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1 **Gaze direction as equilibrium: more evidence from spatial and**
2 **temporal aspects of small-saccade triggering in the rhesus**
3 **macaque monkey**

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15 **Abbreviated title:**

16 Small-amplitude saccade latencies in monkey
17

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38

Abstract

40 Rigorous behavioral studies made in human subjects have shown that small-
41 eccentricity target displacements are associated with increased saccadic reaction
42 times, but the reasons for this remain unclear. Before characterizing the
43 neurophysiological foundations underlying this relationship between the spatial and
44 temporal aspects of saccades, we tested the triggering of small saccades in the male
45 rhesus macaque monkey. We also compared our results to those obtained in human
46 subjects, both from the existing literature and through our own additional
47 measurements. Using a variety of behavioral tasks exercising visual and non-visual
48 guidance of small saccades, we found that small saccades consistently require more
49 time than larger saccades to be triggered in the non-human primate, even in the
50 absence of any visual guidance and when valid advance information about the
51 saccade landing position is available. We also found a strong asymmetry in the
52 reaction times of small upper versus lower visual field visually-guided saccades, a
53 phenomenon that has not been described before for small saccades, even in
54 humans. Following the suggestion that an eye movement is not initiated as long as
55 the visuo-oculomotor system is within a state of balance, in which opposing
56 commands counterbalance each other, we propose that the longer reaction times are
57 a signature of enhanced times needed to create the symmetry-breaking condition
58 that puts downstream premotor neurons into a push-pull regime necessary for
59 rotating the eyeballs. Our results provide an important catalog of non-human primate
60 oculomotor capabilities on the miniature scale, allowing concrete predictions on
61 underlying neurophysiological mechanisms.

62

63

64

65 **Keywords**

66 Microsaccades; saccadic latency; fovea; superior colliculus; cerebellum; fixational

67 eye movements; ocular drift

68

New and noteworthy

70 Leveraging a multitude of neurophysiological investigations in the rhesus macaque
71 monkey, we generated and tested hypotheses about small-saccade latencies in this
72 animal model. We found that small saccades always take longer, on average, than
73 larger saccades to trigger, regardless of visual and cognitive context. Moreover,
74 small downward saccades have the longest latencies overall. Our results provide an
75 important documentation of oculomotor capabilities of an indispensable animal model
76 for neuroscientific research in vision, cognition, and action.

77 **Introduction**

78 The sudden appearance of a visual target is often followed by a saccadic movement
79 of the eyes. In non-pathological conditions, this movement brings the image of the
80 target within the central visual field. During the subsequent fixation, small saccades
81 can still be triggered, even though the target location in space has not changed. This
82 suggests that gaze fixation is a highly active process requiring continuous regulation
83 of the contraction of extraocular muscles, and also constant coordination among
84 them. This physiological fact can sometimes be overlooked, especially given that in
85 the majority of studies using monkeys as behavioral research subjects, so-called
86 computer-controlled “fixation windows” are used to make sure that the animal
87 effectively looks at the appropriate target, and not elsewhere, for a period of time.
88 While such windows can constrain the range of saccade sizes that the monkey is
89 allowed to make during fixation, they do not completely eliminate them. Moreover,
90 the generation of fixational saccades in the monkey is not a mere function of
91 computer-controlled constraints on fixation accuracy. Their amplitude remains small
92 even when large fixation windows are used (e.g. Guerrasio et al. 2010), and high
93 acuity visual tasks often require that small saccades are directed in highly precise
94 manners. In addition, monkeys can make microsaccades that accurately and
95 consistently orient a restricted zone of their retina toward the location of tiny visual
96 spots (Tian et al. 2018; 2016). Another aspect that influences the generation of
97 “fixational” saccades is the target size. Minuscule targets indeed elicit smaller
98 saccades than larger targets (Goffart et al. 2012).

99

100 Besides these spatial aspects, there are also temporal aspects, such as variabilities
101 in the timing of saccade onset. From the excitation of ganglion cells in the retina to
102 the recruitment of motor neurons and the contraction of extraocular muscles, action

103 potentials are transmitted through several relays in the brain (thalamus, cerebral
104 cortex, superior colliculus, and reticular formation). The latency of saccades reflects
105 the time (duration) taken by the action potentials to recruit a sufficient number of
106 neurons to ultimately contract the agonist muscles while relaxing the antagonist
107 ones, and rotate the eyeballs. Thus, any lesion that compromises the visuomotor
108 transmission leads to increasing the oculomotor reaction time. In humans, the
109 visuomotor delay depends upon the eccentricity of the target in the visual field
110 (Kalesnykas and Hallett 1996; 1994; Wyman and Steinman 1973) insofar as the
111 latency of saccades towards foveal targets is much longer, on average, than other
112 saccades. However, since these observations were made, it was not entirely clear
113 whether the origin of these longer latencies was visual or motor. Later experiments
114 testing saccades towards auditory targets (Zambarbieri et al. 1995) or gaze shifts
115 that were rendered dysmetric by a cerebellar pharmacological perturbation (Goffart
116 and Pelisson 1997) suggested that the dependency might be motor-related: the
117 smaller the saccade, the longer the time to initiate it. We hypothesize that this effect
118 is related to a recent proposal that gaze direction is not a passive state, but an active
119 equilibrium, and that an eye movement (saccadic or slow) is not initiated as long as
120 the visuo-oculomotor system is within a mode where opposing commands (or
121 movement tendencies) counterbalance each other (Goffart 2019; Goffart et al. 2018;
122 Krauzlis et al. 2017).

123

124 Here we document the timing of saccade triggering in rhesus macaque monkeys in a
125 variety of behavioral tasks. We particularly focus on very small saccades, as well as
126 differences between saccade directions, in order to investigate hypotheses related to
127 recent neurophysiological findings (Chen et al. 2019; Goffart et al. 2018; Guerrasio et
128 al. 2010; Hafed and Chen 2016; Krauzlis et al. 2017) and also motivate future ones.

129 Our results are consistent with the model positing that saccade triggering, or lack
130 thereof, depends on balance of different opposing oculomotor commands, and with
131 particular dependence on spatial visuomotor maps magnifying the representation of
132 the central visual field.
133

134 **Methods**

135 *Ethics approvals*

136 All monkey experiments were approved by ethics committees at the
137 Regierungspräsidium Tübingen. The experiments were in line with the European
138 Union directives and the German laws governing animal research. Some monkey
139 data were analyzed from (Willeke et al. 2019) for the new purposes of this article. In
140 these cases, the same committees had approved the experiments.

141

142 We also analyzed anew human data from the same study (Willeke et al. 2019), as
143 well as collected additional data from one author (ZH) and three naïve subjects (2
144 males and 1 female, aged 25-33 years). These human experiments were approved
145 by ethics committees at the Medical Faculty of Tübingen University, and the subjects
146 provided informed consent.

147

148 *Laboratory setups*

149 Monkey experiments were performed in the same laboratory environment as that
150 described recently (Buonocore et al. 2019; Chen and Hafed 2018; Chen et al. 2018;
151 Skinner et al. 2019; Willeke et al. 2019). Human experiments were done in the
152 laboratory described in (Grujic et al. 2018; Hafed 2013).

153

154 Briefly, the monkeys viewed stimuli on a cathode-ray-tube (CRT) display running at
155 120 Hz refresh rate. The humans viewed stimuli on a CRT display running at 85 Hz
156 refresh rate. In all cases, the display used was gamma-corrected (linearized), and the
157 stimuli were grayscale. Background and stimulus luminance values are described
158 below with the behavioral tasks. Stimulus control for both monkeys and humans was
159 achieved using the Psychophysics Toolbox (Brainard 1997; Kleiner et al. 2017; Pelli

160 1997). In the monkey experiments, the toolbox acted as a slave device receiving
161 display update commands from a master device and sending back confirmation of
162 display updates. The master system consisted of a real-time computer from National
163 Instruments controlling all aspects of data acquisition (including digitization of eye
164 position signals) and reward of the animals (in addition to display control). The real-
165 time computer communicated with the Psychophysics Toolbox using direct Ethernet
166 connections and universal data packet (UDP) protocols (Chen and Hafed 2013). In
167 the human experiments, the Psychophysics Toolbox was used as the primary
168 controller, and it synchronized display updates with eye tracker data samples (Hafed
169 2013).

170

171 Monkey eye movements were recorded at 1kHz using electromagnetic induction of
172 electrical current in a scleral eye coil (Fuchs and Robinson 1966; Judge et al. 1980).
173 As stated in (Willeke et al. 2019), we used video-based eye tracking for the human
174 subjects, again sampling at 1kHz (EyeLink 1000; desktop mount). For best eye
175 tracking performance, we fixed the heads of the monkeys and humans during the
176 sessions. For the former, this was achieved with surgically-implanted head-holders
177 (Chen and Hafed 2013). For the latter, we used a custom-built chin-and-forehead
178 rest with additional head position guides on the temples and behind the head (Hafed
179 2013).

180

181 *Animal preparation*

182 We collected behavioral data from 2 adult, male rhesus macaques (*Macaca Mulatta*).
183 Monkeys M and N (aged 7 and 10 years, and weighing 8 and 11.5 kg, respectively)
184 were implanted with a scleral coil in one eye to allow measuring eye movements
185 using the electromagnetic induction technique (Fuchs and Robinson 1966; Judge et

186 al. 1980). The monkeys were also implanted with a head holder to stabilize their
187 head during the experiments, with details on all implant surgeries provided earlier
188 (Chen and Hafed 2013; Skinner et al. 2019). They were part of a larger
189 neurophysiology project beyond the scope of the current manuscript.

190

191 *Monkey behavioral tasks*

192 The monkeys were trained to perform a visually-guided saccade task. Each trial
193 started with the presentation of a central white fixation spot (86 cd/m^2) over a uniform
194 gray background (29.7 cd/m^2). The fixation spot was a square of 5.3×5.3 min arc
195 dimensions. After 300-900 ms of fixation (i.e. maintaining eye position within a
196 prescribed distance from the spot; see below), the fixation spot was jumped to a new
197 location, instructing the monkeys to generate a visually-guided saccade to follow the
198 spot. The size of the jump was varied randomly across trials. Target locations were
199 chosen from among 96 predefined possibilities, as follows: the target could jump by a
200 distance of 0.06, 0.1, 0.2, 0.3, 0.5, 0.7, 1, 1.5, 2, 3, 5, or 10 deg in either the
201 horizontal or vertical dimension, or it could jump obliquely along a diagonal (in which
202 case we used the same sampling resolution of each of the horizontal and vertical
203 dimensions of any given jump: 0.06, 0.1, 0.2, 0.3, 0.5, 0.7, 1, 1.5, 2, 3, 5, or 10 deg of
204 each of the horizontal and vertical components). Moreover, the jump could be to
205 either side of display center (rightward or leftward in the horizontal dimension;
206 upward or downward in the vertical dimension). Therefore, we sampled horizontal,
207 vertical, and diagonal target locations of different eccentricities, with denser sampling
208 of foveal and perifoveal locations. In all data analyses and graphs, we used the
209 convention of positive target locations being to the right of or above display center
210 (for either horizontal or vertical dimension, respectively), and negative target
211 locations being to the left of or below display center. If the monkeys fixated the new

212 spot location within 500 ms after it had jumped, and held their eye position there for
213 another approximately 300 ms, they were rewarded with liquid reward.

214

215 We controlled the monkeys' fluid reward system in real-time by employing a virtual,
216 computer-controlled window around target location. If eye position entered the virtual
217 window within the prescribed "grace" period, a reward was triggered. Otherwise, the
218 trial was aborted, and a new trial was initiated. Our virtual "target windows" across
219 trials had radii of 2-2.5 deg. Note that a radius of 2-2.5 deg was still employed even
220 for foveal target locations of smaller eccentricities. This means that for such small
221 target eccentricities, we exploited the natural tendency of the monkeys to perform the
222 task without any computer monitoring to ensure that they generated the required
223 saccades. This was not a problem at all, because after the monkeys were trained on
224 the task with eccentricities of 5 deg and higher, they very naturally generalized their
225 trained rule when tested on smaller target eccentricities. This was also the case in
226 more complicated variants of the task (Willeke et al. 2019), and it was also consistent
227 with human results (e.g. see Fig. 10). We felt that this approach of large virtual target
228 windows was better than the alternative of enforcing tiny target windows, because in
229 the latter case, any potential increases in reaction times of saccades could have
230 been interpreted as being the consequence of increased task difficulty or a potential
231 speed-accuracy tradeoff.

232

233 We analyzed a total of 928 trials from monkey M in this task, and 1246 trials from
234 monkey N.

235

236 We also analyzed visually-guided delayed saccades and memory-guided delayed
237 saccades made by the same two monkeys. These data were collected during an

238 earlier experiment, with detailed methods described elsewhere (Willeke et al. 2019).
239 The purpose of the present re-analysis was to explore saccade latency as a function
240 of target eccentricity, and to examine how this relationship might be affected by task
241 instruction. We also wanted to directly compare results from the same animals used
242 in the (immediate) visually-guided saccade experiments described above. Briefly, the
243 delayed saccade task was similar to the (immediate) visually-guided saccade task
244 described above, except that there was a delay period of 500-1000 ms during which
245 the fixation spot remained visible when the saccade target was visible. The presence
246 of the central spot instructed the monkeys to maintain fixation, despite the presence
247 of the peripheral target. When the fixation spot disappeared, the monkeys could
248 make the saccade to the peripheral target. This task allowed us to investigate
249 whether increased saccadic latencies for small target eccentricities (see Results)
250 were necessarily linked to sudden visual onsets in the (immediate) visually-guided
251 saccade task.

252

253 The memory-guided saccade task was similar to the delayed, visually-guided
254 saccade task, except that the target duration was brief (duration: 58 ms). When the
255 fixation spot disappeared, the monkeys generated an eye movement to the
256 remembered location of the earlier target flash. This task was useful to dissociate
257 increased reaction times for small target eccentricities from the presence of a visual
258 target.

259

260 In all tasks, we started out with the monkeys already being experts in oculomotor
261 tasks requiring fixation of a small target (similar to author ZH in Fig. 10). The
262 monkeys were used in earlier studies demonstrating their level of precision in eye
263 movement control (e.g. Tian et al. 2018; 2016 for monkey N and Buonocore et al.

264 2019; Skinner et al. 2019 for monkey M). Therefore, even though we analyzed
265 thousands of trials in the present study, we did not characterize learning processes.
266 From personal observation, the naïve monkeys naturally fixated similarly sized
267 fixation spots to a precision significantly higher than that required by computer-
268 controlled virtual windows. The quality of their fixation therefore started out being
269 good, and improved fairly quickly within a matter of a few trials within a single
270 session.

271

272 *Human behavioral tasks*

273 For supporting comparisons of the results from our monkeys in the (immediate)
274 visually-guided saccade task to those reported in the literature on human subjects
275 (e.g. Kalesnykas and Hallett 1996; 1994; Wyman and Steinman 1973), we ran one
276 human expert (author ZH) and three naïve subjects on the same task as that
277 performed by our two expert monkeys (see Figs. 10, 11). We analyzed 1966 trials
278 from subject ZH and 783-974 trials from each of the naïve subjects. In separate
279 sessions, we also ran a variant of the same task, but the fixation spot now remained
280 visible after target jump. The subjects' task was to maintain fixation and press a
281 button (with the right thumb) as quickly as possible after target onset. The goal was
282 to measure manual reaction times for perceptual detections not requiring an eye
283 movement. This allowed us to compare and contrast manual reaction times to
284 saccadic reaction times from the original variant of the task. We analyzed 1924 from
285 author ZH in this task variant, and 799-945 trials from each of the three naïve
286 subjects. In all experiments, the fixation spot and target were a small square of 4.4 x
287 4.4 min arc. Their luminance was 97.3 cd/m², and the background luminance was
288 20.5 cd/m². In addition, two of the subjects (ZH and MB) were instructed to perform
289 the manual task first before the saccade task, and two other subjects (FK and HB)

290 performed the saccade task first before the manual task. The results (see Figs. 10,
291 11) did not depend on the order in which the two tasks were performed, and
292 therefore cannot be explained by learning or practice effects in one or the other task.

293

294 Because we were particularly interested in the monkey memory-guided saccade
295 reaction time results as a function of target eccentricity (see Results below), we also
296 decided to explore their generalizability to human memory-guided saccades, an
297 aspect that was not well-explored in the existing human saccade literature so far.
298 Therefore, we re-analyzed human data that we had collected earlier (Willeke et al.
299 2019) with the same task. Briefly, the human subjects made the same memory-
300 guided saccade task with target locations being chosen randomly across trials from
301 among 480 possibilities, with heavy sampling of small eccentricities. Specifically,
302 target eccentricities in this experiment ranged from 6 min arc to 12 deg, with 288 out
303 of the 480 target locations lying within the square of eccentricities within ± 0.8 deg
304 (horizontally) by ± 0.8 deg (vertically).

305

306 *Behavioral analyses*

307 We detected saccades and microsaccades using established methods reported
308 elsewhere (Bellet et al. 2019; Chen and Hafed 2013). Both methods rely on a
309 mathematical differential (i.e. speed) or more (i.e. acceleration) of the digitized eye
310 position signals acquired by our systems, with specific parameters for the
311 classification of saccadic events depending on the specific signal noise levels in the
312 digitized signals. We manually inspected each trial to correct for false alarms or
313 misses by the automatic algorithms, which were rare. We also marked blinks or noise
314 artifacts for later removal. In scleral eye coil data, blinks are easily discernible due to
315 well-known blink-associated changes in eye position. In video-based eye tracking,

316 blinks are equally easy to detect because they are associated with an absence of eye
317 position data due to the closed eyelids.

318

319 In the (immediate) visually-guided saccade task, we analyzed the first saccade that
320 was triggered after the target jump. We excluded all trials in which there was a blink
321 within +/- 100 ms from target jump, since this could impair visual detection of the
322 jump. We also excluded all trials in which a microsaccade occurred within the period
323 from -100 ms to 60 ms relative to target jump occurrence. Our reason was that
324 microsaccades around stimulus onset reduce target visibility and increase reaction
325 time (Beeler 1967; Bellet et al. 2017; Chen and Hafed 2017; Chen et al. 2015; Hafed
326 and Krauzlis 2010; Tian et al. 2016; Zuber and Stark 1966). Similar exclusion criteria
327 were also used in human analyses (e.g. Figs. 10, 11). We defined as a successful
328 reaction any eye movement made within 70-500 ms after target jump (throughout this
329 article, we interchangeably refer to the time interval between target jump and
330 saccade onset as the “saccadic latency” or “saccadic reaction time”). When plotting
331 reaction time as a function of target eccentricity or direction, or both, we binned
332 nearby eccentricities, and we only showed summary measurements (e.g. mean and
333 s.e.m.) if each bin contained at least five measurements. We also only included
334 saccades if the measurements had movements with direction error relative to the
335 target (defined as the difference in the angular direction of a saccade relative to the
336 angular direction of the target displacement vector) of less than 45 deg (this was the
337 great majority of data; e.g. Fig. 9 in Results).

338

339 For the re-analysis of the delayed, visually-guided and memory-guided saccade data
340 of (Willeke et al. 2019), we used similar procedures to those described above. Since
341 the sampling of target locations in these tasks was slightly different from that

342 performed in the present experiments (i.e. for the visually-guided saccade task), we
343 adjusted the binning windows accordingly, and we only included any measurement
344 bins in which there were at least 7 saccades per bin. We also accepted as a
345 minimum reaction time 100 ms instead of 70 ms, since we observed that reaction
346 times in these “delayed” types of saccade tasks were generally longer than in the
347 immediate visually-guided saccade task.

348

349 For the re-analysis of the human memory-guided saccade data of (Willeke et al.
350 2019), we again used similar procedures. Like in the monkey memory-guided
351 saccade task, we considered a minimum reaction time of 100 ms. In reality, this was
352 conservative, since the human reaction times were significantly longer, in general,
353 than those of the monkeys in the same task (as described in Results and also in
354 Willeke et al. 2019).

355

356 We additionally binned trials in the delayed, visually-guided saccade task according
357 to the length of the delay period used in the task. For analyzing trends of reaction
358 time as a function of delay period duration, we used a running average spanning the
359 total range of delay periods (500 to 1000 ms). The running average started at a delay
360 period of 600 ms with time bin steps of 50 ms until 900 ms. At each of these time bin
361 steps, we averaged trials with +/- 100 ms delay period duration from the current bin
362 step. For example, the average in the first bin step of 600 ms had all trials with delay
363 period durations of 500-700 ms, and the average of the next bin step had all trials
364 with delay period durations of 550-750 ms, and so on.

365

366 Finally, for the visually-guided saccade task, we plotted saccade amplitude and
367 direction error as a function of target eccentricity, using similar binning procedures to
368 those described above for reaction times.

369

370 In all analyses, we were interested in comparing saccades to upper and lower visual
371 field target locations, since eye-movement related structures like the superior
372 colliculus (SC) represent them differently (Hafed and Chen 2016). Specifically, SC
373 visual responses to stimulus onsets (as well as neuronal contrast sensitivity) are both
374 significantly stronger and earlier in SC neurons representing the upper visual field
375 than in neurons representing the lower visual field (Hafed and Chen 2016), and there
376 is a concomitant reflection of this difference in saccade reaction times; this
377 corroborates a very strong correlation between SC visual response strength/latency
378 and saccadic reaction times in general and under a variety of conditions (Chen et al.
379 2018; Chen and Hafed 2017). We therefore divided trials according to whether the
380 target location was in the lower visual field (one group) or otherwise (that is, purely
381 horizontal or in the upper visual field; the second group).

382

383 *Statistical analyses*

384 Our purpose was to document patterns of rhesus macaque reaction time values as a
385 function of visual-field location across a variety of well-established oculomotor tasks.
386 We therefore largely present descriptive statistics in all figures, showing mean and
387 s.e.m. measurements, as well as numbers of observations. All trends that we focus
388 on are immediately visible in the mean and s.e.m. plots that we present.

389

390

391

392 *Data availability*

393 All data presented in this paper are stored in institute computers and are available

394 upon reasonable request.

395

396 **Results**

397

398 *Monkeys exhibit increased saccadic reaction times for foveal target eccentricities*

399 Our goal was to document the saccadic reaction times of rhesus macaque monkeys
400 when target displacements are small. We were motivated by the fact that in humans,
401 it is known that small-eccentricity target displacements are associated with increased
402 saccadic reaction times (De Vries et al. 2016; Kalesnykas and Hallett 1996; 1994;
403 Wyman and Steinman 1973). Figure 1 shows example eye position and velocity
404 traces from one monkey (monkey M) when the target displacement was small (Fig.
405 1a) or when it was much larger (Fig. 1b). In both cases, the target displacement was
406 to the right of central fixation, and we plotted horizontal eye position as well as radial
407 eye velocity in the interval around target jump (labeled target onset in the figure). In
408 both cases, a saccade was made to the target, which scaled appropriately in size
409 with target eccentricity (also see Fig. 9 in a later section of Results). However, when
410 the target eccentricity was small (Fig. 1a), the small saccades had significantly longer
411 reaction times than the big saccades generated when the target eccentricity was
412 large (Fig. 1b). This is illustrated in Fig. 1 with dashed vertical lines delineating the
413 reaction times of the fastest small (Fig. 1a, blue dashed line) and large (Fig. 1b, red
414 dashed line) saccades in the two shown data sets. As can be seen, there was a clear
415 difference between fastest reaction times as a function of target eccentricity.

416 Moreover, the overall distribution for the small saccades was shifted towards longer
417 and more variable reaction times when compared to the bigger saccades. These
418 examples demonstrate that rhesus macaque monkeys exhibit the same latency
419 increase for small visually-guided saccades as human subjects (De Vries et al. 2016;
420 Kalesnykas and Hallett 1996; 1994; Wyman and Steinman 1973).

421

422 We summarized the above results across the entire set of measurements. In Fig. 2a,
423 we plotted in the leftmost panel the mean (surrounded by s.e.m. boundaries)
424 saccadic reaction time of monkey M as a function of target eccentricity. The smallest
425 target eccentricities (<1 deg) were associated with long reaction times, reaching a
426 mean of approximately 240 ms. Reaction time then dropped down to approximately
427 150 ms for eccentricities >1 deg. Larger eccentricities (approximately >5 deg) were
428 associated with another increase in saccadic reaction times, albeit not as large as
429 that for the foveal target eccentricities. This strong increase for the foveal targets is
430 more vivid in the middle panel of Fig. 2a, zooming in on only the central 1.5 deg of
431 target eccentricities. Similarly, the rightmost panel of Fig. 2a plots the same data as
432 in the leftmost panel but now on a logarithmic eccentricity scale, again demonstrating
433 the longer saccadic reaction times associated with small target eccentricities. Similar
434 results were obtained in monkey N, except that this monkey showed an even more
435 dramatic increase in reaction times for foveal target eccentricities (from a minimum
436 mean reaction time of <150 ms to a peak of approximately 300 ms). Therefore,
437 across all target locations and eccentricities that we measured, there was a clear and
438 consistent increase in saccadic reaction times of the two monkeys for foveal targets.
439 There was another increase in reaction times, albeit weaker, for large target
440 eccentricities, as also observed in human subjects (Kalesnykas and Hallett 1996;
441 1994).

442

443 To statistically confirm the above interpretations (Fig. 2), we binned target
444 eccentricities into three groups: <1 deg, 2-5 deg, and >7 deg. Reaction times were
445 significantly faster for the <1 deg group than for the 2-5 deg (monkey M: $p=1.6 \times 10^{-17}$;
446 monkey N: $p=1.6 \times 10^{-41}$; t-test). Moreover, reaction times were significantly faster for

447 the 2-5 deg group than for the >7 deg group (monkey M: $p=1.3 \times 10^{-32}$; monkey N:
448 $p=6.2 \times 10^{-43}$; t-test).

449

450 We also inspected overall reaction time distributions to confirm that our method for
451 accepting successful trials during the experiments did not artificially penalize specific
452 ranges of reaction times. Specifically, our monkeys were rewarded based on the use
453 of virtual, computer-controlled windows surrounding target location. If the eye
454 position was not inside the virtual target window within 500 ms from target onset on a
455 given trial (Methods), then the trial was aborted and the monkey was not rewarded. It
456 is therefore conceivable (although unlikely; Methods) that we artificially truncated
457 reaction time distributions at 500 ms, especially for target eccentricities showing
458 increased reaction times (Fig. 2). However, this was not the case. For example, the
459 top panels of Fig. 3a, b show the reaction time distributions when foveal target
460 eccentricities of 12-36 min arc were tested. The distributions were not truncated at
461 500 ms, suggesting that the monkeys were still able to generate visually-guided
462 saccades to these foveal targets within the prescribed “grace” period of 500 ms.
463 Similarly, the bottom panels of Fig. 3a, b demonstrate that for another range of target
464 eccentricities in which reaction times increased (Fig. 2), the increase was again not
465 affected by the truncation at 500 ms forced by our grace period.

466

467 *Targets in the lower visual field are associated with increased reaction times, also for*
468 *foveal eccentricities*

469 Because the SC exhibits a strong asymmetry between the representation of the
470 upper and lower visual fields (Hafed and Chen 2016), with direct consequences on
471 saccadic reaction times for large saccades, we next analyzed the reaction times of
472 small visually-guided saccades to foveal targets in the upper and lower visual fields.

473 Specifically, it was not known so far whether differences in saccadic reaction times
474 between upper and lower visual field target locations also occur for very small eye
475 movements. For the same data as in Fig. 2, we divided trials according to whether
476 the target was in the lower visual field (Fig. 4a, c; red) or whether it was along the
477 horizontal meridian or in the upper visual field (Fig. 4a, c; blue). Using the same
478 formatting conventions as in Fig. 2, we found that there was, essentially, a global
479 upward shift in the relationship between saccadic reaction time and target
480 eccentricity for targets in the lower visual field. That is, the reaction time increase
481 associated with lower visual field target locations also happened for tiny foveal
482 eccentricities (middle panels in Fig. 4a, c). This was confirmed statistically when we
483 tested reaction times across the two groupings of target locations in Fig. 4a, c
484 (monkey M: $p=2 \times 10^{-8}$; t-test comparing the two groups of data in Fig. 4a; monkey N:
485 $p=1.6 \times 10^{-28}$; t-test comparing the two groups of data in Fig. 4c). Moreover, this effect
486 was not restricted to cardinal target/saccade directions. For example, in Fig. 4b, d,
487 we plotted, for each monkey, the saccadic reaction time as a function of oblique
488 target location. We plotted target location bins on log-polar coordinates (Hafed and
489 Krauzlis 2012), in order to cover the large span of eccentricities tested, and we color-
490 coded each binned target location (z-axis) with the mean saccadic reaction time for
491 that location. In both monkeys, the same general dependence of saccadic reaction
492 time on target eccentricity (Figs. 2, 3, 4a, c) occurred for all target directions. That is,
493 foveal locations had the longest reaction times; there was a minimum of reaction
494 times at intermediate eccentricities; and there was then a more modest increase in
495 reaction times once again for larger eccentricities. Moreover, lower visual field
496 locations (including foveal ones) were associated with the longest reaction times
497 (also see Figs. 10, 11 for a human replication of all of these observations).
498

499 *Delayed, visually guided saccades show largely similar reaction time patterns to*
500 *(immediate) visually-guided saccades*

501 To demonstrate that increased reaction times for small saccades are indeed related
502 to motor programming (our equilibrium hypothesis) rather than only due to visual
503 processing of foveal targets, we also ran our monkeys on a delayed saccade task. In
504 this task, the target remained persistent for a certain delay period while the fixation
505 spot was visible. Only when the fixation spot was removed were the monkeys
506 allowed to make the saccade (Methods).

507

508 We found a similar increase in reaction time in the delayed condition as in the
509 immediate visually-guided saccade task for small target eccentricities. This happened
510 even though the target was persistent, and the instruction to trigger the saccade was
511 the offset of a fixation spot instead of the onset of the target. The task also had
512 temporal expectation inherently built into it (discussed further below), since the longer
513 the delay period was, the more likely it was that the “go” signal for the saccade was
514 to come; there was also sufficient time with short delay periods to plan a saccade.

515 Figure 5 plots reaction time data from this task in a format identical to that in Fig. 4
516 for both monkeys. The same general pattern of results was observed. Namely, small,
517 foveal target eccentricities were associated with the longest reaction times, and lower
518 visual field locations were also associated with long reaction times when compared to
519 horizontal and upper visual field locations.

520

521 An interesting difference that emerged in this condition relative to the (immediate)
522 visually-guided saccade condition was the behavior of saccadic reaction times for
523 large eccentricities (e.g. >10 deg). In this variant of the task, the increase in saccadic
524 reaction times with increasing target eccentricities was less consistent than with the

525 (immediate) visually-guided saccade task (Figs. 2-4). Instead, lower visual field
526 targets of intermediate eccentricities (e.g. between ~4 and 10 deg) exhibited a small
527 increase in reaction time relative to larger target eccentricities (and upper visual field
528 target locations). Thus, in the same two animals, changing the task seemingly
529 modified the pattern of results for large eccentricities.

530

531 We also explicitly investigated the potential role of temporal expectations in this task.
532 We divided our trials based on the length of the delay period. That is, we asked
533 whether saccadic reaction times decreased when the delay period was long, since
534 longer delay periods necessarily increase the likelihood of the instruction to generate
535 the required saccade. For each monkey, we plotted in Fig. 6a, c reaction time as a
536 function of target eccentricity (pooling upper and lower visual field locations together),
537 but after dividing the trials into different bins based on the duration of the delay period
538 (different colors). There was indeed an effect of temporal expectations (faster
539 reaction times for longer delay period durations), but this effect was absent for the
540 most foveal target eccentricities. We confirmed this in Fig. 6b, d by plotting reaction
541 time as a function of delay period duration for different target eccentricity bins. In both
542 monkeys, targets within <1 deg of eccentricity did not show a dependence of reaction
543 time on delay period duration. In monkey N, such a dependence emerged for more
544 eccentric targets as close as 2 deg; in monkey M, this dependence emerged for more
545 eccentric targets approximately >7 deg in eccentricity. These effects were the same
546 whether targets were in the upper or lower visual fields (except for the globally
547 elevated reaction times of lower visual field targets shown in Fig. 5).

548

549 Thus, even though knowledge of target location and expectation to generate a
550 saccade altered the detailed patterns of saccadic reaction times for extra-foveal

551 target locations (Figs. 5, 6), the same increases in reaction times for foveal targets
552 were evident in this task just like in the (immediate) visually-guided saccade task.

553

554 *Small memory-guided saccades are also associated with increased reaction times,*
555 *despite the absence of a visual target*

556 To further demonstrate the independence of small saccade reaction times from
557 foveal visual responses (whether in SC or elsewhere), we also trained our monkeys
558 to generate small memory-guided saccades (Willeke et al. 2019). In this case, the
559 instruction to generate a saccade was the offset of a fixation spot displayed on an
560 otherwise blank screen. The saccade itself was not directed to a visual stimulus, but
561 instead to a remembered location (Willeke et al. 2019). We found similar increases in
562 saccadic reaction times for foveal target eccentricities (Fig. 7; formatted identically to
563 Figs. 4, 5). Interestingly, for foveal target eccentricities (middle panels of Fig. 7a, c),
564 there was no clear difference in reaction times between locations in the upper and
565 lower visual fields, unlike when there was a visual stimulus as the target for the
566 saccade (Figs. 4, 5). Thus, even with memory-guided “microsaccades” (Willeke et al.
567 2019), there was an increase in saccadic reaction times, although the presence or
568 absence of a visual target could alter the detailed properties of such an increase. It is
569 also worth noting that the reaction time in this condition did not increase for larger
570 eccentricities as in the (immediate) visually-guided saccade task. Instead, and as in
571 the delayed, visually-guided saccade task, it was specifically the lower visual field
572 saccades for intermediate eccentricities that seemed to increase.

573

574

575

576 *Small memory-guided saccades in humans show patterns similar to small memory-*
577 *guided saccades in monkeys*

578 Intrigued by the results in Fig. 7, we sought to test whether similar observations could
579 also be made in human subjects. We had human subjects perform the same task as
580 the monkeys (Willeke et al. 2019) and found very similar results (Fig. 8). Small
581 memory-guided “microsaccades” (Willeke et al. 2019) were associated with the
582 longest reaction times relative to all other eccentricities, just like in the monkeys.
583 Therefore, in all tasks, small saccades were always associated with the longest
584 average latencies, regardless of whether the saccades were reflexive (Figs. 1-4),
585 delayed (Figs. 5, 6), or memory-guided (Figs. 7, 8).

586

587 *Small visually-guided saccades show differences in spatial accuracy for upward and*
588 *downward targets*

589 Because of the global changes in reaction times in the (immediate) visually-guided
590 saccade task for different visual field locations (Fig. 4), we searched for other
591 asymmetries in saccade parameters that also depended on foveal (or extra-foveal)
592 target location. We found that saccade amplitude and direction differentially
593 depended on visual field target location for foveal targets. Specifically, when we
594 plotted saccade amplitude as a function of target eccentricity (Fig. 9a, c), we found
595 that amplitude scaled nicely with target eccentricity even for foveal target locations,
596 but there was larger overshoot in saccade amplitude for foveal targets in the lower
597 visual field than in the upper visual field or along the horizontal meridian. On the
598 other hand, when we plotted saccade direction error relative to target direction (Fig.
599 9b, d), we found that the overshooting lower visual field small saccades were more
600 directionally accurate than the saccades to foveal targets in the upper visual field or
601 along the horizontal meridian. Therefore, besides strong increases in reaction times

602 for foveal target eccentricities (Figs. 1-4), small visually-guided saccades showed
603 differential effects of amplitude versus directional accuracy as a function of target
604 visual field location. These effects (Fig. 9) were not so clearly visible in the other
605 variants of the task, such as the delayed, visually-guided saccade task or the
606 memory-guided saccade task.

607

608 *Increased reaction times for small eccentricities are specific to eye movements and*
609 *absent in manual reactions*

610 Finally, we were further investigated the absence of increased reaction times for
611 large saccades made in the memory-guided task when compared to the visually-
612 guided saccade task. We hypothesized that the increase in the latter task might
613 critically depend on the perceptual detectability of the appearing target. Specifically,
614 we used a small spot as the target in all of our experiments, even for eccentricities of
615 10 or 15 deg. This means that, at these eccentricities, the small spot would be harder
616 to perceptually detect than in the foveal or parafoveal regions (due to limits of the
617 contrast sensitivity function). Therefore, even without saccadic responses, decreased
618 perceptual detectability at far eccentricities could delay reaction times.

619

620 We explicitly tested this hypothesis by performing additional experiments with one of
621 us (ZH) being the experienced subject (similar to our two experienced monkey
622 subjects). In Fig. 10a, we replicated the findings of human saccadic reaction times as
623 a function of target eccentricity (Kalesnykas and Hallett 1996; 1994). Note how, in
624 addition to the dramatic increase for small saccades, saccadic reaction times
625 increased with increasing target eccentricity for extra-foveal targets (curved black
626 arrow in the figure; similar to our monkeys in Fig. 2). Critically, for Fig. 10b, we ran
627 the same subject on a perceptual detection task, in which no saccade was required

628 at all. Instead, the subject had to press a button as soon as the target appeared in
629 the periphery (Methods), and we confirmed that no microsaccades occurred between
630 target onset and button press. Two notable observations are clear from the data.
631 First, there was no strong increase in reaction times for foveal target eccentricities,
632 suggesting that the increased reaction times of small saccades are specific to the
633 fact that the motor behavior was to generate small saccades. Second, the same
634 increase in reaction times for larger target eccentricities as in Fig. 10a was still
635 evident (curved black arrow).

636

637 This latter observation is much more obvious when the two curves are superimposed
638 together in Fig. 10c using the same y-axis scaling (but with arbitrary y-axis
639 positioning of the curves due to the different absolute values of saccadic and manual
640 reaction times). Both tasks were associated with increased reaction times for
641 peripheral targets, but only the saccadic task was associated with increased reaction
642 times for foveal targets. Therefore, the increases in Fig. 2 and Fig. 10a for large
643 eccentricities were not specific to saccade generation.

644

645 These same conclusions were reached when we repeated these same experiments
646 on 3 additional naïve subjects (Fig. 11a). Interestingly, all 4 subjects also showed the
647 dependence of saccadic reaction times on upper versus lower visual field target
648 locations (Fig. 10d and Fig. 11b) that we observed in our monkeys (Fig. 4), but this
649 effect was again specific only to saccade generation (Fig. 10e and Fig. 11c).

650

651

652 **Discussion**

653 We investigated spatial and temporal aspects of triggering small saccades in the
654 rhesus macaque monkey and compared our results to those obtained in human
655 subjects both from the existing literature and through our own additional
656 measurements. We specifically found that, in the monkey, small saccades require
657 more time than larger saccades to be triggered. This observation is true whether the
658 small saccades are visually-driven, delayed (but still visually-driven), or memory-
659 guided. We also found a strong asymmetry in the reaction times of small visually-
660 guided saccades to upper and lower visual field locations, similar to larger saccade
661 results (Hafed and Chen 2016; Schlykova et al. 1996; Zhou and King 2002). For
662 larger saccades, there was a gradual increase in reaction times with increasing target
663 eccentricities, but primarily in the (immediate) visually-guided saccade task and not in
664 the delayed, visually-guided saccade task or the memory-guided saccade task.

665

666 Our results are important to document in the oculomotor system literature because
667 there has been no systematic attempt to investigate small-saccade triggering
668 properties in the rhesus macaque monkey. In humans, it is well-known that small-
669 saccade reaction times are long (Kalesnykas and Hallett 1996; 1994; Wyman and
670 Steinman 1973), although the mechanistic reasons for this phenomenon seem to be
671 still not fully understood. In the monkey, there have basically been only casual
672 inferences about small-saccade reaction times in macaques (Boch et al. 1984;
673 Skinner et al. 2019; Willeke et al. 2019), but either with tasks that were not explicitly
674 designed for such analyses or without sufficient sampling of small target
675 eccentricities. Therefore, our results provide an important reference catalog of small-
676 saccade triggering in macaque monkeys. This is especially important nowadays to

677 guide investigations of neural mechanisms associated with foveal visual and motor
678 processing (Chen et al. 2019; Guerrasio et al. 2010; Willeke et al. 2019).

679

680 One interesting aspect of our results is the observation that the reaction times of
681 small saccades are shorter for upper visual field target locations than for lower visual
682 field target locations (e.g. Fig. 4). This was in addition to the observation of increased
683 reaction times in general for small saccades (Figs. 1-3). Therefore, not only are
684 foveal targets associated with long saccadic reaction times (Figs. 1-3), but longer
685 times are particularly prominent with foveal targets located in the lower visual field
686 (Fig. 4). Interestingly, in one of their control conditions, Wyman and Steinman (1973)
687 required a small downward saccade, which exhibited prolonged reaction times in
688 humans as well, although this aspect of the data was not explicitly mentioned in that
689 study. This is consistent with our human results of Figs. 10, 11. It is also consistent
690 with the asymmetric representations of upper and lower visual fields in the SC, in
691 such a manner that can directly affect gaze direction, saccadic reaction times, and
692 landing errors (Hafed and Chen 2016; Goffart et al. 2006). As we elaborate more
693 below, these effects are also consistent with our theory of gaze direction as an
694 equilibrium insofar as an eye movement is not initiated as long as the visuo-
695 oculomotor system is within a state of balance among opposing commands (Goffart
696 2019; Goffart et al. 2018; Goffart et al. 2012; Krauzlis et al. 2017).

697

698 We also noticed interesting contrasts between the reaction times of small and large
699 saccades. For example, immediate visually-guided saccades showed a marked
700 increase in reaction times for large saccades (e.g. Fig. 2), but this effect was not as
701 strong as that for small saccades. It has been reported in humans that large
702 saccades also become associated with increased reaction times (Kalesnykas and

703 Hallett 1996; 1994). However, are the causes similar to the causes of increased
704 reaction times of small saccades? This issue remains unaddressed. Based on our
705 data, we believe that the two increases are driven by quite different underlying
706 causes. Specifically, in the delayed and memory-guided saccade tasks, the increase
707 in reaction times for large saccades was much less obvious than in the (immediate)
708 visually-guided saccade task, even though small saccades showed strong increases
709 in all three tasks. Therefore, increased reaction times for large saccades are likely to
710 be driven by different mechanisms from those affecting small-saccade reaction times.
711 Indeed, our experiments of Figs. 10, 11 demonstrate that perceptual detectability of
712 far peripheral targets might explain the increased reaction times associated with
713 large eccentricities.

714

715 If perceptual detectability can affect reaction times of large target eccentricities (Figs.
716 10, 11), we think that equilibrium states in the oculomotor system explain the long
717 reaction times of small saccades. Specifically, evidence from pharmacological
718 inactivation experiments in either the SC or the caudal fastigial nucleus suggests that
719 gaze direction is an equilibrium, and that an eye movement (saccadic or slow) is not
720 initiated as long as the visuo-oculomotor system is within a state of balance where
721 opposing commands counterbalance each other (Goffart 2019; Goffart et al. 2018;
722 Goffart et al. 2012; Krauzlis et al. 2017). Thus, the longer reaction times of small
723 saccades are the signature of enhanced times to create a symmetry-breaking
724 condition, which puts the downstream premotor neurons into a push-pull regime that
725 is responsible for the firing rates of motor neurons innervating the agonist and
726 antagonist extraocular muscles (reciprocal innervation). Such enhanced times can
727 occur because of the following reason. Prior to bursting during both contralateral and
728 ipsilateral saccades, saccade-related neurons in the rostral SC and caudal fastigial

729 nucleus fire in a sustained manner during visual fixation (Hafed and Krauzlis 2012;
730 Kleine et al. 2003). More importantly, they also increase firing before and during both
731 contralateral and ipsilateral saccades. Such bilateral activity carries, at the level of
732 saccade-related premotor neurons, commands that are antagonist to each other (see
733 Fig. 10 in Goffart et al. 2004). Thus, the longer reaction times of small saccades
734 result from the fact that the bilateral and conflicting drives exerted by collicular and
735 fastigial neurons become stronger as the activity becomes more rostral in the SC
736 and/or as the ipsilateral and contralateral presaccadic spikes emitted by fastigial
737 neurons are simultaneous. The longer lead times of firing activity (before saccade
738 bursts) that some inhibitory premotor neurons emit prior to small saccades strikingly
739 illustrate this concept (e.g. see Fig. 8 in Scudder et al. 1988).

740

741 A second mechanistic reason for enhanced times is related to spatial representation
742 itself. Consistent with the large amount of foveal magnification in the SC (Chen et al.
743 2019), the equilibrium idea is actually a natural extension of SC population coding of
744 saccade metrics, but this time to aid in the specification of gaze direction during
745 fixation. Specifically, Sparks and colleagues proposed that “precise saccadic
746 movements are not produced by the discharge of a small population of finely tuned
747 neurons but result from the weighted sum of the simultaneous movement tendencies
748 produced by the activity of a large population of less finely tuned neurons” (Sparks et
749 al. 1976). If the deep SC is a continuum representing different movement tendencies,
750 then the absence of movement during fixation may be viewed as the simple result of
751 simultaneous movement tendencies for small saccades counterbalancing each other.
752 Indeed, rostral SC neurons active during fixation do individually represent small
753 movement vectors (Hafed and Krauzlis 2012). Thus, the foveal magnification in the
754 SC contributes not only to ensure precise microsaccades (Chen et al. 2019;

755 Guerrasio et al. 2010; Ko et al. 2010; Tian et al. 2018), but it does also imply that a
756 sizable population of neurons is active at any one moment in time to represent the
757 current fixated goal (Goffart et al. 2012; Hafed et al. 2008; Hafed and Krauzlis 2008).
758 The implication of this is that a given displacement (in anatomical coordinates) of the
759 center of mass of such active population would correspond to only a tiny
760 displacement of the represented “movement vector” in visual coordinates (the same
761 displacement in the caudal SC would correspond to much larger changes in the
762 represented movement vector). Thus, achieving a shifted center of mass to create
763 sufficient imbalance in the downstream readout of SC activity is harder because of
764 the tiny visual field locations represented by the rostral SC. Movements effected by
765 readout of the rostral SC would indeed be infinitesimally small for very small shifts of
766 rostral SC populations.

767

768 If balance among multiple gaze commands is what maintains gaze stability and
769 increases reaction times for small saccades, then one might wonder how an
770 imbalance may be generated at all during fixation in the first place. In other words,
771 why is reaction time not infinite once balance among competing gaze shift
772 commands is achieved? One possible explanation is behavioral and invokes the slow
773 fixational eye movements that often happen in between saccades. These ocular drifts
774 change the retinotopic location of the fixated object and thus create the imbalance
775 needed to activate the colliculoreticular streams innervating the eye muscles. In fact,
776 we recently found that the generation of tiny microsaccades during fixation is highly
777 consistently associated with small, instantaneous retinotopic gaze position errors,
778 even in the presence of peripheral “attention-capturing” cues (Tian et al. 2018; 2016).
779 Another explanation is physiological and lies upon the fluctuations of the activity of
780 neurons, which, from the foveal ganglion cells to the saccade-related premotor burst

781 neurons, exhibit sustained firing rates whenever gaze is held stable. Among this
782 immense number of neurons, we find not only long-lead burst neurons in the pontine
783 reticular formation, but also neurons in the caudal fastigial nucleus (Kleine et al.
784 2003; Sun et al. 2016). After unilateral inactivation of this nucleus, fixational
785 saccades are not only dysmetric (Guerrasio et al. 2010), but the direction of gaze
786 during fixation and pursuit is also always deviated towards the lesioned side
787 (Bourrelly et al. 2018; Goffart et al. 2004; Guerrasio et al. 2010). The fact that the
788 head can also be deviated following a unilateral SC or fastigial lesion indicates that
789 the balancing of activity is a process that is not restricted to the determination of eye
790 gaze direction (Goffart et al. 2018); head direction is also an equilibrium. Thus, gaze
791 and head movements, instead of reducing putative signals encoding the angular
792 distance between gaze (or head) and target locations in physical space, may be
793 separate processes which consist of restoring symmetries (Goffart 2019; Goffart et
794 al. 2018).

795

796 An interesting additional consequence of the oculomotor balance idea is that we can
797 predict express, rather than slow, reaction times for small saccades under the right
798 conditions related to instantaneous gaze position error. Indeed, so-called “express
799 microsaccades” can happen when peripheral stimulus onsets momentarily bias a
800 state equivalent to “unstable equilibrium” out of equilibrium (Tian et al. 2018).
801 Specifically, in that study, it was found that a peripheral stimulus onset during fixation
802 was sometimes associated with a distinct population of so-called express
803 microsaccadic reactions, which were highly precise in their timing and direction
804 relative to the appearing stimulus. These movements had latencies significantly <100
805 ms even though they were small eye movements (like in the present study), but it
806 was found that they occurred under very specific conditions of lack of prior

807 microsaccades for a prolonged period of time as well as eye position being in a state
808 of almost “zero” position error relative to the fixated spot (Tian et al. 2018).

809

810 Of course, the oculomotor balance referred to in all of the above can be implemented
811 in different forms in different oculomotor nuclei. For example, omnipause neurons
812 (OPN’s) in the nucleus raphe interpositus exhibit tonic activity in the absence of
813 saccades, similar in principle to other neurons in other brain areas (e.g. rostral deep
814 SC neurons or caudal fastigial nucleus neurons) (Krauzlis et al. 2017). Because
815 these OPN’s completely pause during saccades, they are believed to be an all-or-
816 none mechanism for “fixing gaze”. However, OPN’s do show evidence for reflecting
817 the state of balance among multiple movement tendencies, which is consistent with
818 our equilibrium hypothesis. For example, OPN’s clearly modulate their tonic rate with
819 eye velocity in a continuous manner (Missal and Keller 2002). It is thus conceivable
820 that even during so-called “gaze fixation”, their tonic rate is systematically variable,
821 reflecting fixational drift eye movements. In that case, even these neurons would
822 show variability that is inconsistent with a theoretical “command to fix gaze”. These
823 neurons, like other brainstem premotor neurons, can be part of a network likely
824 coordinating balance or imbalance from among multiple competing movement
825 tendencies. However, there is no convincing evidence to date that inactivating OPN’s
826 results in impairments in gaze fixation or even saccade latency (Soetedjo et al. 2002;
827 Kaneko 1996).

828

829 Naturally, the role of vision needs to be also considered when thinking about
830 oculomotor behaviors, and that is why we performed our delayed and memory-
831 guided saccade tasks. Previous experiments in humans have attempted to dissociate
832 between visual and oculomotor (or other) sources of increased reaction times for

833 small target eccentricities, and they attributed the increase to a difficulty in specifying
834 the saccade metrics (Kalesnykas and Hallett 1996; Wyman and Steinman 1973).
835 Similarly, in the rhesus macaque SC, while some visual bursts for foveal target
836 onsets might show dependence on foveal eccentricity in their response latency (first-
837 spike latency), this does not seem to be a general property of foveal SC neurons
838 (Chen et al. 2019). Specifically, superficial SC neurons (which generally exhibit
839 marginally shorter visual response latencies than deeper SC neurons) show
840 decreases in first-spike latency of the visual response with increasing foveal
841 eccentricity (consistent with our behavioral findings above); on the other hand,
842 deeper SC neurons show no such dependence of visual burst latency on foveal
843 target eccentricity (Chen et al. 2019). Since it is the deeper SC neurons that show
844 higher correlations between visual burst latency and saccadic reaction times (Chen
845 and Hafed 2017; Marino et al. 2012), this might suggest that increased reaction times
846 for small target eccentricities may not be intrinsically visual in nature (i.e. caused
847 purely by visual-only mechanisms). Consistent with this, other studies showed that
848 the latencies of gaze shifts increase for the smallest gaze displacements, though not
849 for the smallest target eccentricities (Goffart and Pelisson 1997; Zambarbieri et al.
850 1995), suggesting that saccade triggering can depend on premotor signals related to
851 the impending movement in addition to incoming visual signals from the retina. Our
852 results from the delayed and memory-guided saccade tasks (e.g. Fig. 5) further
853 corroborate these ideas.

854

855 Finally, future experiments could investigate the neural mechanisms for learning to
856 fixate visual objects under different visual and oculomotor conditions, and in which
857 various amounts of asymmetry would be incorporated. For example, if target shape is
858 changing, whether for the currently fixated position or for next target positions, what

859 are the consequences on the oculomotor balance? How does this change alter the
860 SC and caudal fastigial nucleus population activity? It will also be important to
861 characterize the neural mechanisms underlying the coordination between saccades
862 and slow eye movements (including the ocular drifts), with or without a concurrent
863 head movement.
864

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874 **Author contributions**

875 ZMH collected the data. ZMH and LG analyzed the data and wrote the manuscript.

876

877 **Declaration of interests**

878 The authors declare no competing interests.

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1012 **Figure legends**

1013

1014

1015 **Figure 1 Example horizontal visually-guided saccades of different amplitudes**
1016 **in a rhesus macaque monkey. (a)** Eye position (top) and velocity (bottom)
1017 measurements from 7 example trials in monkey M, for rightward target onsets at
1018 eccentricities between 9 and 15 min arc. Upward deflections in each eye position
1019 trace (top) mean rightward eye position displacements, and the position scale bar
1020 denotes 6 min arc. The vertical dashed blue line indicates the reaction time of the
1021 fastest saccade to occur in the shown set, to facilitate comparison to the data in **b**.
1022 **(b)** Similar analyses for 9 example movements from the same monkey, but now for
1023 target eccentricities between 9 and 11 deg. The position scale bar (top) now
1024 indicates 1 deg. The vertical dashed red line indicates the reaction time of the fastest
1025 movement to occur in the shown set. Comparison of the blue and red traces reveals
1026 a clear increase in reaction times for the small saccades. Subsequent figures further
1027 characterize such an increase.
1028

1029

1030 **Figure 2 Longer visually-guided saccade reaction times for small target**
1031 **eccentricities in rhesus macaque monkeys. (a)** In monkey M, we plotted visually-
1032 guided saccade reaction times as a function of target eccentricity (left). Reaction
1033 times for small-amplitude saccades were the longest. Zooming in to the central 1.5
1034 deg (middle) revealed a monotonic decrease in reaction time with increasing
1035 amplitude within foveal target eccentricities. The rightmost plot shows the same data
1036 in the left and middle panels but using a logarithmic x-axis scale to clarify the strong
1037 increase in reaction time when small-amplitude saccades are triggered. Note that the
1038 reaction times also increased again for larger target eccentricities (e.g. > 5 deg).
1039 n=928 trials; error bars in each panel denote s.e.m. **(b)** Similar results from monkey
1040 N. There was an even stronger increase in reaction times for foveal target
1041 eccentricities. n=1246 trials.
1042

1043

1044 **Figure 3 Distributions of visually-guided saccade reaction times for different**
1045 **representative target eccentricities. (a)** In monkey M, we plotted the distributions
1046 of saccade reaction times for three ranges of eccentricities chosen based on the
1047 results of Fig. 2. The faint-colored curves in the top and bottom panels are copies
1048 (with arbitrary y-axes) of the curve in the middle panel to facilitate comparison of the
1049 distributions. Note how the distributions of the top and bottom panels demonstrate
1050 that the increased reaction times observed in Fig. 2 at these eccentricities were not
1051 due to a potential artifact caused by a cut-off grace period of 500 ms for responding
1052 with an eye movement (Methods). **(b)** Similar results from monkey N. In all panels,
1053 target directions (e.g. lower versus upper visual field target locations) were equally
1054 distributed across all trials. Also note that numbers of observations are directly
1055 inferable from the histogram counts in each panel.
1056

1057

1058 **Figure 4 Dependence of monkey visually-guided saccade reaction times on**
1059 **upper versus lower visual field target location. (a)** Similar analyses as in Fig. 2a
1060 for monkey M. However, here, we separated targets as being located in the lower
1061 visual field relative to the line of sight (red) or otherwise (that is, located horizontally
1062 or in the upper visual field; blue). Reaction times were longer for lower visual field
1063 targets, consistent with (Hafed and Chen 2016). This also happened for small target
1064 eccentricities (middle panel of **a**). **(b)** Log-polar plot of the same data as in **a**
1065 demonstrating how intermediate eccentricities had the lowest reaction times in all
1066 directions, and how lower visual field target locations were associated with longer
1067 reaction times than upper visual field target locations at all eccentricities tested. **(c, d)**
1068 Same as **a, b** but for monkey N. Error bars denote s.e.m.
1069

1070
1071 **Figure 5 Increased reaction times for small delayed, visually-guided saccades**
1072 **in the rhesus macaque monkey. (a)** Similar analyses to those in Fig. 4a for monkey
1073 M, but now during the delayed, visually-guided saccade task. As in the (immediate)
1074 visually-guided saccade task, small saccades had increased reaction times
1075 compared to larger saccades. Also like in the visually-guided saccade task, upper
1076 visual field target locations were associated with faster reaction times than lower
1077 visual field target locations. However, an increase in reaction times for large target
1078 eccentricities was less clear here than in the (immediate) visually-guided saccade
1079 task. Instead, lower visual field targets of intermediate eccentricities (e.g. 5-12 deg;
1080 red reaction time curves in **a**) were associated with increased reaction times relative
1081 to eccentricity-matched upper visual field targets. n=3265 trials; error bars denote
1082 s.e.m. **(b)** Log-polar plot showing the underlying data of **a** across space. **(c, d)**
1083 Similar results were obtained with monkey N. n=4277 trials.
1084

1085
1086 **Figure 6 Impacts of temporal expectations on small and large delayed, visually-**
1087 **guided saccades. (a)** For monkey M, we plotted the same data of Fig. 5a, but after
1088 dividing trials based on delay period duration. For the smallest target eccentricities,
1089 the same reaction time increases seen in Fig. 5a were present, regardless of delay
1090 period duration. For large eccentricities, longer delay periods were clearly associated
1091 with shorter reaction times. **(b)** We plotted the same data as a function of delay
1092 period duration. Each curve shows targets of a given eccentricity bin. Foveal targets
1093 (eccentricities <1 deg) did not show dependence of reaction time on delay period
1094 duration. More eccentric targets did (most prominently for targets >7 deg). **(c, d)**
1095 Same as **a, b**, but for monkey N. In this monkey, the dependence of reaction time on
1096 delay period duration emerged for targets as close as 2 deg in eccentricity **(d)**. Like in
1097 monkey M, more foveal targets (<1 deg) still showed reaction times that were largely
1098 independent of delay period duration. Error bars denote s.e.m.
1099

1100
1101 **Figure 7 Increased reaction times for small memory-guided saccades in the**
1102 **rhesus macaque monkey. (a, b)** Similar analyses to Fig. 4a, b for monkey M but
1103 during the memory-guided saccade task. Small memory-guided saccades were
1104 associated with increased reaction times (compared to larger saccades) despite the
1105 absence of a visual target for the saccades. Note that for memory-guided saccades,

1106 the increase in reaction time for larger target eccentricities that was obvious for
1107 (immediate) visually-guided saccades (e.g. Fig. 2) did not take place so clearly.
1108 Instead, lower visual field saccades of intermediate sizes (e.g. 5-12 deg amplitudes;
1109 red curves) showed elevated reaction times compared to upper visual field saccades.
1110 Also note that there was no strong difference in reaction time between upper and
1111 lower visual field targets for small amplitudes (middle panel in **a**), unlike for visually-
1112 guided saccades (Figs. 2-5). n=6346 trials; error bars denote s.e.m. (**c**, **d**) Same
1113 results for monkey N. n=4245 trials.
1114

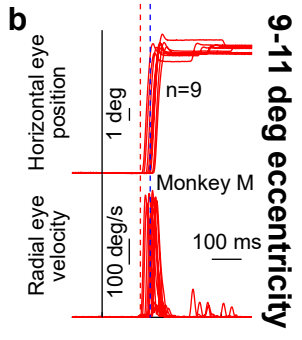
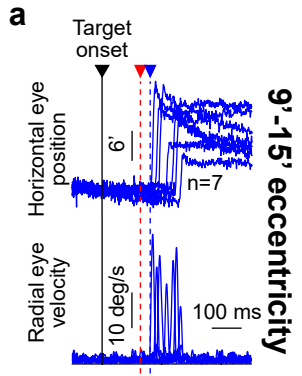
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1116 **Figure 8 Memory-guided saccades in humans showed the same eccentricity-**
1117 **dependencies as monkey memory-guided saccades. (a)** Similar analyses to Fig.
1118 2 but for our human subjects' data combined. The smallest saccades were
1119 associated with the longest reaction times, as in the monkeys (Fig. 7). n=13531 trials;
1120 error bars denote s.e.m. (**b**) The same data but now with upper and lower visual field
1121 target locations separately, as in Fig. 7. Similar results to those in the monkeys were
1122 obtained. Note that for small amplitudes (middle panel), there was a clearer
1123 difference between upper and lower visual field saccades than in the monkeys (Fig.
1124 7). Thus, the data appeared more similar to those in visually-guided saccades (Fig.
1125 4a, c; middle panels). (**c**) The same data but in a format similar to that of Fig. 7b, d,
1126 demonstrating that, in humans as well, small memory-guided "microsaccades" in all
1127 directions are associated with increased reaction times.
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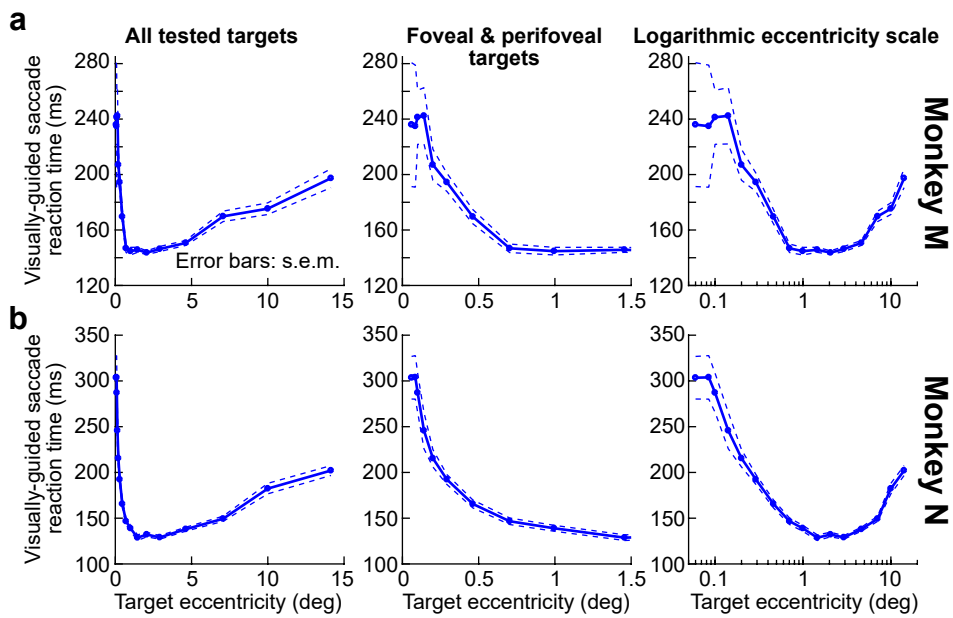
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1130 **Figure 9 Small visually-guided saccades in the rhesus macaque monkey were**
1131 **more accurate in size for upper visual field targets but more accurate in**
1132 **direction for lower visual field targets. (a)** Saccade amplitude as a function of
1133 target eccentricity in monkey M. We used logarithmic axes to display the data such
1134 that the effects with small eccentricities are more visible. Small saccades to lower
1135 visual field targets (red) overshoot the target significantly more than small saccades to
1136 horizontal and upper visual field targets (blue). n=928 trials. (**b**) For the same data as
1137 in **a**, we plotted saccade direction error (relative to target direction) as a function of
1138 target eccentricity. Direction error was smaller for small saccades to lower visual field
1139 targets (red) than for small saccades to horizontal and upper visual field targets
1140 (blue). (**c**, **d**) Similar results for monkey N. n=1246 trials. In all panels, error bars
1141 denote s.e.m.
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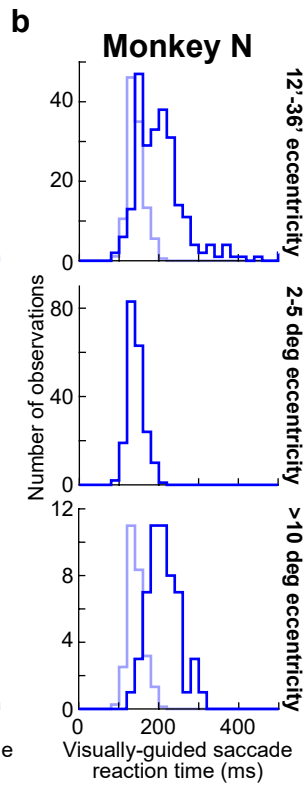
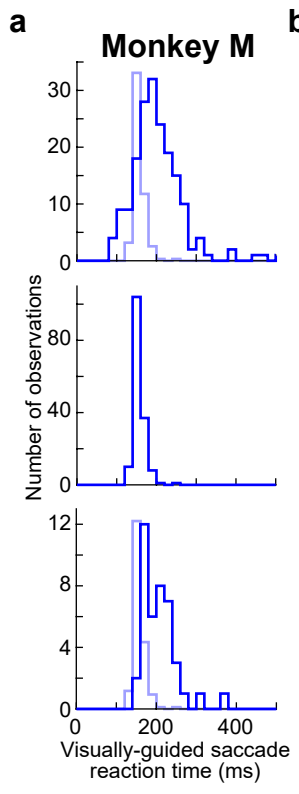
1143
1144 **Figure 10 Both saccadic and manual reaction times increased for large target**
1145 **eccentricities in a human subject; only saccadic, but not manual, reaction**
1146 **times increased for small saccades as well as for lower visual field target**
1147 **locations. (a)** Author ZH performed the same task as in Fig. 2. Small saccades had
1148 very long reaction times. Large saccades also showed a modest reaction time
1149 increase (curved black arrow). (**b**) Results from the same subject in the manual
1150 version of the task (Methods). (**c**) Same data from **a**, **b** but now using the same y-
1151 axis scaling (see vertical scale bar) but arbitrary y-axis placement to visually align the
1152 curves. Both tasks showed increased reaction times for large target eccentricities
1153 (black curved arrows), but only saccadic responses had strong increases for small

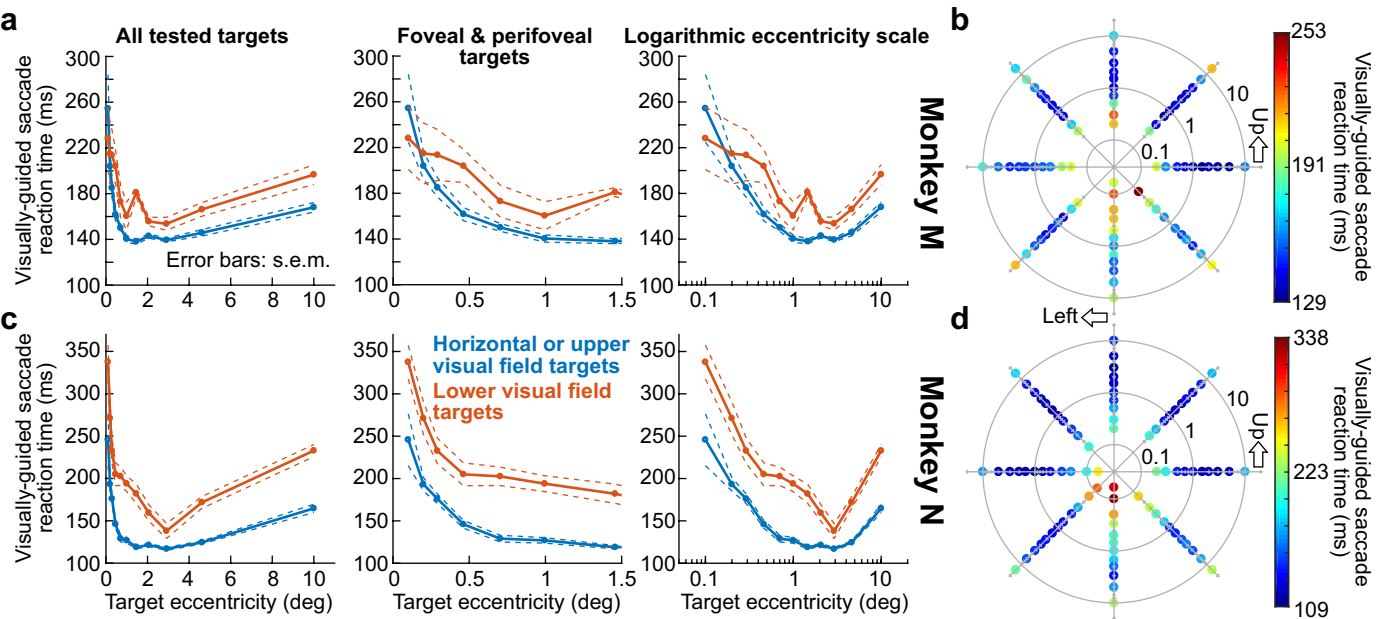
1154 target eccentricities (gray rectangle). **(d)** Same data as in **a** but separating upper and
1155 lower visual field target locations, as in Fig. 4. **(e)** Similar to **d** but for the manual
1156 task's data. Error bars denote s.e.m. Figure 11 shows similar results from three
1157 additional naïve subjects.
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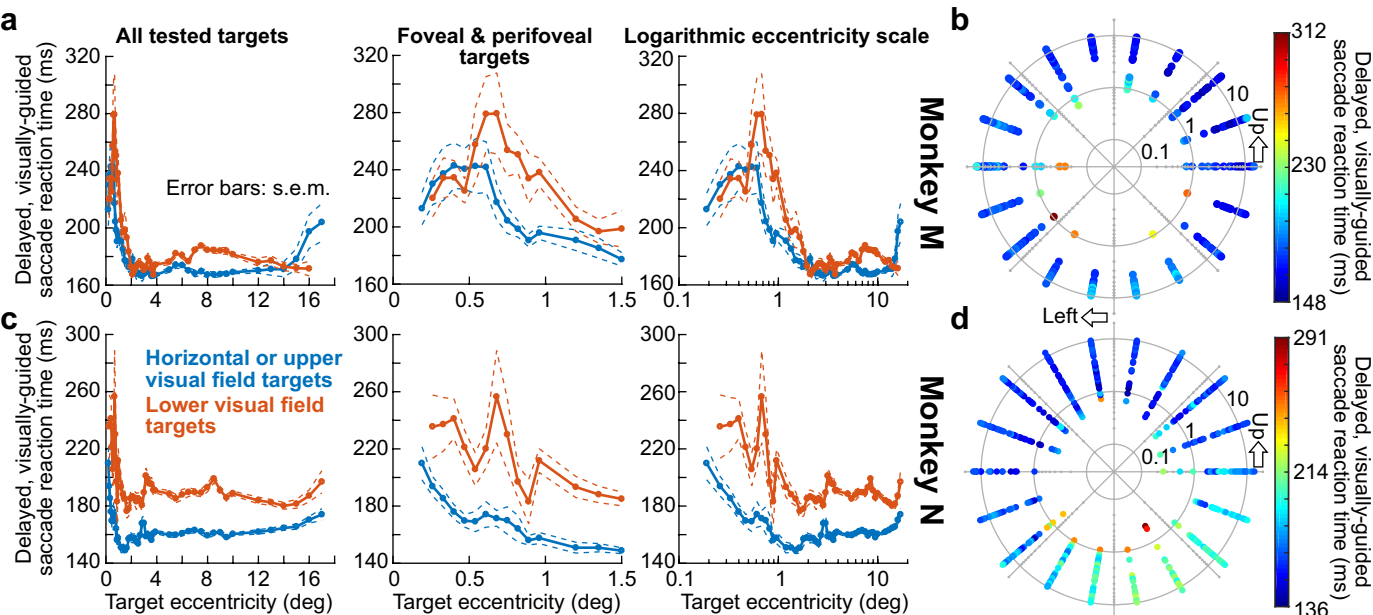
1159 **Figure 11 Same observations as in Fig. 10, but with data from three additional**
1160 **naïve subjects.** Each row of plots represents data from a single subject. **(a)** Same
1161 as Fig. 10c showing a comparison between manual and saccadic reaction times. The
1162 same y-axis scale bar applies to both tasks, but absolute values are not presented
1163 (for reference, absolute values are shown from one data point per curve). **(b)** Same
1164 data as in **a** from the saccade task, but separating targets as being either in the
1165 upper or lower visual fields, as in Fig. 10d. **(c)** Same data as in **a** from the manual
1166 task, but separating targets as being either in the upper or lower visual fields, as in
1167 Fig. 10e. For each subject, the same y-axis scaling was used in **b**, **c** to facilitate
1168 comparison of effect sizes between the two tasks. All other conventions are identical
1169 to those in Fig. 10.
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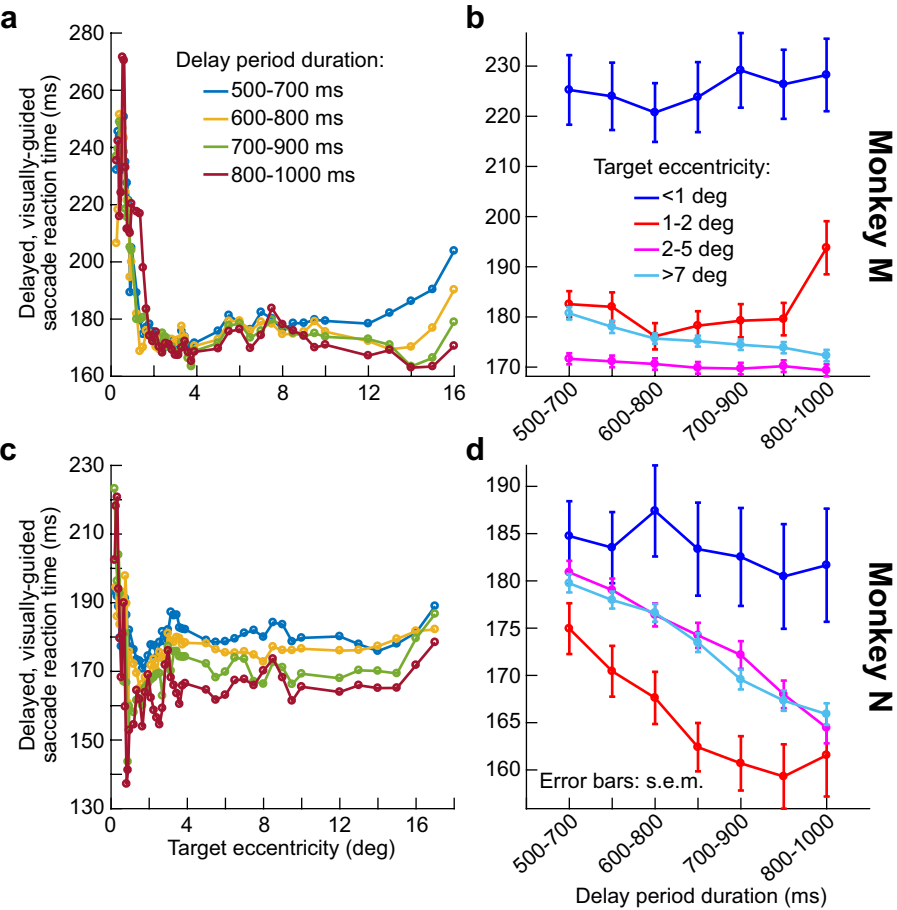


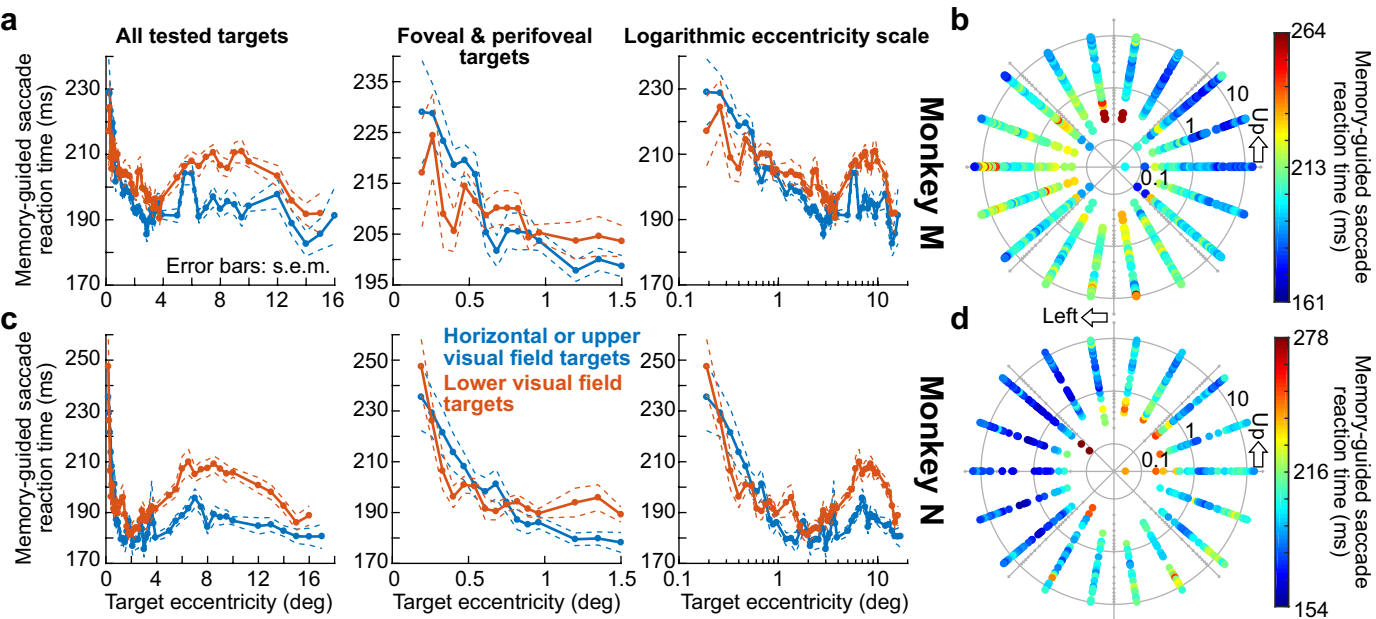


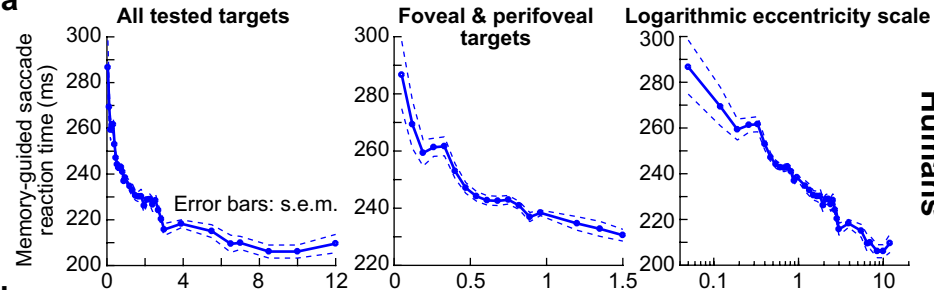
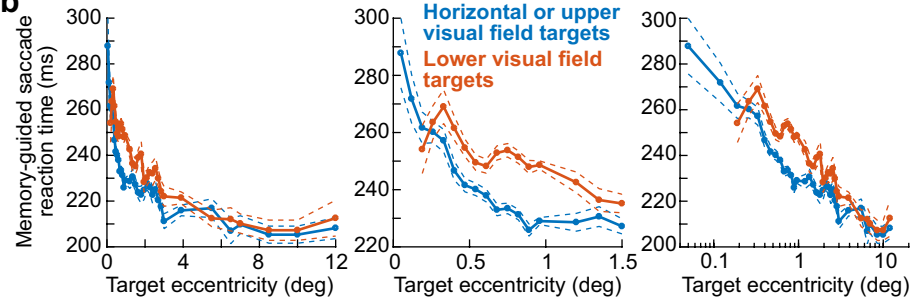










a**b****c**