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**The transfer function of the rhesus macaque oculomotor system for small-amplitude slow motion trajectories**

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31 **small-amplitude slow motion trajectories**

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42 **Abstract**

43 Two main types of small eye movements occur during gaze fixation: microsaccades and  
44 slow ocular drifts. While microsaccade generation has been relatively well-studied,  
45 ocular drift control mechanisms are unknown. Here we explored the degree to which  
46 monkey smooth eye movements, on the velocity scale of slow ocular drifts, can be  
47 generated systematically. Two male rhesus macaque monkeys tracked a spot moving  
48 sinusoidally, but slowly, along the horizontal or vertical directions. Maximum target  
49 displacement in the motion trajectory was 30 min arc (0.5 deg), and we varied the  
50 temporal frequency of target motion from 0.1 to 5 Hz. We obtained an oculomotor  
51 “transfer function” by measuring smooth eye velocity gain (relative to target velocity) as  
52 a function of frequency, similar to past work with large-amplitude pursuit. Monkey eye  
53 velocities as slow as those observed during slow ocular drifts were clearly target-motion  
54 driven. Moreover, like with large-amplitude smooth pursuit, eye velocity gain varied with  
55 temporal frequency. However, unlike with large-amplitude pursuit, exhibiting primarily  
56 low-pass behavior, small-amplitude motion tracking was band-pass with the best ocular  
57 movement gain occurring at ~0.8-1 Hz. When oblique directions were tested, we found  
58 that monkey oblique pursuit gain for small-amplitude slow motion trajectories was >1.  
59 Our results provide a catalogue of the control abilities of the monkey oculomotor system  
60 for slow target motions, and they also support the notion that smooth fixational ocular  
61 drifts are controllable. This has implications for neural investigations of drift control and  
62 the image-motion consequences of drifts on visual coding in early visual areas.

63  
64

## 65 **Introduction**

66 Small fixational eye movements continuously move the retinal image, even though they  
67 never deviate the center of gaze (or fovea) away from objects of interest. Such continuous  
68 movements mean that the neural signals representing input images in a variety of early  
69 visual areas are continuously modulated, and this has implications for theoretical  
70 interpretations of neural variability across trials, as well as population correlations in  
71 simultaneously recorded neurons (McFarland et al. 2016; Rucci and Victor 2015).  
72 Therefore, understanding the neural control mechanisms for fixational eye movements is  
73 an important first step towards understanding the full impact of these eye movements on  
74 neural coding, and ultimately visual perception.

75

76 Fixational eye movements come in two main flavors: microsaccades, which are rapid  
77 gaze shifts that look like big saccades; and smooth ocular drifts, which are slow changes  
78 in eye position occurring in between microsaccades (Barlow 1952; Murphy et al. 1975;  
79 Nachmias 1961). Even though microsaccades have received a substantial amount of  
80 research attention recently (Hafed 2011; Hafed et al. 2015; Krauzlis et al. 2017; Rolfs  
81 2009), drifts remain to be relatively underexplored. For example, the mechanisms for  
82 generating ocular drifts are unknown, whereas microsaccade generation has been studied  
83 in a variety of different brain areas (Arnstein et al. 2015; Hafed et al. 2009; Hafed and  
84 Krauzlis 2012; Peel et al. 2016; Sun et al. 2016; Van Horn and Cullen 2012). Moreover,  
85 uncovering detailed neural mechanisms for microsaccade generation in certain key brain  
86 areas was instrumental for uncovering important, previously unappreciated, consequences  
87 of these eye movements on vision, perception, and even cognition (Chen et al. 2015;

88 Hafed 2013; 2011; Hafed et al. 2015; Krauzlis et al. 2017; Tian et al. 2016; Veale et al.  
89 2017). Thus, exploring the neural mechanisms for slow ocular drift generation is a  
90 worthwhile effort, especially given the fact that during fixation, microsaccades are brief  
91 events in an otherwise continuous sea of ocular drifts.  
92  
93 Here, towards approaching that ultimate goal, we aimed to characterize the degree to  
94 which the control system for eye position in the macaque monkey brain is able to  
95 generate very slow smooth pursuit eye movements, on the velocity scale of fixational  
96 ocular drifts. In other words, is it possible for monkeys to volitionally generate a slow eye  
97 movement that is as small in amplitude and velocity as slow ocular drifts, but that is  
98 clearly controlled and with a predictable motion trajectory? We designed behavioral  
99 experiments motivated by potential analogies that one can make between slow ocular  
100 drifts and smooth pursuit eye movements (Cunitz 1970; Martins et al. 1985; Nachmias  
101 1961), similar to analogies that one makes between microsaccades and larger saccades  
102 (Hafed 2011; Krauzlis et al. 2017). After all, smooth pursuit eye movements are  
103 (relatively) slow rotations of the eyeball, similar in nature to slow ocular drifts, and the  
104 circuits for generating such smooth pursuit eye movements are well studied (Krauzlis  
105 2004).  
106  
107 We presented macaque monkeys with small-amplitude sinusoidal target trajectories, and  
108 we asked how well their small-amplitude slow eye movements can track such  
109 trajectories. Our approach was to assume that for the frequency ranges that we studied,  
110 the oculomotor system may behave, to a first approximation, like a linear system. This

111 means that we can present a single frequency and measure the response, and then test  
112 another frequency, and so on. The gain and phase lag of tracking at each frequency can  
113 thus allow estimating an “equivalent” transfer function of the oculomotor system (Ohashi  
114 and Mizukoshi 1991). Previous attempts like this with larger-amplitude (and faster) eye  
115 movements in smooth pursuit were effective, and showed that pursuit tracks very well for  
116 low frequencies ( $<1$  Hz), but that it then behaves relatively poorly with higher  
117 frequencies (exhibiting both lower gain and larger phase lag) (Bahill and McDonald  
118 1983; Collewijn and Tamminga 1984; Fabisch et al. 2009; Martins et al. 1985; Ohashi  
119 and Mizukoshi 1991; Rottach et al. 1996). We were interested in what happens in the  
120 monkey with much smaller and slower eye movements. The key comparison was to see  
121 whether controlled slow eye movements as slow as fixational ocular drifts would be  
122 possible. Critically, we performed our experiments on monkeys in order to demonstrate  
123 that these animals are instrumental for ultimately uncovering the neural control  
124 mechanisms for slow ocular drifts, and also in order to complement earlier human work  
125 on the topic (Cunitz 1970; de Bie and van den Brink 1986; Martins et al. 1985; Murphy et  
126 al. 1975; Nachmias 1961; Wyatt and Pola 1981).

127

128

129 **Materials and Methods**

130 *Animal preparation and laboratory setup*

131 We recorded eye movements from two male rhesus macaque (*macaca mulatta*) monkeys  
132 (monkey A and monkey M) aged 6-7 years. We implanted one eye (left for monkey A  
133 and right for monkey M) in each animal with a scleral search coil for eye tracking using  
134 the magnetic induction technique (Fuchs and Robinson 1966; Judge et al. 1980). Surgical  
135 procedures for implantation were similar to those described earlier (Chen and Hafed  
136 2013; Hafed and Ignashchenkova 2013), and the experiments were approved by ethics  
137 committees at the regional governmental offices of the city of Tübingen. These  
138 experiments were in accordance with European Union guidelines on animal research, as  
139 well as the associated implementations of these guidelines in German law.

140

141 We used monkeys in this study for two important reasons. First, the monkeys had scleral  
142 search coils implanted, which allowed the most precise measurement of small-amplitude  
143 slow eye movements, including fixational drifts. Video-based eye trackers (used in most  
144 human studies) are less reliable than scleral search coils for measuring slow eye  
145 movements. Second, and more importantly, the monkeys are now being used in  
146 neurophysiological recording experiments, such that direct neural correlates of our  
147 observations here can be identified and disseminated; particularly to complement earlier  
148 human work on similar questions (Cunitz 1970; de Bie and van den Brink 1986; Martins  
149 et al. 1985; Murphy et al. 1975; Nachmias 1961).

150

151 During data collection, the animals were seated in a primate chair 73 cm from a CRT  
152 computer monitor in an otherwise dark room. The monitor had a pixel resolution of 34  
153 pixels/deg and a refresh rate of 120 Hz. Stimuli were presented over a uniform gray  
154 background (29.7 Cd/m<sup>2</sup> in Experiment 1, and either 29.7 or 4.4 Cd/m<sup>2</sup> in Experiment 2).  
155 A small white spot (~5 x 5 min arc square) having 86 Cd/m<sup>2</sup> luminance in Experiment 1  
156 and either 86 or 48.1 Cd/m<sup>2</sup> in Experiment 2 was used as the moving target for smooth  
157 pursuit eye movements (see *Behavioral tasks* below).

158

159 Graphics on the CRT monitor were presented by a computer running Matlab's  
160 Psychophysics Toolbox (Brainard 1997; Kleiner et al. 2007; Pelli 1997). This computer  
161 in turn received commands from a real-time I/O system from National Instruments  
162 (Austin, USA), which ensured control of the display on a frame-by-frame basis, as well  
163 as real-time monitoring of animal behavior and reward. The system was described  
164 recently (Chen and Hafed 2013; Tian et al. 2018; 2016).

165

166 *Behavioral tasks*

167 *Experiment 1: Temporal frequency series*

168 The monkeys fixated a small white spot for 350-550 ms at trial onset, after which the spot  
169 started moving either horizontally or vertically along a sinusoidal position trajectory of  
170 only 30 min arc (0.5 deg) amplitude. The monkeys had to track this moving target with  
171 their eyes, and target position in deg (along either the horizontal or vertical axis) could be  
172 described by the following equation

173

174 
$$\text{target position} = 0.5 \times \sin(2\pi ft + \varphi) \quad (1)$$

175

176 where  $f$  is the temporal frequency of target trajectory,  $t$  is time from motion onset, and  $\phi$   
177 could be either 0 or  $\pi$  across trials. The temporal frequency,  $f$ , of target motion was  
178 chosen randomly from trial to trial from among the following values: 0.1, 0.2, 0.3, 0.4,  
179 0.5, 0.6, 0.8, 1, 2, 3, 4, or 5 Hz. Target motion duration was constant within a session, but  
180 could vary across sessions in the range of 3000-4200 ms, depending on animal  
181 motivation on any one day. In all cases, we had a long enough target motion duration to  
182 ensure that we were analyzing steady-state tracking behavior, even for the smallest values  
183 of  $f$  (associated with the slowest target position changes). Horizontal and vertical target  
184 trajectories were collected in different blocks of trials, and we analyzed a total of 867  
185 trials from monkey A and 1392 trials from monkey M. We did not penalize the monkeys  
186 (e.g. by aborting trials) for making catch-up saccades as long as they stayed within a  
187 radius of  $\sim 1$ -1.5 deg around the instantaneous target position.

188

189 *Experiment 2: Amplitude series*

190 The monkeys performed a similar experiment to that described above, but this time, the  
191 temporal frequency,  $f$ , was maintained at 0.5 Hz. Also, we interleaved different target  
192 motion directions, and we varied the amplitude of the target motion. Target motion  
193 trajectory was now described by the following equations

194

195 
$$\text{horizontal target position} = \text{Amp}_h \times \sin(2\pi ft) \quad (2)$$

196 
$$\text{vertical target position} = \text{Amp}_v \times \sin(2\pi ft) \quad (3)$$



197

198 where  $f$  was fixed at 0.5 Hz, and  $Amp_h$  and  $Amp_v$  specified the target motion amplitudes.

199 For purely horizontal target motions,  $Amp_h$  and  $Amp_v$  were chosen to result in radial

200 amplitudes of 0.25, 0.5, 1, or 2 deg. We also introduced two oblique directions: “+45 deg

201 oblique pursuit” was used to describe the case when  $Amp_h$  and  $Amp_v$  were equal and

202 positive (again from among 0.25, 0.5, 1, or 2 deg); “+135 deg oblique pursuit” was used

203 to describe the case when  $Amp_v$  had an opposite sign from  $Amp_h$  and  $Amp_h$  was negative

204 (e.g. -0.25 deg for  $Amp_h$  and +0.25 deg for  $Amp_v$ ). In other words, the two oblique

205 directions both started with upward motion trajectory, but with one first moving

206 rightward/upward (+45 deg) and the other first moving leftward/upward (+135 deg).

207 During the sessions, we interleaved all amplitude and direction conditions. We analyzed a

208 total of 969 trials from monkey A and 2145 trials from monkey M.

209

210 *Experiment 3: Fixation comparison*

211 For a subset of analyses, we compared eye velocity during tracking of small-amplitude

212 motion trajectories to eye velocity during fixation. The monkeys simply fixated the same

213 small spot for 1000-1400 ms before getting rewarded. We analyzed a total of 3160 trials

214 from monkey A and 5222 trials from monkey M.

215

216 *Data analysis*

217 *Detecting catch-up saccades*

218 We detected catch-up saccades using velocity and acceleration criteria (Chen and Hafed

219 2013; Hafed et al. 2009; Krauzlis and Miles 1996), and we manually inspected all

220 movements to correct for misses or false detections. For a subset of the data, we used  
221 instead a novel state-of-the-art machine-learning approach for saccade detection using  
222 convolutional neural networks, which we have developed (Bellet et al. 2018).

223

224 Catch-up saccade detection was necessary for performing focused analyses on smooth  
225 pursuit eye movements (see below), but we also analyzed interesting properties of these  
226 saccades themselves. For example, we explored both the frequency of occurrence and  
227 amplitude of these eye movements as a function of either target motion temporal  
228 frequency,  $f$ , or amplitude ( $Amp_h$ ,  $Amp_v$ ).

229

230 *Measuring smooth pursuit gain and phase lag*

231 We plotted eye velocity as a function of time for either horizontal or vertical eye  
232 movements. For oblique motion trajectories (Experiment 2), we performed a coordinate  
233 rotation such that one component of eye velocity was along the motion trajectory and the  
234 other was orthogonal, and we plotted eye velocity for the component along the motion  
235 trajectory (in other analyses, we also analyzed the horizontal and vertical components of  
236 oblique eye velocity independently). We then picked a period of steady-state smooth  
237 pursuit execution by excluding the first 1000 ms of eye movement data after target  
238 motion onset (in Experiment 2, we relaxed this to 300 ms). In each velocity trace, we  
239 then excised any interval during which a catch-up saccade was being executed, and we  
240 also removed 10 ms before and 10 ms after each such saccade. The data that were excised  
241 were replaced by Not-a-Number (NaN) labels, such that averages of eye velocity across

242 trial repetitions of a given condition did not include the large velocity transients  
243 associated with catch-up saccades.  
244  
245 After plotting saccade-free eye velocity from any one trial, we fitted the resulting curve,  
246 using a least-squares fitting algorithm, with a sinusoidal function (of appropriate temporal  
247 frequency for the condition) in which the amplitude and phase values of the sinusoid  
248 were the fitting parameters. This resulted in a population of amplitudes and phases from  
249 the fitting procedure across trial repetitions of a given condition. For example, for 0.5 Hz  
250 horizontal target trajectories in Experiment 1, we could have a population of  $N$  fitted  
251 gains or phase lags across trials. We then summarized these  $N$  values into the mean gain  
252 or mean phase lag at 0.5 Hz target motion temporal frequency, and with appropriate 95%  
253 confidence intervals. “Gain” was defined as the ratio of the fitted eye velocity amplitude  
254 in a sinusoid divided by the true amplitude of the target velocity sinusoid. For example,  
255 for  $f$  Hz horizontal target trajectory with  $Amp_h$  deg position amplitude in equation 1 above  
256 (and also equations 2 and 3), the target velocity amplitude was  $2\pi f Amp_h$ . Similar  
257 procedures were performed for all conditions. In all analyses, we had >25 trials per  
258 condition in each animal (most often, significantly more; e.g. see Fig. 2).  
259  
260 In a subset of analyses (e.g. Fig. 9), we measured eye velocity directly. For example, we  
261 estimated eye velocity during smooth pursuit initiation or during baseline fixation (before  
262 target motion onset). We defined a measurement interval of 50 ms, starting either at -100  
263 ms or +100 ms from motion onset. The earlier interval measured eye velocity during

264 fixation, whereas the latter interval measured eye velocity during smooth pursuit  
265 initiation.

266

267 *Spectral analysis of eye positions*

268 For some analyses of the data from Experiment 1, we performed a discrete Fourier  
269 transform decomposition of eye position traces from the different values of  $f$  in equation  
270 1. We picked, in each trial, an epoch of steady-state smooth pursuit (i.e. removing the  
271 initial component immediately after motion onset as described above) that was 2500 ms  
272 long. We then applied a Hanning window followed by discrete Fourier transformation to  
273 investigate whether low-gain tracking was still modulated by the temporal frequency of  
274 the target motion. We then plotted the average spectrum across the individual trial  
275 spectra.

276

277 In all figures presented in this paper, we designated 95% confidence intervals as error  
278 bars, such that the statistical robustness of our results can be easily assessed.

279

## 280 **Results**

### 281 *Band-pass tuning for small-amplitude slow motion tracking in the monkey*

282 Our goal was to systematically characterize the quality of monkey ocular control when  
283 tracking small-amplitude slow motion trajectories. We were motivated by the more  
284 general question of how slow ocular drifts that occur during gaze fixation may be  
285 controlled, and how similar such control may be to the control needed when volitionally  
286 tracking a moving target. We therefore asked two monkeys to pursue a small spot that  
287 moved sinusoidally with an amplitude of only 30 min arc (0.5 deg) and different temporal  
288 frequencies (Experiment 1; Material and Methods). For temporal frequencies of <1 Hz,  
289 the peak velocities of target motion (based on equation 1) were always <3.14 deg/s, and  
290 they were even smaller for even lower frequencies like 0.4 Hz, and also at off-peak-  
291 velocity epochs of tracking. Therefore, the target velocities involved in our experiments  
292 were similar in scale to the velocities with which the eye may drift on its own during  
293 steady fixation (Cherici et al. 2012; Martins et al. 1985).

294

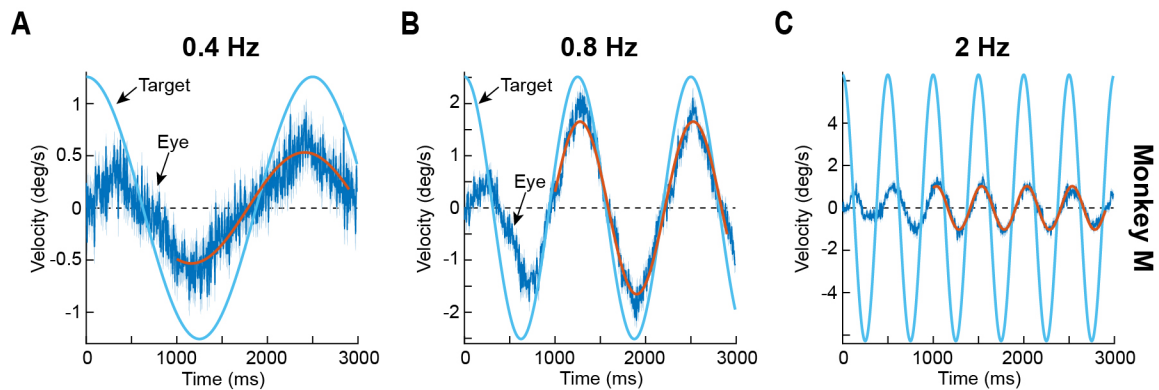
295 We found that eye velocity always tracked the temporal frequency of the target, albeit to  
296 varying degrees of success. For example, Fig. 1A shows average saccade-free (Materials  
297 and Methods) eye velocity from monkey M when this monkey tracked a horizontally  
298 moving spot at 0.4 Hz in Experiment 1. Error bars denote 95% confidence intervals  
299 across trials, and the solid blue line shows the true target velocity (based on the derivative  
300 of equation 1). As can be seen, the eye moved sinusoidally at a similar temporal  
301 frequency to the target, but eye velocity gain was quite low; fitting a sinusoid to the eye  
302 velocity data (in the sustained pursuit interval; Materials and Methods; red line in Fig 1A)

303 showed a peak velocity amplitude in the fit of 0.532 deg/s relative to the true target peak  
304 velocity of 1.26 deg/s, resulting in a gain of only 0.4235. There was also a phase lead of  
305 ~90 ms, which amounted to a lead of 0.036 of a full cycle of motion trajectory (3.6% of a  
306 full cycle). When the target temporal frequency was 0.8 Hz instead, eye velocity gain was  
307 significantly better (Fig. 1B), but it then decreased once again for even higher frequencies  
308 (e.g. Fig. 1C; temporal frequency of 2 Hz). Phase lead or lag also matched the gain  
309 changes by progressively shifting towards larger and larger lags, with 0.8 Hz showing  
310 now a minimal phase delay (28 ms, or 0.022 of a full cycle) in tracking (as opposed to a  
311 lead at 0.4 Hz), and the higher frequency showing an even more substantial delay of 35  
312 ms or 0.07 of a full cycle. Therefore, monkey smooth ocular tracking of small-amplitude  
313 slow motion trajectories may be described as being band-pass in nature, unlike the classic  
314 description of smooth pursuit tuning (with much faster target speeds) as being low-pass  
315 (Collewijn and Tamminga 1984; Fabisch et al. 2009; Rottach et al. 1996). This difference  
316 is not due to the use of monkeys in our current study, as opposed to humans in the earlier  
317 ones, because monkeys are indeed capable of high-gain sinusoidal pursuit of foveal spots  
318 when faster target speeds (but similar low temporal frequencies) are used (Hafed et al.  
319 2008; Hafed and Krauzlis 2008). It is very intriguing to us, nonetheless, that very highly  
320 trained human subjects performed significantly better at low temporal frequencies than  
321 our monkeys when face with similar small-amplitude motions (Martins et al. 1985).

322

323

324



325

326 **Figure 1 Band-pass nature of monkey smooth pursuit of small-amplitude slow motion trajectories.**

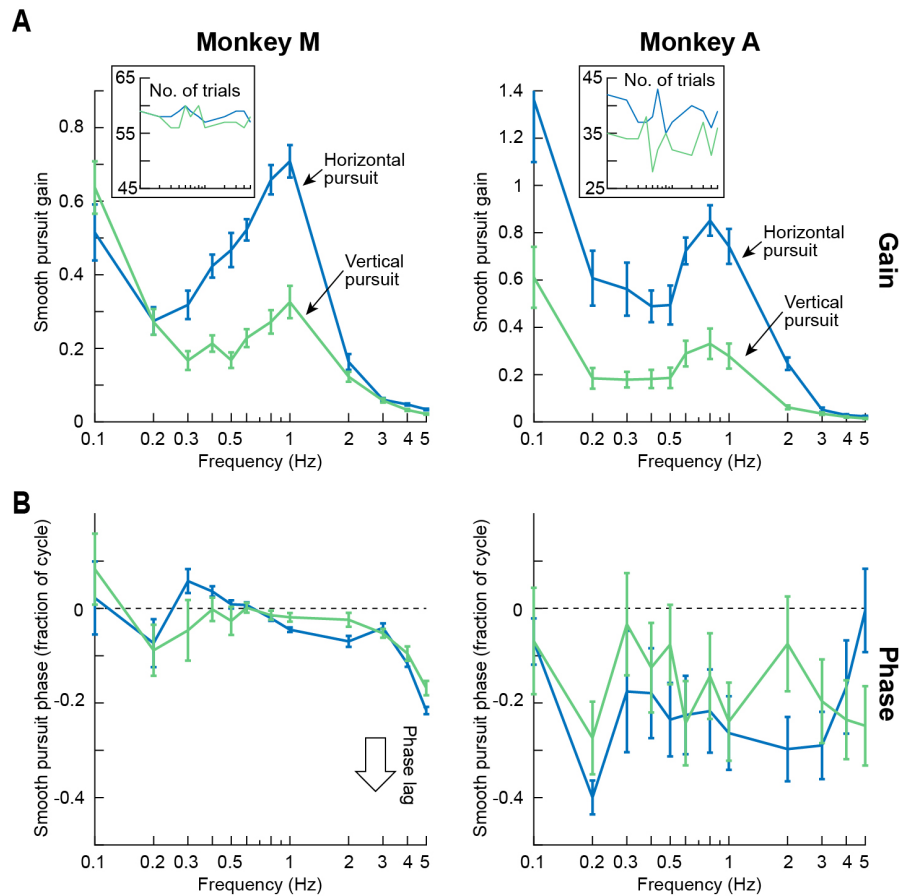
327 (A) Example tracking behavior from monkey M with 0.4 Hz sinusoidal target motion. The solid blue  
328 sinusoid represents target velocity. The dark blue data plot shows mean eye velocity across trials  
329 (surrounded by 95% confidence interval bands in a fainter color). The red sinusoid is a fit of the eye  
330 velocity data in a sustained interval starting 1000 ms after target motion onset. As can be seen, the eye  
331 tracked the frequency of target motion well, but with a markedly low peak velocity (i.e. low gain). (B)  
332 Tracking gain was significantly higher at 0.8 Hz. This panel is formatted identically to A. (C) For even  
333 higher frequencies, pursuit gain decreased again, as evidenced by the much smaller amplitude of the  
334 sinusoid describing eye velocity relative to that describing target velocity (red and blue sinusoids,  
335 respectively). Note that phase lag also increased (compare the phase of the solid red and blue sinusoids,  
336 respectively). Error bars, when visible, denote 95% confidence intervals.

337

338

339 We confirmed the band-pass nature of small-amplitude slow motion tracking in our two  
340 monkeys, and also with both horizontal and vertical tracking. For each temporal  
341 frequency,  $f$ , in equation 1 (Materials and Methods), we estimated the gain of pursuit  
342 (similar to Fig. 1; Materials and Methods) and plotted it for horizontal and vertical  
343 tracking, along with 95% confidence intervals (Fig. 2A). In both monkeys, pursuit gain  
344 peaked at  $\sim 0.8$ -1 Hz, and this happened for both horizontal and vertical tracking,  
345 although vertical tracking always had significantly worse pursuit gain than horizontal  
346 tracking (Rottach et al. 1996). For a frequency of 0.1 Hz, pursuit gain in both monkeys  
347 seemed to increase relative to, say, 0.2 Hz and 0.3 Hz. This was because at 0.1 Hz, the  
348 target was barely moving with a peak speed of only 0.314 deg/s. At such speeds, the  
349 monkeys seemed to rely much more on saccades than slow eye movements to correct eye

350 position errors (e.g. see Fig. 5A), and their own fixational ocular drifts were significantly  
 351 faster than the target motion (e.g. see Fig. 3A). Therefore, for all frequencies other than  
 352 0.1 Hz, we observed a band-pass characteristic of monkey smooth pursuit gain for small-  
 353 amplitude slow motion trajectories.  
 354



355

356 **Figure 2 Band-pass nature of slow motion smooth pursuit in both monkeys.** (A) Each panel shows the  
 357 gain of smooth pursuit (i.e. the ratio of red sinusoid amplitude to blue sinusoid amplitude in Fig. 1) as a  
 358 function of target motion frequency. The left panel shows data from monkey M, and the right panel shows  
 359 data from monkey A. Error bars denote 95% confidence intervals, and the insets indicate the number of  
 360 trials per condition used for analysis. As can be seen, pursuit gain peaked at around 0.8-1 Hz for both  
 361 monkeys, and was lower for both lower and higher frequencies. In both animals, pursuit gain seemed high  
 362 at 0.1 Hz; at this frequency, the target was barely moving and ocular drift velocities could be substantially  
 363 higher than target velocities (Martins et al. 1985). Also, in both animals, pursuit gain was significantly  
 364 worse for vertical tracking as opposed to horizontal tracking. (B) A similar analysis but now for pursuit  
 365 phase (e.g. the phase difference between the red and blue sinusoids of Fig. 1). In monkey M, higher  
 366 frequencies were associated with larger phase lags. This dependence of phase lag on frequency was not so  
 367 evident in monkey A, for which an overall lag existed even at low frequencies. Note that the phase lag is  
 368 displayed here as a fraction of a cycle. Thus, a constant temporal lag would translate into a larger fraction  
 369 with increasing frequency (see text). All error bars indicate 95% confidence intervals.



370

371 We similarly analyzed pursuit phase lag, reporting it as a fraction of a full cycle (Fig.  
372 2B); that is, a constant temporal delay in phase would mean a larger fraction of a cycle  
373 with increasing frequencies. In monkey M, this was the case: higher target motion  
374 frequencies resulted in progressively more and more pursuit lag when represented as a  
375 fraction of a full cycle. However, this was less so in monkey A, for which there was an  
376 overall lag in pursuit that was independent of frequency. The insets in Fig. 2A show the  
377 total numbers of trials analyzed for each condition.

378

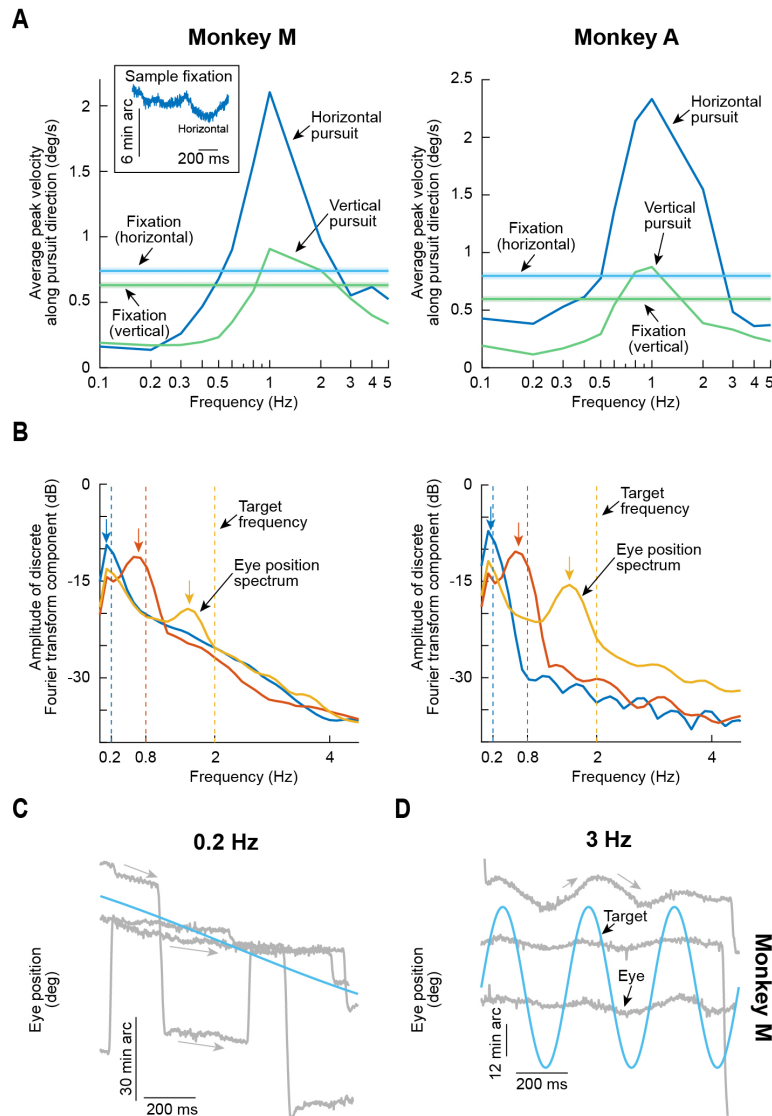
379 Therefore, for both horizontal and vertical smooth pursuit eye movements, tracking of  
380 very slow motion trajectories in monkeys is seemingly different from classical  
381 experiments with faster target speeds; for the small-amplitude slow motions, pursuit  
382 efficacy at low frequencies is significantly impaired, and only recovers at  $\sim 0.8$ -1 Hz. For  
383 larger target speeds, evidence from the literature shows that smooth pursuit typically  
384 exhibits low-pass behavior, with high gain at all low frequencies up to  $\sim 1$  Hz (Collewijn  
385 and Tamminga 1984; Fabisch et al. 2009; Hafed et al. 2008; Hafed and Krauzlis 2008;  
386 Martins et al. 1985; Rottach et al. 1996). As stated above, in highly trained humans, such  
387 a low-pass behavior of smooth pursuit seemed to also still persist for small-amplitude  
388 target trajectories like the ones that we used (Martins et al. 1985); perhaps this difference  
389 from our monkey results is due to extensive training of the humans to avoid making  
390 catch-up saccades.

391

392 *Controllability of monkey ocular velocities as slow as those during fixational ocular*  
393 *drifts*

394 Despite the low gain of smooth pursuit at low temporal frequencies in Figs. 1, 2, eye  
395 velocity in our monkeys was still clearly controllable. For example, sinusoidal tracking  
396 was still evident at 0.4 Hz even with the reduced gain (Fig. 1A). As stated earlier, we  
397 were interested in this phenomenon particularly because the velocities with which  
398 tracking occurred at these low temporal frequencies seemed similar to the velocities with  
399 which ocular drifts during fixation normally take place. For example, peak target velocity  
400 at 0.1, 0.2, and 0.3 Hz was 0.314, 0.628, and 0.942 deg/s, respectively, which are all  
401 within the range of eye velocity during fixational ocular drifts (Cherici et al. 2012;  
402 Martins et al. 1985). To confirm this, we collected control fixation data from the same  
403 animals. In these trials, the spot never moved, and the monkeys simply fixated it for  
404 approximately 1000 ms (Materials and Methods). We measured eye velocity during  
405 microsaccade-free fixation epochs, and we related them to the peak eye velocity at each  
406 temporal frequency during tracking (Fig. 3A). Specifically, in Fig. 3A, we plotted the  
407 same data as in Fig. 2A but now as raw measurements of peak eye velocity instead of as  
408 gain values. We then plotted the average velocities observed during gaze fixation  
409 (horizontal lines), again along with 95% confidence intervals. At the lowest and highest  
410 tracking frequencies (e.g. 0.1-0.2 Hz or 4-5 Hz), peak eye velocity during pursuit of slow  
411 motion trajectories was significantly lower than eye velocity during fixation (error bars in  
412 Fig. 3A denote 95% confidence intervals). However, the eye was still well-controlled  
413 because gain was not zero (Fig. 2A). We also further confirmed this by analyzing the  
414 frequency spectrum of eye position traces for different temporal frequencies (particularly

415 the small ones associated with the slowest peak velocities). We found that there was a  
416 peak in the power spectrum of eye position traces near the frequency with which the  
417 target was moving (Fig. 3B). This means that eye position had a harmonic component  
418 that was close in frequency to that present in the target motion trajectory even at the low  
419 gain values observed in Fig. 2A. Finally, we also inspected example eye position traces  
420 for low (Fig. 3C) or high (Fig. 3D) tracking frequencies, and clear modulation of  
421 saccade-free eye position was still present (e.g. see the gray arrows in Fig. 3C, D).  
422 Therefore, slow ocular movements at velocities similar to or lower than the velocities of  
423 slow fixational ocular drifts are relatively well-controlled in this behavior (Wyatt and  
424 Pola 1981).  
425



426

427 **Figure 3 Monkey ocular velocities as slow as those during fixational drifts occurred during smooth**  
428 **pursuit of slow motion, but they were still systematically controlled to track the motion trajectory.**  
429 (A) The curves show the same data as in Fig. 2A, but this time as real measurements of peak eye velocity  
430 as opposed to a gain ratio. The solid horizontal lines show average eye velocity during fixation (Materials  
431 and Methods), surrounded by 95% confidence intervals (the inset shows an example 1-second fixational  
432 eye position trace, demonstrating how ocular drift has substantial non-zero eye velocity even with a  
433 stationary fixation spot). Fixational drift velocity was higher than pursuit peak velocities at pursuit  
434 frequencies of, say, 0.2 Hz, 0.3 Hz, and 4 Hz. This means that eye velocities as slow as those during ocular  
435 drifts are controllable by the central nervous system of the monkey. (B) This idea is supported by analyzing  
436 the spectral content of eye position traces for different pursuit target frequencies. Even at very low  
437 frequencies (e.g. 0.2 Hz and 0.8 Hz) associated with low pursuit velocities (as in A), eye position still  
438 exhibited a peak in the spectrum at a frequency near target motion. This indicates that eye position was still  
439 following target motion (even if at low gain). (C, D) Sample 1-second eye position traces (shown in gray)  
440 from three example trials at 0.2 Hz (C) or 3 Hz (D), both of which exhibited very weak pursuit gain (A and  
441 Fig. 2). In both cases, eye position was systematically controlled to follow target trajectory (e.g. see the  
442 gray arrows). Thus, monkeys are capable of slow control of their drift velocities in our task.  
443

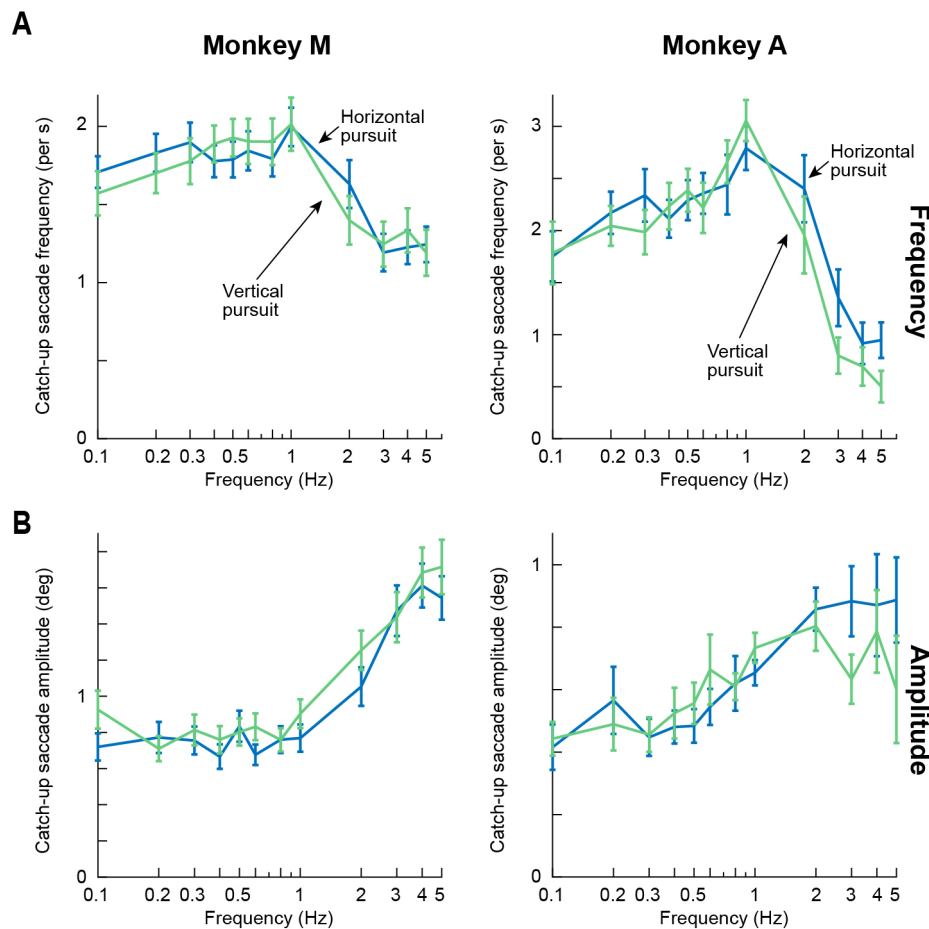
444

445 *Dependence of monkey catch-up saccade frequency and amplitude on temporal frequency*

446 Our results so far have focused on smooth eye velocity effects. However, we also  
447 analyzed and catalogued catch-up saccade frequency and amplitude. We found that catch-  
448 up saccades behaved in different ways for temporal frequencies higher or lower than the  
449 frequency associated with peak smooth pursuit gain (~0.8-1 Hz). For example, in Fig.  
450 4A, we plotted the frequency of catch-up saccades as a function of temporal frequency in  
451 Experiment 1. In both animals, catch-up saccade frequency reached a peak at the same  
452 temporal frequency for which smooth pursuit gain was maximum. This suggests that eye  
453 position was continuously adjusted with both smooth pursuit and saccadic eye  
454 movements when overall tracking was particularly effective (i.e. with high gain). Catch-  
455 up saccade frequency then dropped dramatically for higher temporal frequencies, but this  
456 drop was not so dramatic for lower temporal frequencies. This suggests that for the lower  
457 temporal frequencies, when the spot was barely moving, catch-up saccades played a role  
458 more similar to that of fixational microsaccades: they optimized eye position on the target  
459 on average (Guerrasio et al. 2010; Ko et al. 2010; Tian et al. 2018; 2016), especially  
460 when slow eye movements (Fig. 2) were significantly less effective in keeping the eye on  
461 target because of low gain. On the other hand, for very rapid oscillations (high  
462 frequencies), the oculomotor system was unable to keep track of the frequent flips in  
463 target position (even with saccades as opposed to smooth pursuit), and saccades were  
464 therefore more or less random events. Consistent with this, catch-up saccade amplitudes  
465 (Fig. 4B) were always small for all frequencies <1 Hz; on the other hand, catch-up  
466 saccade amplitudes increased for higher frequencies.

467

468



469

470 **Figure 4 Catch-up saccade frequency was highest for frequencies resulting in maximal smooth**  
471 **velocity gain; catch-up saccade amplitude increased for high frequencies. (A)** For both animals in  
472 Experiment 1, we estimated the frequency of catch-up saccades during steady-state smooth pursuit. The  
473 highest rate of catch-up saccades occurred at the frequencies associated with maximal smooth velocity gain  
474 (Figs. 1-3). For yet higher frequencies, both animals showed a marked decrease in catch-up saccade  
475 frequency, suggesting that the reduction in smooth velocity gain associated with these frequencies (Figs. 1-  
476 3) was not compensated for by rapid back and forth saccades to try to track the target. **(B)** Instead, catch-up  
477 saccades at higher frequencies were apparently random, infrequent movements that were increasingly large  
478 in amplitude. These patterns of results **(A and B)** were identical for horizontal and vertical pursuit, despite  
479 the quantitative difference in smooth velocity gain for these different pursuit directions (Figs. 2-3). All  
480 error bars denote 95% confidence intervals.

481

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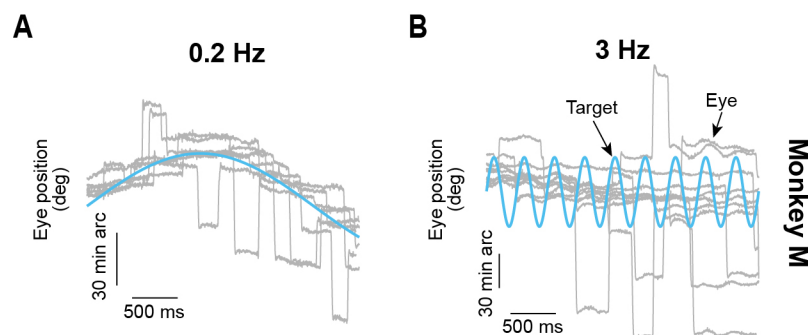
483 The above interpretations are also supported by inspecting sample eye position traces

484 from two example temporal frequencies from Experiment 1 (Fig. 5). Saccades were

485 frequent at low temporal frequencies, and they kept the eye hovering around target  
486 location, consistent with the role of fixational microsaccades in continuously optimizing  
487 eye position (Guerrasio et al. 2010; Ko et al. 2010; Tian et al. 2018; 2016). On the other  
488 hand, saccades at high temporal frequency were less frequent, large, and very often  
489 increasing eye position error, rather than decreasing it, for substantial amounts of time  
490 (>500 ms).

491

492



493

494 **Figure 5 Monkey catch-up saccades at low temporal frequencies behaved like microsaccades during**  
495 **fixation.** (A) Example eye position traces (gray) when tracking a target moving at 0.2 Hz (true target  
496 position is shown by the blue sinusoid). Smooth velocity (i.e. slow ocular drifts) tracked target motion,  
497 albeit at a low gain, and there were plenty of catch-up saccades. Thus, the slow eye movements here  
498 appeared similar to fixational ocular drifts in terms of velocity (e.g. inset in Fig. 3A). Moreover, catch-up  
499 saccades were quite frequent, and resulted in the eye “hovering” around target position on average, as with  
500 fixational microsaccades. (B) At high frequencies, slow movements also tracked the target motion (at low  
501 gain). However, this time, catch-up saccades were less frequent, and they were large, often deviating the  
502 eye substantially away from the target, and for substantial periods of time (>500 ms).  
503

504

505 It is also interesting to note that despite the large difference in smooth pursuit gain  
506 between horizontal and vertical tracking in Experiment 1 (Fig. 2), catch-up saccade  
507 frequency and amplitude were not at all different from each other across tracking  
508 directions (Fig. 4). This might suggest that there is a larger tolerance for oculomotor

509 errors along the vertical dimension, perhaps because of potential asymmetries in  
510 oculomotor circuits (Hafed and Chen 2016), although this remains to be just a hypothesis  
511 at the moment.

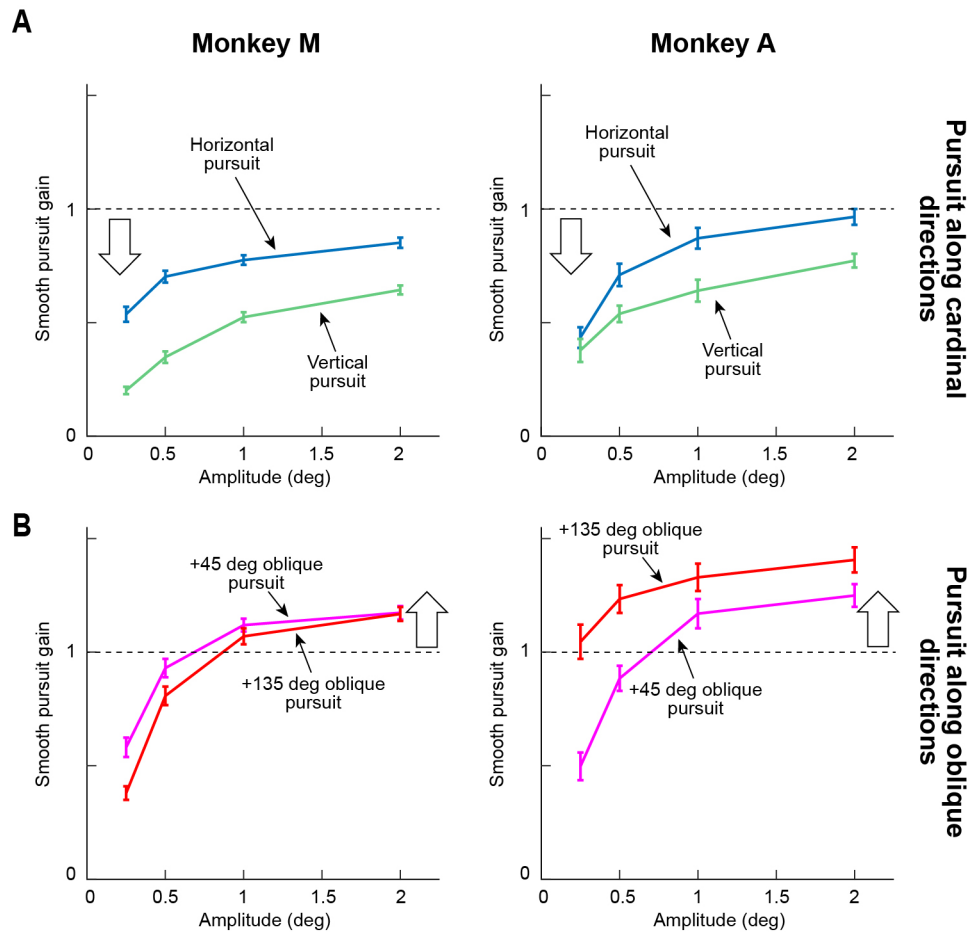
512

513 *Over-tracking of oblique small-amplitude slow motion trajectories by monkeys*

514 We also sought to compare the effects of temporal frequency that we observed above to  
515 those of movement amplitude and direction for a given frequency. We therefore  
516 conducted Experiment 2 (Materials and Methods) in which temporal frequency was  
517 pegged at 0.5 Hz but movement amplitude varied between ~15 min arc (0.25 deg) and ~2  
518 deg (Materials and Methods). Movement direction also included oblique tracking  
519 (Materials and Methods). Overall, we found expected results in terms of smooth pursuit  
520 gain as a function of target motion trajectory amplitude. For example, for both cardinal  
521 (horizontal and vertical) and oblique pursuit, smooth pursuit gain increased with  
522 increasing target motion amplitude (Fig. 6). This might explain why our results from  
523 Experiment 1 above showed band-pass behavior (Fig. 2) when the target amplitude was  
524 small; this band-pass effect was primarily due to the very small motion trajectory  
525 amplitudes (and, correspondingly, velocities) used when compared to classic studies, and  
526 increasing amplitude in the current experiment has alleviated this.

527





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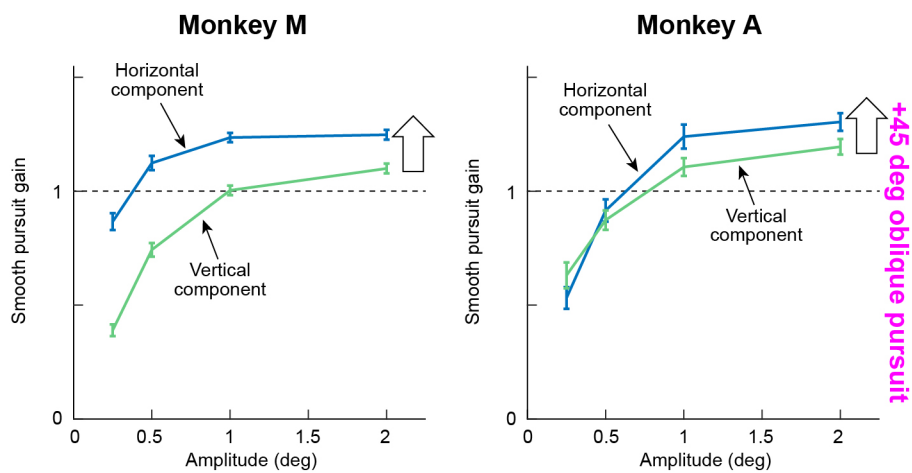
529 **Figure 6 Higher pursuit gain for tracking of small-amplitude oblique motion trajectories.** (A) In  
 530 Experiment 2, we varied target sinusoidal position amplitude, and also introduced oblique pursuit  
 531 trajectories. For cardinal directions, we obtained expected results based on what we found in Experiment 1.  
 532 Pursuit gain was higher for horizontal than vertical pursuit, and pursuit gain progressively increased with  
 533 increasing target amplitude. Note, however, that gain seemed to asymptote near a value of 1. (B) For  
 534 oblique pursuit directions, there was still an increase in pursuit gain with target amplitude. However, this  
 535 increase eventually resulted in an overshoot of target speeds (gain going substantially >1). Even at 0.5 deg  
 536 amplitudes, oblique pursuit showed higher gain than cardinal pursuit (compare the 0.5 deg point in this  
 537 panel to the corresponding point in panel A). Thus, oblique pursuit was associated with overshooting of  
 538 target velocity in both animals. All error bars denote 95% confidence intervals.  
 539

540

541

542 The most striking result from Experiment 2, which is also evident in Fig. 6, was that  
 543 smooth pursuit gain was significantly >1 for oblique tracking directions (Fig. 6B). This is  
 544 different from pursuit of large-amplitude motions, in which oblique pursuit might be

545 expected to be worse in gain than pursuit along cardinal directions, perhaps due to  
546 oblique effects in motion perception (Krukowski and Stone 2005). When we analyzed the  
547 horizontal and vertical components of oblique pursuit independently, we found that the  
548 “overshoot” was primarily occurring in the horizontal dimension (Fig. 7). These results  
549 are reminiscent of overshoot in visually-guided saccade amplitudes in humans for very  
550 small retinal eccentricities (Kalesnykas and Hallett 1994), and they demonstrate an  
551 additional difference in the control capabilities of the slow movement oculomotor sub-  
552 system between small and large motion amplitudes. For example, in large-amplitude  
553 pursuit, horizontal gain can be higher than vertical gain during oblique tracking (Rottach  
554 et al. 1996), but overall gain still always stays below or very close to 1. We found marked  
555 increases above a gain value of 1.  
556  
557



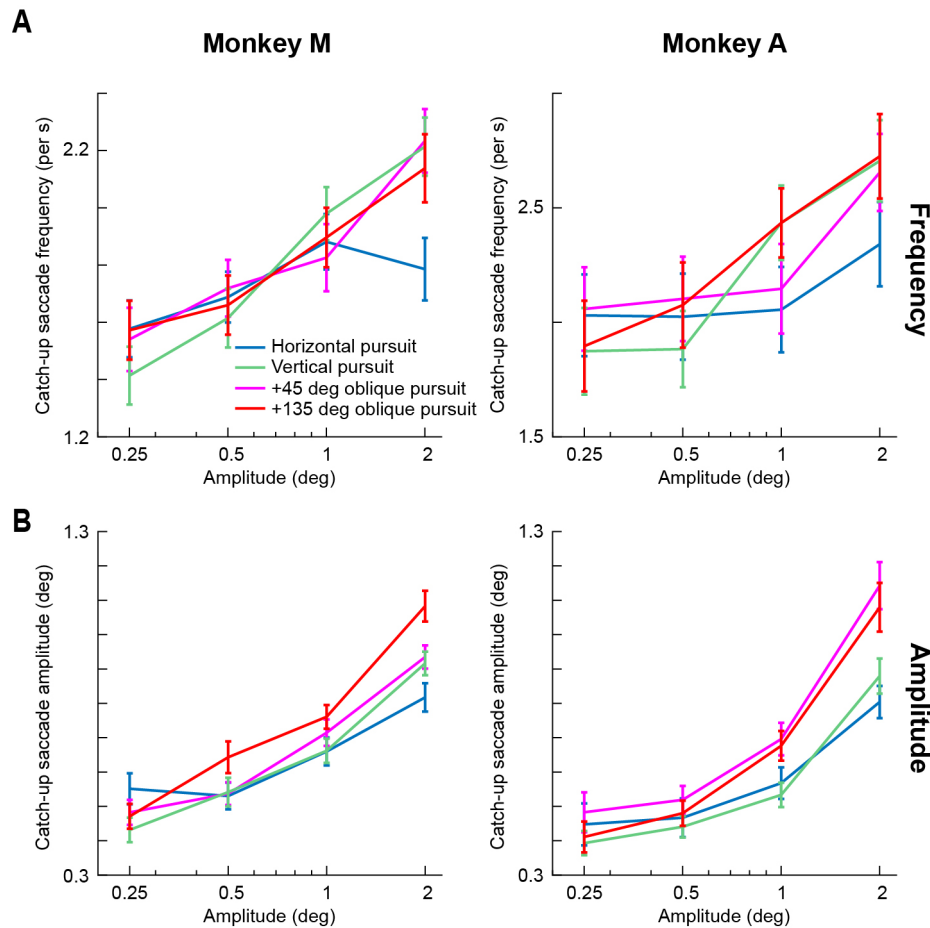
558

559 **Figure 7 Over-tracking in the horizontal dimension during smooth pursuit of small-amplitude**  
560 **oblique motion trajectories.** We investigated the overshoot observed in Fig. 6B by plotting the horizontal  
561 and vertical components of eye velocity separately for an example oblique pursuit condition. In both  
562 animals, pursuit gain was higher in the horizontal component of eye velocity than the vertical component.  
563 Thus, the over-tracking observed in Fig. 6B was primarily driven by over-tracking in the horizontal  
564 dimension. All error bars denote 95% confidence intervals.  
565

566

567 The over-tracking of oblique motion trajectories was also accompanied by larger catch-  
568 up saccades for these trajectories. In Fig. 8, we plotted catch-up saccade frequency (Fig.  
569 8A) and amplitude (Fig. 8B), as we had done earlier for Experiment 1. Consistent with  
570 Experiment 1, increased smooth pursuit gain was associated with an increase in catch-up  
571 saccade frequency (Fig. 8A), suggesting synergistic interactions between smooth pursuit  
572 eye movements and saccades to optimize eye position on the target (de Brouwer et al.  
573 2002); this is similar to us seeing the most catch-up saccades in Experiment 1 for the  
574 temporal frequencies in which smooth velocity gain was also at a maximum. In terms of  
575 catch-up saccade amplitude, it also increased with increasing target motion amplitude; in  
576 addition, while an increase in saccade amplitude was expected with increasing target  
577 position trajectory amplitude, the increase was stronger for oblique directions (Fig. 8B).  
578 For example, in monkey A, both oblique directions had higher saccade amplitudes than  
579 horizontal or vertical trajectories, and in monkey M, one of the oblique directions did.  
580 This result might reflect the slightly higher peak velocities associated with oblique  
581 tracking (for example, oblique tracking with a horizontal and vertical amplitude of 2 deg  
582 each meant an overall radial amplitude of 2.82 deg; Materials and Methods).

583



584

585 **Figure 8 Catch-up saccade frequency and amplitude in Experiment 2. (A)** Consistent with Experiment  
586 1, when smooth velocity gain was high (Figs. 6-7), catch-up saccade frequency was high. **(B)** Catch-up  
587 saccade amplitude also expectedly increased with larger target motion excursions. All error bars denote  
588 95% confidence intervals.

589

590

591 *Dependence of monkey first catch-up saccade latency and smooth pursuit initiation on*  
592 *target motion*

593 We also analyzed the properties of the very first catch-up saccade during smooth pursuit  
594 initiation, as well as the smooth component of initial eye acceleration itself. For all  
595 saccades (including fixational microsaccades) occurring in the interval 0-300 ms after  
596 target motion onset, we plotted these movements' amplitudes as a function of their  
597 occurrence time. We also plotted either baseline eye velocity (in the 50 ms interval

598 starting at -100 ms from target motion onset) or smooth pursuit initiation eye velocity (in  
599 the 50 ms starting 100 ms after target motion onset; ensuring no saccades within each  
600 interval). We observed expected relationships between initial catch-up saccades and  
601 initial smooth pursuit eye velocity. For example, in Experiment 2, with 0.5 Hz target  
602 trajectory variation, eye position error of the target (relative to initial fixation location if  
603 the eye did not start tracking) monotonically increased in the first 300 ms of any trial (and  
604 up to 500 ms). Therefore, if a saccade were to occur during initiation (and there was no  
605 associated smooth acceleration after motion onset), then saccade amplitude was expected  
606 to increase with increasing time after motion onset. However, this was not the case for  
607 most target amplitudes that we tested (Fig. 9A). We think that this is so because of a  
608 concomitant increase in smooth eye velocity to track the target (Fig. 9A, B; only  
609 horizontal tracking data is shown for clarity). In other words, after motion onset, the eye  
610 often started to accelerate smoothly, therefore already reducing eye position error. Such  
611 reduction may have alleviated the need to increase first catch-up saccade amplitude. Only  
612 when target position amplitude was large enough (2 deg) did there arise a need for  
613 increasing initial catch-up saccade amplitude. For such a larger position amplitude of the  
614 motion trajectory, even the initial component of smooth pursuit acceleration was not  
615 sufficient to reduce eye position error sufficiently; a larger saccade was therefore  
616 necessary. This idea is illustrated in Fig. 9C showing raw pursuit velocities with saccades  
617 excised from the averages as per Materials and Methods (shown from horizontal tracking  
618 only for clarity). Pursuit initiation velocity increased for trajectories with amplitudes of 2  
619 deg compared to, say, 0.5 deg. However, the increase in velocity did not necessarily  
620 allow for completely eliminating eye position error, resulting in the need for an initial

621 catch-up saccade whose amplitude gradually increased with increasing time after motion  
622 onset (Fig. 9A; 2 deg motion position amplitude). Therefore, there was a synergistic  
623 interaction between smooth pursuit initiation and initial catch-up saccade execution,  
624 which also likely occurs between slow ocular drifts and microsaccades (Chen and Hafed  
625 2013). Note that in Fig. 9A, saccades occurring <50-60 ms after target motion onset were  
626 fixational microsaccades and not really target-driven catch-up saccades because they  
627 occurred too early to reflect the new visual error signal introduced by target motion onset.  
628 This is why these movements were also small in amplitude even for 2 deg motion  
629 amplitudes.

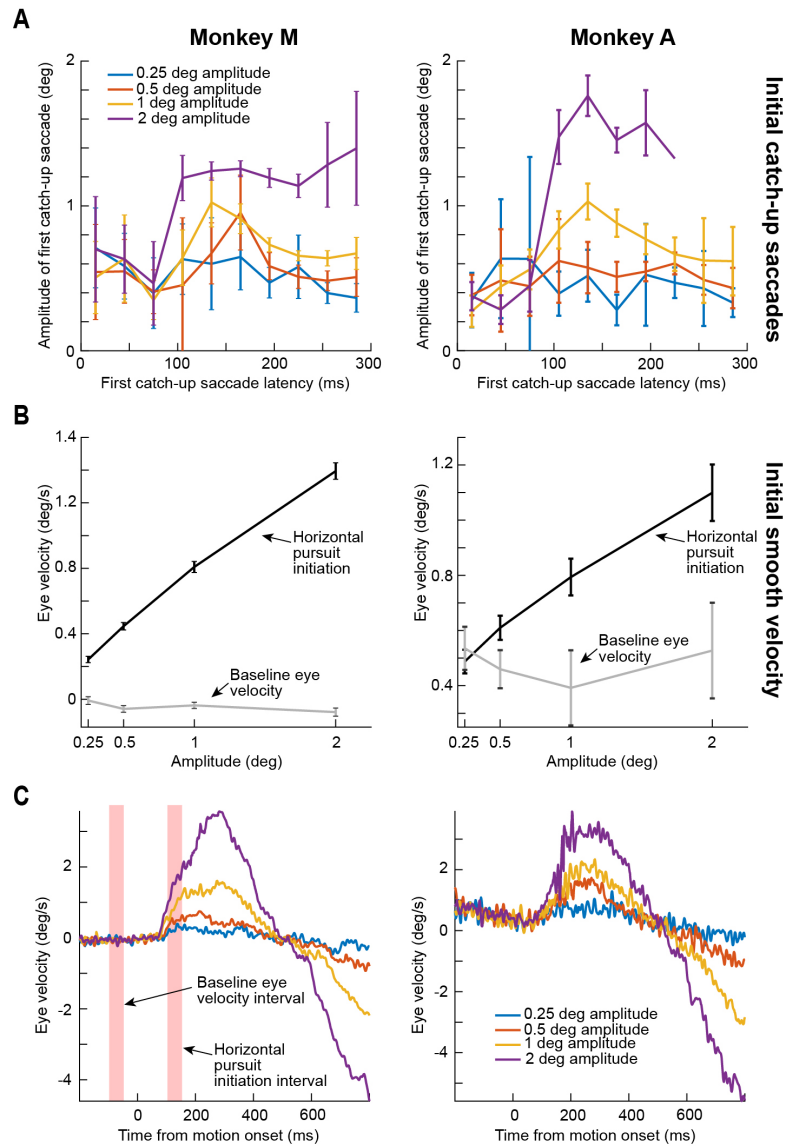
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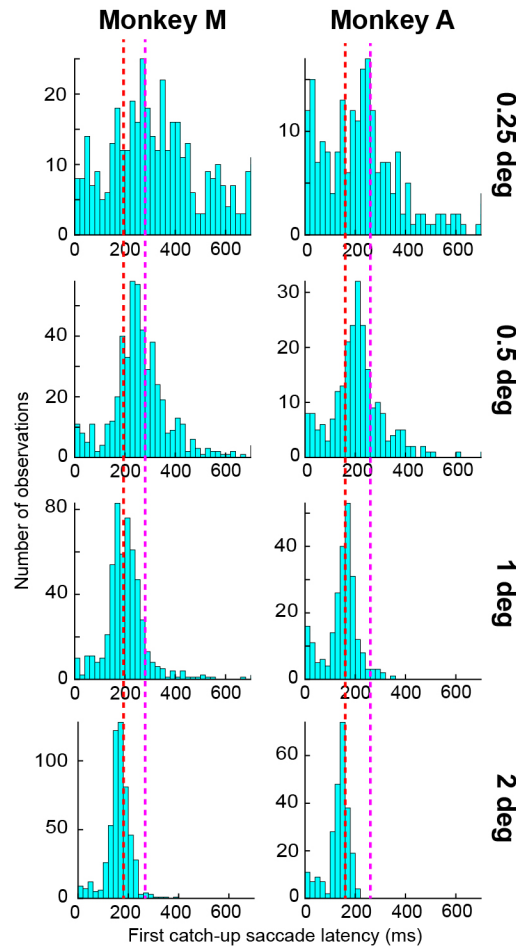
636 **Figure 9 Interactions between saccades and smooth pursuit eye movements during initiation of**  
 637 **tracking.** (A) We found evidence of synergistic interactions between smooth pursuit and catch-up saccades  
 638 during initiation. The amplitude of the first catch-up saccade after target motion onset did not increase  
 639 convincingly as a function of time (even though eye position error was monotonically increasing), except  
 640 for 2 deg amplitude trajectories (dark purple). (B) This might be because saccade-free smooth pursuit  
 641 initiation may have already acted to reduce eye position error. For example, initial eye velocity during  
 642 saccade-free initiation (see pink measurement intervals in the left panel of C) increased with increasing  
 643 target amplitude. Thus, saccades did not necessarily need to increase in amplitude in A for small target  
 644 amplitudes. For 2 deg trajectories, the increase in smooth eye velocity may have not been sufficient to  
 645 completely obviate the need for a catch-up saccade, and that is why catch-up saccade amplitudes in this  
 646 particular condition increased with time from motion onset when compared to all of the other conditions  
 647 that we tested. Note that in A, saccades with latencies less than ~50-60 ms were likely not initial catch-up  
 648 saccades but instead fixational microsaccades. That is why their amplitudes were low for all conditions. (C)  
 649 Example average saccade-free smooth velocity traces from horizontal tracking (like B) showing the  
 650 measurement intervals for B and also the idea that smooth velocity effects increased with increasing target  
 651 amplitude. All error bars denote 95% confidence intervals.  
 652

653

654 Finally, we checked whether the first catch-up saccade latency itself depended on target  
655 amplitude. In Experiment 2, we plotted histograms of first catch-up saccade latency in the  
656 different amplitude conditions (Fig. 10). For the smallest amplitude trajectories, catch-up  
657 saccade latencies were long and variable. As target amplitude increased, latency became  
658 more precise, as well as shorter. Since Fig. 9 showed that it was more likely for catch-up  
659 saccade amplitudes to increase with increasing target position amplitude, these results  
660 constitute a monkey replication of human studies, showing that saccade latencies are  
661 substantially longer for very small-amplitude visually-guided saccades compared to  
662 larger ones (Kalesnykas and Hallett 1994).

663





664

665 **Figure 10 Dependence of first catch-up saccade latency on target amplitude.** We plotted histograms of  
666 first catch-up saccade latency for different target amplitudes in Experiment 2. We show results only from  
667 horizontal tracking for clarity; other directions showed similar effects. Since larger target amplitudes  
668 resulted in larger catch-up saccades (e.g. Fig. 9), the present histograms show monkey replication of human  
669 observations that very small visually-guided saccades are associated with longer reaction times than larger  
670 ones (Kalesnykas and Hallett 1994). For example, for each monkey, the red dashed line marks the latency  
671 bin with most observations at 2 deg target motion amplitude (bottom panel), and the magenta dashed line  
672 marks the latency bin with the most observations at 0.25 deg target motion amplitude (top panel). As can be  
673 seen, there was a substantial differential in saccade times for the different target motion amplitudes. Note  
674 that, like in Fig. 9, the small distribution of saccades occurring with latencies <100 ms in this figure are  
675 likely not genuine first catch-up saccades, but instead fixational microsaccades. This is further supported by  
676 the noticeable dip in the histograms at ~100 ms, which is similar to the phenomenon of microsaccadic  
677 inhibition reported in the literature for both humans and monkeys (Buonocore et al. 2017; Haged and  
678 Ignashchenkova 2013; Rolfs et al. 2008).

679

680

681

## 682 **Discussion**

683

684 We attempted to characterize monkey oculomotor behavior with small-amplitude slow  
685 motion trajectories. We catalogued both smooth velocity effects as well as catch-up  
686 saccade effects. For smooth velocity effects, we found that pursuit gain was low for both  
687 low and high temporal frequencies, only reaching a peak in mid-frequencies near 1 Hz.  
688 This is in contrast to previous human experiments with large-amplitude (Collewijn and  
689 Tamminga 1984; Fabisch et al. 2009; Rottach et al. 1996) or small-amplitude (Martins et  
690 al. 1985) sinusoidal motions, in which low-pass behavior was observed. In terms of  
691 catch-up saccades, we found that they (perhaps paradoxically) increased in frequency  
692 when smooth velocity gain was high. Moreover, we found that catch-up saccades during  
693 presentation of low temporal frequencies acted more like fixational microsaccades,  
694 whereas catch-up saccades during presentation of high temporal frequencies were large  
695 and infrequent.

696

697 Our results provide a necessary foundation for exploring the neural mechanisms  
698 subserving fixational ocular drifts in awake monkeys. This complements early  
699 characterizations of awake monkey smooth pursuit eye movements with higher speeds  
700 (Lisberger and Westbrook 1985). These early characterizations were themselves a major  
701 boon for a wide range of significant and seminal subsequent discoveries about the neural  
702 mechanisms for oculomotor control in general, and about the neural mechanisms for  
703 smooth pursuit in particular (Krauzlis 2004). Our next goal is to extend on our current  
704 results by uncovering neural substrates in the same animals.

705

706 To that end, we were careful to avoid unnecessarily penalizing the monkeys for making  
707 saccades during tracking. Specifically, we aimed to minimize over-training on one  
708 particular movement modality. For example, early human studies with small-amplitude  
709 motions barely had any saccades in the experiments, to focus almost solely on slow  
710 control effects (Martins et al. 1985). However, we wanted the animals to engage in as  
711 naturalistic a behavior as possible, such that we could understand important interactions  
712 between slow control and micro/saccadic control. This has allowed us to make the  
713 interesting observation that smooth pursuit gain in our monkeys exhibited band-pass  
714 behavior, unlike in (Martins et al. 1985). This has also allowed us to make the interesting  
715 observation that there were actually more saccades when pursuit gain was high (i.e. when  
716 retinal position and motion errors were presumably low) than when it was low.

717

718 Such an observation of a concomitant increase in catch-up saccade frequency along with  
719 an increased velocity gain might suggest that catch-up saccades normally behave like  
720 fixational microsaccades. The latter eye movements continuously re-align gaze with a  
721 foveal target under a variety of stimulus conditions (Guerrasio et al. 2010; Ko et al.  
722 2010), and even when competing peripheral stimuli are presented (Tian et al. 2018;  
723 2016). Their frequency of occurrence might therefore increase when the target is sharp,  
724 providing a clear spatial reference frame for re-aligning gaze. During pursuit, similar re-  
725 alignment of gaze may be necessary. This is consistent with observations that foveal  
726 targets increase catch-up saccade frequency in humans (Heinen et al. 2018; Heinen et al.  
727 2016); presumably, foveal targets not only support good smooth velocity gain, but they

728 also provide the oculomotor system with a punctate spatial reference point to which gaze  
729 can be re-directed. We also found in monkeys that there was a tendency for higher catch-  
730 up saccade frequencies for smaller foveal pursuit targets than for bigger and fuzzier ones  
731 (Hafed et al. 2008). It would be interesting to analyze the relationship between eye  
732 position error and catch-up saccade likelihood with a foveal target during smooth pursuit,  
733 such that one can uncover an almost-deterministic estimate of whether a catch-up saccade  
734 can occur at any one moment of time or not (de Brouwer et al. 2002). This kind of  
735 approach was recently made for microsaccades (Tian et al. 2018), and it is very intriguing  
736 because predicting whether and when a microsaccade might take place can then, at least  
737 in principle, be used to estimate the occurrence of distinct cognitive performance effects  
738 associated with such movements (Bellet et al. 2017; Chen et al. 2015; Hafed 2013).

739

740 Our interest in relying on more naturalistic tracking (i.e. with combined smooth and  
741 saccadic eye movements) may also explain why we observed band-pass smooth pursuit  
742 gain effects in our monkeys, even though a similar human experiment with low  
743 frequencies and small-amplitude trajectories found very good gain (Martins et al. 1985).  
744 As stated earlier, in that study, the human subjects tested were highly trained, and they  
745 were instructed to minimize saccade generation. As a result, substantial systematic eye  
746 position drifts occurred in their experiments, whereas we did not observe such systematic  
747 drifts. In our case, we relied more on the natural behavior of the monkeys in being  
748 intrinsically interested to foveate the small white spot that was presented on the display.  
749 Yes, the monkeys became highly trained in the lab after multiple sessions, but their  
750 behavior was not shaped by us, say, by aborting trials whenever a saccade occurred.

751 Instead, we rewarded them for tracking the target to within a reasonable radius, which  
752 may not be too different from natural variability in human fixation among untrained  
753 individuals (Cherici et al. 2012). As a result, our monkeys tracked the target with both  
754 smooth and saccadic eye movements.

755

756 We were also intrigued by our oblique tracking effects in Experiment 2. Both smooth  
757 velocity gain and catch-up saccade amplitudes increased for oblique tracking, with  
758 smooth velocity gain surpassing a value of 1 by quite a margin. While the catch-up  
759 saccade amplitude increase may have reflected the slightly faster trajectories associated  
760 with oblique target motions in our stimulus design relative to cardinal target motions  
761 (Materials and Methods), the smooth velocity gain measure is a normalized measure that  
762 should not depend on absolute target velocity. Instead, it does reflect a real observation  
763 that pursuit in these oblique conditions substantially over-tracked the small-amplitude  
764 motions that we tested. This is intriguing to us because small visually-guided saccades in  
765 humans are known to overshoot their targets (Kalesnykas and Hallett 1994). We may  
766 have thus observed a similar phenomenon for smooth pursuit, adding to evidence that  
767 pursuit and saccades share neural resources (Krauzlis and Dill 2002; Krauzlis 2004;  
768 Krauzlis et al. 1997; Krauzlis et al. 2017). Similarly, even our catch-up saccade effects of  
769 Fig. 10 demonstrate a monkey correlate of human observations that visually-guided  
770 saccade latency increases for small target eccentricities. It would be interesting to extend  
771 these effects for other types of saccades, like delayed visually- or memory-guided  
772 saccades.

773

774 In all, our results add to an extensive cataloguing in the literature of rhesus macaque  
775 sensory, perceptual, cognitive, and motor capabilities, testifying to the tremendous value  
776 of such an animal model for systems neuroscience research.

777

778

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780

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787

788

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790

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