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# **Decisions in motion: Vestibular contributions to saccadic target selection**

*Running head: Decisions in Motion*

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38 **Abstract**

39  
40           The natural world continuously presents us with many opportunities for action,  
41 thus a process of target selection must precede action execution. While there has  
42 been considerable progress in understanding target selection in stationary  
43 environments, little is known about target selection when we are in motion. Here we  
44 investigated the effect of self-motion signals on saccadic target selection in a  
45 dynamic environment. Human subjects were sinusoidally translated ( $f=0.6$  Hz, 30 cm  
46 peak-to-peak displacement) along an inter-aural axis using a vestibular sled. During  
47 the motion two visual targets were presented asynchronously but equidistantly on  
48 either side of fixation. Subjects had to look at one of these targets as quickly as  
49 possible. Using an adaptive approach, the time delay between these targets was  
50 adjusted until the subject selected both targets equally often. We determined this  
51 balanced time delay for different phases of the motion in order to distinguish the  
52 effects of body acceleration and velocity on saccadic target selection. Results show  
53 that acceleration (or position, as these are indistinguishable during sinusoidal  
54 motion), but not velocity, affect target selection for saccades. Subjects preferred to  
55 look at targets in the direction of the acceleration – the leftward target was preferred  
56 when the sled accelerated to the left, and vice versa. Saccadic reaction times  
57 mimicked this selection bias by being reliably shorter to targets in the direction of  
58 acceleration. Our results provide evidence that saccade target selection mechanisms  
59 are modulated by self-motion signals, which could be derived directly from the otolith  
60 system.

61

62 **New & Noteworthy**

63 The neural mechanisms of decision-making for actions have been studied  
64 extensively, but mostly when the subject is stationary. Our results directly examine  
65 decision-making in a dynamic environment, i.e. when the subject is in motion.  
66 Findings emphasize the impact of vestibular information on decision-making,

67 extending the importance of this sensory modality beyond its known role in reflexive  
68 responses and spatial orientation, and opening up new avenues for  
69 neurophysiological investigations.

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73 **Introduction**

74  
75 The natural world continuously presents us with many potential targets for action,  
76 necessitating a decision process that selects one target for execution. This selection  
77 can be influenced by both bottom-up factors, such as sensory information and  
78 saliency, and top-down influences, such as internal goals or expectations based on  
79 rewards and costs (Glimcher, 2003; Bisley and Goldberg, 2010; Padoa-Schioppa,  
80 2011; Schall et al., 2011; Sumner, 2011 for reviews). Signatures of these influences  
81 are often seen in behavioral performance. For example, in the saccadic system,  
82 stimulus intensity and contrast influence reaction time (Boch et al., 1984; Carpenter,  
83 1988; Burr and Corsale, 2001; Bell et al., 2006; Marino et al., 2012), likely reflecting a  
84 bottom-up effect. Conversely, reaction times are reduced when targets are  
85 anticipated or more rewarding, which may reflect a top-down effect (Basso and  
86 Wurtz, 1998; Dorris and Munoz, 1998; Rezvani and Corneil, 2008; Bray and  
87 Carpenter, 2015).

88         While these selection mechanisms have mostly been studied in stationary  
89 subjects, many of our saccadic decisions are made while we are in motion, for  
90 example during walking or in a moving vehicle. The study of saccadic decisions in  
91 such a dynamic (from a self-motion perspective) environment has received little  
92 study, although such dynamic situations could introduce a host of new bottom-up and  
93 top-down influences.

94         One likely source of influence in dynamic situations could be the vestibular  
95 system, the sensor in the inner ear that detects linear and angular acceleration of the  
96 head (Angelaki and Cullen, 2008). It is known that the vestibular system interacts  
97 with eye movements to stabilize gaze (Galiana and Guitton, 1992; Paige et al., 1998;  
98 Angelaki et al., 1999), and the brainstem circuits for saccades and quick-phase  
99 responses converge in the brainstem burst generator (Scudder et al., 2002). Such  
100 low-level overlap between vestibular and saccadic circuits within the brainstem may  
101 impose strong bottom-up, reflexive, influences on saccadic decisions.

102           The brain may also bias saccadic decisions by anticipating the effects of  
103   upcoming motion, perhaps to optimize orbital reserve, eye position in space, or  
104   energy usage (Fuller, 1996; Tweed, 1997; Oommen et al., 2004; Monteon et al.,  
105   2012). For this, the brain will need to build an internal model of the motion dynamics  
106   based at least in part on vestibular inputs (Prsa et al., 2015) and incorporate the  
107   predictions based on the internal model in its optimality calculations.

108           The objective of this study is to test the influence of whole-body sinusoidal  
109   translational motion on saccadic decisions. While in motion, human subjects freely  
110   chose to look to one of two visual targets presented equidistantly from a fixation  
111   point, with presentation times staggered by a stimulus-onset asynchrony (SOA). At  
112   different phases of the sinusoidal motion, SOAs were adjusted to ensure that each  
113   target was selected equally often.

114           Given the inherent links between the various signal derivatives (position,  
115   velocity, acceleration, etc) during sinusoidal whole-body motion, we can begin to  
116   distinguish between bottom-up and top-down influences on saccadic decisions. For  
117   example, because otolith afferents respond nearly in phase with acceleration  
118   (Fernández and Goldberg, 1976; Jamali et al., 2009; Yu et al., 2012), a low-level,  
119   bottom-up influence of vestibular information on saccadic choices predicts the largest  
120   biasing effects at peak acceleration (when velocity is zero), and negligible effects at  
121   peak velocity (when acceleration is zero). In contrast, if the brain uses top-down  
122   information, saccadic choice may be influenced by anticipated motion dynamics  
123   (Prsa et al., 2015), and hence may be more related to the direction of motion, i.e. to  
124   velocity-based signals

125           During sinusoidal motion, acceleration and position signals are  
126   indistinguishable. Our results show that saccadic choice is affected most strongly by  
127   acceleration or position, rather than velocity. To avoid the repeated use of a  
128   cumbersome “acceleration or position” phrase throughout our results, we will frame  
129   our methods and results in terms of acceleration or velocity, but the reader is asked

130 to keep in mind that an alternative phrasing in terms of position is conceivable. In the  
131 Discussion, we will forward arguments for while we prefer to interpret our results in  
132 terms of acceleration rather than position.

133

134

## 135 **Methods**

136

137 Twenty healthy subjects (7 males, 13 females, aged 19-32 yrs.) with normal or  
138 corrected-to-normal vision and free of any known sensory, perceptual, or motor  
139 disorders participated in this study. Seventeen of them were naïve as to the purpose  
140 of the experiment. All participants gave their written informed consent in accordance  
141 with the institutional guidelines of the ethics committee of the Social Sciences Faculty  
142 of Radboud University. Participants were given both a written and oral description of  
143 the task as well as practice trials. Each subject participated in two sessions of  
144 approximately 60 minutes each, which were completed on different days.

145

### 146 *Experimental setup*

147 Participants performed a saccadic target selection task in a completely dark room  
148 (except for the target lights) while sitting on a custom-built vestibular sled that moved  
149 side-to-side along a magnetic track, aligned to the subjects' inter-aural axis. The sled  
150 chair was mounted on a linear motor (TB15N; Technotion, Almelo, The Netherlands)  
151 that was controlled by a Kollmorgen S700 drive (Danaher, Washington, DC).  
152 Participants were restrained using a five-point seat belt and their head was firmly  
153 fixated to the sled using an over-ear headphone, which also provided feedback  
154 during the experiment. Emergency buttons on either side of the chair allowed  
155 participants to stop the motion at any time if needed. The vestibular sled moved  
156 sinusoidally with an amplitude of 0.15 m and a period of 1.6 s, which resulted in peak  
157 velocity and peak acceleration of 0.6 m/s and 2.3 m/s<sup>2</sup>, respectively.

158           A horizontal bar with three lights (LEDs) was attached to the sled and located  
159 50 cm away from the subject at eye level. LEDs had a luminance  $< 1 \text{ cd/m}^2$ . The  
160 central LED served as the fixation light and was aligned to the subject's midsagittal  
161 plane. The peripheral lights had visual angles of  $-10^\circ$  and  $+10^\circ$  relative to the  
162 cyclopean eye. The onset latency (the stimulus onset asynchrony, SOA) between the  
163 two peripheral lights could be controlled in steps of 2 ms using an Arduino  
164 microcontroller (Smart Projects, Torino, Italy).

165           Binocular eye position was recorded at 500 Hz using an eye tracker (Eyelink  
166 II, SR Research) tightly secured by a helmet on the subject's head. Mounting the eye  
167 tracker to a head-mounted helmet, rather than to the sled, minimized relative motion  
168 between the head and helmet during sled motion. Stable recording of eye position  
169 was ensured by measuring corneal reflections in combination with pupil tracking,  
170 which reduces the errors caused by any helmet slip and vibration. Saccade choice  
171 (left versus right) was detected online using a position threshold of  $2.5^\circ$  (supported by  
172 a liberal velocity threshold of  $170^\circ/\text{s}$ , which was needed since eye traces on the sled  
173 were noisier), and used to adjust the stimulus onset asynchrony in the next trial  
174 following an adaptive psychometric procedure. Stimuli, eye position signals, and sled  
175 motion were controlled using a custom written Python code.

176

#### 177 *Task*

178 Subjects performed the following target selection task, both without (stationary  
179 paradigm) and with sled motion (dynamic paradigm). They initiated a trial by fixating  
180 the center light, which remained on during the whole experiment (Figure 1A). After  
181 the subject had looked at this fixation point for at least 500 ms within a  $2.5^\circ$  position  
182 threshold, the two peripheral lights were illuminated with a small timing difference  
183 between their onsets. Participants were instructed to look as fast as possible to one  
184 of these lights and then return to the center light. In 4% of the trials only a single  
185 target was presented, to serve as catch trials.

186           The SOA was adjusted across trials based on the directional responses in the  
187 preceding trials using an adaptive approach (Psi procedure, Kontsevich and Tyler,  
188 1999). This method updates posterior probabilities after every trial in the two-  
189 dimensional (mean, slope) parameter space of psychometric functions in order to  
190 compute for each possible SOA the expected information to be gained by completion  
191 of a trial with this SOA. On each trial the method selects the SOA that maximizes this  
192 expected information. While the number of trials for a particular SOA is not constant  
193 in this procedure, it converges quickly and determines the mean and slope in fewer  
194 trials than a fixed interval approach. The mean indicates the stimulus onset  
195 asynchrony for which a given subject selected both targets equally often. We refer to  
196 this value as the balanced time delay (BTD). In the dynamic paradigm (see below),  
197 SOAs for different phases of motion were adjusted independently. SOAs could vary  
198 between -250 to 250 ms in steps of 2 ms. In practice, we found that the choice  
199 preference plateaued at choices for  $|\text{SOA}| > 150$  ms, with subjects always looking to  
200 the first stimulus. These large SOA trials in combination with the single target 'catch'  
201 trials ensured that subjects were paying attention to visual stimuli and making  
202 choices based on each trial's visual input instead of a predefined directional choice.  
203 Accordingly, trials with  $|\text{SOA}| > 150$  ms were combined with single target 'catch' trials.

204           A self-paced pause of about 1 min was provided every 100 trials  
205 (approximately every 5 minutes), during which the sled was stationary and the room  
206 lights were turned on in order to avoid dark adaptation. After every pause, the Eyelink  
207 system underwent drift correction. In all trials, auditory feedback was given to inform  
208 participants if they responded too fast (reaction time  $< 100$ ms relative to the  
209 presentation of the first target), too slow (saccade reaction time  $> 450$ ms), or looked  
210 in the non-target direction during catch trials. If a trial was not performed according to  
211 these criteria, it was repeated at the next instance of the corresponding motion  
212 phase.

213



214 *Paradigms*

215           As indicated above, the target selection task was incorporated in two  
216 paradigms: stationary and dynamic. In the stationary paradigm we tested the  
217 saccadic target preference while the sled remained stationary. Each subject  
218 completed this paradigm at the beginning of each of the two sessions, providing us  
219 with a measure of test-retest reliability. The stationary paradigm lasted about 15  
220 minutes with a total of 250 trials. Stimuli were presented every 1.5 sec.

221           In the dynamic paradigm (Figure 1A), targets could be presented at 8 different  
222 phase angles (from 0 to 360° in steps of 45°) of the sinusoidal sled motion. Figure 1B  
223 illustrates the phase-plane plot, showing velocity against acceleration. Each phase  
224 was tested following its own independent adaptive procedure that ran in parallel with  
225 the other phases being tested. Since it was only possible to have four psychometric  
226 procedures converge in one session, the dynamic paradigm was split across two  
227 days, with four different phase angles per day, counterbalanced across subjects. On  
228 one day, targets were presented at the motion reversals (phases 0° and 180°), when  
229 the sled was at maximum acceleration and had zero velocity, and at the center of the  
230 motion sinusoid (phases 90° and 270°), when the sled was at maximum velocity and  
231 had zero acceleration. On the other day, these phase angles were shifted by 45°, so  
232 that targets were presented at 45°, 135°, 225°, and 315°. On both days, the first of  
233 the two stimuli was always presented at the exact time of the selected phase, while  
234 the second stimulus was delayed by the SOA determined from the adaptive  
235 procedure.

236           Subsequent trials were tested 1¼ motion cycle apart, i.e., probing the phase  
237 that was shifted 90° forward compared to the former, so the minimum time between  
238 trials was 2.0 s. However, if the subject did not accurately fixate the central target at  
239 the time required, one or more motion cycles would pass until fixation criteria were  
240 met and stimuli could be presented. Each session lasted about 45 minutes with a  
241 total of 700-900 trials per session and a pause of one minute every 100 trials. As a

242 result, with this design, targets were presented ~175-225 times at a given phase of  
243 motion.

244

#### 245 *Data Analysis*

246 We performed off-line data analyses in Matlab (MathWorks). Of the correctly  
247 performed trials, we quantified choice preference by calculating the probability of a  
248 rightward saccade as a function of SOA. We used a maximum likelihood fit of a  
249 cumulative Gaussian function including a lapse rate parameter to summarize the  
250 psychometric data of each participant:

$$f(x) = \lambda + (1 - 2\lambda) \frac{1}{\sigma\sqrt{2\pi}} \int_{-\infty}^x e^{-\frac{(y-\mu)^2}{2\sigma^2}} dy$$

251 in which  $x$  represents the magnitude of the SOA. The mean of the Gaussian,  $\mu$ ,  
252 represents the balanced time delay (BTD), which is the SOA for which the participant  
253 selected both targets equally often. A positive value of  $\mu$ , that is, a positive BTD,  
254 reflects that the rightward target needed to be turned on first to balance the choices  
255 and thus corresponds to a preference for the leftward target. Parameter  $\sigma$ , inversely  
256 proportional to the slope of the curve, serves as a measure of the participant's  
257 variability in the responses. Parameter  $\lambda$ , representing the lapse rate, accounts for  
258 stimulus-independent errors caused by subject lapses or mistakes. It was restricted  
259 to small values ( $\lambda < 0.06$ ).

260 Having established the BTDs for saccadic choice in the stationary condition  
261 and for the different phases of the sled motion, we compared BTDs from different  
262 phases of the sled motion. This yielded a number of contrasts of interest. To examine  
263 the influence of acceleration, we compared the BTDs at phases with equal velocity  
264 but opposing accelerations. For example, comparing BTDs at the 0° and 180° phases  
265 allowed examination of the effect of peak acceleration on choice preference, while  
266 velocity was zero (see Fig 1B). Similarly, the effects of leftward vs. rightward

267 acceleration were also investigated by comparing the BTDs of 45° vs. 135° (same  
268 leftward velocity) and 315° vs. 225° (same rightward velocity).

269 We used a similar approach to examine the influence of velocity, comparing  
270 BTDs with equal accelerations but opposing velocities. For example, comparing  
271 BTDs of 90° vs. 270° phases tested for an influence at peak velocity, when  
272 acceleration was zero, while the 45° vs. 315° and 135° vs. 225° comparisons tested  
273 other leftward vs. rightward velocities at equal, non-zero, accelerations (see Figure  
274 1B). In addition we analyzed the stationary and dynamic data in combination using a  
275 2-way ANOVA containing three levels of acceleration (leftward, zero, rightward) and  
276 three levels of velocity (leftward, zero, rightward) (see Figure 1B).

277 After documenting these results, we computed, separately for each subject,  
278 as an overall dependency measure the correlation between his/her BTDs and the  
279 acceleration and velocity amplitudes at each of the probed phases. We tested  
280 whether mean correlations differed significantly from zero using a *t*-test on the Fisher  
281 z-transformed correlation coefficients from the 20 individual subjects.

282 If the BTD results indicate a choice bias, one could also expect the reaction  
283 time to differ between saccades to preferred and non-preferred targets. Targets at  
284 preferred locations would be processed faster than targets at non-preferred locations.  
285 To test this, we defined saccadic reaction time (SRT) as the time interval between  
286 the onset of the saccade target and the initiation of the saccade. We further  
287 computed, per subject, for all phases of the motion, the difference between the  
288 average SRT for the leftward and rightward target, denoted by  $\Delta$ SRT. We used a  
289 correlation analysis, similar to that described as above, to examine the relationship  
290 between  $\Delta$ SRT and acceleration, and  $\Delta$ SRT and velocity, at each of the probed  
291 phases. This analysis was performed separately for each subject.

292 To further test whether the saccades are the outcome of a decision process,  
293 we examined whether a linear race model could account for the observed SRTs  
294 (Carpenter and Williams, 1995). To this end, we measured the SRTs in catch trials

295 and in trials with  $|SOA| > 150$  ms (which we considered as single-target trials, see  
296 Task section above). The SRT distributions of these trials were assumed to be  
297 directly related to the rate and variance of rise of an internal decision signal from a  
298 single target. Using this information, we then modeled a race with two decision  
299 processes arising from two targets, staggering the second process by the SOA. From  
300 these races, we selected trials in which the process for the second stimulus won the  
301 race, calculated predicted SRT distributions of saccades to the second target as a  
302 function of SOA, and then compared the predicted and observed SRTs using a  
303 correlation analysis.

304

## 305 **Results**

306 We investigated the effect of passively-induced sinusoidal body translations on  
307 saccadic target selection by measuring subjects' selection bias in a two-alternative  
308 forced choice task. Using an adaptive approach, the stimulus onset asynchrony  
309 (SOA) of these targets for the different phases of motion was adjusted until the  
310 participant selected both targets equally often, which corresponds to the Balanced  
311 Time Delay (BTD).

312         At the beginning of each of two sessions we performed a stationary paradigm  
313 to quantify the test-retest reliability of the BTD across the two days of the experiment.  
314 Figure 2 illustrates the probability of a rightward saccade as a function of SOA in a  
315 single subject, and the fitted psychometric curve, separately for sessions tested in  
316 the first and second day. Circle size represents the number of trials for in a given bin  
317 of SOA. The psychometric fits provide an estimate of the balanced time delay (BTD)  
318 for each session, which is the SOA at which the subject equally often chooses to  
319 make a rightward or leftward saccade. In this subject, the respective BTDs did not  
320 change much across sessions (3 vs 6 ms). The same was found across all subjects.  
321 The mean BTD was -1 ms on day 1 and 6 ms on day 2. A paired samples t-test

322 revealed no significant differences between the BTDs in the two sessions ( $t(19)=-1.3$ ,  
323  $p=0.2$ ). This result confirms the consistency of the BTD across days.

324 We next investigated the effects of whole body motion on saccadic choice  
325 preference at 8 different phase angles of sled motion, which probed different  
326 combinations of whole body acceleration and velocity. Figure 3 presents data from a  
327 representative subject. Figure 3A shows that at peak acceleration, when the subject  
328 crossed the right turning point and accelerated to the left (gray circles and fitted  
329 curve), the right target needed to be turned on earlier (BTD = 12 ms) than the left to  
330 balance left- and rightward saccadic choices. Thus, the subject's choice bias was  
331 toward the left target. In contrast, the left target needed to be turned on earlier when  
332 the subject crossed the left turning point (open circles, black fit curve), accelerating to  
333 the right (BTD = -18 ms). Thus, the subject's choice bias was toward the right target.  
334 Since velocity is the same (zero) in both these conditions, this finding suggests that  
335 this subject's preference for saccadic targets depends on the direction of acceleration  
336 and not velocity.

337 Figure 3B shows the choice biases at the 225° and 315° phases, which also  
338 have different directions of acceleration while sharing the same velocity (here,  
339 rightward). Qualitatively we see the same pattern as above: when accelerating to the  
340 left (phase 315°), the right target needed to be turned on earlier than the left (BTD =  
341 19 ms) to obtain equally balanced choices. When accelerating to the right, the left  
342 target needed to be turned on earlier than the right (BTD = -24 ms).

343 Such choice biases were virtually absent at peak velocity, i.e. at zero  
344 acceleration (phase 90° and 270°). As shown in Figure 3C, leftward and rightward  
345 targets needed to be switched on about simultaneously to balance saccadic choices,  
346 irrespective of whether the subject's velocity was to the right (filled circle, BTD = 1  
347 ms) or to the left (open circle, BTD = -1 ms). This result suggests that velocity alone  
348 does not affect the subject's preferences. BTDs were also very similar in two other  
349 phases featuring opposite directions of velocity but the same acceleration. Figure 3D

350 illustrates this for the 45° and 315° phases, showing BTDs of 13 and 19 ms,  
351 respectively.

352 Together, this subject's data suggest that the selection bias reverses with the  
353 direction of the acceleration, rather than with the direction of motion. Leftward  
354 accelerations, i.e. the motion toward and away from the right turning point (see  
355 Figure 1B) biases selection to the leftward targets; rightward accelerations, i.e.  
356 motion toward and away from the left turning point, biases the preference to  
357 rightward targets.

358

### 359 ***Acceleration affects choice bias***

360 The results of the exemplar subject are characteristic for subjects in general. Figure 4  
361 plots the BTD, averaged across subjects, as a function of acceleration. At peak  
362 accelerations, i.e. at the turning points of the motion, there are clear differences in  
363 the BTD. For leftward accelerations, on average, the right target needed to be turned  
364 on 11 ms earlier than the left target to balance left- and rightward saccadic choices.  
365 For rightward accelerations, at the left turning point, the left target needed to be  
366 presented 9 ms earlier than the right. Across subjects, the difference between these  
367 BTDs is  $20 \pm 6$  ms (mean  $\pm$  SE), which is significantly different from zero ( $t(19)=3.1$ ,  
368  $p=.006$ ). This indicates that the direction of peak acceleration affects the choice bias,  
369 with higher BTD scores for leftward than rightward acceleration.

370 If this choice bias reflects a pure bottom-up effect of the vestibular system on  
371 saccadic choice, we would expect it to disappear at peak velocity, when acceleration  
372 is zero. Indeed, results indicate small BTD values across subjects (2 ms at phase  
373 90°, and -4 ms at phase 270°) and the difference between these BTDs was not  
374 significant ( $t(19)=0.9$ ,  $p=.42$ ). This result suggests that when subjects have to make  
375 saccadic choices at peak velocity, thus experiencing zero acceleration, saccadic  
376 preferences are unbiased.

377           If the hypothesis that acceleration, not velocity, biases choice is accepted we  
378 can make two predictions when comparing other phases of motion (45°, 135°, 225°,  
379 and 315°). The first prediction is that choice bias should be the same for comparisons  
380 featuring the same (non-zero) acceleration, even if velocity is different. This was  
381 confirmed. Comparing the BTDs between leftward (45°, 135°) and rightward (225°,  
382 315°) velocity, pooled across acceleration directions revealed no significant  
383 differences ( $F(1,19)=0.87$ ,  $p=0.36$ ). The second prediction is that choice biases  
384 should be different for comparisons featuring different accelerations but the same  
385 (non-zero) velocities. This was also confirmed by comparing the BTDs between  
386 leftward (45°, 315°) and rightward (135°, 225°) acceleration, pooled across velocity  
387 directions ( $F(1,19)=10.05$ ,  $p=0.005$ ), with the overall mean BTD for leftward  
388 acceleration (14.9 ms) higher than the BTD for rightward acceleration (4.5 ms).

389           We also analyzed stationary and dynamic data together by employing a 3x3  
390 design, i.e. a 2-way ANOVA with factors acceleration and velocity. Because of the  
391 reliability of the day 1 and day 2 stationary data, we collapsed these two data sets  
392 into one averaged stationary BTD score for each subject. In combination with the  
393 eight dynamic conditions, this yields three conditions for each direction of  
394 acceleration, leftward (0°, 45°, 315°), zero (90°, 270°, stationary), and rightward  
395 (135°, 180°, 225°). Similarly, there are three conditions for each direction of velocity,  
396 leftward (45°, 90°, 135°), zero (0°, 180°, stationary), and rightward (225°, 270°,  
397 315°). The BTD data were analyzed in a corresponding 3x3 acceleration by velocity  
398 Repeated Measures Anova, using Greenhouse-Geisser corrected p values. This  
399 analysis resulted in a significant main effect of acceleration ( $F(2,37.1)=8.5$   $p=.001$ ),  
400 with leftward accelerations having significantly higher BTD scores than rightward  
401 accelerations; BTDs for zero acceleration fell in between. There was no indication of  
402 a main effect of velocity ( $p=0.28$ ) or an interaction effect between velocity and  
403 acceleration ( $p=.21$ ). All of this confirms the previous results on the individual  
404 contrasts of different phases.

405 To also capture quantitatively the relation between BTM and the magnitude of  
406 the acceleration in the dynamic paradigm at the individual level, we computed per  
407 subject the correlation between his/her BTM scores and the corresponding actual  
408 acceleration amplitudes. For 19 out of the 20 subjects this correlation was negative,  
409 with the mean  $r=-0.39$  significantly different from zero (Fisher's  $r$  to  $z$  transform,  $t=-$   
410  $3.4$ ,  $p=.003$ ). Repeating the same procedure with velocity instead of acceleration  
411 produced a mixed bag of 12 negative and 8 positive correlations, and a  
412 nonsignificant ( $p=0.26$ ) mean correlation.

413 Figure 4 depicts this linear relation between BTM and acceleration. It contains  
414 the mean BTM values with error bars for the specific phases, ordered by  
415 acceleration, as well as the average regression line across participants. We  
416 computed the 95%-confidence interval around the average slope, represented in the  
417 figure by the gray zone around the average regression line. While the error bars  
418 show considerable between-subject variability for each of the phase conditions, this  
419 95%-CI in gray contains only lines with negative slopes, indicating the consistent  
420 relation between BTM and acceleration levels as expressed in the significant  
421 negative correlation found.

422

### 423 **Reaction times reflect a decision process**

424 The observation that the choice bias varies along the motion cycle in the  
425 dynamic paradigm brings up the question whether this is also expressed in SRT: are  
426 the choice biases accompanied by SRT differences? Figure 5 demonstrates the SRT  
427 differences of saccades to rightward vs leftward targets ( $\Delta$ SRT), averaged across  
428 subjects, as a function of acceleration. The goodness-of-fit across subjects was  
429 characterized by a value of 0.64. The pattern nicely mimics the patterns of choice  
430 biases based on the BTM analysis shown in Fig. 4. While  $\Delta$ SRT is quite variable  
431 between subjects, as indicated by the error bar of each point, the within-subject  
432 variability of its relationship with acceleration is confined to negative values. Across



433 individual subjects, the mean correlation of SRT with acceleration amplitude was -  
434 0.23 ( $p=0.02$ ). For leftward accelerations, for which the BTD results show a  
435 preference to leftward targets, the SRT to rightward targets is larger than to leftward  
436 targets. The opposite pattern is seen for rightward accelerations, i.e., shorter SRTs  
437 for rightward targets. In contrast, SRT did not correlate with velocity ( $r =0.005$ ;  $p$   
438  $=0.95$ ).

439         To further examine whether SRTs are indicative of a neural decision process  
440 we used a straightforward linear rise-to-threshold modeling approach (Carpenter and  
441 Williams, 1995). In this analysis, the release of the saccade is assumed to reflect the  
442 final outcome of two independent linear rise-to-threshold processes, related to the  
443 two targets, which race to the same threshold (race model). To account for the  
444 stimulus onset asynchrony, the process for target 2 starts later than that for target 1.  
445 It is further assumed that in isolation target 1 and 2 yield the same reaction time  
446 distribution. Hence, to win the race, the process for target 2 must proceed  
447 progressively faster to compensate for progressively longer SOAs. Using this simple  
448 framework, we can predict SRTs for target 2. Figure 6 shows that the predicted  
449 pattern of how BTD affects the SRT (black line) for the second target, expressed  
450 relative to the onset of the second target, nicely fits the observed SRT-BTD pattern  
451 ( $R^2>0.85$ ,  $p<0.001$ ), for each of the eight phase angles. Together with the results of  
452 the previous section, these results are indicative of a neural decision process in  
453 which the selection process is biased by a self-motion (acceleration) signal.

454

## 455 **Discussion**

456         The main purpose of this study was to understand how whole body motion  
457 influences saccadic target selection. In particular, we focused on how the velocity  
458 and acceleration of body motion affect the choice between two targets, presented  
459 asynchronously but equiluminantly and equidistantly from the fixation point. Using an  
460 adaptive psychometric procedure, we adjusted the temporal difference between the

461 two target onsets until the subject selected both targets equally often as the goal of  
462 the saccade. We determined this balanced time delay (BTD) for different phases of  
463 the motion so we could distinguish the effects of whole body velocity and  
464 acceleration on saccadic target selection. Of these two, our results show that  
465 acceleration but not velocity correlates significantly with target selection. The  
466 observed BTDs may represent a bottom-up effect of acceleration, presumably  
467 derived from the otolith system, on saccadic target selection. In support of this notion,  
468 saccadic reaction times were reliably shorter to targets in the acceleration direction,  
469 which is a further reflection of the selection bias. A simple race model could capture  
470 the pattern of saccadic reaction times quite well, which suggests that the saccade  
471 reflects the final outcome of a stochastic decision processes, modulated by a low-  
472 level acceleration signal.

473         As mentioned in the Introduction, we have framed our results in terms of  
474 acceleration rather than position, even though these are indistinguishable during  
475 sinusoidal motion. Every relationship showing an influence of leftward or rightward  
476 acceleration can be alternatively interpreted as showing a biasing influence of  
477 position to the right or left toward the center of sinusoidal motion. Our preference of  
478 an interpretation based on acceleration rather than position, while speculative, is  
479 more parsimonious since the otoliths sense linear acceleration rather than position;  
480 accordingly derivation of position from acceleration requires double integration.  
481 Previous work has suggested that such integration is leaky, and thus the neural  
482 representation of integrated position should lag behind that of acceleration  
483 (Mittelstaedt and Mittelstaedt, 2001; Merfeld et al., 2005; Vingerhoets et al., 2006).  
484 Given that a phase lag should be inherent to an acceleration-to-position  
485 transformation, we find it difficult to explain why BTD values are similar at matched  
486 phases of acceleration, even though the integrated position signals would be  
487 different. In the same way, we find it difficult to explain why we observed a negligible  
488 influence of velocity on BTD, since integration position signals after maximum

489 velocity are non-zero. Instead, our results show that the largest dynamic influence  
490 comes from the “snapshot” of motion when the first target is presented, regardless of  
491 whether acceleration (or position) is increasing or decreasing.

492         An alternative line of reasoning favoring an interpretation based on  
493 acceleration rather than position stems from a top-down perspective. Anecdotally,  
494 subjects indicated that they did not recognize the phases at which they were tested  
495 throughout the ongoing motion, illustrating an inability to predict fine details of  
496 upcoming motion. Moreover, if subjects opted to simply select the target that is in the  
497 direction of the center, then we would have expected response bias to depend simply  
498 on whether the subject is left or right from this center at the time of target  
499 presentation, irrespective of velocity or acceleration. This is not what the data  
500 showed: we observed instead a systematic modulation of motion phase on response  
501 bias that appeared most consistent with a phase-dependent bottom-up modulation.  
502 For future work, it would be interesting to address the dissociation of acceleration  
503 and position effects further, e.g., by using more complicated motion profiles, possibly  
504 including abrupt onsets of acceleration.

505         The vast majority of studies in the literature have examined the mechanisms  
506 of target selection in body-stationary environments. This work has broadly  
507 differentiated between top-down and bottom-up influences on target selection, with  
508 the former driven by the internal goals of the subject and the latter related to the  
509 physical characteristics of the environment. Clearly, target selection mechanisms  
510 have evolved during more complex situations when the body is in motion, which is a  
511 common but largely unstudied situation. Our results point to the incorporation of  
512 acceleration signals, presumably transmitted by the vestibular system, in saccadic  
513 target selection. Of course, we cannot rule out that other potential signals convey  
514 acceleration information, such as pressure receptors in the skin. It would also be  
515 interesting to test to what extent the present findings with passive motion generalize  
516 to target selection in more natural environments and with active self-generated body

517 motion which, in contrast to the present study, would involve motor planning and  
518 predictions about the course and the outcome of the action (Carriot et al., 2013;  
519 Foulsham et al., 2014; Hayhoe and Ballard, 2014).

520 We consider it unlikely that inertial factors or anticipated biomechanical costs  
521 serve as an explanation for the selection bias in the dynamic condition. Anticipated  
522 biomechanical costs have been shown to influence the outcome of action decisions  
523 for upper limb movement in a static situation (Cos et al., 2011, 2014). Such  
524 biomechanical costs would change when the arm is undergoing acceleration, and  
525 numerous experiments show that the brain anticipates Coriolis torques on the limb  
526 generated during torso rotation (e.g. Sainburg et al., 1999; Pigeon et al., 2013) and  
527 learns to adapt during reaches made in rotating environments (Lackner and Dizio,  
528 1994). This suggests that for the upper limb, top-down prediction of biomechanics  
529 influence target selection. But compared to the limb, the eyes have a negligible  
530 inertial component, rendering biomechanical cost a rather insignificant factor in the  
531 selection of saccadic targets. Interesting questions to address in future work are  
532 whether and how bottom-up and/or top-down influences of acceleration influence  
533 saccadic decisions when the head is free to move, bias target selection of reaching  
534 movements, or affect the choice of which hand to use.

535 Using the dynamic paradigm, we showed that the preference for saccadic  
536 targets was biased by the direction (i.e. the sign) of acceleration. SRTs were also  
537 shorter for targets in the direction of acceleration, comparable to the shorter SRTs  
538 observed during saccade-smooth pursuit interactions (Tanaka et al., 1998). Because  
539 sinusoidal motion is predictable (Barnes, 1993; Han et al., 2005; Prsa et al., 2015),  
540 subjects could potentially also rely on velocity or position signals in the selection  
541 process. However, selection in our task appears not to be biased by velocity  
542 information, rendering such top-down effects on target selection less likely.  
543 Alternatively, the dependent measure in our study may not have been sensitive  
544 enough to uncover such an effect.

545           In fact, our results show the same selection bias for the same magnitude of  
546 acceleration (see Figures 3 and 4), irrespective of whether the subject's velocity is  
547 leftward or rightward, and thus moving in opposite directions in space. This is also  
548 inconsistent with an explanation of the selection bias based on anticipated motion  
549 dynamics, such as a strategy where subjects look in the direction that they are about  
550 to go.

551           It is known that intervening eye, head, and body motion is taken into account  
552 when programming saccades to world-fixed targets (Snyder and King, 1992; Telford  
553 et al., 1997; Crane and Demer, 1998; Medendorp, 2011). In the present study,  
554 targets were presented at head-fixed locations, meaning that such compensatory  
555 mechanisms should be switched off, or suppressed, in the generation of the saccade.  
556 Nonetheless, the question remains: does the choice bias relate to the magnitude of  
557 the instantaneous acceleration signal at the onset of the stimuli or at the onset of the  
558 saccade? After the onset of the stimuli, the phase of the acceleration signal changes  
559 by about 45° during the ~200 ms saccadic reaction time. Because of the periodicity of  
560 the motion, we cannot completely exclude the possibility that the selection bias in a  
561 single condition depends on the acceleration signal slightly before saccade onset, i.e.  
562 about 45° further than stimulus onset. However, here again, it is difficult to explain  
563 why BTD values would be similar at phases where neither the acceleration nor the  
564 related velocity information is the same (e.g. 45° and 315° phase onsets, where the  
565 saccade starts around peak velocity and peak acceleration, respectively). Based on  
566 this reasoning, we think that the present results are best interpreted as a bottom-up  
567 effect of the instantaneous acceleration signal at the moment of stimulus  
568 presentation on the mechanisms of target selection for saccades.

569           To our knowledge there are no other studies in the literature that have  
570 examined target selection during either whole-body rotational or translational motion.  
571 In fact, only a few studies have investigated saccade-vestibular interactions during  
572 whole-body rotations. Van Beuzekom and Van Gisbergen (2002a) asked human

573 subjects to make pro- or anti-saccades in oblique directions while being rotated  
574 sinusoidally in yaw. They tested how the saccadic system would cope with the  
575 interfering effects of ongoing horizontal nystagmus, in particular with the quick-phase  
576 eye movements. While the vertical component of the voluntary saccade was typically  
577 correct, the horizontal component was compromised, and biased in the direction of  
578 the quick phase. The same authors also tested how oblique saccades induced by  
579 electrical microstimulation in the monkey superior colliculus (SC) are modified by  
580 concurrent sinusoidal yaw rotation (Van Beuzekom and Van Gisbergen, 2002b).  
581 Again, results showed a kinematic effect only on the horizontal component of the  
582 induced saccade, not the vertical component. Together, these results suggest an  
583 interaction between the vestibularly-induced quick phase eye movement and a  
584 voluntary or induced saccade. The differential effect on horizontal versus vertical  
585 components indicates that such an interaction takes place downstream from the SC  
586 (where saccades are encoded in a vectorial fashion), consistent with other studies  
587 (Kitama et al., 1995; Anastasio, 1997), as well as lesion experiments (Schiller et al.,  
588 1980; Hepp et al., 1993).

589         The SC has been implicated in target selection (Glimcher and Sparks, 1992;  
590 Basso and Wurtz, 1998; Krauzlis and Dill, 2002; McPeck and Keller, 2002; White and  
591 Munoz, 2011). Would the quick-phase results from Van Beuzekom and Van  
592 Gisbergen, as described above, suggest that no vestibular information arrives in the  
593 SC? To our knowledge, there is only little experimental data that would allow us to  
594 infer an answer. The few studies that have looked at the influence of vestibular  
595 information on SC activity have employed rotation (Maeda et al., 1979), not  
596 translation. Although quick phase eye movements during rotation persist after the SC  
597 is either ablated (Schiller et al., 1980) or temporarily inactivated (Hepp et al., 1993),  
598 such quick phase eye movements are associated with bursts of activity on SC  
599 saccade-related neurons (Schiller and Stryker, 1972; Hepp et al., 1993). Vestibular  
600 rotation does not modulate the activity of another class of SC neurons related to

601 head-only movements (Walton et al., 2007). Together, these observations indicate  
602 that vestibular information arising from rotation can access the SC, impacting the  
603 activity on saccade-related neurons. Whether vestibular information arising from  
604 translation also influences saccade-related activity in the SC remains unknown, but  
605 this seems possible, given that signals related to eye-in-head position (Van Opstal et  
606 al., 1995; Campos et al., 2006) and head-on-body position (Nagy and Corneil, 2010)  
607 also impact activity on saccade-related SC neurons.

608         It is known that periodic linear acceleration induces a horizontal nystagmus,  
609 with quick phases in the direction of the acceleration (thus, against the inertial force)  
610 (Niven et al., 1966; Katayama and Mori, 2001). Although quick phase saccades were  
611 suppressed in the present study (due to the head-fixed fixation point), our results  
612 suggest a selection bias to targets in that direction. Therefore, a plausible  
613 explanation of our results is that vestibular information from the otolith organs  
614 modulates SC activity during our target selection paradigm, favoring development of  
615 a saccade-related burst in one SC versus the other. This mechanism is consistent  
616 both with our saccadic choice biases and with the shortened saccadic reaction times.  
617 Future neurophysiological work using dynamic motion should be performed to test  
618 this proposal.

619         An alternative scenario is that the vestibular signals modulate activity in  
620 cortical areas that have been implicated in target selection, such as the lateral  
621 intraparietal area (Bisley and Goldberg, 2010) or the frontal eye fields (Schall and  
622 Hanes, 1993). Indeed, there are pathways that transmit vestibular signals to parietal  
623 cortex (Kaufman and Rosenquist, 1985; Meng et al., 2007; Shinder and Taube,  
624 2010) and frontal cortex (Fukushima, 1997), which could potentially bias processing  
625 in the SC, but this has not been tested. Ascertaining whether the influence of  
626 vestibular information from translation on the oculomotor system arises from trans-  
627 cortical pathways or those confined solely to the brainstem would represent another  
628 fruitful avenue for future neurophysiological investigations of this phenomenon.





630

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807 **Legends**

808

809 Figure 1. Dynamic paradigm. A. Subjects were translated sinusoidally while  
810 fixating a central, body-fixed light. At different phases of the motion (here at  
811 the right turning point), two peripheral lights were presented with a small  
812 stimulus onset asynchrony. Subjects had to look as fast as possible to one of  
813 these lights, but were free to choose either light. B. Phase-plane plot, showing  
814 the combination of acceleration and velocity (i.e. phase) at which the stimuli  
815 were presented. Note, a rightward deceleration means a leftward  
816 acceleration, and vice versa. AL/AR=Acceleration Left/Right, VL/VR=Velocity  
817 Left/Right.

818

819 Figure 2. Single-subject results in the stationary paradigm. Panels shown the  
820 probability of a rightward saccade as a function of SOA in a single subject,  
821 together with the fitted psychometric curve. BTD, balanced time delay. Top  
822 panel, day 1; bottom panel, day 2. Circle size indicates the number of trials for  
823 a particular bin of SOAs.

824

825 Figure 3. Single-subject results in the dynamic paradigm. Format as in Figure  
826 2, now comparing two phases of motion. A: target selection at leftward and  
827 rightward peak acceleration, both at zero velocity. B: target selection for  
828 opposite acceleration, but with same non-zero velocity. C: target selection at  
829 leftward and rightward peak velocity, both at zero acceleration. D: target  
830 selection at the same non-zero acceleration, but with opposite velocities.

831 Insets on the right show phase-plane plots of the compared phases  
832 (corresponding colors).

833

834 Figure 4. BTD results shown as a function of acceleration. Error bars on each  
835 point represents between-subject variability (SE). Black line represents the  
836 best fit through these data points, with  $R^2$  the goodness-of-fit across subjects.  
837 The between-subject variability of the best-fit slope is depicted by the gray  
838 zone around the average slope, representing the 95%-confidence interval.

839

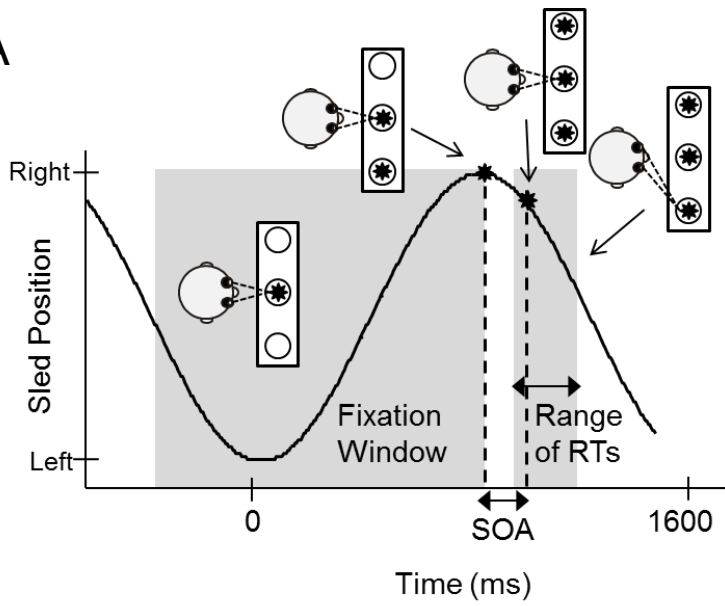
840 Figure 5. SRT results. Difference in SRTs between rightward and leftward  
841 saccades, shown as a function of acceleration. Same format as Fig. 4.

842

843 Figure 6. SRTs, averaged across subjects, to the first (black circles) and  
844 second stimulus (gray circles) as a function of stimulus onset asynchrony.  
845 Each panel represents one of the eight phase angles. Lines show expected  
846 SRT according to a linear rise-to-threshold modeling approach.

847



**A****B**