

1           The superior colliculus and the steering of saccades  
2                           toward a moving visual target

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28 **SIGNIFICANCE STATEMENT**

29 By comparing the movement field (MF) of saccade-related neurons between saccades  
30 toward static and moving targets, we show that the motor burst issued by neurons in the  
31 superior colliculus does not convey commands related to the future location of a moving  
32 target. During interceptive saccades, the active population consists of a continuum of  
33 neurons, ranging from cells exhibiting a shift in the center or boundary of their MF to cells  
34 which exhibit no change. The shifts correspond to residual activity related to the fact that  
35 the active population does not change as fast as the target in the visual field. By contrast, the  
36 absence of shift indicates commands related to the current target location, as if it were  
37 static.

38

39 **ABSTRACT**

40 Following the suggestion that a command encoding the expected here-and-now target  
41 location feeds the oculomotor system during interceptive saccades, we tested whether this  
42 command originates in the deep superior colliculus (SC). Monkeys generated saccades to  
43 targets that were static or moving along the preferred axis, away from (outward) or toward a  
44 fixated target (inward) with a constant speed (20°/s). Vertical and horizontal motions were  
45 also tested. Extracellular activity of 57 saccade-related neurons was recorded in 3 monkeys.  
46 The movement field (MF) parameters (boundaries, center and firing rate) were estimated  
47 after spline fitting the relation between the saccade amplitude and the average firing rate of  
48 the motor burst. During radial motion, the inner MF boundary shifted in the same direction  
49 as the target motion for some neurons, not all. During vertical motion, both lower and  
50 upper boundaries were shifted upward during upward motion whereas the upper boundary  
51 only shifted during downward motions. For horizontal motions, the medial boundaries were  
52 not changed. The MF center was shifted only for outward motion. Regardless of the motion  
53 direction, the average firing rate was consistently reduced during interceptive saccades. Our  
54 study shows an involvement of the saccade-related burst of SC neurons in steering the gaze  
55 toward a moving target. When observed, the shifts of MF boundary in the direction of  
56 target motion correspond to commands related to antecedent target locations. The absence  
57 of shift in the opposite direction shows that SC activity does not issue predictive commands  
58 related to the future target location.

59

60 **INTRODUCTION (648 <= 650 words)**

61           The primate oculomotor system has been used as a model to understand the  
62 neuronal processes underlying the localization of an object in the external world and the  
63 generation of movements toward its location (Goffart, 2017). In most studies, the stimulus  
64 was static, leaving unexplored the processes generating saccades toward a moving target.  
65 An involvement of the deep superior colliculus (SC) and caudal fastigial nucleus (CFN) is  
66 however suggested by the emission of bursts of action potentials by their neurons during  
67 interceptive and catch-up saccades aimed at a moving target (Keller et al., 1996; Fuchs et al.,  
68 1994). Moreover, their anatomical situation between the cerebral and cerebellar cortices  
69 where neurons responsive to the motion of a target are found (Cassanello et al., 2008;  
70 Robinson and Fuchs, 2001) and the saccade-related premotor neurons in the reticular  
71 formation (Scudder et al., 2002; Sparks, 2002) corroborates their involvement.

72           According to the "dual drive" hypothesis, interceptive saccades are driven by a  
73 combination of commands issued by these two subcortical structures (Optican 2009). The  
74 locus of SC activity encodes the location where the target first appears whereas the CFN  
75 component encodes the command related to the target motion after the collicular  
76 "snapshot" (see also Optican & Pretegeiani 2017). This hypothesis rests upon the observation  
77 that the centers of the movement field (MF) of SC neurons (i.e., the amplitude and direction  
78 of saccades associated with the most vigorous burst) shifts to larger amplitudes during  
79 saccades toward a target moving away from the central visual field (Keller et al., 1996).  
80 However, the magnitude of the shift spans over a notable range since some neurons exhibit  
81 no change (see their Fig. 3A). This scattering suggests instead that the population of neurons  
82 which burst during interceptive saccades consists of a continuum of cells ranging from  
83 neurons issuing commands related to past locations of the target (cells with a shift) to  
84 neurons issuing commands related to its current location (cells with no shift). Thus, as an  
85 alternative to the dual drive hypothesis, the "remapping" hypothesis proposed that the  
86 population of active neurons in the SC does not correspond to a snapshot, but expands  
87 across the SC (Fleuriet et al. 2011). In other words, the supplementary command envisioned  
88 by the dual drive hypothesis would be incorporated within the SC itself, making its output a  
89 possible origin of the expected here-and-now command that has been proposed to feed the  
90 saccade premotor system during interceptive saccades (Fleuriet & Goffart 2012).

91           The goal of this study was to evaluate these hypotheses. We also examined whether  
92 SC neurons bursting during interceptive saccades issue commands related to future locations  
93 of the target along its motion path, i.e., locations which are going to be reached. Such a  
94 possibility would be indicated by shifts in the *boundaries* of the MF in the direction *opposite*  
95 to the target motion, an option which was not addressed in the study of Keller et al. (1996)  
96 since they focused on the MF centers. Furthermore, we complemented the  
97 electrophysiological characterization of saccade-related neurons in the SC by comparing  
98 their MF between saccades to static and moving targets. Our results show a continuum of  
99 neurons, ranging from cells which exhibit a shift in the boundary (or center) of their MF to  
100 cells which do not exhibit any change. When shifts were observed, they were always in the  
101 same direction as the target motion, never in the opposite direction. This absence of shift in  
102 the opposite direction indicates no recruitment of neurons which issue commands related to  
103 any future target location. When they are observed, the shifts correspond to a residual  
104 activity due to the fact that the locus of active neurons across the SC does not change as fast  
105 as the target in the visual field. The observation of cells with no shift is consistent with their  
106 involvement in steering the saccade toward the current location of a moving target, as if it  
107 were static.  
108

## 109 **MATERIALS AND METHODS**

### 110 ***Subjects and surgical procedures***

111 All surgical and experimental protocols were approved by the University of Pittsburgh  
112 Animal Care and Use Committee and performed in accordance with the National Institutes  
113 of Health Guide for the Care and Use of Laboratory Animals. Three adult rhesus monkeys  
114 (*Macaca mulatta*; Male: BB & BL; Female: WI) underwent aseptic surgeries to secure a small  
115 head-restraint device to the skull, cement a stainless steel chamber over a craniotomy, and  
116 attach a Teflon-coated stainless steel wire (search coil) on the sclera of one eye. The  
117 chamber was placed stereotaxically on the skull, slanted posteriorly at an angle of 38° in the  
118 sagittal plane. This approach allowed access to both SC and permitted electrode  
119 penetrations roughly perpendicular to the SC surface. Antibiotics and analgesics were  
120 administered postoperatively as detailed in an approved protocol.

121

### 122 ***Behavioral tasks and experimental apparatus***

123 After full recovery, the subjects were trained to sit in a primate chair with their head  
124 restrained and a sipper tube placed near the mouth for reward delivery. They were  
125 subsequently trained to perform standard oculomotor tasks involving stationary targets.  
126 The monkeys were not previously trained to pursue moving targets, which were introduced  
127 only during the recording sessions. Visual stimuli, behavioral control, and data acquisition  
128 were implemented by a custom-built program that uses LabVIEW conventions on a real-time  
129 operating system supported by National Instruments (Austin, TX) (Bryant and Gandhi, 2005).  
130 Each animal sat inside a frame containing two alternating magnetic fields that induced  
131 voltages in the search coil thereby permitting measurement of horizontal and vertical eye  
132 orientations (Robinson 1963). Visual targets were red dots subtending ~0.5° of visual angle  
133 that were displayed on a 55 inch, 120 Hz resolution LED monitor.

134 Every trial began with the illumination of an initial target (T0) that the subjects were  
135 required to fixate for a variable duration (300-700ms, 100ms increments). Trials were  
136 aborted if the gaze direction deviated beyond a computer-defined window (3° radius)  
137 surrounding T0. If fixation was maintained, then T0 was extinguished and another target

138 (T1) was simultaneously presented in the visual periphery. During static trials, the subjects  
139 were rewarded for orienting their gaze within a window that surrounded T1 with a radius of  
140 3-6° for a minimum of 350 ms. During motion trials, target T1 moved at a constant speed of  
141 20°/sec immediately after it appeared on the screen. The reward window associated with T1  
142 was elliptical with a long axis that extended from the starting position of T1 to at least 5°  
143 beyond its final position. The subjects were required to be within this window for at least  
144 500ms before receiving reward. The starting position and the direction of target motion  
145 depended upon the movement field properties of the recorded cell as determined during  
146 static trials (see below).

147

### 148 ***Single-unit recording and movement fields***

149 Tungsten microelectrodes (Microprobe) were used to record extracellular activity  
150 from the intermediate and deep layers of SC. The SC was identified online by the presence  
151 of distinctive bursts of activity associated with flashes of room lights and saccades as well as  
152 identifiable saccade-related cells during static trials. After we isolated a single saccade-  
153 related neuron, we estimated the boundaries of its movement field by pseudo-randomly  
154 presenting targets and observing peak firing rates displayed online by the acquisition  
155 software. Once the optimal vector was approximated, a series of static target locations was  
156 chosen along either 1) an imaginary line that passed through the center of the movement  
157 field and the initial target T0; or 2) an imaginary line that passed through the center of the  
158 movement field and parallel to the vertical meridian; or 3) an imaginary line that passed  
159 through the center of the movement field and parallel to the horizontal meridian.

160 Approximately 75-100 static trials were collected before static and motion trials were  
161 pseudo-randomly intermixed. The starting positions of moving targets (T1 ini) were located  
162 along the same axis used for the targets during static trials. Target motion could be radial  
163 (inward or outward relative to T0), vertical (upward or downward relative to T1 ini) or  
164 horizontal (rightward or leftward relative to T1 ini). Data were collected across the three  
165 axes in block mode. Introducing variability in the location of T1 ini during the motion trials,  
166 as well as the natural variability in the subjects' reaction times, allowed the collection of  
167 neural data during interceptive saccades that fell both within and outside of the boundaries  
168 of the movement field as defined during static trials.

169

170 ***Data set and analysis***

171           The horizontal and vertical eye positions for each trial were digitized and stored with  
172 a resolution of 1 ms and then analyzed off-line analysis with a custom software and Matlab.  
173 The onset and offset of saccades were identified using a velocity criterion of 15°/s. Saccade  
174 metrics (amplitude, peak velocity, latency, etc.) reported here were obtained by measuring  
175 the first saccade (primary saccade) made after the presentation of T1 (equivalently, offset of  
176 T0). The primary saccade needed to occur between 100ms and 500ms after the offset of T0  
177 in order to be considered for further analysis.

178           The present study concerns the discharge properties of 57 neurons which fired a  
179 burst of action potentials during saccades. Response fields were obtained by plotting firing  
180 rate (calculated as the number of spikes per second during a period beginning 20 ms before  
181 saccade onset and continuing until 10 ms before saccade end) as a function of horizontal,  
182 vertical, or radial saccade amplitude during either the static or motion trials. The boundaries  
183 and optimal vector encoded by the MF were estimated from a smoothing spline fit of the  
184 data with the curve-fitting toolbox in Matlab. For each neuron, the same spline parameter  
185 was used for fitting the data of both tasks. The boundary was defined as the saccade  
186 amplitude from which the neuron starts firing with a rate larger than 30 spikes/s. When the  
187 saccade-related burst was preceded by a prelude activity, the threshold was adjusted to the  
188 minimal value that characterizes the burst onset. The Wilcoxon test ( $P < 0.05$ ) was used to  
189 test for statistically significant differences in MF properties across neurons between the  
190 saccades toward a static and a moving target.

191



## 192 RESULTS

193 Figure 1A illustrates the firing rate of a typical visuomotor SC neuron during a static  
194 target trial. The first phasic response occurred approximately 100 ms after the onset of the  
195 visual target and was followed by a second, more vigorous burst timed with the saccade  
196 toward its location. The neuron also produced a weaker burst during saccades whose  
197 amplitude and direction slightly deviated from the neuron's preferred vector (Fig. 1B); the  
198 visual response was absent for this particular location. In response to a target moving  
199 upward at the same horizontal eccentricity, the neuron's discharge was different. When the  
200 target motion started from the location that elicited vigorous visual and perisaccadic  
201 responses during the static condition (Fig. 1A), the visual response was not followed by the  
202 saccade-related burst (Fig. 1C). Thus, the response of this neuron could signal the presence  
203 of the target within its response field, but it did not participate to the population activity  
204 which drives this particular interceptive saccade. The cell was active during saccades whose  
205 vectors matched the vectors that elicited the most vigorous perisaccadic bursts with a static  
206 target (compare Fig. 1A to Fig. 1D). Another observation is the absence of firing when the  
207 monkey made an interceptive saccade whose vector was associated with a perisaccadic  
208 burst if the target had been static (compare Fig. 1B to Fig. 1E). During this particular  
209 condition, the neuron was silent even though the saccade vector belonged to the movement  
210 field measured with static targets (hereafter referred to as "static MF") and even though the  
211 target was going to enter within this MF.

212 Figure 2 plots a slice through the MF of the same cell during three target conditions:  
213 static (2A), moving upward (2B) and downward (2C). The three MFs were generated by  
214 presenting targets along a vertical axis situated at a horizontal eccentricity of  $8^\circ$  to the right.  
215 During these target conditions, saccades had horizontal amplitudes ranging from  $7.2$  to  $9.2^\circ$ .  
216 The center of the static MF was identified during rightward saccades with a small ( $-4.4^\circ$ )  
217 downward component (Fig. 2A); the discharge of this neuron was weaker when the saccade  
218 deviated from this preferred vertical amplitude. Estimated by a spline fitting procedure, the  
219 lower and upper boundaries of the static MF as were  $-11.2^\circ$  and  $0.1^\circ$ , respectively.  
220 Compared to the static MF, the center and the boundaries of the dynamic MF (Fig. 2B) were  
221 shifted upward (toward positive values) during saccades made to a target moving upward  
222 (center:  $-2.3^\circ$ , shift  $\Delta = 2.1^\circ$ ; lower boundary =  $-7.3^\circ$ ,  $\Delta = 2.9^\circ$ ; upper boundary =  $2.4^\circ$ ,  $\Delta =$

223 2.3°). When the target appeared below the lower edge of the static MF and moved upward  
224 toward the center of the MF, the neuron did not fire unless the interceptive saccade  
225 involved a vertical component larger than  $-7.3^\circ$  (see arrow in Fig. 2B). Thus, instead of  
226 emitting spikes that would promote the foveation of a target which was going to enter in its  
227 MF, the neuron remained silent. Likewise, when the vertical amplitude of the interceptive  
228 saccade exceeded the amplitude corresponding to the upper boundary of the static MF  
229 ( $0.1^\circ$ ), instead of pausing and facilitating the generation of saccades with a larger upward  
230 component, this neuron emitted spikes, biasing the population of active neurons with a  
231 command encoding an oblique downward vector. While differences between the static and  
232 dynamic MFs were clearly visible during saccades directed to a target moving upward,  
233 changes were barely visible in the saccade-related burst of this neuron when the target  
234 moved downward (Fig. 2C). Thus, the effects of a moving target on the MF properties of this  
235 particular neuron were consistent with the "dual drive" hypothesis when the saccades were  
236 made to a target moving upward, and with the "remapping" hypothesis when they were  
237 made to a target moving downward.

238         Next, we examine the saccade-related burst of the same neuron during saccades  
239 made along the radial axis of its MF. During saccades to static targets, the neuron fired  
240 during saccades of radial amplitudes ranging from  $5.5^\circ$  (inner boundary) to  $20.7^\circ$  (outer  
241 boundary) with the most vigorous bursts occurring for  $8.9^\circ$  saccades (Fig. 3A). During  
242 saccades to a target moving from the peripheral to the central visual field (inward saccades),  
243 the entire MF was shifted toward smaller amplitude values (Fig. 3B). When the target  
244 started its motion from outside the MF and moved inward, the neuron did not fire unless the  
245 monkey made a  $17^\circ$  saccade (see arrow in Fig. 3B). Thus, instead of emitting spikes that  
246 would promote the reduction of saccade amplitudes, the neuron remained silent.  
247 Moreover, although no firing was observed during small saccades toward static targets with  
248 eccentricity less than  $5^\circ$ , the neuron discharged during small inward saccades. A small shift  
249 of the entire MF was also observed in the direction of the target motion during outward  
250 saccades: the outer boundary shifted toward larger amplitudes ( $\Delta = 2.1^\circ$ ; Fig. 3C) whereas  
251 the inner boundary barely changed ( $\Delta = 0.4^\circ$ ).

252         Many of the cells that we recorded exhibited open movement fields, so only the  
253 proximal boundary could be identified. Figure 4 shows four examples of such neurons  
254 where the movement field exhibited a shift in boundary (consistent with the "dual drive"

255 hypothesis) whereas Figure 5 shows examples of neurons where the shift was absent or  
256 barely visible (consistent with the "remapping" hypothesis). Fig. 4 shows the movement  
257 fields during saccades made to a static target (black symbols) or to a target moving (grey  
258 symbols) along an axis orthogonal to the vertical meridian (A: rightward motion), a radial  
259 axis (B: outward motion) or an axis perpendicular to the horizontal meridian (C: downward  
260 motion; D: upward). For each of these neurons, the boundary of the MF is shifted in the  
261 same direction as the target motion. By contrast, Fig. 5 shows examples of neurons which  
262 exhibited no shift or barely visible shift in the MF boundary during interceptive saccades (like  
263 in Fig. 3C). Some of them exhibited a lower firing rate during saccades made to the center of  
264 the movement field (Fig. 5A-C and F). However, this reduced firing rate was not observed  
265 during small (Fig. 5A,D) or large (Fig. 5C,F) saccades.

266 Figure 6 compares, for all neurons, the boundaries of static MF to those of MF  
267 measured during saccades made toward a target that moved radially (A), horizontally (B), or  
268 vertically (C: upward or D: downward) across their MF. In comparison to the static target  
269 conditions, the inner boundary shifted toward small amplitude values when the saccades  
270 were made to a target that moved inward, i.e., toward the central visual field (Fig. 6A, left  
271 graph; average difference=-1.6+/-1.6 deg, non-parametric Wilcoxon test,  $P<0.05$ ). During  
272 outward motion (Fig. 6A, right graph), a small, but significant shift toward larger amplitude  
273 values, in the same direction as the target motion, was also observed (0.7+/-0.8 deg,  
274  $P<0.05$ ). When the target moved horizontally across the MF (Fig. 6B), no significant  
275 difference in the medial boundary were observed during leftward (0.9+/-2.2 deg;  $P$ -value =  
276 0.25) or rightward (1.4+/-3.8 deg;  $P$ -value = 0.29) motion. The absence of significant  
277 difference is likely due to the small sample of neurons recorded during this motion condition  
278 of target motion. In contrast, when the target moved upward (Fig. 6C), a shift in the same  
279 direction as the target motion was observed for the lower boundary (leftmost graph in C;  
280 2.3+/-2.0 deg,  $P<0.05$ ). For the upper boundary (rightmost graph in C), the difference failed  
281 to reach our threshold of statistical significance (1.1+/-2.0 deg;  $P$ -value=0.07). During  
282 downward target motion (Fig. 6D), a significant shift was observed for the upper boundary (-  
283 1.9+/-1.7 deg,  $P<0.05$ ; rightmost graph in D) but not for the lower boundary (0.0+/-1.2 deg,  
284  $P$ -value=0.81; leftmost graph in D,). In summary, average shifts in the MF boundaries were  
285 observed but not in every condition. Crucially, whenever a significant difference was found

286 between the static and dynamic MFs, the shift was always in the same direction as the target  
287 motion.

288 While Keller et al. (1996) did not describe the MF boundaries, they reported a shift in  
289 MF centers during saccades made toward stimuli moving outward; other directions of target  
290 motion were not tested. Figure 7 complements and extends their study by comparing the  
291 preferred amplitude values during radial (panel A), vertical (B) and horizontal (C) target  
292 motions. The center of MF significantly changed during outward saccades (Fig. 7A, right  
293 graph; average difference =  $3.0 \pm 4.2$  deg,  $P < 0.05$ ). No consistent shift was observed  
294 during inward saccades ( $0.4 \pm 3.6$  deg;  $P$ -value = 0.54). During vertical motions (Fig. 7B), a  
295 shift was observed when the target moved upward ( $3.1 \pm 3.2$  deg,  $P < 0.05$ ; rightmost graph)  
296 but not when it moved downward ( $-0.2 \pm 3.3$  deg,  $P$ -value = 0.81; leftmost graph). During  
297 horizontal target motion (Fig. 7C), we could not detect any significant change for leftward ( $-$   
298  $3.6 \pm 4.4$ ;  $P$ -value=0.052) and rightward ( $1.7 \pm 4.3$  deg;  $P$ -value=0.29) motions. In summary,  
299 shifts in the MF center were observed but not in every condition. Whenever a significant  
300 difference was found between the static and dynamic MF, the shift was always in the same  
301 direction as the target motion.

302 Finally, when the average firing rates were compared between saccades toward a  
303 static and moving target, significant reductions were consistently observed during radial  
304 motions (Fig. 8A;  $-96 \pm 96$  and  $-101 \pm 85$  spikes/second for inward and outward saccades,  
305 corresponding to 24 and 25 % reductions), during vertical motions (Fig. 9B;  $-54 \pm 85$  and  $-$   
306  $62 \pm 110$  spikes/second for downward and upward saccades; 15 and 17 % reductions) and  
307 during horizontal motions (Fig. 8C;  $-121 \pm 98$  and  $-153 \pm 106$  spikes/second for leftward and  
308 rightward saccades; 31 and 39 % reductions). Contrary to the suggestion made by Berthoz et  
309 al. (1986), the firing rate of SC cells during saccades made toward a moving target is not  
310 related to their velocity. Figure 9 shows two examples of cells where the largest difference in  
311 MF was found between inward and outward saccades. For the first neuron, when one  
312 considers the saccades of amplitudes less than 5 degrees, the firing rate was higher during  
313 inward saccades than during outward saccades whereas for saccades of amplitudes larger  
314 than 5 degrees, the firing rate was lower during inward saccades than during outward  
315 saccades (Fig. 9A; left panel). Yet, the relation between the amplitude and the peak velocity  
316 of saccades does not show any difference between the two groups of saccades (Fig. 9A; right  
317 panel). For the other neuron, the firing rate was always smaller during outward saccades

318 than during inward saccades (Fig. 9B; left panel) and again, no difference in velocity was  
319 observed between the two saccade types (Fig. 9B; right panel). Our results contrast the  
320 qualitative impression illustrated in the work of Keller et al. (1996) (see their Figure 1).  
321 Perhaps the attenuation reflected as a “shoulder” or double peaks in the velocity waveform  
322 was due to an accompanying gaze-evoked blink (Gandhi, 2012).  
323

324 **DISCUSSION (1493 <= 1500 words)**

325 In this work, we studied the movement field (MF) of saccade-related neurons in the  
326 SC while monkeys made saccades toward a static or moving visual target. For some neurons,  
327 significant shifts were found in the center of the MFs, in their boundaries and in the firing  
328 rate. The changes in boundaries and centers indicate that for a given saccade, the  
329 population of bursting neurons is not identical between the two types of saccade. However,  
330 the shifts were not always observed and their size varied across the cells. When present,  
331 they were always in the direction of motion, never in the opposite direction. The absence of  
332 shift of boundaries in the direction opposite to the target motion indicates that the SC  
333 activity does not issue commands related to upcoming locations of the moving target (no  
334 predictive coding). A reduction in the discharge was also observed during interceptive  
335 saccades. Unrelated to any change in saccade velocity, this lower firing rate is likely due to  
336 the fact that less photons bombarded the retinal cells (and their subsequent recipient visual  
337 neurons) when their response field was smoothly "traveled" by a moving target than when it  
338 was excited by a static stimulus.

339

340 ***No predictive coding in the SC for the generation of interceptive saccades***

341 The idea has diffused that the SC would identify the position and speed of an object  
342 and, in a predictive and anticipatory manner, trigger the movement required to orient the  
343 gaze toward its future location (Berthoz, 2012; Optican & Pretegianni, 2017). Target motion  
344 would be "used to predict the future target position so as to assure a spatial lead of the gaze  
345 at the saccade end, instead of attempting a precise capture of the target" (Klam et al., 2001).  
346 The present study and other works (Hafed et al., 2008; Fleuriet & Goffart, 2012; Quinet &  
347 Goffart, 2015a) do not support this suggestion. During the saccade-related burst, the active  
348 population does not include cells which code for saccades toward future locations of a  
349 moving target. During inward motions, when the target moved from a location outside the  
350 MF toward its inside, none of our neurons emitted action potentials that would promote the  
351 reduction of saccade amplitude; the outer boundary of their MF did not shift toward larger  
352 values of saccade amplitude (Fig. 2B-C and 3B-C). Likewise, during outward motions, when  
353 the target moved from a location inside the MF toward a location outside, instead of pausing  
354 and facilitating the amplitude increase, the neuron continued to fire, biasing the vector

355 encoded by the population of active neurons toward past locations of the target (Fig. 2B-C  
356 and 3B-C) and not to its upcoming locations. In summary, contrary to what would be  
357 expected if the SC neurons fired in a predictive manner, the boundaries did not shift in the  
358 direction opposite to the target motion. The neurons did not “predictively” fire during  
359 saccades toward a target which was going to enter inside their response field. Moreover,  
360 their firing persisted when the target, after crossing the response field, moved away from it.

361 It may be argued that our testing conditions did not favor the possibility of predictive  
362 responses because our subjects were not trained to pursue the target, or because the target  
363 motion direction and the trials with static and moving targets were pseudo-randomly  
364 interleaved. Anticipatory saccades would have likely been observed if the target always  
365 moved from the same starting location and in the same direction. Such saccades might even  
366 be triggered before the target appears, associated with bursting activities in the SC.  
367 However, these premature saccades do not necessarily involve a shift of MF in the direction  
368 opposite to the target motion. If the SC activity steers the interceptive saccades like  
369 saccades toward a static target, viz., toward the target location (here and now), then the  
370 movement fields should overlap between saccades toward static and moving targets.

371

### 372 ***The “dual drive” and “remapping” hypotheses***

373 Consistent with the study of Keller et al. (1996), we found that, on average, the MF  
374 center shifted in the direction of the target motion during outward saccades (Fig. 7A,  
375 rightmost graph). But the shift was small and not consistently observed across all neurons  
376 (see examples in Fig. 3C and Fig. 5), comparable to observations made in the frontal eye  
377 fields (Cassanello et al., 2008). Should we consider that the generation of outward saccades  
378 involves two sub-groups within the active population, with one sub-group composed of  
379 neurons which exhibit a shift and another of neurons which do not? This option would  
380 require that we consider sub-groups of neurons also for the generation of inward saccades,  
381 and likewise for upward and downward saccades. Indeed, the MF center of our example  
382 neuron was shifted during inward (Fig. 3B) and upward ones (Fig. 2B) but not during outward  
383 (Fig. 3C) or downward saccades (Fig. 2C). The current knowledge of the SC physiology does  
384 not support such a segregation (Hall and Moschovakis, 2003; May, 2006; Gandhi and  
385 Katnani, 2011). The only known segregation takes place in the pontomedullary and  
386 mesencephalic reticular formations, at the level of the premotor neurons which are targeted

387 by the saccade-related SC neurons and which are respectively involved in the generation of  
388 the horizontal and vertical components of saccades (Moschovakis et al., 1996; Barton et al.,  
389 2003). Therefore, instead of segregation, we propose a continuum of commands within the  
390 SC.

391           Neurophysiological studies indicate that the generation of saccades is under the  
392 influence of activity originating in the SC and the CFN. According to the dual drive  
393 hypothesis, the MF changes observed during interceptive saccades result from the fact that  
394 the saccade-related premotor neurons in the reticular formation are summing commands  
395 from the CFN and the SC. Several data are consistent with independent influences of CFN  
396 and SC onto the reticular formation, viz., that the fastigial-induced changes in premotor  
397 activity do not influence the distribution of active neurons in the SC (see discussion of Quinet  
398 and Goffart, 2015b). However, several other observations indicate that the CFN influence on  
399 the premotor neurons is modulatory rather than additive (Goffart et al., 2004; Quinet and  
400 Goffart, 2007). If the CFN provided a command which compensates for motions of the  
401 target away from the vertical meridian (like in Quinet & Goffart, 2015a), one should expect  
402 that this supplementary command be constant (or zero) when the target is static. This  
403 inference is not consistent with the amplitude-dependent horizontal deviation (ipsipulsion)  
404 of vertical saccades during unilateral inactivation of CFN with muscimol (Iwamoto and  
405 Yoshida, 2002; Goffart et al., 2004; Quinet and Goffart, 2007). Finally, the dual drive  
406 hypothesis considers that the SC encodes the location of the target appearance, overlooking  
407 the possibility of subsequent changes in the distribution of active neurons in the SC.  
408 However, this view is neither supported by our results nor by the demonstration that the  
409 population of active neurons can change during saccades made toward a target which jumps  
410 toward a new location (McPeck et al., 2003; Port and Wurtz, 2003).

411           The shift of the MF boundaries indicates that the locus of activity in the SC is different  
412 between identical saccades made toward a static and moving target. The fact that on  
413 average the shift is in the same direction as the target motion indicates that the population  
414 of active neurons includes commands for generating a saccade toward a past location of the  
415 target. The larger shifts of MF centers observed by Keller et al. (1996) are consistent with  
416 this view since in their work, the target moved 2 to 3 times faster than in our study.  
417 Moreover, the examination of the shift for each individual neuron shows a continuum of  
418 neurons ranging from cells which exhibited a shift to cells with no change or very a small



419 shift. Therefore, instead of considering that all SC neurons provide a discrete “snapshot”  
420 command and that another drive is added downstream, we propose that the shifts illustrate  
421 the fact that the population of active neurons does not change in the SC as fast as the target  
422 does in the visual field. Thus, the population in the SC would consist of a continuum of  
423 neurons issuing commands, ranging from commands related to antecedent target locations  
424 to commands related to its current location. More generally, our study and two others  
425 (Hafed et al., 2008; Goffart et al. 2012) show that the SC activity steers the oculomotor  
426 system for target foveation, regardless of whether the target is located in the peripheral or  
427 central visual field, static or moving. Downstream adjustments for improving the accuracy of  
428 foveation are still possible, from the CFN, but from other regions also, since the CFN seems  
429 to essentially control their horizontal component (Sato & Noda, 1991; Goffart et al., 2004;  
430 Guerrasio et al., 2010; Quinet and Goffart, 2015b). These adjustments would be modulatory  
431 and contribute to the spatial and temporal coordination of eye movements with the motion  
432 of a visual target in the external world, in a kind of spatial synchronization (Bourrelly et al.,  
433 2016).  
434

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507

508 **FIGURE LEGENDS**

509

510 **Figure 1:** Illustration of the firing rate of a SC visuomotor neuron during single trials. A-B:  
511 Visual and saccade-related activity following the appearance of a static target at different  
512 locations (Cartesian coordinates) of the right visual field. C-E: Activity of the same neuron  
513 when the target moves upward at the same horizontal eccentricity. In A and C, the target  
514 appears at a location corresponding to the center of the neuron's movement field (MF). In D,  
515 the saccade is aimed at the same location as in A: the visual response is absent because the  
516 moving target appears outside the neuron's response field. In E, the saccade is aimed at the  
517 same location as in B: the neuron does not fire when the target moves.

518 **Figure 2:** Movement field of the same neuron as in Figure 1 during saccades toward targets  
519 located on an axis parallel to the vertical meridian. A: static target; B: target moving upward;  
520 C: target moving downward. The arrow in B shows the shift in the lower boundary of the MF.

521 **Figure 3:** Movement field of the same neuron as in Figures 1 and 2 during saccades toward  
522 targets located along the radial axis of its MF. A: static target; B: target moving inward  
523 (toward the fixation target); C: target moving outward (away from the fixation target). The  
524 arrow in B shows the shift in the outer boundary of the MF when the target moves toward it.

525 **Figure 4:** Movement fields of four other neurons exhibiting a shift during saccades toward a  
526 moving target (grey) in comparison to saccades toward a static target (black). A: target  
527 moves to the right; B: target moves outward along the radial axis; C: target moves  
528 downward; D: target moves upward.

529 **Figure 5:** Movement fields of six other neurons exhibiting no shift, neither in the center nor  
530 the inner boundary. Grey: firing rate during interceptive saccades, black: firing rate during  
531 saccades toward a static target.

532 **Figure 6:** Comparison of the MF boundaries between saccades toward a static target  
533 (abscissa) and saccades toward a target (ordinate) moving along the radial axis (A), a  
534 horizontal axis (B) and a vertical axis passing through the MF center (C and D). The moving  
535 target moves upward in C, downward in D.

536 **Figure 7:** Comparison of the MF center between saccades toward a static target (abscissa)  
537 and saccades toward a target (ordinate) moving along the radial axis (A), the vertical axis (B)  
538 and the horizontal axis passing through the MF center (C). In B, the MF center could not be  
539 estimated for two neurons because of the absence of sharp peak in the curve fitting the  
540 relation between firing rate and saccade amplitude.

541 **Figure 8:** Comparison of the average firing rate (at MF center) of the motor burst between  
542 saccades toward a static target (abscissa) and saccades toward a target (ordinate) moving  
543 along the radial axis (A), the vertical axis (B) and the horizontal axis passing through the MF  
544 center (C).

545 **Figure 9:** The firing rate of SC cells is not related to the velocity of interceptive saccades. Two  
546 examples of cells are shown where the largest difference in MF was found between inward  
547 and outward saccades. For the neuron shown in A, the firing rate was higher during inward  
548 saccades than during outward saccades of amplitude < 5 degrees, but lower during inward  
549 saccades than during outward saccades of amplitude > 5 degrees (left panel). The relation  
550 between the amplitude and the peak velocity of saccades does not show any difference  
551 between the two groups of saccades (right panel). For the neuron shown in B, the firing rate  
552 was lower during outward saccades than during inward saccades (left panel). Again, the  
553 relation between the amplitude and the peak velocity of saccades does not show any  
554 difference between the two groups of saccades (right panel).

Figure 1

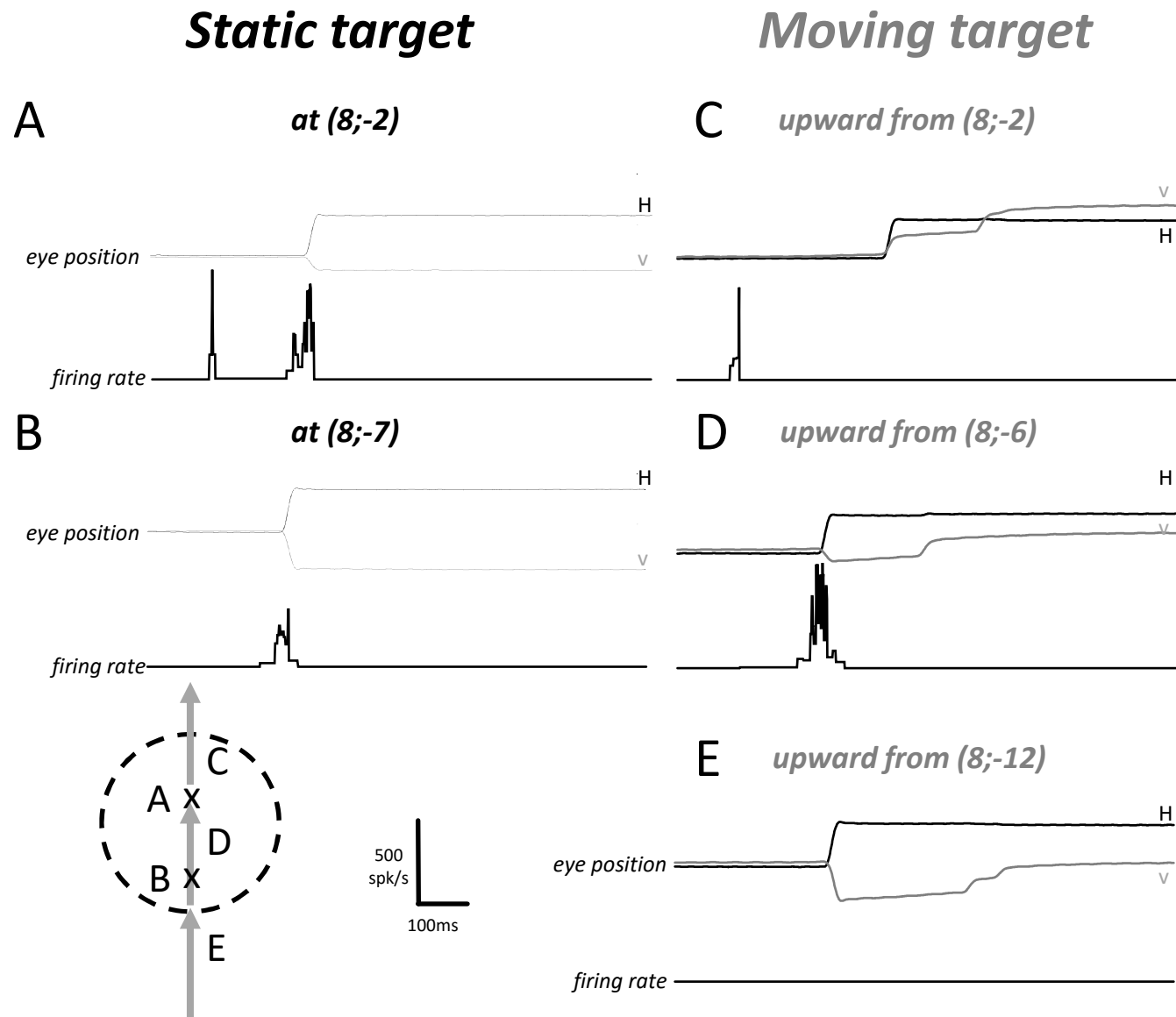


Figure 2

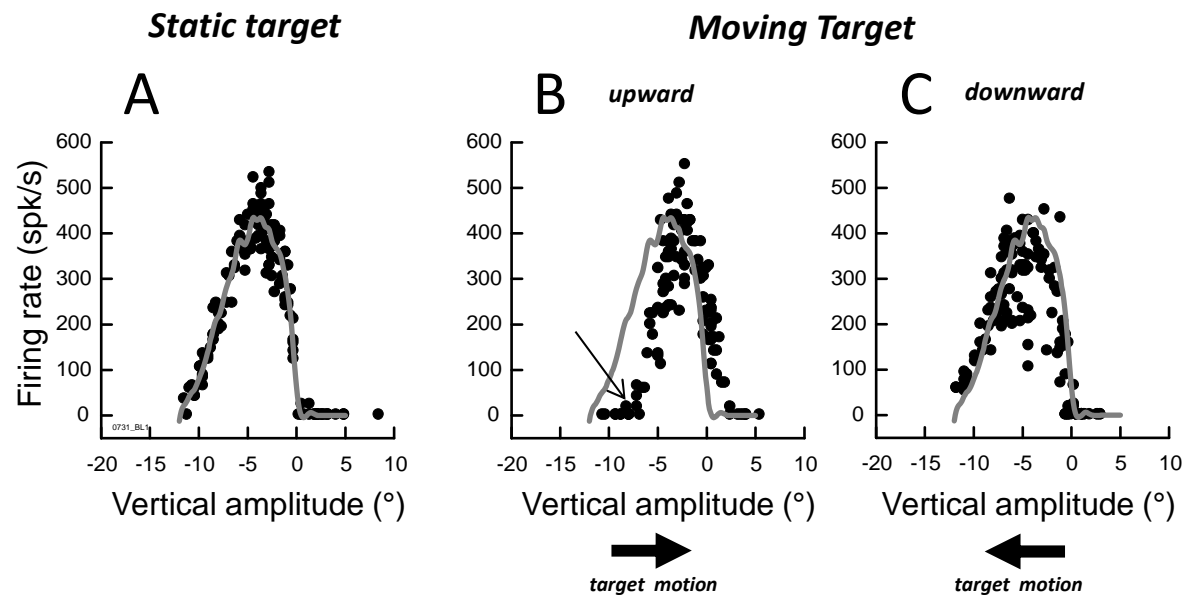




Figure 3

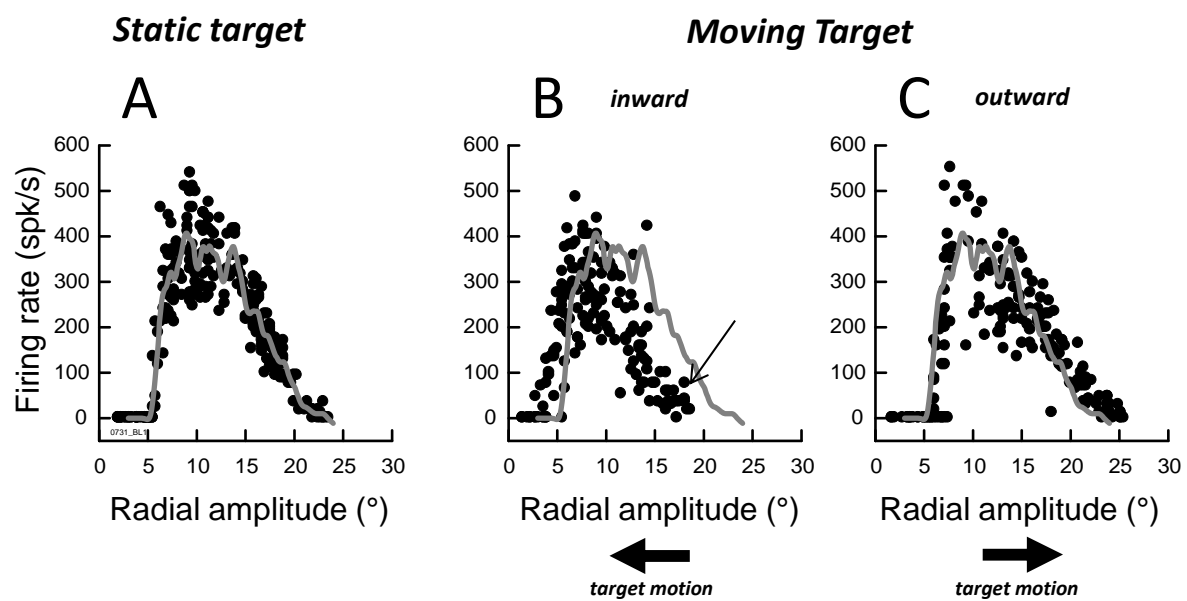


Figure 4

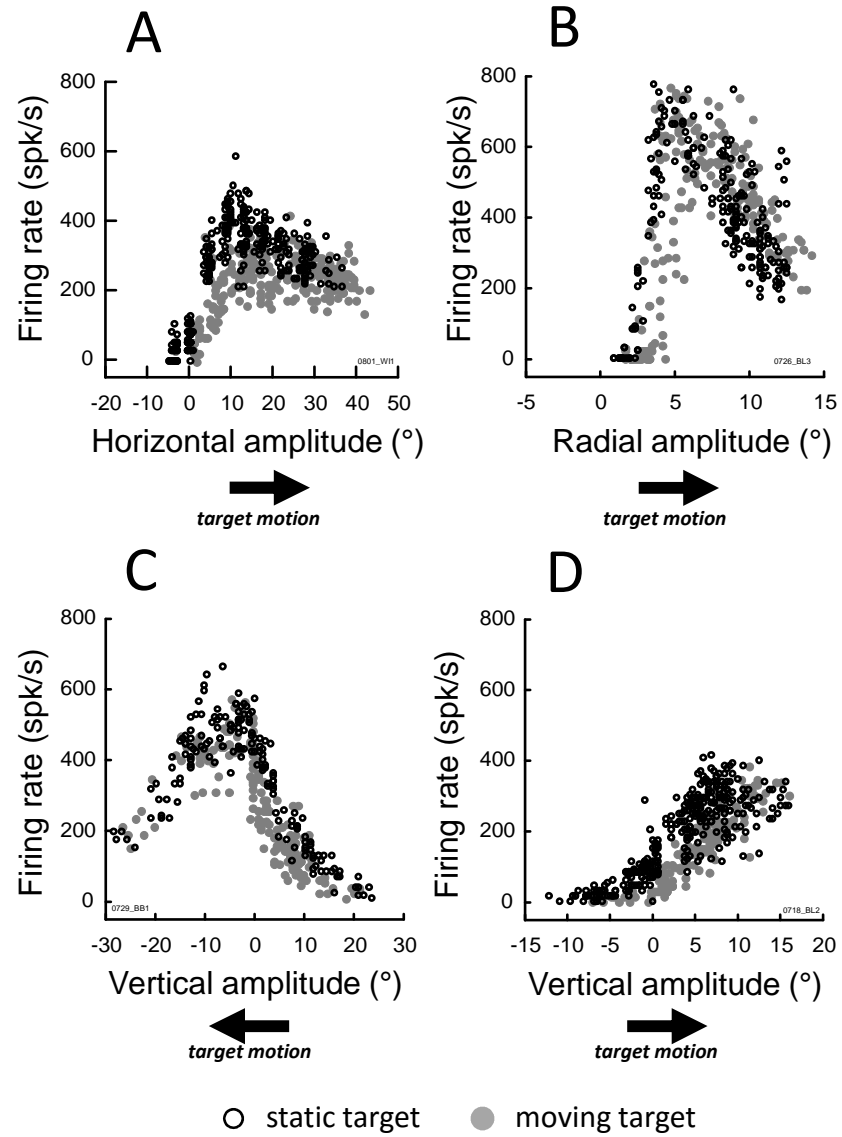


Figure 5

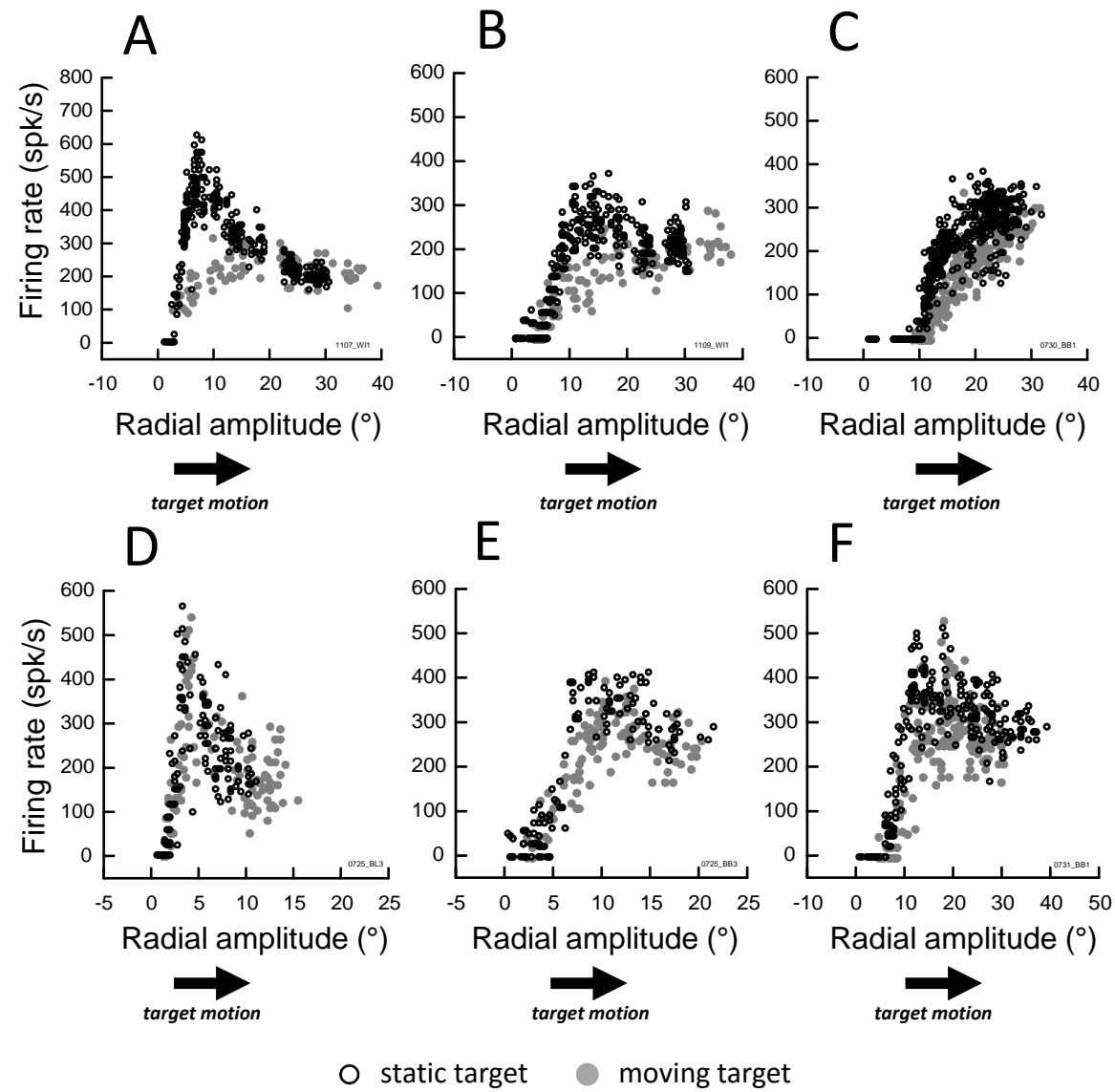
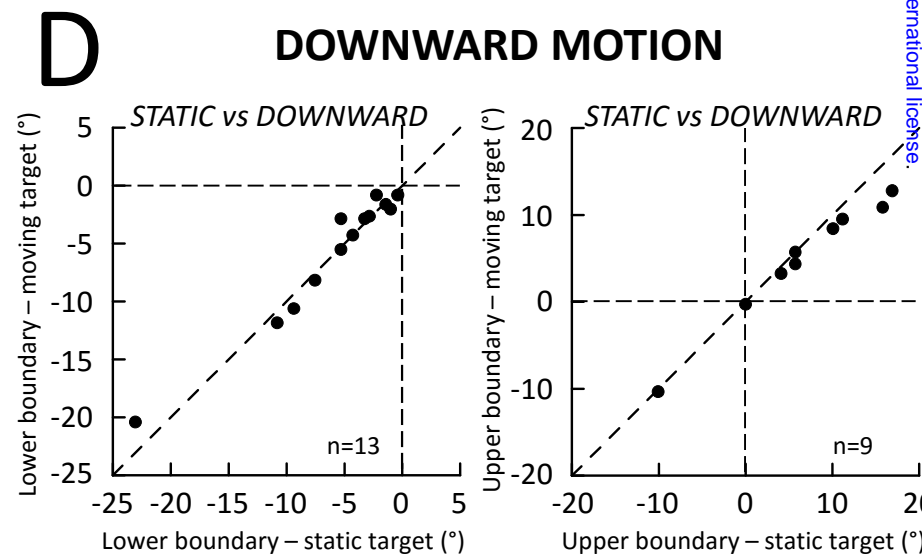
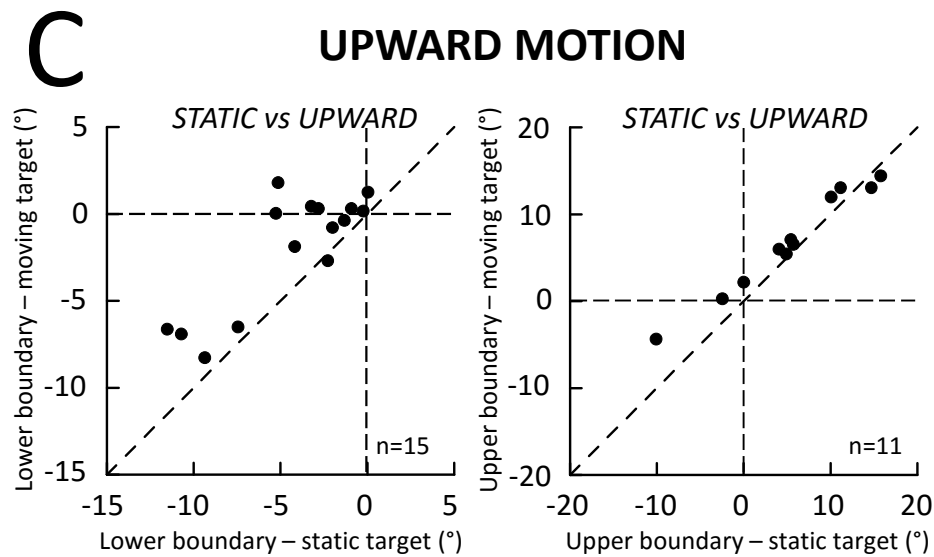
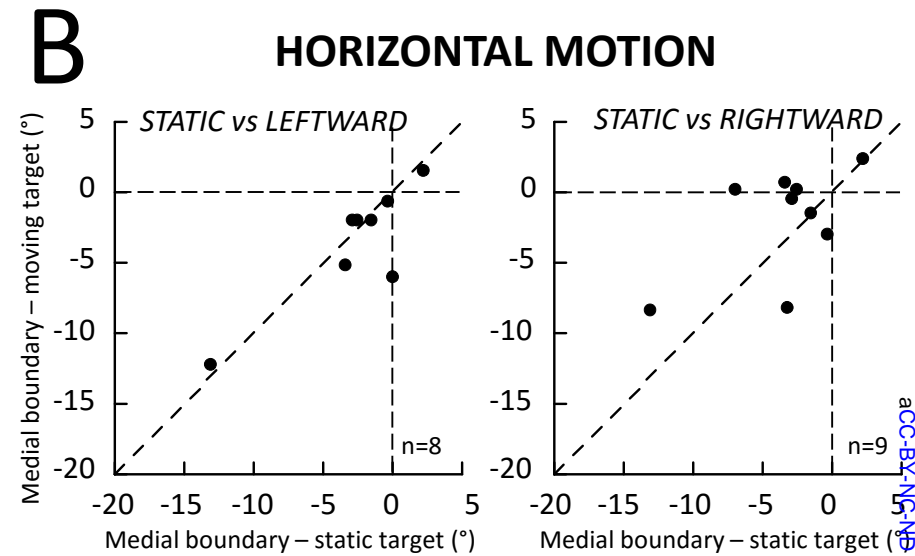
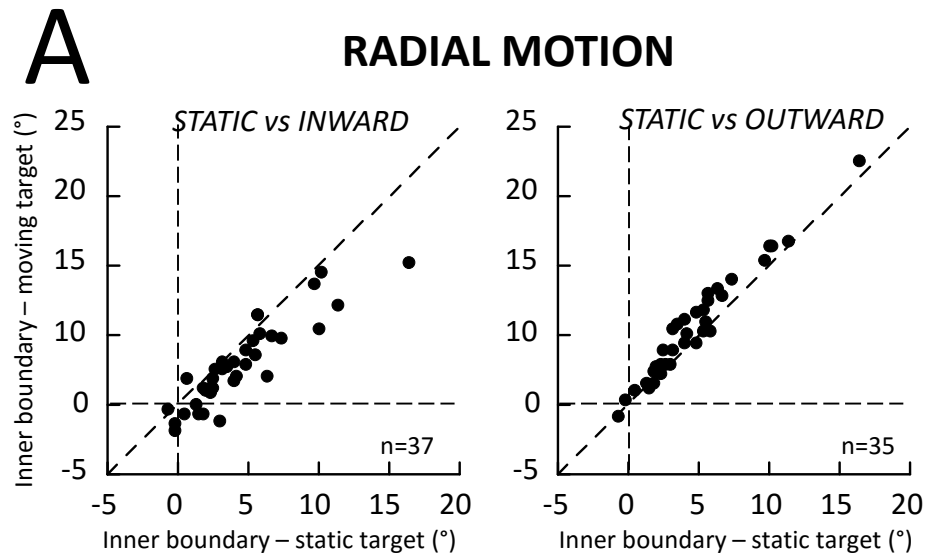
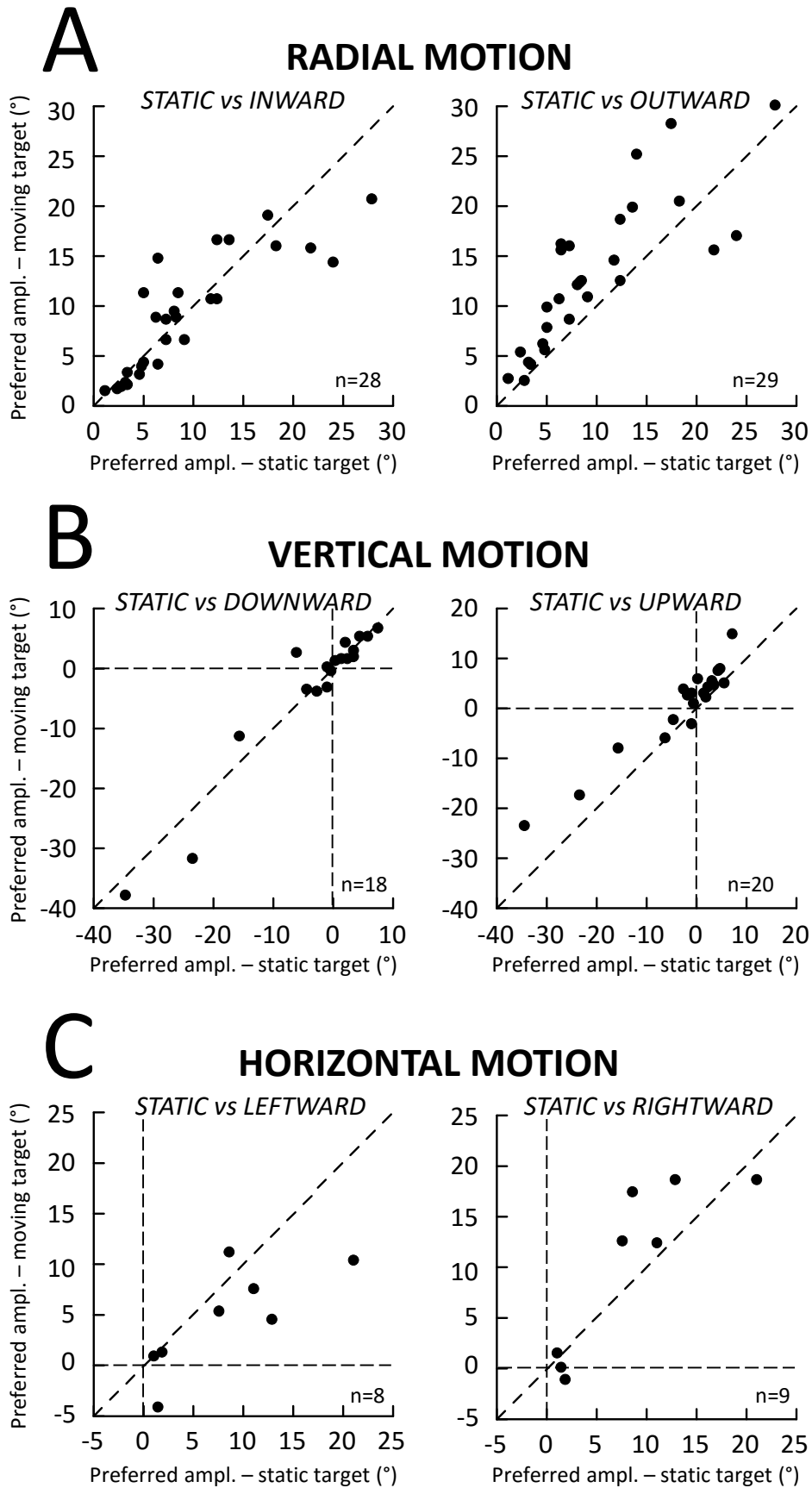


Figure 6





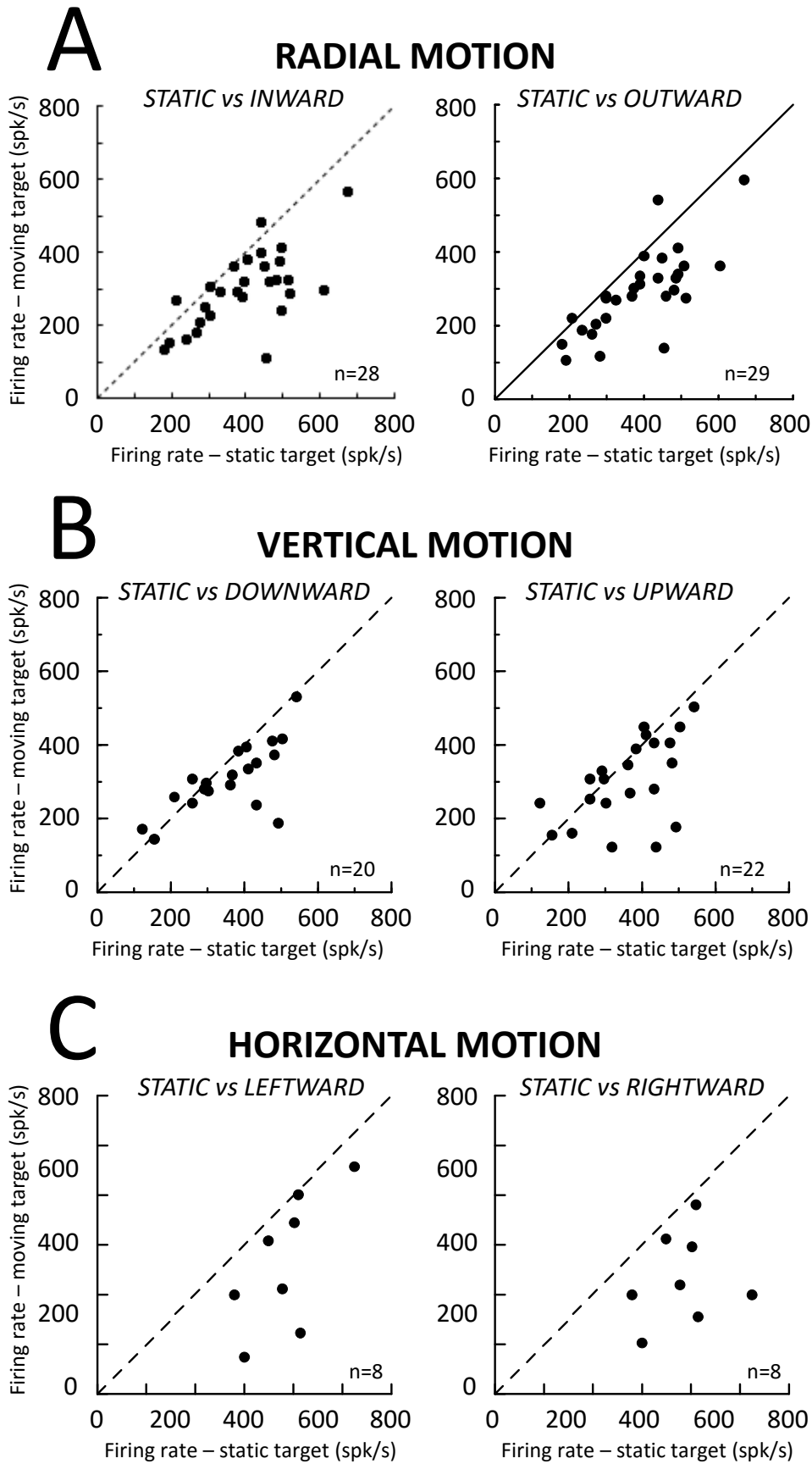


Figure 9

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