

*Research Article: New Research / Sensory and Motor Systems*

## Eye Tracking of Occluded Self-Moved Targets: role of Haptic Feedback and Hand-Target Dynamics

### Eye tracking of occluded self-moved targets

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DOI: 10.1523/ENEURO.0101-17.2017

Received: 23 March 2017

Revised: 6 June 2017

Accepted: 8 June 2017

Published: 26 June 2017

**Author Contributions:** FD and RF designed research; FD and JM performed research, and analysed data; FD prepared the figures; FD and RF interpreted the results and wrote the paper.

**Funding:** Centre National de la Recherche Scientifique (CNRS)  
501100004794  
PICS N{degree sign}191607

**Funding:** Agence Nationale de la Recherche (ANR)  
501100001665  
REM ANR-13-APPR-0008

**Conflict of Interest:** Authors report no conflict of interest.

Support for this research was provided by the CNRS (PICS N°191607) and a French National Grant (REM ANR-13-APPR-0008).

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**Cite as:** eNeuro 2017; 10.1523/ENEURO.0101-17.2017

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Accepted manuscripts are peer-reviewed but have not been through the copyediting, formatting, or proofreading process.

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# Eye tracking of occluded self-moved targets: role of haptic feedback and hand-target dynamics

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## Author Contributions

FD and RF designed research; FD and JM performed research, and analysed data; FD prepared the figures; FD and RF interpreted the results and wrote the paper.

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## Numbers

Number of pages (including figures): **33**

Number of figures: **6**

Number of tables: **0**

Number of words-Abstract: **246**

Number of words-Introduction: **749**

Number of words-Significance statement: **115**

Number of words-Discussion: **1461**

**Keywords:** smooth pursuit, prediction, eye-hand coordination, internal models, hand-target mappings, target occlusion, haptic feedback

## Acknowledgements

We would like to thank Martin York and Mohamed Albaghdadi for technical support and logistical support. We would like also to thank the anonymous reviewers for helpful comments and suggestions.

## Conflict of Interest

No conflicts of interest, financial or otherwise, are declared by the authors.

## Funding Sources

Support for this research was provided by the CNRS (PICS N°191607) and a French National Grant (REM ANR-13-APPR-0008).

51 **ABSTRACT**

52 Previous studies on smooth pursuit eye movements have shown that humans can  
53 continue to track the position of their hand, or a target controlled by the hand, after it is  
54 occluded, thereby demonstrating that arm motor commands contribute to the prediction of  
55 target motion driving pursuit eye movements. Here we investigated this predictive mechanism  
56 by manipulating both the complexity of the hand-target mapping and the provision of haptic  
57 feedback. Two hand-target mappings were used, either a rigid (simple) one in which hand and  
58 target motion matched perfectly, or a non-rigid (complex) one in which the target behaved as  
59 a mass attached to the hand by means a spring. Target animation was obtained by asking  
60 participants to oscillate a lightweight robotic device that provided, or not, haptic feedback  
61 consistent with the target dynamics. Results showed that as long as 7s after target occlusion,  
62 smooth pursuit continued to be the main contributor to total eye displacement (about 60%).  
63 However, the accuracy of eye-tracking varied substantially across experimental conditions. In  
64 general eye-tracking was less accurate under the non-rigid mapping, as reflected by higher  
65 positional and velocity errors. Interestingly, haptic feedback helped to reduce the detrimental  
66 effects of target occlusion when participants employed the non-rigid mapping, but not when  
67 they used the rigid one. Overall we conclude that the ability to maintain smooth pursuit in the  
68 absence of visual information can extend to complex hand-target mappings, but the provision  
69 of haptic feedback is critical for the maintenance of accurate eye-tracking performance.

70

71 **SIGNIFICANCE STATEMENT**

72       The ability to predict visual consequences arising from our actions is central in daily  
73 activities. Here we tested this ability by means of a task that required participants to track  
74 with the eyes a target that was occluded and whose motion was driven by the hand using  
75 simple or complex hand-target mappings both with and without haptic feedback. Our results  
76 showed that, despite a general drop in performance after target occlusion, smooth pursuit  
77 activity persisted under all conditions. Although haptic feedback was not critical under the  
78 simple mapping, it clearly improved performance under the complex one. We conclude that  
79 haptic feedback is critical to supplement vision when predicting the behavior of objects with  
80 complex dynamics.

81

82 **INTRODUCTION**

83       The ability to anticipate sensory consequences resulting from self-initiated movement  
 84 is central for current theories of motor control (Shadmehr et al., 2010; Wolpert et al., 2011;  
 85 Wolpert and Flanagan, 2001). This ability can be demonstrated in various motor tasks ranging  
 86 from object manipulation to eye-hand coordination. For instance, it is well established that  
 87 smooth pursuit eye movements are substantially improved when the viewed target is moved  
 88 by the subject's hand in comparison to when it is moved by an external agent. This  
 89 improvement is characterized by a higher gain in smooth pursuit (Gauthier et al., 1988;  
 90 Mather and Lackner, 1975; Vercher et al., 1995), fewer saccades (Angel and Garland, 1972;  
 91 Mather and Lackner, 1975; Steinbach, 1969; Steinbach and Held, 1968), and a shorter  
 92 temporal lag between target and eye position (Domann et al., 1989; Gauthier and Hofferer,  
 93 1976; Steinbach and Held, 1968; Vercher et al., 1996). To account for these observations, it is  
 94 proposed that the oculomotor system has access to an estimate of the current hand position  
 95 through the combination of sensory feedback, arm efferent copy and knowledge of the hand-  
 96 target dynamics (Ariff et al., 2002; Scarchilli et al., 1999). Overall, it is postulated that eye  
 97 tracking profits from the ability to both predict future states of the limb (Ariff et al., 2002) and  
 98 learn the mapping between hand actions and their visual consequences (Sailer et al., 2005).

99       The advantage of self-generated versus externally generated target motion in pursuit  
 100 eye tracking is also seen when vision of the moving target is occluded. A large number of  
 101 studies have examined eye movement behavior when vision of an externally driven moving  
 102 target is transiently occluded (Bennett and Barnes, 2003, 2006; Madelain and Krauzlis, 2003;  
 103 Orban de Xivry et al., 2008). A typical observation is that about 200ms after target blanking,  
 104 performance in eye-tracking starts to deteriorate as indicated by a drop in smooth pursuit  
 105 velocity and an increase in the contribution of catch-up saccades. Although only a few studies  
 106 have investigated eye tracking when a self-moved target is temporarily masked, they indicate

107 improved performance. In a seminal study Gauthier and Hofferer (1976) explored the ability  
108 of participants to track a visual target that was moved either by oscillating the finger or the  
109 elbow. At some point the target was masked, and participants were asked to keep oscillating  
110 their limb while tracking the target as if it was still visible. Their results showed that  
111 participants were able to maintain smooth pursuit (albeit with a lower gain) over several  
112 successive cycles of movement lasting several seconds, which contrasts with the rapid decay  
113 of smooth pursuit when using an externally-moved target. More recently Berryhill and  
114 colleagues (2006), who investigated the ability to track a self-moved pendulum in the dark,  
115 also showed that participants could maintain smooth pursuit for several seconds (albeit with a  
116 low gain). Overall, the benefit of self-moving a target on smooth pursuit performance extends  
117 to situations in which the target is occluded.

118       The goal of the current study was to further investigate the ability of humans to track  
119 an invisible self-moved target, focusing on two key issues. First, we asked whether this ability  
120 extends to situations in which participants employ a more complex mapping between hand  
121 and target motion. Second, we asked how this ability depends on receiving haptic feedback  
122 about the interaction between hand and target motion. To date the contribution of haptic  
123 feedback to eye tracking has been (indirectly) investigated with deafferented patients under a  
124 simple hand-target mapping (Vercher et al, 1996), but not under a complex mapping and not  
125 when the target is occluded. To achieve these goals we designed an experiment in which  
126 participants were asked to track a target on a screen whose animation was obtained by  
127 oscillating horizontally a grasped object attached to a lightweight robotic device. Two visual  
128 hand-target mappings were used, either a rigid one in which hand and target motion matched  
129 perfectly (simple dynamics), or a non-rigid one in which the target behaved as a mass  
130 attached to the hand by means a spring (complex dynamics). Using the robotic device, haptic  
131 feedback congruent with the target dynamics could be provided or removed. Although

132 previous studies have shown that people can learn to control non-rigid objects both when  
 133 appropriate haptic feedback is provided (Dingwell et al., 2002, 2004; Mehta and Schaal,  
 134 2002; Nagengast et al., 2009) and when it is not (Mah and Mussa-Ivaldi, 2003; Mehta and  
 135 Schaal, 2002), performance is typically improved by haptic feedback (Danion et al., 2012;  
 136 Farshchiansadegh et al., 2016). Based on these results, we predicted that whereas eye tracking  
 137 performance following target occlusion would be reduced when moving the non-rigid target  
 138 in comparison to the rigid target, this deficit would be limited when haptic feedback is  
 139 provided.

140

## 141 **METHOD**

### 142 *Participants*

143 Fourteen self-proclaimed right-handed participants (age:  $22.2 \pm 1.8$  yrs., 9 female)  
 144 participated in this study. None of the participants had neurological or visual disorders. They  
 145 were naïve as to the experimental conditions and hypotheses, and had no previous experience  
 146 of ocular motor testing. All participants gave written informed consent prior to the study.  
 147 Each participant received 10\$ for his/her participation. The Author University ethics  
 148 committee approved the experimental paradigm (N°2014-12-3-04), which complied with the  
 149 Declaration of Helsinki.

150

### 151 *Apparatus*

152 The experimental setup is illustrated in Figure 1. Participants were comfortably seated  
 153 facing a screen positioned in a frontal plane 57 cm away from the participant's eye (see Fig.  
 154 1A). Thus, at the center of the screen a target displacement of 1cm corresponded to 1deg in  
 155 terms of visual angle. To minimize measurement errors, participants' head movements were  
 156 restrained by a chin rest and a padded forehead rest so that the eyes in primary position were

157 directed toward the center of the screen. A bib was positioned under the participants' chin to  
158 block vision of their hands. Participants controlled the position of a target on the screen by  
159 moving a grasped object attached to a lightweight robotic arm (Phantom Haptic Interface  
160 3.0L, Sensable Technologies, Woburn, MA, USA) in a frontal plane (see Fig. 1B). When the  
161 target was at the center of the screen, the elbow and shoulder were comfortably positioned so  
162 that both hand and target lied in the participant's mid-sagittal plane (see Fig. 1A). Hand  
163 movements were recorded at a sampling rate of 1000 Hz with a resolution of 0.1 mm.

164  
165 The target (filled red circle  $0.5^\circ$  in diameter) was projected on the screen using a laser  
166 beam (39080; Edmund Optics, Inc., Barrington, NJ) moved by an optical scanner  
167 (MG350DT; General Scanning, Inc., Watertown MA) servo-controlled by a PC (see Fig. 1C).  
168 The delay in the servo-command was less than 1 ms. The optical scanner motion was  
169 restricted to one dimension so that the target moved only along the horizontal axis. An  
170 infrared video-based eye tracker (RK-726PCI pupil/corneal tracking system; ISCAN, Inc.,  
171 Burlington, MA) was used to record the position of gaze of the left eye in the work plane at  
172 400 samples/sec. Before the experiment, we calibrated the output from the eye tracker by  
173 recording the raw eye positions as participants fixated a grid composed of 25 known  
174 locations. The mean values during fixation intervals at each location were then used for  
175 converting off line raw eye tracker values to horizontal and vertical eye position in degrees of  
176 visual angle.

177 Two types of hand-target visual mapping were employed. When participants had to  
178 move the 'rigid target' (RIGID), its motion was an exact replicate of the actual hand trajectory  
179 in the frontal plane: if the hand moved by 1cm to the left, the target also moved by 1cm to the  
180 left on the screen. When haptic feedback was implemented for the rigid target (RIGID-  
181 HAPT), interaction forces provided by the robotic device simulated the physical behavior of a



182 1kg point mass. In the no haptic version of the rigid target (RIGID-NOHAP), the motors of  
 183 the robotic device were simply turned off. When subjects had to move the non-rigid target  
 184 (SPRING), the visual target was simulated as a mass-spring object with the following  
 185 properties: mass = 1 Kg, stiffness = 40 N/m, damping = 1.66 N/m/s, resting length = 0 m.  
 186 These values are about one third of values used in previous studies investigating the  
 187 manipulation of non-rigid objects (Danion et al., 2012; Dingwell et al., 2004, 2004; Landelle  
 188 et al., 2016; Nagengast et al., 2009). The rationale for decreasing object inertia was to prevent  
 189 possible fatigue effects while keeping a 1Hz resonance frequency as in other studies; the  
 190 resonance frequency ( $F$ ) of a mass-spring system depends on its mass ( $m$ ) and its stiffness ( $k$ )  
 191 such that  $F = \frac{1}{2\pi} \sqrt{\frac{k}{m}}$ . Depending on the experimental conditions, haptic feedback of the  
 192 non-rigid target could be implemented in 3 different ways. First haptic feedback could be  
 193 provided such that it was congruent with the visual dynamics of the object (SPRING-HAPT),  
 194 meaning that the same parameters were employed to simulate physical and visual behaviour.  
 195 Second haptic feedback could be removed in the sense that motors of the robotic device were  
 196 turned off (SPRING-NOHAPT). Third haptic feedback could be incongruent with the visual  
 197 dynamics of the object (SPRING-DISSHAPT). In this case we introduced a dissociation  
 198 between the visual and haptic stiffness of the mass-spring (VISUAL stiffness = 48 N/m,  
 199 HAPTIC stiffness = 32 N/m) while keeping mass and damping similar to previous values.  
 200 This dissociation led to distinct resonance frequencies for the visual and haptic dynamics  
 201 (1.25 vs 0.8 Hz).

202

### 203 *Procedure*

204 In all trials participants were instructed to track as accurately as possible the target  
 205 moving on the screen. The target motion was always driven by the subject's hand. However,  
 206 depending on the experimental condition, the visual mapping between hand movement and

207 target motion could either be rigid (RIGID) or elastic (SPRING) with either no haptic  
 208 feedback, congruent haptic feedback, or incongruent haptic feedback (see above). Overall the  
 209 following five experimental conditions were tested: RIGID-HAPT, RIGID-NOHAPT,  
 210 SPRING-HAPT, SPRING-NOHAPT, and SPRING-DISSHAPT. Each subject completed first  
 211 a familiarization session in which they practiced the task with visual feedback followed by an  
 212 experimental session in which, in each trial, visual feedback was initially present and then  
 213 removed.

214         During the familiarization session, subjects were asked to perform random oscillatory  
 215 movements to move the target (for a similar procedure see Steinbach and Held, 1968; Angel  
 216 and Garland, 1972). The underlying motivation was to favor the acquisition of knowledge  
 217 about hand-target dynamics. Subjects were encouraged to use the whole extent of the screen  
 218 ( $\pm 20^\circ$ ) while making sure that the target did not fall outside the screen boundaries. To  
 219 facilitate the production of random movements, a template was given prior to the training  
 220 session. During demonstration trials, subjects did not move their hand and simply had to  
 221 observe the replay of a trial performed by one of the experimenters under the same mapping  
 222 condition. When subjects subsequently moved the target, we ensured that absolute target  
 223 speed was comparable across conditions by encouraging subjects to maintain an average  
 224 absolute target velocity close to  $30^\circ/\text{s}$ ; this was possible by computing on-line mean absolute  
 225 target velocity, while the experimenters provided verbal feedback to the subject when  
 226 necessary. This procedure ensured an overall mean target velocity of  $30.2^\circ/\text{s}$  with minimal  
 227 changes across subjects ( $\text{SD} = 0.23^\circ/\text{s}$ ), experimental conditions ( $\text{SD} = 0.52^\circ/\text{s}$ ), and trials ( $\text{SD}$   
 228  $= 0.80^\circ/\text{s}$ ). Each subject completed one block of 20 trials in each of the 5 experimental  
 229 conditions. Each trial was 16 s long. Subjects were not explicitly informed about the nature of  
 230 the mapping between their hand movement and the target motion before completing these

231 experimental conditions. The order of blocks was randomized across subjects. Overall a total  
 232 of 100 trials (5×20 trials) were collected in this familiarization session.

233        Trials in the continuation session were similar to those in the familiarization session  
 234 except that subjects were asked to produce target motion that was sinusoidal and that target  
 235 was blanked after 7s. Sinusoidal target motion was encouraged to simplify data analysis and  
 236 to allow comparison with previous work (Gauthier and Hofferer, 1976). A template with a  
 237 target moving sinusoidally (Period = 1000ms, peak-to-peak Amplitude = 15°, resulting in  
 238 30°/s mean abs target velocity) was given prior to the continuation session. Subjects were  
 239 encouraged to reproduce this pattern in the subsequent trials (effective mean Period = 1.067  
 240 ms, and effective mean Amplitude = 17.3°). Each trial was 16s long. Approximately 7s after  
 241 trial initiation, the target was removed from the screen (i.e., blanked) until the end of the trial.  
 242 During the blanking period, subjects were instructed to keep oscillating the target while  
 243 tracking it with their gaze as if it was still displayed on the screen. Each subject completed a  
 244 block of 3 trials in each experimental condition. The order of the blocks was randomized  
 245 across subjects. A total of 15 trials (5×3 trials) was collected during this experimental session.  
 246 The overall duration of the familiarization with the experimental session averaged 60 minutes.  
 247 Participants could request additional breaks at any time but most of them only took the break  
 248 offered between blocks.

249

#### 250 *Data analysis*

251        Because the stimuli were moving exclusively along the horizontal meridian, we  
 252 focused our analyses on the horizontal component of eye movements. We performed a  
 253 sequence of analysis to separate periods of smooth pursuit, saccades and blinks from the raw  
 254 eye position signals. The identification of the blinks was performed by visual inspection. This  
 255 procedure led to the removal of about 1% of eye recordings. Eye position time series were

256 then low-pass filtered with a Butterworth (4th order) using a cutoff frequency of 25 Hz. The  
 257 resultant eye position signals were differentiated to obtain the velocity traces. The eye  
 258 velocity signals were low-pass filtered with a cutoff frequency of 25 Hz to remove the noise  
 259 from the numerical differentiation. The resultant eye velocity signals were then differentiated  
 260 to provide the accelerations traces that we also low-pass filtered at 25 Hz to remove the noise.  
 261 A dedicated Matlab script was run to identify saccades. This identification was based on the  
 262 acceleration and deceleration peaks of the eye ( $>1500^\circ/s^2$ ). Further visual inspection allowed to  
 263 identify smaller saccades ( $<1^\circ$ ) that could not be identified automatically by our program.  
 264 Based on these computations, periods of pursuit and of saccades were extracted.

265       During the experimental (continuation) trials we distinguished regular pursuit from  
 266 the periods of target occlusion (after about 7s). The first part and last part of each trial were  
 267 analyzed separately. Each continuation trial was segmented into 1s bins. The bin  
 268 segmentation was set with respect to the initiation of target blanking. The first bin that  
 269 followed the target blanking was named +1, and the bin just preceding the target blanking was  
 270 named -1. We used the same policy to name the surrounding bins. A total of 7 bins preceding  
 271 the target blanking, and 8 bins following target blanking could be reliably extracted from each  
 272 trial. For each of these 1s bin, we computed the same dependent variables. To assess baseline  
 273 performance (i.e. in the presence of visual feedback), dependent variables were averaged  
 274 across the 5 bins preceding target blanking (-5, -4, -3, -2, -1; bins -6 -7 were discarded  
 275 because stable performance was not reached yet). To assess performance during continuation  
 276 (i.e. when target was invisible), dependent variables were averaged across the last 5 bins (+4,  
 277 +5, +6, +7, +8).

278       To assess the participants' ability to predict the dynamics of the target we extracted the  
 279 following dependent variables. First we computed the mean absolute position error (PE) by  
 280 averaging the absolute difference in position between the target and the eye over the whole

trial, including both periods of saccades and smooth pursuit (note that excluding saccades from PE evaluation did not change our findings). Second we computed the mean absolute velocity error (VE), i.e. the average absolute difference between the eye and target velocity. Note that although PE was evaluated over the whole trial (i.e. including both periods of saccades and smooth pursuit), VE was computed only during smooth pursuit periods. Third, as a gross index of temporal coupling, we computed the coefficient of correlation between eye and target position. Fourth, to evaluate more closely the temporal relationship between eye and target movements, we computed the lag between the two using a crosscorrelation technique based on the eye and target position signal (a positive lag indicating the eye is lagging behind the target).

Finally to assess the relative contribution of saccades and smooth pursuit, we computed for each trial the total distance travelled by the eye with saccades (Orban de Xivry et al., 2006) and then expressed this as a percentage of the total distance travelled by the eye using both saccades and smooth pursuit. To better characterize smooth pursuit, we computed the smooth pursuit gain by averaging the ratio between instantaneous eye and target velocities during phases of smooth pursuit (to avoid numerical instabilities, only situations where absolute target velocity was greater than  $10^\circ/\text{s}$  were considered).

#### *Statistical analysis*

Two-way ANOVA was used to assess the effects of target MAPPING and HAPTIC, but data before and after target blanking were analyzed separately. To subsequently investigate the effect of dissociating visual and haptic feedback, the condition SPRING-DISSHAPT was contrasted to SPRING-NOHAPT and SPRING-HAPT by means of one-way ANOVA. To obtain a normal distribution, Z-score transformation was used for coefficients of

correlation. Newman-Keuls corrections were used for post-hoc T-tests to correct for multiple comparisons. A conventional 0.05 significance threshold was used for all analyses.

## RESULTS

### *Typical trials*

Figure 2 plots five typical trials performed by the same subject in each experimental condition. As can be seen when the target was visible (first half of each trial) accurate smooth pursuit was observed in all 5 conditions. After target occlusion, although the rate and the amplitude of catch-up saccades increased, episodes of smooth pursuit were still observable (albeit with a lower gain). We also noticed a temporal drift between eye and target motion such that the eye started to lead the target, especially under the two conditions with the SPRING mapping.

### *Kinematics of target motion*

Prior to target blanking, average group data indicated a mean period of target oscillation of 1065 ms which was fairly close from the intended value (1000 ms). Blanking the target did not alter the mean period of oscillation (1061 ms). Concerning overall target movement amplitude, its mean value was 17.8° before target occlusion which was slightly above the intended value (15°). After target blanking, this amplitude decreased by 10% under RIGID-NOHAPT ( $t(26)=2.11$ ;  $p<0.05$ ), while it increased by 13% under SPRING-NOHAPT ( $t(26)=3.37$ ;  $p<0.01$ ).

### *Eye motion: smooth pursuit vs. saccades*

Figure 3A presents mean group data showing the relative contribution of smooth pursuit to eye tracking. This figure shows that before target occlusion the percentage of total

330 distance covered by the eye with smooth pursuit was high (about 83%), thereby confirming  
 331 that the task was primarily performed using smooth pursuit eye movements. After target  
 332 occlusion, this contribution decreased substantially (down to 60%; see also Figure 2), but  
 333 smooth pursuit remained the main contributor for eye movement. For both regular and  
 334 blanked periods, ANOVAs showed no significant main effects of MAPPING and HAPTIC, as  
 335 well as no interaction ( $F(1,13) < 3.75$ ,  $p > 0.05$ ). Further analyses showed that the increased  
 336 contribution of saccades following target blanking was associated with a 30% increase in  
 337 saccade rate and an approximate doubling of saccade amplitude (see Figure 2). Overall,  
 338 despite an increase in the contribution of saccades, the key observation is that smooth pursuit  
 339 activity persisted several seconds after target occlusion.

340       Regarding the gain of smooth pursuit, mean group data are presented in Figure 3B. As  
 341 expected from previous studies (Berryhill et al., 2006; Gauthier and Hofferer, 1976), target  
 342 occlusion was followed by a drop in smooth pursuit gain, which was observed in all  
 343 conditions. Averaged across conditions, the gain decreased from 0.74 to 0.61, representing an  
 344 18% drop. Further analyses showed that, both before and after target occlusion, the gain was  
 345 not significantly affected by MAPPING, HAPTIC, or the interaction between these factors  
 346 ( $F(1,13) < 0.89$ ,  $p > 0.05$ ).

347

#### 348 *Accuracy of eye tracking performance at the spatial level*

349       Having shown that smooth pursuit persists after target occlusion, we now assess its  
 350 accuracy with respect to target motion. In Figure 4 we present key parameters accounting for  
 351 the spatial accuracy of eye tracking. Figure 4A presents the time course of position error (PE)  
 352 across our five experimental conditions. Consider first the period before target occlusion. As  
 353 expected we found an effect of MAPPING ( $F(1,13) = 5.94$ ;  $p = 0.03$ ), consistent with the view  
 354 that our task was more difficult under SPRING than RIGID. On average PE was 37% greater



under SPRING than RIGID (2.37 vs. 1.73°). However we found no effect of HAPTIC ( $F(1,13)=0.02$ ;  $p=0.88$ ) and no interaction ( $F(1,13)=2.56$ ;  $p=0.13$ ). Following target blanking, PE increased substantially in all experimental conditions. This time the effect of HAPTIC ( $F(1,13)=6.56$ ,  $p=0.02$ ), MAPPING ( $F(1,13)=86.02$ ,  $p<0.001$ ), and the interaction ( $F(1,13)=13.75$ ;  $p=0.003$ ) were all significant. Post-hoc analysis showed that whereas haptic feedback did not influence PE under RIGID, PE was 25% smaller under SPRING-HAPT in comparison to SPRING-NOHAPT (6.36 vs. 8.49°;  $p<0.001$ ). Overall this analysis of PE shows that, although haptic feedback had little influence on eye tracking accuracy as long as the target was visible, it became very important after target blanking under the SPRING mapping.

Most of these observations were further supported by the analysis of the velocity error (VE; see Figure 4B). Indeed when the target was visible, we also found an effect of MAPPING ( $F(1,13)=7.15$ ;  $p=0.02$ ) consistent with the view that tracking error was greater under SPRING than RIGID (16.4 vs. 20.3°/s; +24%). Again we found no effect of HAPTIC ( $F(1,13)=0.006$ ;  $p=0.94$ ) as well as no interaction ( $F(1,13)=0.16$ ;  $p=0.69$ ). Furthermore, following target blanking, VE increased substantially in all conditions. However, once again this alteration was limited by the provision of haptic feedback under SPRING but not under RIGID as indicated by an interaction between HAPTIC and MAPPING ( $F(1,13)=10.71$ ,  $p=0.006$ ). Post-hoc analysis confirmed that whereas VE were similar in RIGID-HAPT and RIGID-NOHAPT (28.4 vs 25.9°/s;  $p=0.17$ ), VE was 13% smaller in SPRING-HAPT compared to SPRING-NOHAPT (38.0 vs 43.5°/s;  $p<0.001$ ).

#### *Accuracy of eye tracking performance at the temporal level*

As for spatial accuracy, temporal accuracy of eye tracking decreased following target occlusion. To investigate the temporal coordination between eye and target, we first present



381 the correlation coefficient between the two corresponding position signals (see Figure 5A).  
 382 When the target was visible, we found no significant main effect of MAPPING and HAPTIC  
 383 as well as no interaction ( $F(1,13) < 1.39$ ;  $p > 0.26$ ). In contrast, when the target was blanked we  
 384 found a MAPPING by HAPTIC interaction ( $F(1,13) = 54.88$ ;  $p < 0.001$ ) such that R values were  
 385 similar under the two RIGID conditions (NOHAPT=0.71 vs. HAPT=0.65;  $p = 0.12$ ), but were  
 386 greater under SPRING-HAPT compared to SPRING-NOHAPT (0.30 vs. -0.01;  $p < 0.001$ ).  
 387 Overall this analysis adds further evidence that haptic feedback was helpful when the target  
 388 was occluded, but only under the SPRING mapping.

389 To further examine this alteration in temporal accuracy, Figure 5B and C present  
 390 respectively the temporal lag between eye and target, and between eye and hand. Importantly  
 391 one should keep in mind that, in contrast to RIGID where hand and target motion are  
 392 inherently synchronized, there is a temporal delay between hand and target motion under  
 393 SPRING. Due to the mass-spring dynamics, the motion of the target lagged hand motion by  
 394 about 200 ms (see bottom three rows in Fig. 2). Mean group lags—combining data from pre-  
 395 and post-occlusion—were respectively 182, 171 and 245 ms in the SPRING-NOHAPT,  
 396 SPRING-HAPT, and SPRING-DISS (in the latter condition the delay was greater because of  
 397 the lower stiffness of the ‘visual’ spring).

399 Concerning the temporal relationship between eye and target (see Figure 5B), we  
 400 found that when the target was visible, eye and target were rather well synchronized under  
 401 RIGID (mean lag=-13ms) whereas a clear eye lead was seen under SPRING (mean lag=-53  
 402 ms). This difference in eye behavior was corroborated by a main effect of MAPPING  
 403 ( $F(1,13) = 11.06$ ;  $p = 0.005$ ). Unexpectedly when the target was blanked, the eye began to lead  
 404 even more on the target, a phenomenon observed in all conditions albeit with different  
 405 intensity. First this effect was more pronounced under SPRING than RIGID (-208 vs -100 ms;

406  $F(1,13)=73.94$ ;  $p<0.001$ ). Second, we also found an interaction between MAPPING and  
 407 HAPTIC ( $F(1,13)=12.95$ ;  $p=0.003$ ), such that a smaller phase lead was observed under  
 408 SPRING-HAPT than SPRING-NOHAPT (-186 vs. -230 ms;  $p<0.05$ ). In contrast, the phase  
 409 lead was similar under both RIGID conditions ( $p=0.14$ ). Overall haptic feedback appeared  
 410 helpful in limiting the temporal drift of the eye induced by the target blanking under SPRING.

411 To provide a better understanding of eye-hand temporal coordination, we present now  
 412 the temporal lag between eye and hand (see Figure 5C). As expected when the target was  
 413 visible, there was a clear effect of MAPPING ( $F(1,13)=232.3$ ;  $p<0.001$ ). Whereas under  
 414 SPRING the eye lagged behind the hand (mean lag=117 ms), the eye and hand were  
 415 synchronized under RIGID (mean lag=-12 ms). After target blanking, the timing between eye  
 416 and hand changed substantially, with the eye leading the hand under all conditions. However,  
 417 the magnitude of this eye lead depended on both MAPPING and HAPTIC as revealed by an  
 418 interaction between the two factors ( $F(1,13)=50.06$ ;  $p<0.001$ ). Post-hoc analysis indicated that  
 419 in the absence of haptic feedback, the lead of the eye became similar under RIGID-NOHAPT  
 420 and SPRING-NOHAPT (respectively -82 and -88ms;  $p=0.46$ ), despite substantial differences  
 421 prior to target blanking. In contrast when haptic feedback was provided, the differences in  
 422 eye-hand lag persisted between the two mappings (RIGID-HAPT=-118ms vs. SPRING-  
 423 HAPT=-38ms;  $p<0.001$ ). Overall this analysis reinforces the view that the provision of haptic  
 424 feedback is important for eye-hand coordination after target masking.

#### 426 *Dissociation between haptic and visual feedback*

427 Many dependent variables (PE, VE, eye-target correlation, and eye-target lag) showed  
 428 that the provision of haptic feedback was helpful in reducing the detrimental effects of target  
 429 blanking under the SPRING mapping. For each of these variables, we ran an additional  
 430 ANOVA that compared the 3 SPRING conditions, namely SPRING-DISSHAPT, SPRING-

431 NOHAPT, and SPRING-HAPT. Except for VE, we found in all cases a significant difference  
 432 across these 3 conditions ( $F(2,26) > 4.15$ ;  $p < 0.05$ ). Post-hoc analyses consistently showed a  
 433 lack of difference between SPRING-DISSHAPT and SPRING-NOHAPT, while showing  
 434 reliably a difference between SPRING-DISSHAPT and SPRING-HAPT ( $p < 0.05$ ). Overall  
 435 these additional analyses show that when haptic feedback was not congruent with visual  
 436 dynamics of the target, the benefit provided by haptic feedback was lost.

437

#### 438 *Comparison between a self-moved and an externally moved target*

439 One major conclusion drawn from this study is that, following target occlusion,  
 440 smooth pursuit remains the major contributor of eye motion, with about 60% of the total  
 441 distance covered by the eye. An implicit assumption is that the contribution of smooth pursuit  
 442 would have been smaller for an externally moved target. To test this assumption, we tested 7  
 443 new participants using a similar paradigm except this time the motion of the target was  
 444 preprogrammed and the hand was immobile. After a familiarization session, each participant  
 445 was tested successively with pure sinusoidal trajectories (Freq=1Hz, Amp=15°), and target  
 446 trajectories taken from a randomly selected participant of the previous experiment (with a  
 447 different previous participant matched to each new participant). As in the former conditions  
 448 the target was blanked after 7 seconds, and each participant performed a block of 3 trials in  
 449 each condition. In Figure 6 we present the results of this control experiment separately for the  
 450 pure sinusoidal trajectories (EXT-PURESINE) and the playback trajectories (EXT-  
 451 REPLAY). For comparison purposes, we also present the mean performance of the 7  
 452 participants whose trajectories were utilized for playback (SELF-MEAN). Although there was  
 453 no significant difference between EXT-PURESINE and EXT-REPLAY ( $F(1,6)=2.01$ ;  
 454  $p=0.21$ ), the contribution of smooth pursuit was always smaller in EXT compared to SELF  
 455 ( $F(1,6)=41.65$ ;  $p < 0.001$ ). This control experiment shows that for both visible and occluded

456 targets, there is a greater contribution of smooth pursuit when tracking a self-moved target as  
 457 compared to an externally moved one. Those results extend earlier observations made in the  
 458 context of non-occluded targets (Landelle et al., 2016; Steinbach and Held, 1968) in the sense  
 459 that they are also valid for occluded targets.

460

## 461 **DISCUSSION**

462       The goal of this study was to investigate the ability of humans to track with their eyes  
 463 a self-moved target in the absence of visual feedback. Specifically, we asked whether haptic  
 464 feedback could ameliorate the effects of removing visual feedback when the dynamics  
 465 relating hand and target motion were either simple or complex. Our experiment resulted in  
 466 four key findings. First, we found that participants were able to maintain smooth pursuit  
 467 activity after target occlusion, even under a complex hand-target mapping. Second, although  
 468 largely expected, target occlusion was detrimental for the accuracy of eye tracking under all  
 469 conditions. Third, the detrimental effects of target occlusion on eye tracking depended to a  
 470 large extent on both the target dynamics and the availability of haptic feedback. Specifically,  
 471 although haptic feedback did not provide much benefit to eye tracking under the RIGID  
 472 mapping, it limited the detrimental effects of target occlusion under the SPRING mapping.  
 473 Finally, when haptic and visual feedback were dissociated (i.e. incongruent), the benefit of  
 474 haptic feedback (seen under SPRING-HAPT) was no longer observed. We will now discuss  
 475 in more detail these findings and their implications.

476

### 477 *Maintenance of smooth pursuit after target occlusion*

478       The current study showed that participants can maintain reliable smooth pursuit  
 479 activity for several seconds after the masking of a self-moved target, which further reinforces  
 480 the view that retinal slip is not the only input to the smooth pursuit control system (Berryhill

et al., 2006; Gauthier and Hofferer, 1976; Vercher et al., 1996). However, the contribution of smooth pursuit to tracking was reduced when the target was occluded (switching from 83 to 60%) and the smooth pursuit gain decreased (from 0.74 to 0.61). These detrimental effects are consistent, at least qualitatively, with two earlier seminal studies (Gauthier and Hofferer, 1976; Jordan, 1970). In the study of Jordan (1970) smooth pursuit contribution dropped from 98 to 38% when the target was occluded. In the study of Gauthier and Hofferer (1976), the gain of smooth pursuit dropped approximately from 1 to 0.7, while their Figure 4 also speaks for a decreased contribution of smooth pursuit after target occlusion. Because both studies only used conventional hand-target mappings (i.e. rigid), one novel contribution of our study is to extend the ability of participants to maintain smooth pursuit activity under more complex mappings. In a recent study by Landelle et al (2016), target occlusions were also investigated under a SPRING mapping, but their duration (400ms) was less challenging than in the current experiment. Thanks to longer periods of target occlusion (7s) in our study, we showed that at least 2s were necessary to stabilize the eye behavior (see Figures 3, 4, and 5).

#### *The role of hand-target mapping and haptic feedback*

Smooth pursuit activity can be maintained consistently after target occlusion, but the accuracy of eye tracking was altered by this procedure. Although this was largely expected (Berryhill et al., 2006), this alteration depended both on the type of hand-target mapping, and the availability of haptic feedback. More specifically all our analyses of spatial and temporal accuracy (see Figures 4 and 5) indicated an interaction between MAPPING and HAPTIC. In all cases haptic feedback was helpful to circumvent the detrimental effects of target occlusion under the SPRING mapping but not under the RIGID one. For instance when maneuvering the spring target, the provision of haptic feedback led to a reduction in PE and VE of respectively 25 and 13%.

506       The temporal coordination between eye and target was also altered by the occlusion,  
507 but the largest changes were observed under the SPRING mapping, with the eye starting to  
508 lead substantially the target (see Figure 5B), and even the hand, a phenomenon that was also  
509 observed under the RIGID mapping (see Figure 5C). In the absence of haptic feedback, this  
510 temporal drift was so large under SPRING that ultimately the eye-hand lag became similar  
511 under RIGID, suggesting that participants failed to maintain a representation of the spring  
512 linking target and hand motion. In contrast when haptic feedback was provided, the drift was  
513 smaller (-20%) allowing to maintain different eye-hand timing under SPRING and RIGID.  
514 We conclude that the provision of haptic feedback under SPRING was helpful in maintaining  
515 the initial coordination between eye, hand, and target.

516       More generally the contribution of haptic is very context specific. When manipulating  
517 the rigid target both with and without occlusion, haptic feedback did not influence eye hand  
518 coordination. In that sense, our results are consistent with earlier observations made by  
519 Vercher et al (1996) who reported that, under a simple (i.e. rigid) mapping, deafferented  
520 patients did not differ from control participants when tracking a non-occluded target.  
521 Moreover, when manipulating the non-occluded spring target, we did not find any obvious  
522 contribution of haptic. However, as soon as the spring target was occluded, a contribution of  
523 haptic emerged. Overall, those results suggest that when participants maneuver familiar  
524 objects, haptic feedback is unnecessary to drive their eye-motion (visual information and hand  
525 efference copy being sufficient). In contrast, when conditions become more challenging, such  
526 as with an unfamiliar object (i.e. with complex dynamics) and in the absence of visual  
527 feedback, haptic feedback can provide a critical input for eye tracking.

528

529   *Dissociation between haptic and visual feedback*

530 Results showed that when the haptic and visual dynamics were dissociated, the benefit  
531 of haptic feedback under target occlusion was lost, namely eye tracking performance became  
532 as poor as with no haptic feedback. In principle participants could have learned, prior to target  
533 occlusion, the rather arbitrary mapping between haptic and visual feedback and use it to  
534 predict target motion after target occlusion. However, our results indicate that this did not  
535 occur. Alternatively, following target occlusion, participants could have interpreted that  
536 haptic feedback was congruent with visual target motion (e.g., as in the SPRING-HAPT or  
537 RIGID-HAPT conditions) and used this mapping to predict target motion. However, this is  
538 unlikely because eye tracking performance should have become worse than with no haptic  
539 feedback. Instead it seems that participants simply ignored the incongruent haptic feedback,  
540 presumably after learning that it was not consistent with visual feedback during the pre-  
541 blanking phase. All in all, this suggests that participants can flexibly rely on haptic feedback  
542 when it is helpful for the task, but can also ignore it when it is potentially harmful for the task.

543

#### 544 *Eye lead following target occlusion*

545 Under all experimental conditions eye motion was shifted forward in time after the  
546 target was occluded. Averaged across conditions, the mean lead of the eye over the hand was  
547  $76 \pm 31$ ms. Similarly Gauthier and Hofferer (1976) reported that “*the eye led the finger by an*  
548 *averaged 60ms delay in all tests involving tracking of an imaginary target actively moved by*  
549 *the finger*“. They suggested that this lead arises because hand and eye movements have  
550 different response times to motor commands, mainly because the eye has considerably lower  
551 inertia, and is driven by relatively stronger muscles. It was proposed that in total darkness,  
552 since there is no more need to compensate for this asymmetry in motor systems, a phase lead  
553 of the eye would emerge. More recently a rather similar phenomenon was observed when  
554 participants were asked to try to look at the perceived position of their hand during unseen



555 reaching movements (Ariff et al., 2002). In that context saccades provided an unbiased  
556 estimate of hand position at  $t+200\text{ms}$ . Namely participants initiated saccades that landed close  
557 to the location of their hand would be 200ms later. The authors interpreted that finding as  
558 evidence that the brain uses a forward model allowing the eye to estimate the future hand  
559 position in real time as movement unfolds (see also Scarchilli et al., 1999). Although  
560 attractive this scheme does not account for the eye lead when participants are explicitly  
561 required to track their hand. A possible reason for this behavior may stem from natural eye-  
562 hand coordination during object manipulation. Indeed when participants are asked to transport  
563 an object, their gaze is typically leading the hand (Johansson et al., 2001; Sailer et al., 2005).  
564 Specifically, participants make so-called proactive saccades, meaning that their gaze is  
565 directed toward the location where they plan to bring the object. We propose that when the  
566 target was occluded, even though our participants were explicitly required to track the current  
567 position of the target, they might experience difficulties refraining from this proactive gaze  
568 behavior.

569

## 570 *Conclusions*

571 Overall we conclude that the ability to maintain smooth pursuit in the absence of  
572 visual information extends to complex hand-target mappings, but the provision of haptic  
573 feedback is critical for the maintenance of accurate eye-tracking performance. More  
574 generally, this study extends the view that haptic feedback is critical not only for  
575 manipulating non-rigid objects efficiently (Danion et al., 2012; Huang et al., 2006; Sternad et  
576 al., 2001), but also to coordinate proficiently eye and hand actions.

577



578 **BIBLIOGRAPHY**

- 579
- 580 Angel RW, Garland H (1972) Transfer of information from manual to oculomotor control  
581 system. *J Exp Psychol* 96:92–96.
- 582 Ariff G, Donchin O, Nanayakkara T, Shadmehr R (2002) A real-time state predictor in motor  
583 control: study of saccadic eye movements during unseen reaching movements. *J Neurosci*  
584 22:7721–7729.
- 585 Bennett SJ, Barnes GR (2006) Smooth ocular pursuit during the transient disappearance of an  
586 accelerating visual target: the role of reflexive and voluntary control. *Exp Brain Res* 175:1–  
587 10.
- 588 Bennett SJ, Barnes GR (2003) Human ocular pursuit during the transient disappearance of a  
589 visual target. *J Neurophysiol* 90:2504–2520.
- 590 Berryhill ME, Chiu T, Hughes HC (2006) Smooth pursuit of nonvisual motion. *J*  
591 *Neurophysiol* 96:461–465.
- 592 Danion F, Diamond JS, Flanagan JR (2012) The role of haptic feedback when manipulating  
593 nonrigid objects. *J Neurophysiol* 107:433–441.
- 594 Dingwell JB, Mah CD, Mussa-Ivaldi FA (2004) Experimentally confirmed mathematical  
595 model for human control of a non-rigid object. *J Neurophysiol* 91:1158–1170.
- 596 Dingwell JB, Mah CD, Mussa-Ivaldi FA (2002) Manipulating objects with internal degrees of  
597 freedom: evidence for model-based control. *J Neurophysiol* 88:222–235.
- 598 Domann R, Bock O, Eckmiller R (1989) Interaction of visual and non-visual signals in the  
599 initiation of smooth pursuit eye movements in primates. *Behav Brain Res* 32:95–99.
- 600 Farshchiansadegh A, Melendez-Calderon A, Ranganathan R, Murphey TD, Mussa-Ivaldi FA  
601 (2016) Sensory Agreement Guides Kinetic Energy Optimization of Arm Movements during  
602 Object Manipulation. *PLoS Comput Biol* 12:e1004861.
- 603 Gauthier GM, Hofferer JM (1976) Eye tracking of self-moved targets in the absence of vision.  
604 *Exp Brain Res* 26:121–139.
- 605 Gauthier GM, Vercher JL, Mussa Ivaldi F, Marchetti E (1988) Oculo-manual tracking of  
606 visual targets: control learning, coordination control and coordination model. *Exp Brain Res*  
607 73:127–137.
- 608 Huang FC, Gillespie RB, Kuo AD (2006) Human adaptation to interaction forces in visuo-  
609 motor coordination. *IEEE Trans Neural Syst Rehabil Eng Publ IEEE Eng Med Biol Soc*  
610 14:390–397.
- 611 Johansson RS, Westling G, Bäckström A, Flanagan JR (2001) Eye-hand coordination in  
612 object manipulation. *J Neurosci Off J Soc Neurosci* 21:6917–6932.
- 613 Jordan S (1970) Ocular pursuit movement as a function of visual and proprioceptive  
614 stimulation. *Vision Res* 10:775–780.
- 615 Landelle C, Montagnini A, Madelain L, Danion F (2016) Eye tracking a self-moved target  
616 with complex hand-target dynamics. *J Neurophysiol* 116:1859–1870.
- 617 Madelain L, Krauzlis RJ (2003) Effects of learning on smooth pursuit during transient  
618 disappearance of a visual target. *J Neurophysiol* 90:972–982.
- 619 Mah CD, Mussa-Ivaldi FA (2003) Evidence for a specific internal representation of motion-  
620 force relationships during object manipulation. *Biol Cybern* 88:60–72.
- 621 Mather J, Lackner J (1975) Adaptation to visual rearrangement elicited by tonic vibration  
622 reflexes. *Exp Brain Res* 24:103–105.
- 623 Mehta B, Schaal S (2002) Forward models in visuomotor control. *J Neurophysiol* 88:942–  
624 953.
- 625 Nagengast AJ, Braun DA, Wolpert DM (2009) Optimal control predicts human performance  
626 on objects with internal degrees of freedom. *PLoS Comput Biol* 5:e1000419.

- 627 Orban de Xivry J-J, Bennett SJ, Lefèvre P, Barnes GR (2006) Evidence for synergy between  
 628 saccades and smooth pursuit during transient target disappearance. *J Neurophysiol* 95:418–  
 629 427.
- 630 Orban de Xivry J-J, Missal M, Lefèvre P (2008) A dynamic representation of target motion  
 631 drives predictive smooth pursuit during target blanking. *J Vis* 8:6.1-13.
- 632 Sailer U, Flanagan JR, Johansson RS (2005) Eye-hand coordination during learning of a  
 633 novel visuomotor task. *J Neurosci* 25:8833–8842.
- 634 Scarchilli K, Vercher JL, Gauthier GM, Cole J (1999) Does the oculo-manual co-ordination  
 635 control system use an internal model of the arm dynamics? *Neurosci Lett* 265:139–142.
- 636 Shadmehr R, Smith MA, Krakauer JW (2010) Error correction, sensory prediction, and  
 637 adaptation in motor control. *Annu Rev Neurosci* 33:89–108.
- 638 Steinbach MJ (1969) Eye tracking of self-moved targets: the role of efference. *J Exp Psychol*  
 639 82:366–376.
- 640 Steinbach MJ, Held R (1968) Eye tracking of observer-generated target movements. *Science*  
 641 161:187–188.
- 642 Sternad D, Duarte M, Katsumata H, Schaal S (2001) Bouncing a ball: tuning into dynamic  
 643 stability. *J Exp Psychol Hum Percept Perform* 27:1163–1184.
- 644 Vercher JL, Gauthier GM, Guédon O, Blouin J, Cole J, Lamarre Y (1996) Self-moved target  
 645 eye tracking in control and deafferented subjects: roles of arm motor command and  
 646 proprioception in arm-eye coordination. *J Neurophysiol* 76:1133–1144.
- 647 Vercher JL, Quaccia D, Gauthier GM (1995) Oculo-manual coordination control: respective  
 648 role of visual and non-visual information in ocular tracking of self-moved targets. *Exp Brain*  
 649 *Res* 103:311–322.
- 650 Wolpert DM, Diedrichsen J, Flanagan JR (2011) Principles of sensorimotor learning. *Nat Rev*  
 651 *Neurosci* 12:739–751.
- 652 Wolpert DM, Flanagan JR (2001) Motor prediction. *Curr Biol CB* 11:R729-732.
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- 654

655 **FIGURE CAPTIONS**

656

657

658 **Figure 1.** Photographs of the experimental setup. A. Overview of the experimental setup. The  
659 red dot indicates target position when the laser is on. B. The grasped object and the  
660 lightweight robotic device. C. The laser and optical scanner. See text for more details.

661

662 **Figure 2.** Typical trials performed by the same subject in each experimental condition. The  
663 vertical dotted line indicates the moment of target occlusion. Note the progressive drift in the  
664 temporal coupling between eye and target, and the larger contribution of saccades.

665

666 **Figure 3.** Contribution of saccades and smooth pursuit as a function of experimental  
667 condition and time in the vicinity of target occlusion. **A.** Percentage of total distance covered  
668 by smooth pursuit. **B.** Gain of smooth pursuit velocity. Error bars represent SE. The vertical  
669 dotted lines denote the initiation of target occlusion. The numbers circled (in red or black)  
670 denote the numbering of each bin (following the rational described in the method section).

671

672 **Figure 4.** Spatial accuracy of eye tracking as a function of experimental condition and time in  
673 the vicinity of target occlusion. **A.** Position error. **B.** Velocity error between eye and target.  
674 Error bars represent SE. The vertical dotted lines denote the initiation of target occlusion.  
675 Note how the detrimental effects of target blanking are reduced by the provision of haptic  
676 feedback under SPRING. The numbers circled (in red or black) denote the numbering of each  
677 bin.

678

679 **Figure 5.** Temporal accuracy of eye tracking as a function of experimental condition and time  
680 in the vicinity of target occlusion. **A.** Coefficient of correlation between eye and target. **B.**  
681 Temporal lag between eye and target. A negative lag indicates that the eye precedes the target.

682 C. Temporal lag between eye and hand. A negative lag indicates that the eye precedes the  
683 hand. Error bars represent SE. The vertical dotted lines denote the initiation of target  
684 occlusion. The numbers circled (in red or black) denote the numbering of each bin. Note how  
685 the detrimental effects of target blanking are reduced by the provision of haptic feedback  
686 under SPRING.

687

688 **Figure 6.** Percentage of total distance covered by smooth pursuit as a function of  
689 experimental condition and time in the vicinity of target occlusion. This figure compares the  
690 performance of 2 groups of participants that either tracked a self-moved target or an  
691 externally moved one. See text for more details. Error bars represent SE. The vertical dotted  
692 line denotes the initiation of target occlusion. The numbers circled (in red or black) denote the  
693 numbering of each bin.

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