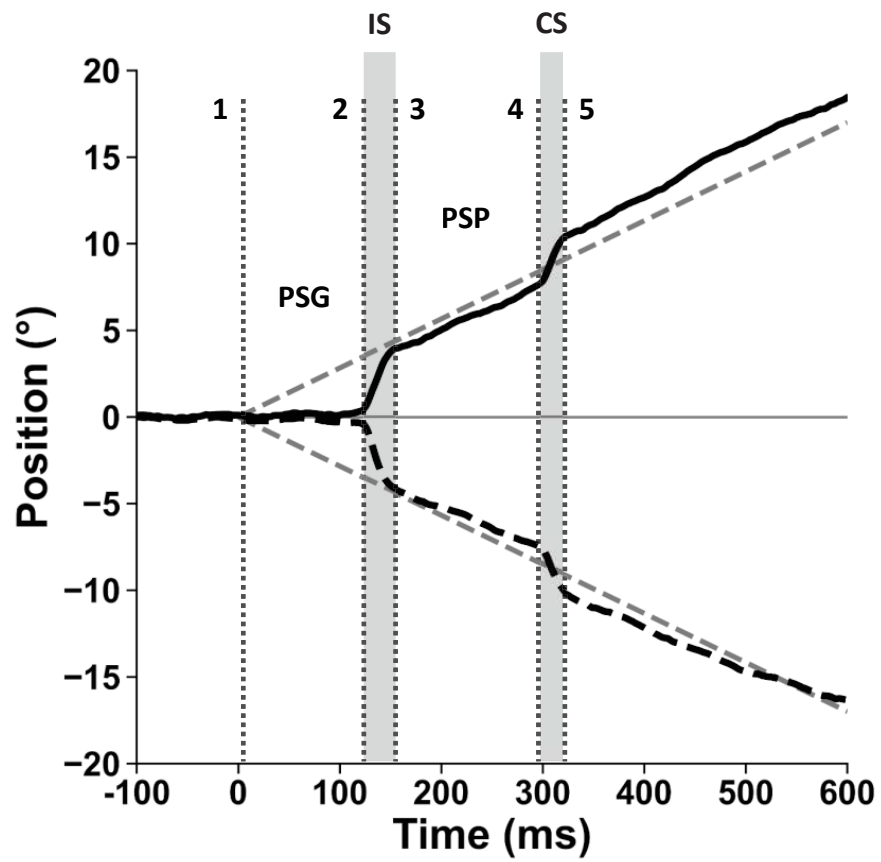
1054 and interquartile range (IQR) values of position/time landing ratio of interceptive saccades (y-  
 1055 axis) are compared to the post saccadic pursuit eye velocity (x axis) for the uncertain (top row)  
 1056 and certain (bottom) sessions. Different symbols correspond to different quadrants of 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

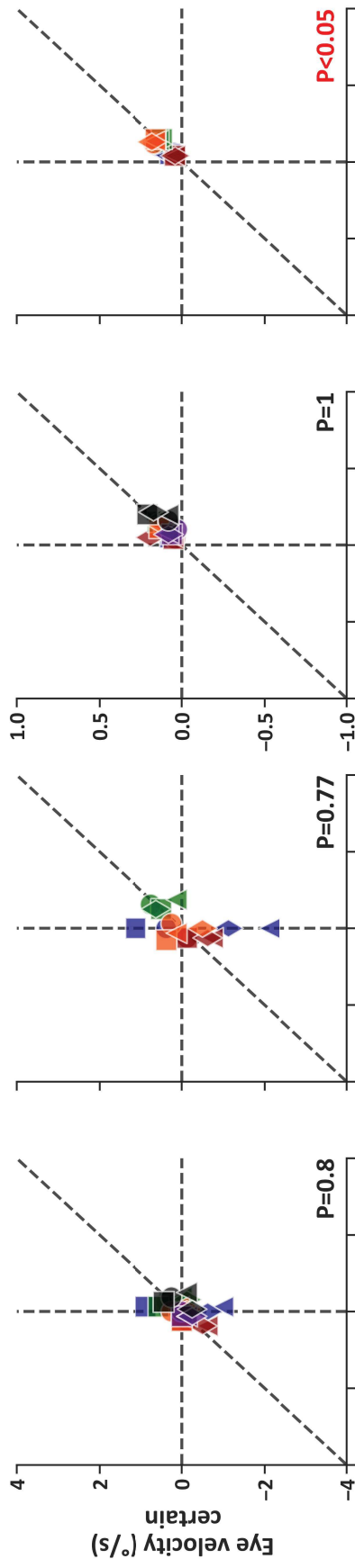
IQR

20°/s

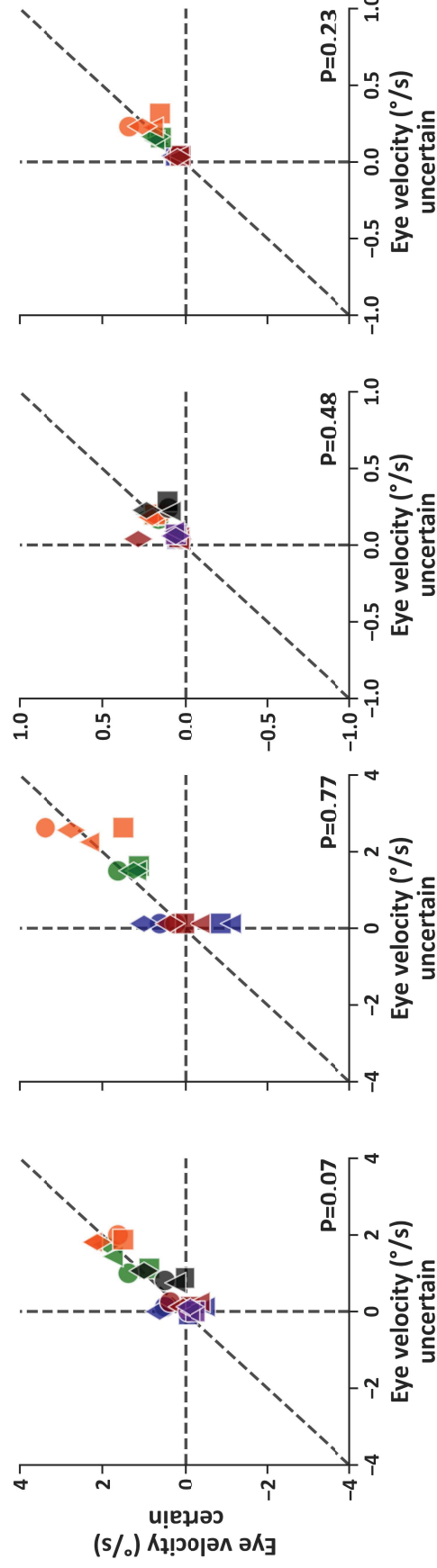
40°/s

20°/s

40°/s

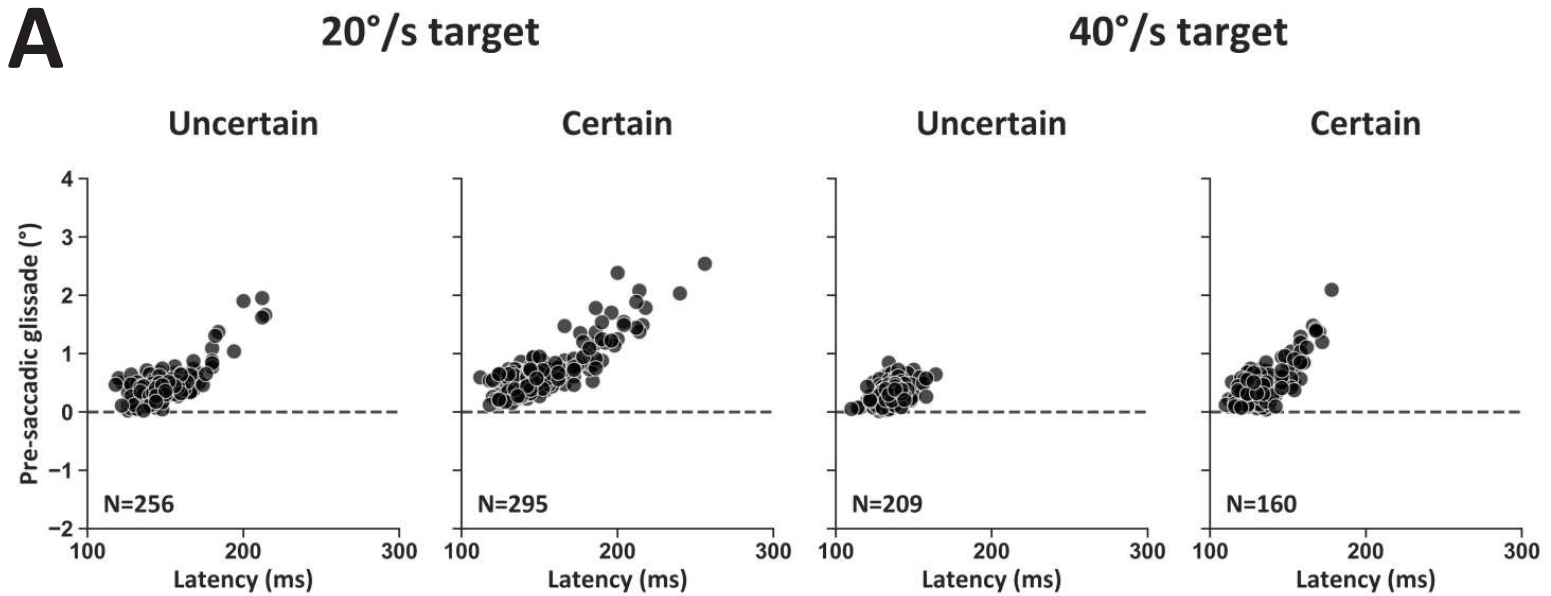
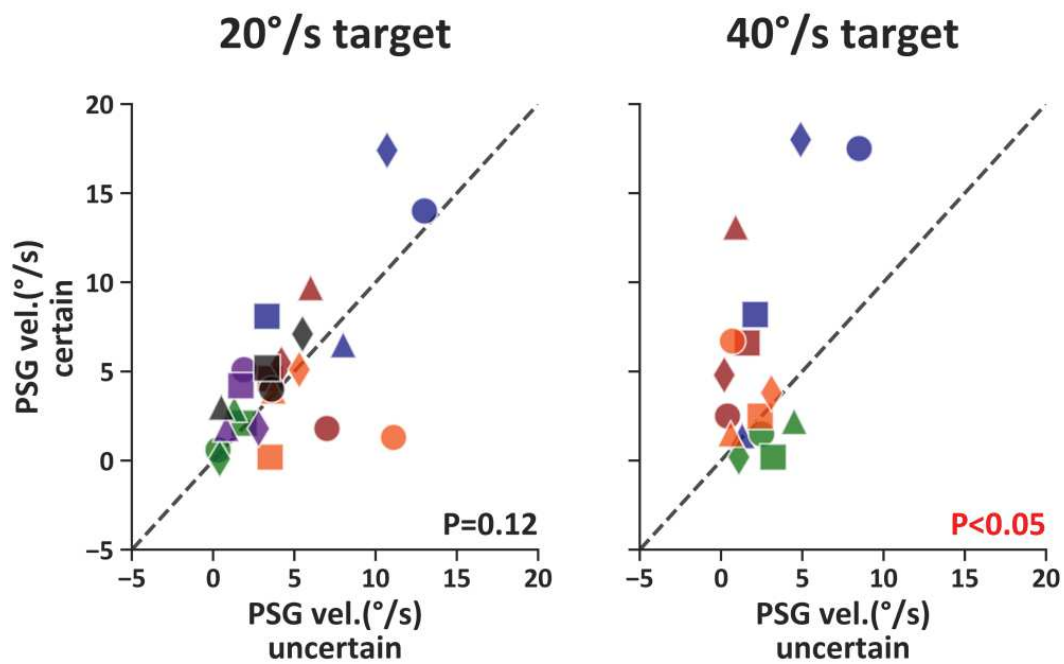


Hor.



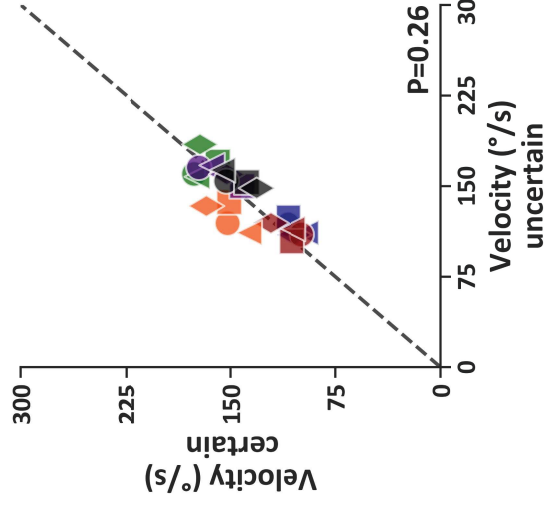
Ver.



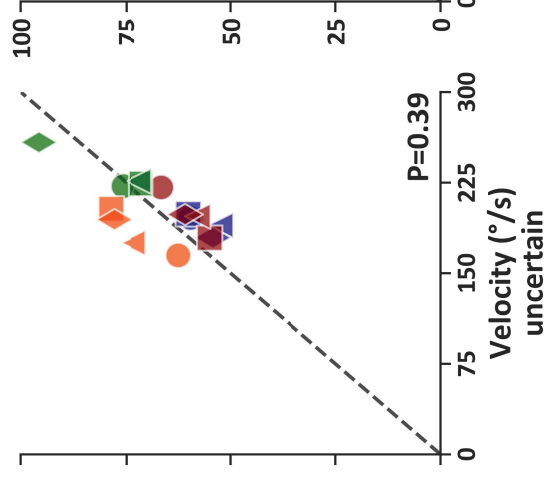
**A****B**

## Median

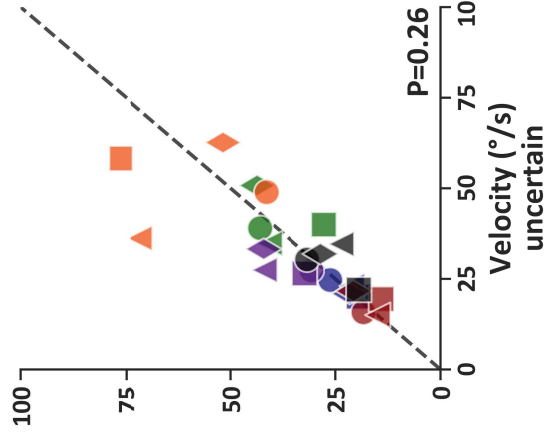
20°/s



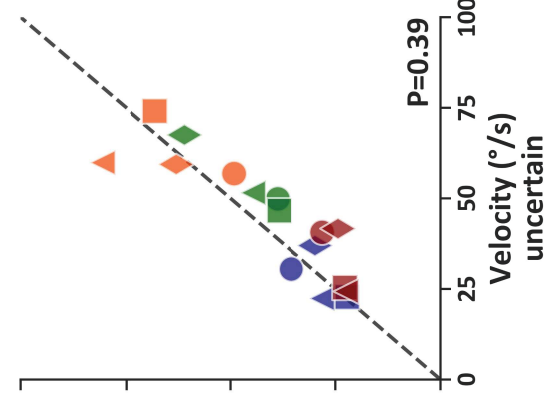
40°/s



20°/s

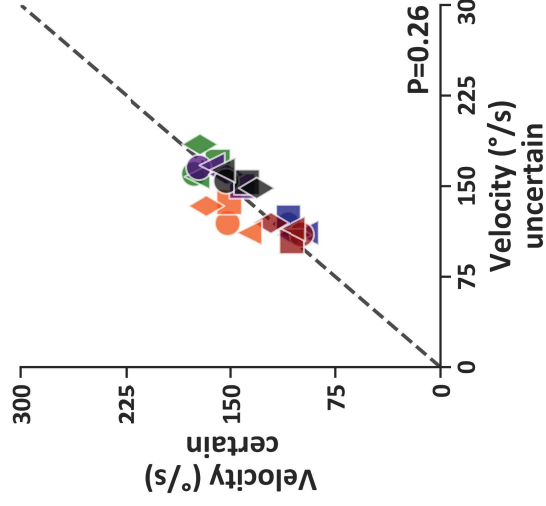


40°/s

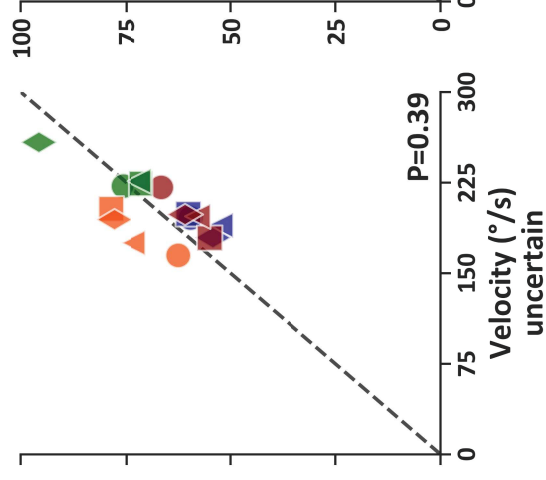


## IQR

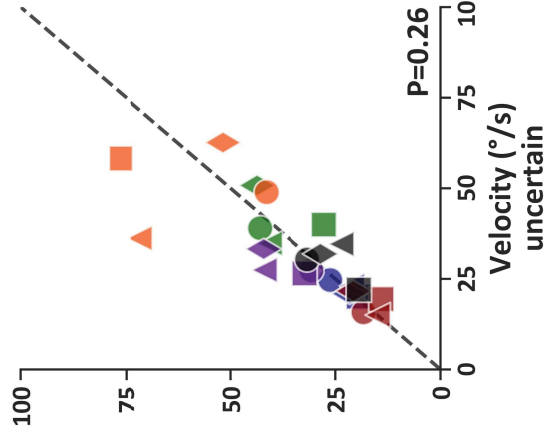
20°/s



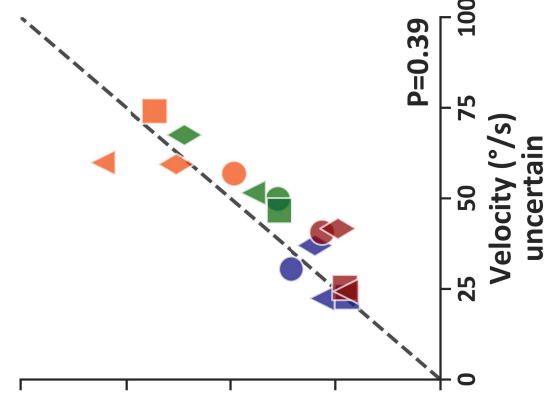
40°/s

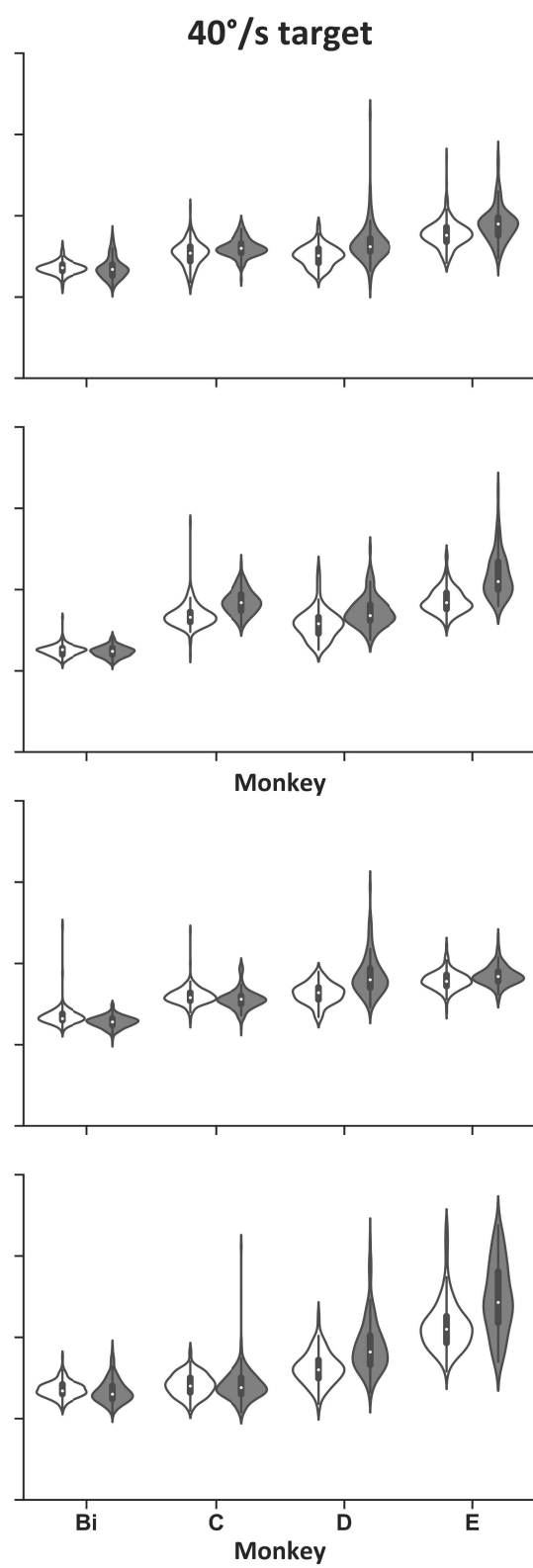
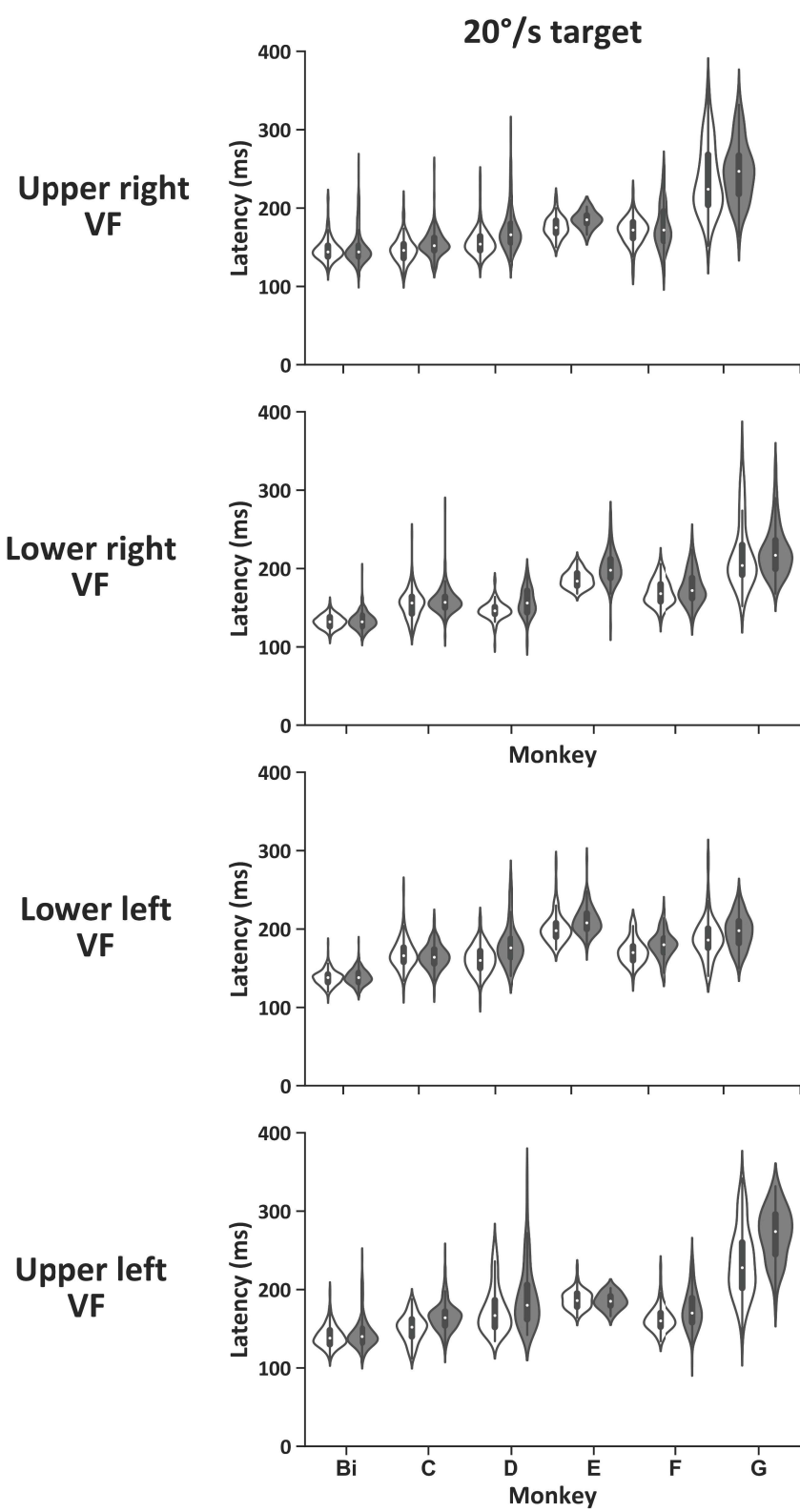


20°/s

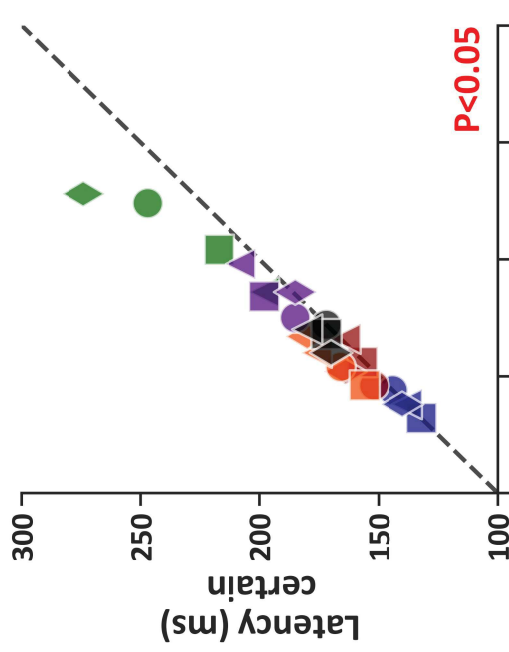


40°/s



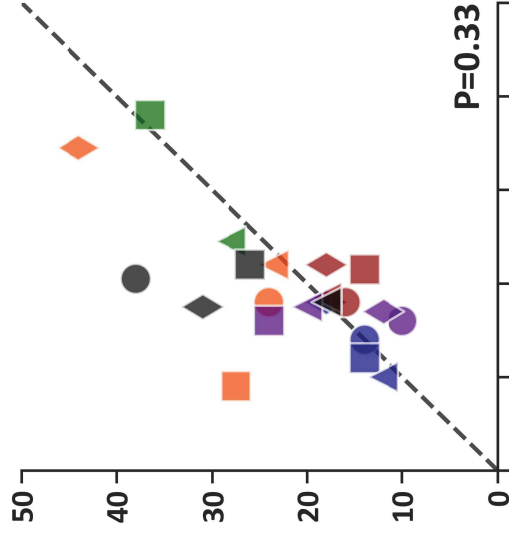


Median



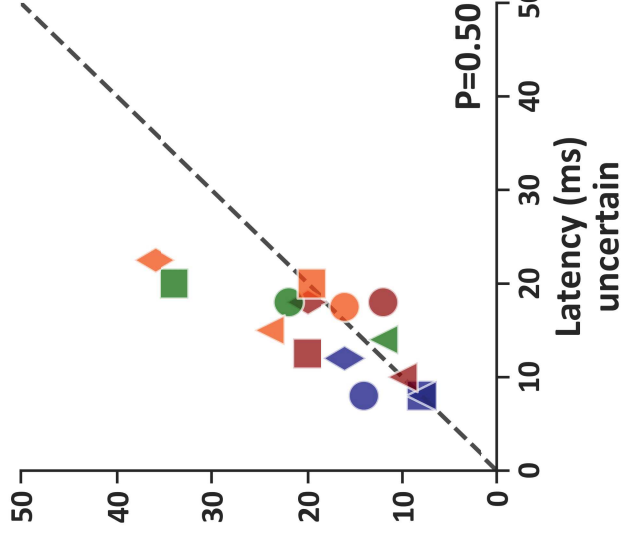
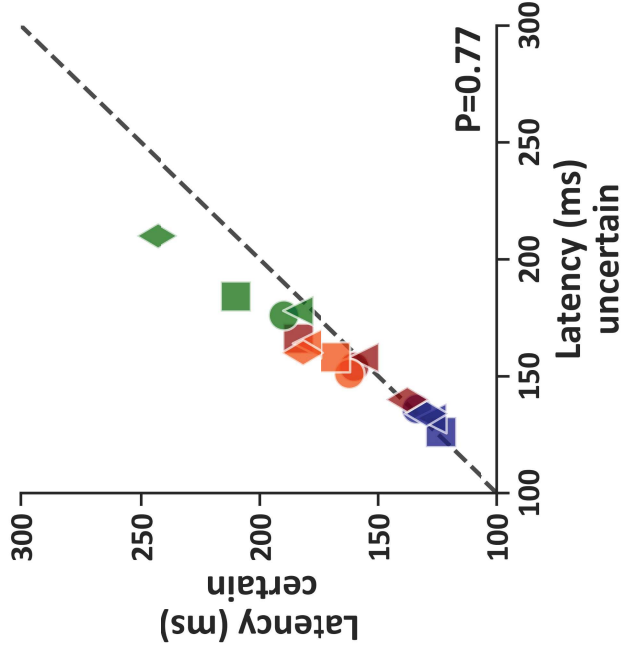
20°/s  
target

IQR

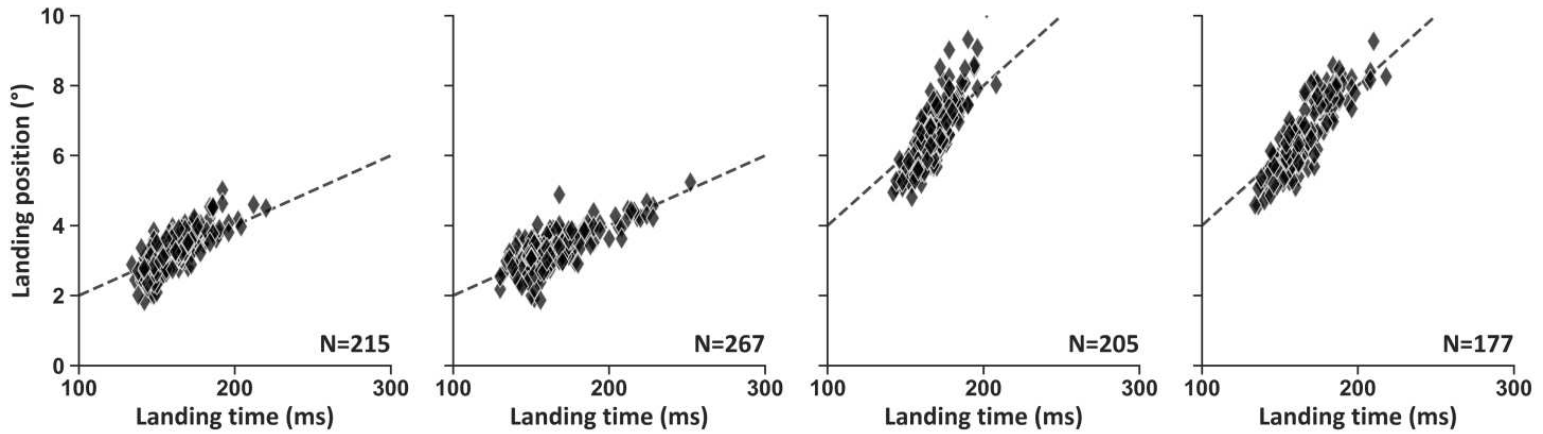
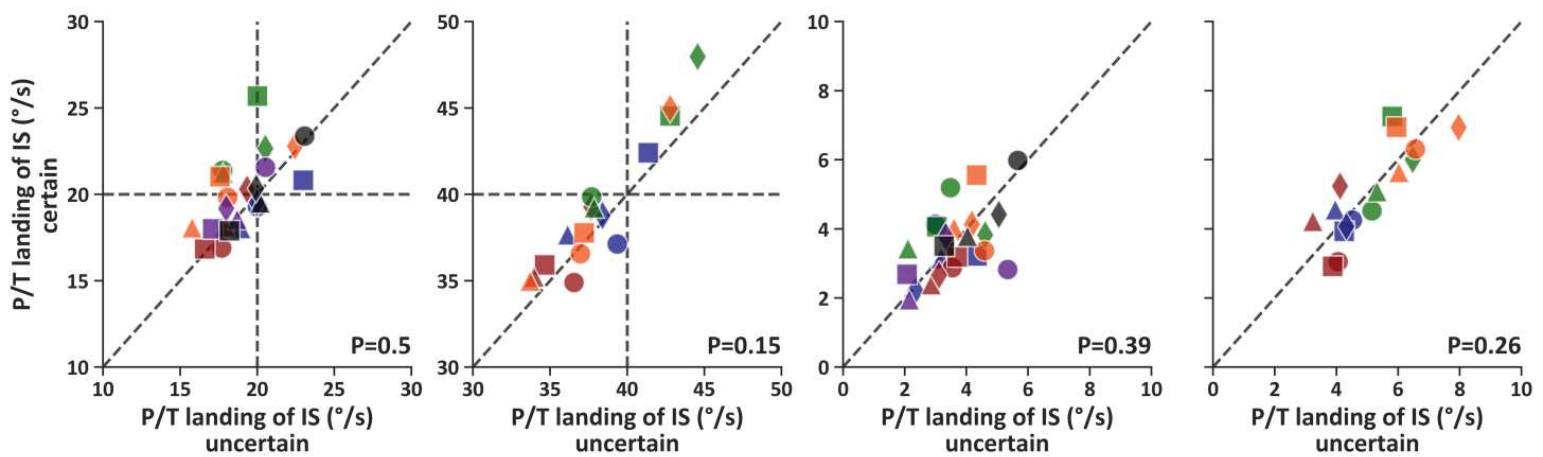


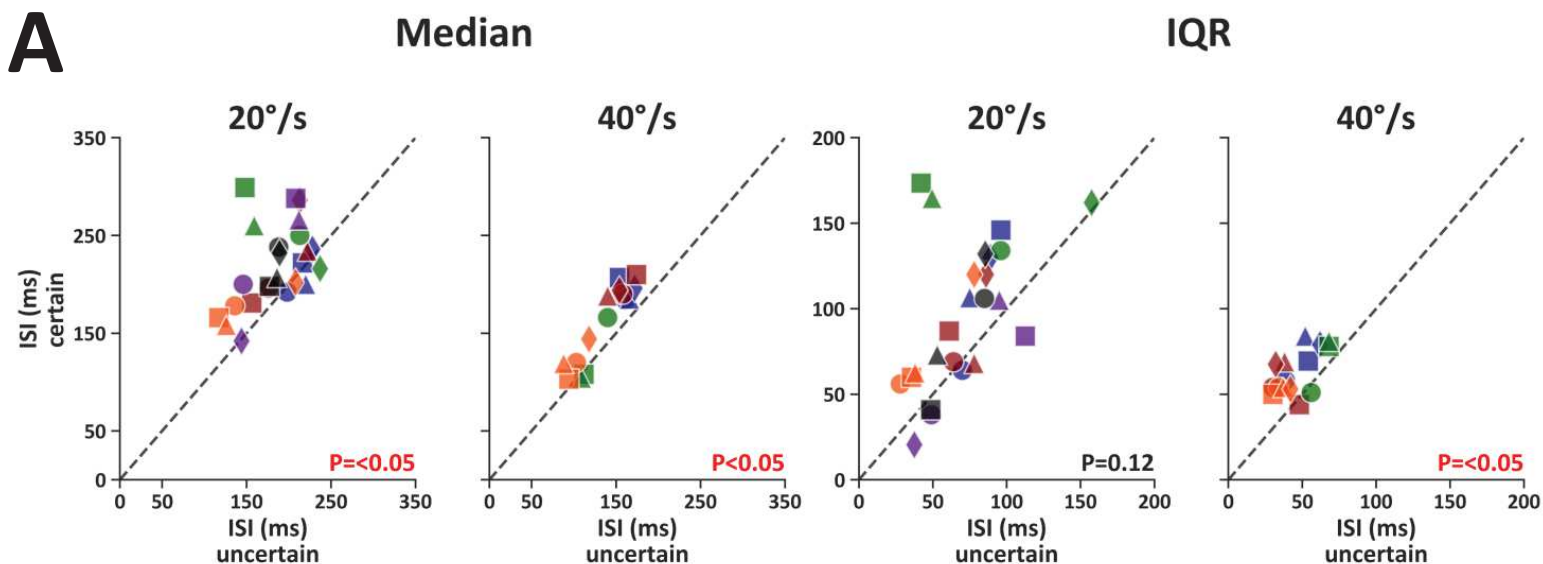
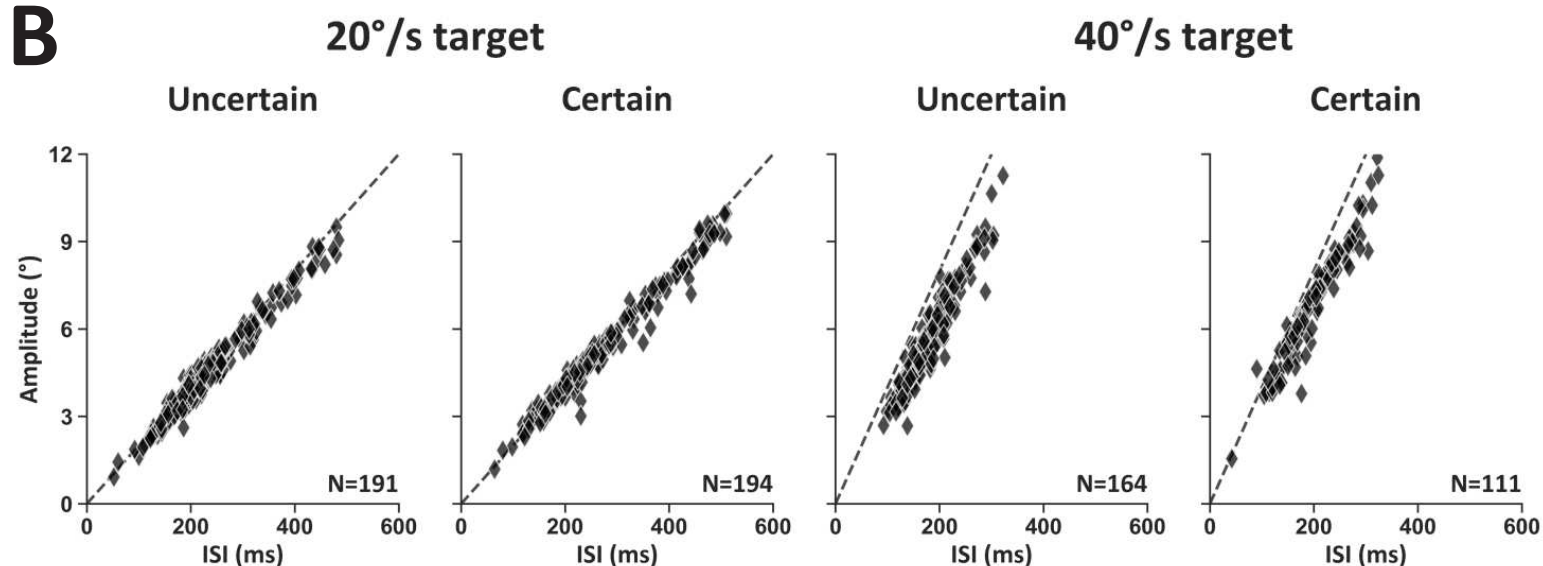
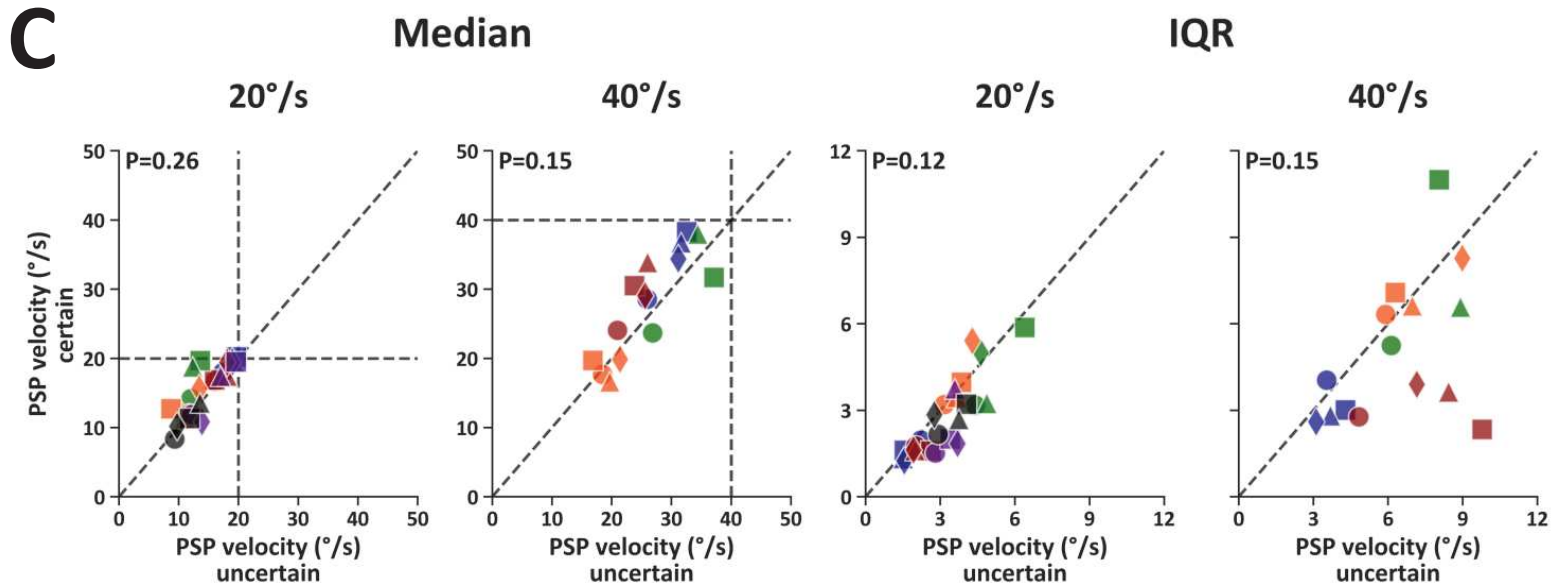
- Upper right VF
- Lower right VF
- ▲ Lower left VF
- ◆ Upper left VF

40°/s  
target

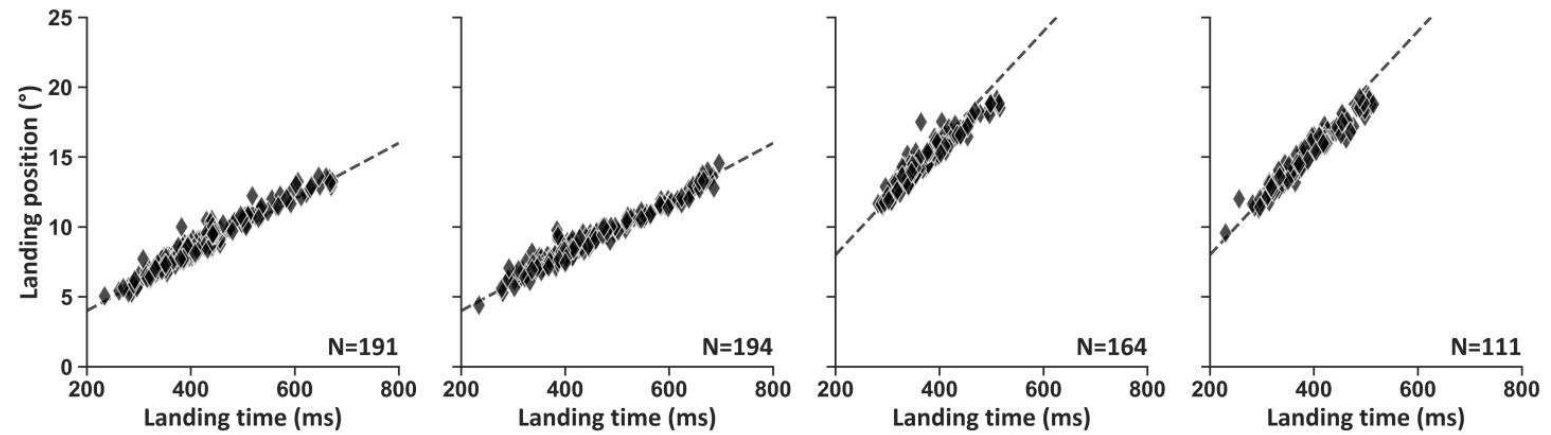
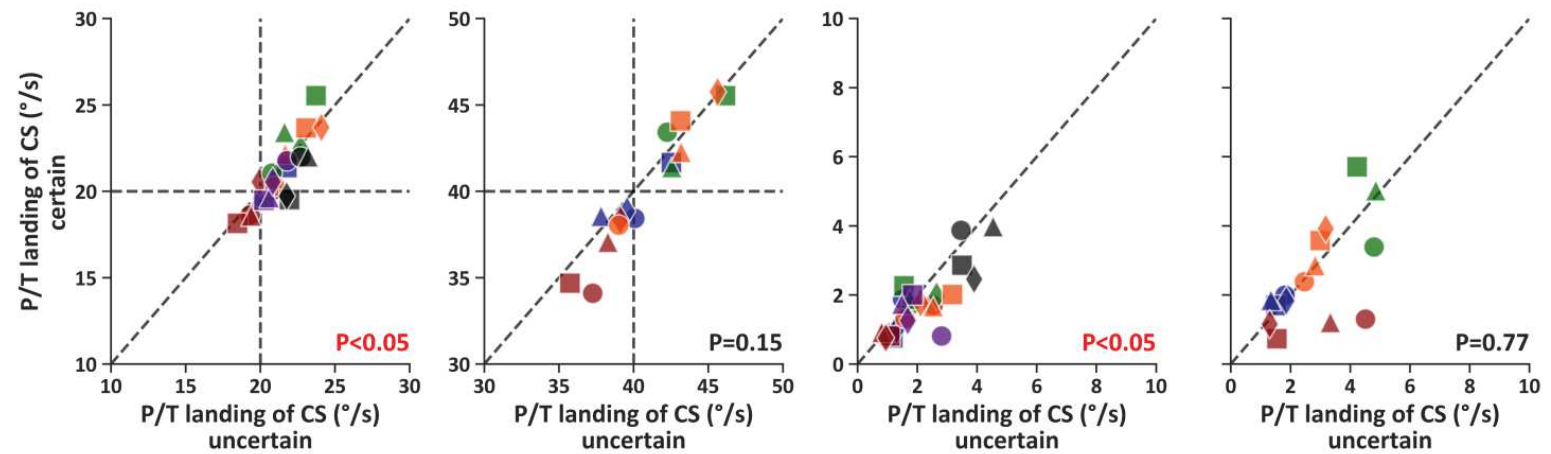


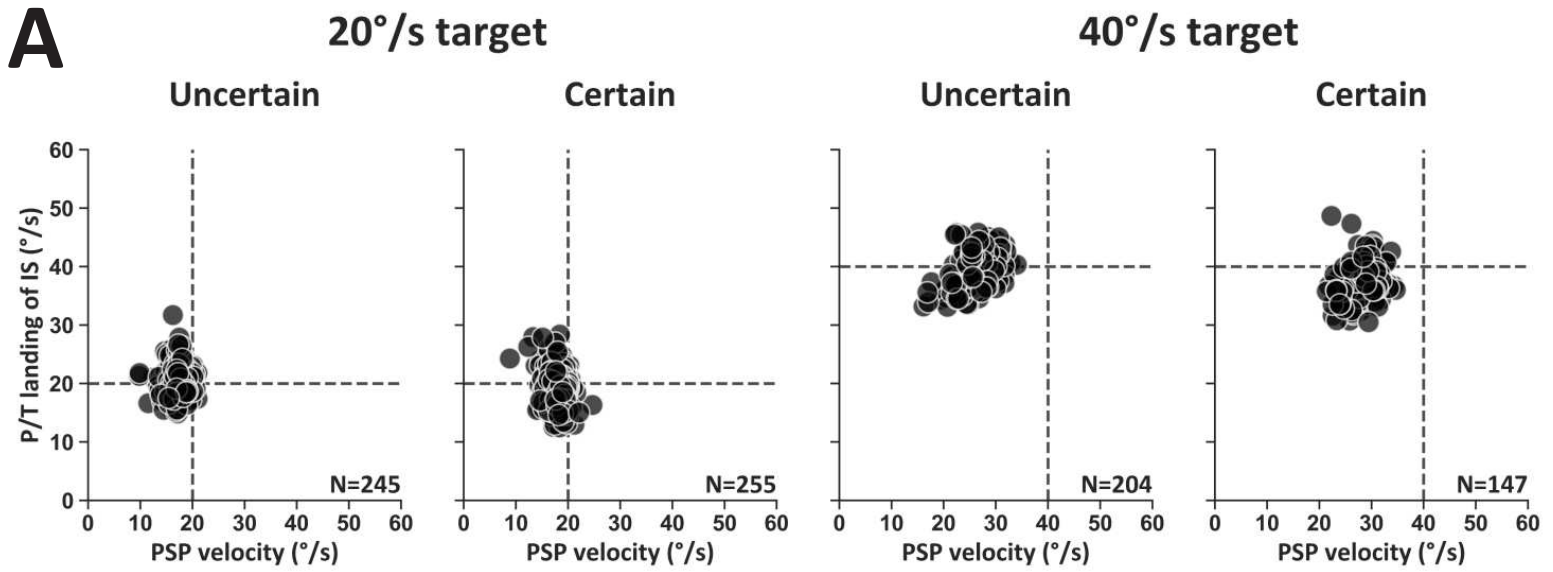
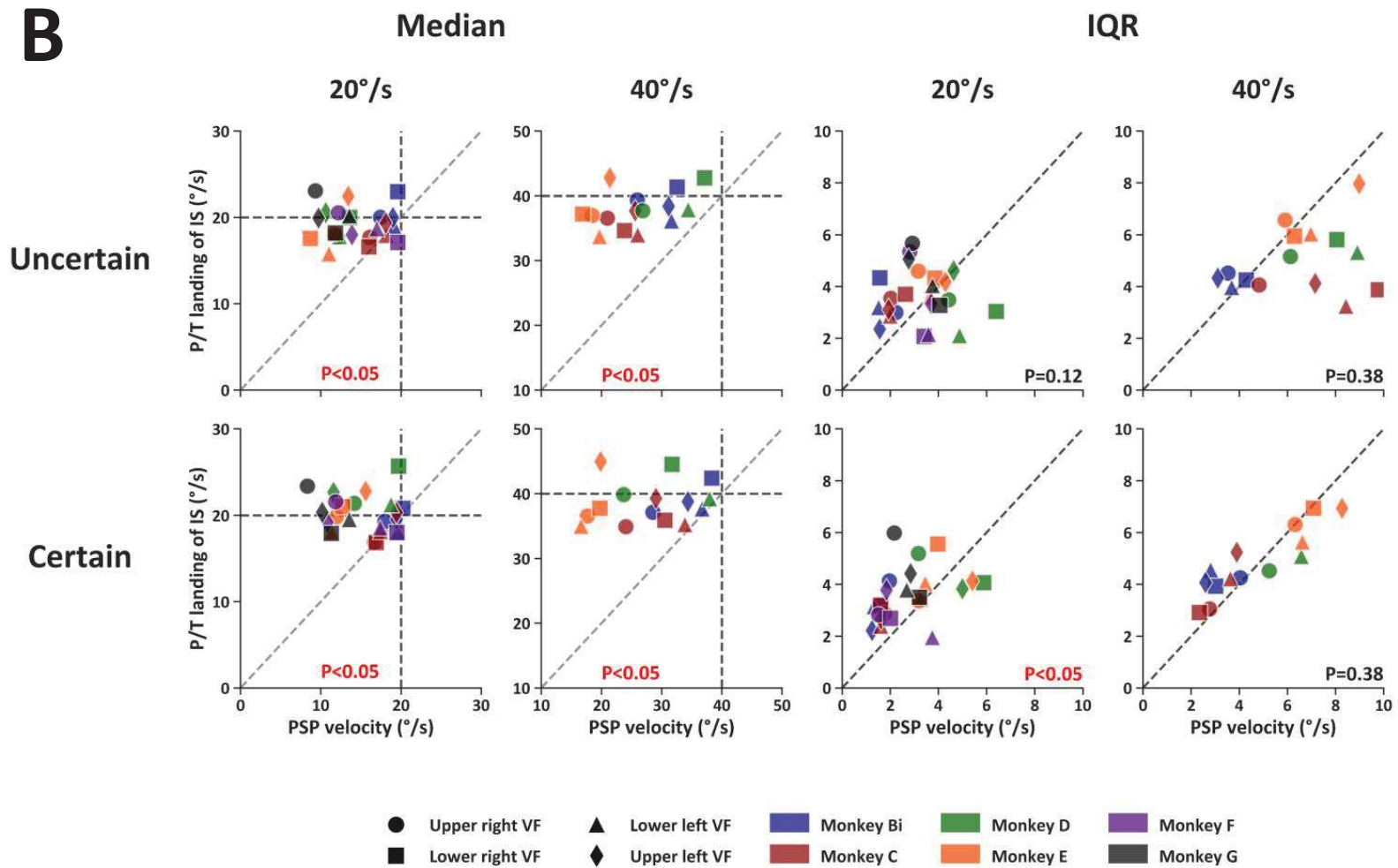
- Monkey Bi
- Monkey C
- Monkey D
- Monkey E
- Monkey F
- Monkey G

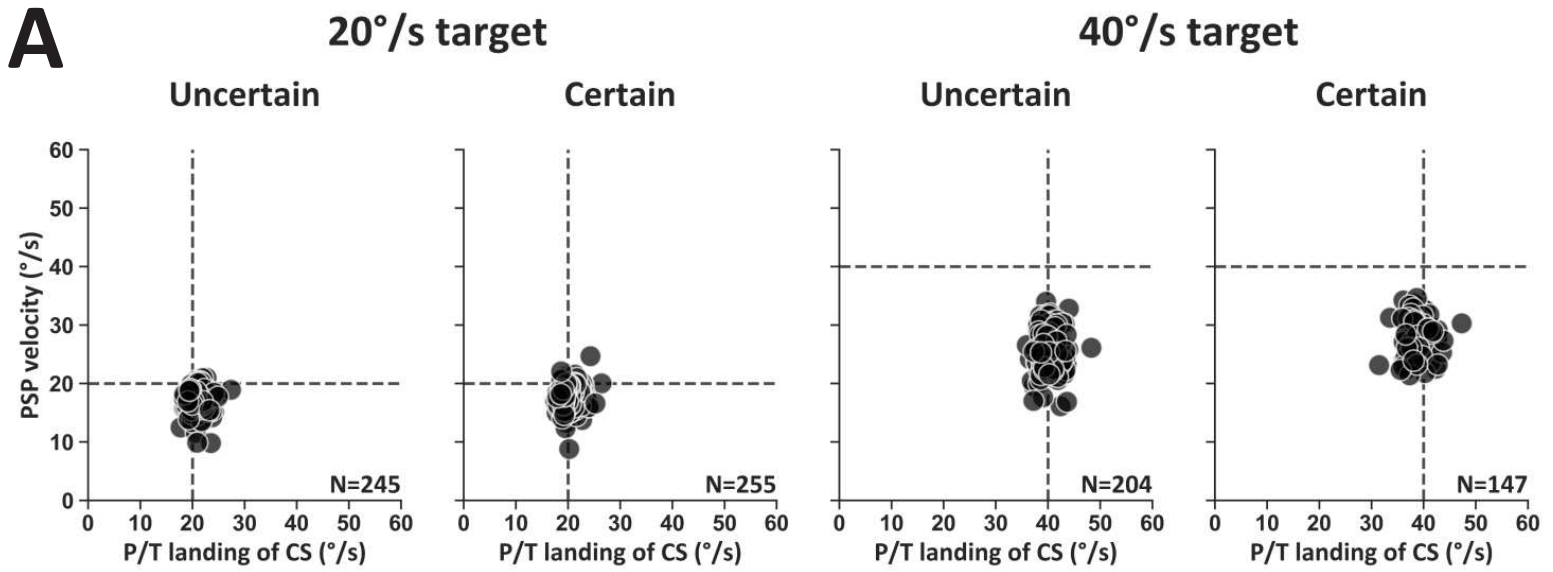
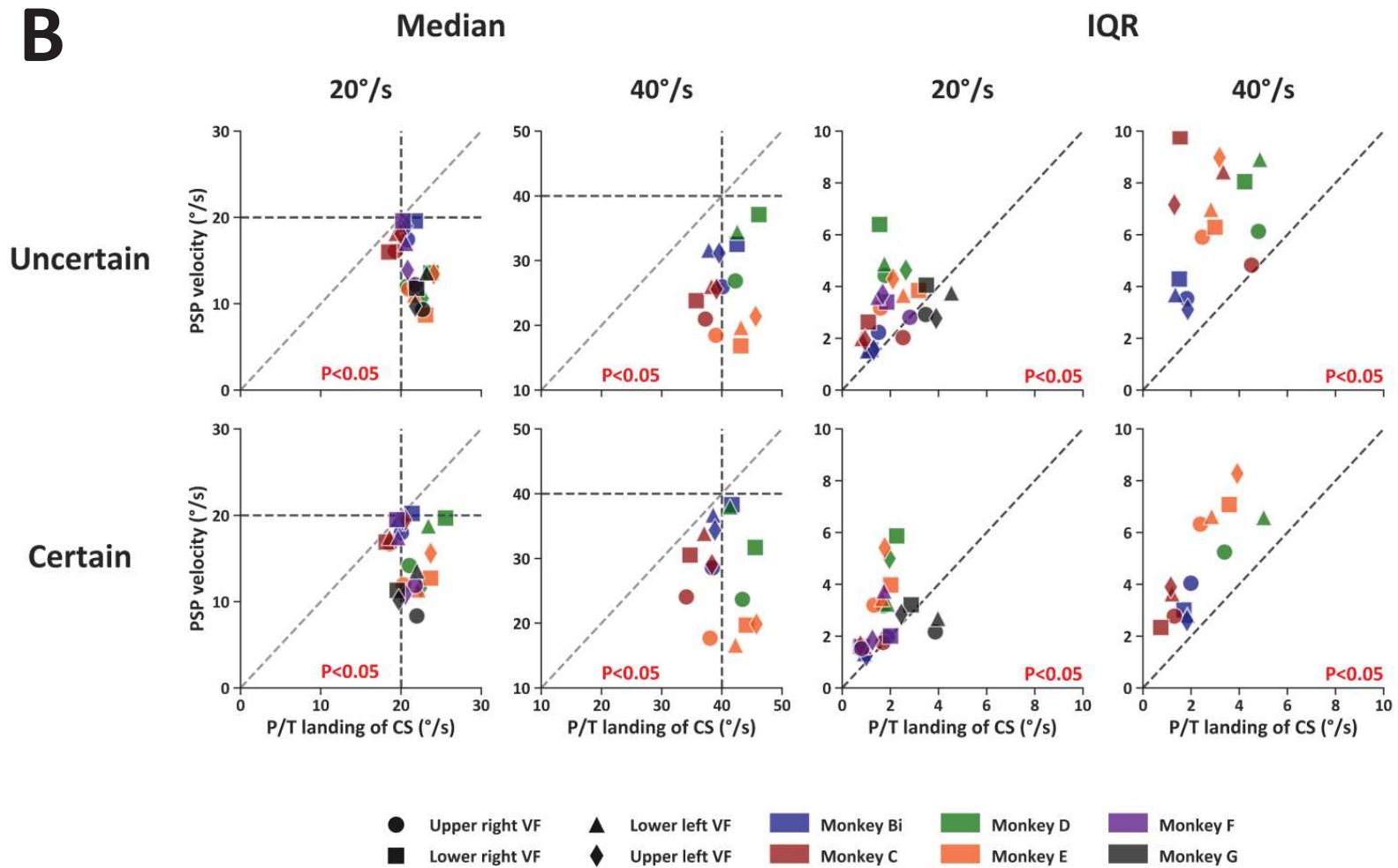
**A****20°/s target****40°/s target****Uncertain****Certain****Uncertain****Certain****B****Median****IQR****20°/s****40°/s****20°/s****40°/s**

**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

