



**HAL**  
open science

# Composition and decomposition of visuomotor maps during manual tracking

Pierre-Michel Bernier, James Mathew, Frédéric Danion

► **To cite this version:**

Pierre-Michel Bernier, James Mathew, Frédéric Danion. Composition and decomposition of visuomotor maps during manual tracking. *Journal of Neurophysiology*, 2021, 126 (5), pp.1685-1697. 10.1152/jn.00058.2021 . hal-03375231

**HAL Id: hal-03375231**

**<https://hal.science/hal-03375231v1>**

Submitted on 17 Nov 2022

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1                   **Composition and decomposition of visuomotor maps during**  
2   **manual tracking**

3                             Pierre-Michel Bernier<sup>1</sup>, James Mathew<sup>2,3</sup>, Frederic R. Danion<sup>2,4</sup>

4                   <sup>1</sup>Département de Kinanthropologie, Université de Sherbrooke, Sherbrooke, Québec, Canada

5                   <sup>2</sup>Aix Marseille Univ, CNRS, INT, Institut Neurosci Timone, Marseille, France

6                   <sup>3</sup>current affiliation: Institute of Neuroscience, Institute of Communication & Information  
7                   Technologies, Electronics & Applied Mathematics, Université Catholique de Louvain,  
8                   Belgium

9                   <sup>4</sup>University of Poitiers, CNRS, Center for Research on Cognition and Learning (CERCA)  
10                   UMR 7295, Poitiers, France

11                   *Running Head:* Modularity of visuomotor adaptation

12                   *Key-words:* hand tracking; sensorimotor adaptation; visuomotor rotation; modular learning;  
13                   interference; kinematic perturbation; mass-spring mapping

14                   *Corresponding author:*

15                   Email: [frederic.danion@univ-poitiers.fr](mailto:frederic.danion@univ-poitiers.fr)

16                   *Number of figures:* 9

17                   *Number of pages:* 40  
18

19                   *Acknowledgement:*

20                   Support for this research was provided by the CNRS (IEA N°00070). We also wish to thank  
21                   Nabawiat Mondoha and Léa Dupony for technical assistance during data collection. Finally,  
22                   we are thankful to all the reviewers for their scrupulous work and helpful feedback.  
23

24                   *Conflict of interest:*

25                   The authors state they have no conflict of interest.  
26

27                   *Contributions:*

28                   PMB and FRD designed the study, collected and analysed the data. All authors drafted the  
29                   manuscript.

30 **ABSTRACT**

31           Adapting hand movements to changes in our body or the environment is essential for  
32 skilled motor behavior, as is the ability to flexibly combine experience gathered in separate  
33 contexts. However it has been shown that when adapting hand movements to two different  
34 visuomotor perturbations in succession, interference effects can occur. Here we investigate  
35 whether these interference effects compromise our ability to adapt to the superposition of the  
36 two perturbations. Participants tracked with a joystick a visual target that followed a smooth  
37 but unpredictable trajectory. Four separate groups of participants (total n = 83) completed one  
38 block of 50 trials under each of three mappings: one in which the cursor was rotated by 90°  
39 (ROTATION), one in which the cursor mimicked the behavior of a mass-spring system  
40 (SPRING), and one in which the SPRING and ROTATION mappings were superimposed  
41 (SPROT). The order of the blocks differed across groups. Although interference effects were  
42 found when switching between SPRING and ROTATION, participants who performed these  
43 blocks first performed better in SPROT than participants who had no prior experience with  
44 SPRING and ROTATION (i.e., composition). Moreover, participants who started with  
45 SPROT exhibited better performance under SPRING and ROTATION than participants who  
46 had no prior experience with each of these mappings (i.e., decomposition). Additional  
47 analyses confirmed that these effects resulted from components of learning that were specific  
48 to the rotational and spring perturbations. These results show that interference effects do not  
49 preclude the ability to compose/decompose various forms of visuomotor adaptation.

50

51

52 **NEW AND NOTEWORTHY**

53           The ability to compose/decompose task representations is critical both for cognitive  
54 and behavioral flexibility. Here we show that this ability extends to two forms of visuomotor  
55 adaptation in which humans have to perform visually guided hand movements. Despite the  
56 presence of interference effects when switching between visuomotor maps, we show that  
57 participants are able to flexibly compose or decompose knowledge acquired in previous

58 sessions. These results further demonstrate the flexibility of sensorimotor adaptation in  
59 humans.

## 60 **INTRODUCTION**

61 A critical issue that is still unresolved in the field of sensorimotor control pertains to  
62 the modularity of sensorimotor mappings, and especially whether multiple internal models  
63 can interact, be flexibly combined and whether they can be stored in common vs. separate  
64 working memory systems (Burgos et al. 2018; Davidson and Wolpert 2004; Flanagan et al.  
65 1999; Haruno et al. 2001; Imamizu et al. 2007; Pearson et al. 2010; Wolpert and Kawato  
66 1998).

67 One type of paradigm that has long been used to address the degree of modularity and  
68 independence between sensorimotor representations is that of interference (Duncker et al.  
69 2020; Krakauer et al. 1999, 2019; Lerner et al. 2020). Generally, when participants are  
70 sequentially exposed to a perturbation (e.g., force-field or visuomotor rotation) and its mirror-  
71 reversal soon thereafter, adaptation to the second perturbation is hampered (anterograde  
72 interference) or memory of the first one is impaired (retrograde interference) (Krakauer et al.  
73 2005; Miall et al. 2004). There have been multiple explanations for this phenomenon, with  
74 early work emphasizing that interference arises whenever error signals for each perturbation  
75 are encoded via the same sensory modality (proprioception, vision) or within the same  
76 reference frame (intrinsic, extrinsic) (Krakauer et al. 1999). Later work brought nuance and  
77 suggested that the critical factor may not be the sensory modality (or reference frame) per se,  
78 but the state variable of the perturbation. For instance, interference has been shown to occur  
79 for different types of perturbations (force-field and visuomotor rotation) if they are both made  
80 to depend on the same state variable, being position, velocity or acceleration (Tong et al.  
81 2002). In more recent work, the notion of context (e.g., color of background or target) and  
82 task goal (e.g., location in the workspace) have been brought forward, with evidence that two  
83 perturbations interfere when they affect movements that are directed toward a common goal,

84 or more subtly when they share common motor preparatory activity (Howard et al. 2012;  
85 Krakauer et al. 2019; Sheahan et al. 2016).

86 Another type of paradigm that has been used to address the modularity of  
87 sensorimotor mappings is that of composition/decomposition, in which participants are  
88 sequentially exposed to separate single sensorimotor mappings or one that consists of their  
89 combination. An early study by Flanagan and colleagues (Flanagan et al. 1999) showed that  
90 participants can flexibly compose and decompose adaptation to different types of  
91 perturbations, namely a dynamic viscous force-field and a kinematic 60° visuomotor rotation,  
92 even though they influence behaviour in opposite directions. For instance, after participants  
93 had adapted to each single perturbation separately, they exhibited immediate benefits on the  
94 combined perturbation as compared to naïve participants. A critical factor in their study,  
95 which may have facilitated composition, was that the perturbations were “orthogonal” to each  
96 other, influencing different state variables and being mediated by different sensory modalities,  
97 thus minimizing potential interference between the two (an issue which was not explicitly  
98 tested in their study).

99 Hence, it remains unclear whether composition and decomposition remain possible  
100 when two perturbations share attributes and interfere with each other. To address this issue,  
101 we used two kinematic perturbations that pertained to the same sensory modality (visual), for  
102 which the state variables were partially shared, and for which all features pertaining to task  
103 goal and context were the same. The first one is a visuomotor rotation, in which a cursor is  
104 rotated by 90° with respect to hand motion. The second one consists of a cursor that mimics  
105 the behaviour of a damped mass-spring system. Although this perturbation is less  
106 conventional, several reports have shown its relevance for motor learning (Dingwell et al.  
107 2002, 2004; Huang et al. 2007; Landelle et al. 2016; Nagengast et al. 2010). In contrast to the

108 visuomotor rotation which relies on a single state variable (cursor position), the effect of the  
109 mass-spring mapping depends upon position, velocity as well as acceleration.

110 We used a pursuit tracking task in which participants had to keep the cursor as close as  
111 possible to a moving target that followed an unpredictable trajectory (Danion and Flanagan  
112 2018; Mathew et al. 2018). Although this task differs from more traditional discrete reaching  
113 tasks in the sense that it relies more heavily on feedback control rather than feedforward  
114 control (Yang et al. 2020), pursuit tracking has nonetheless been shown to be under adaptive  
115 control as demonstrated by the presence of potent aftereffects, a hallmark of adaptation  
116 (following a 90° visuomotor rotation; Gouirand et al. 2019; Mathew et al. 2018; Yang et al.  
117 2020). One of the main advantages of using this task is that it minimizes the possibility for  
118 exploiting explicit mechanisms known to be at play during visuomotor adaptation, such as  
119 cognitive strategizing and re-aiming (Fernandez-Ruiz et al. 2011; Haith et al. 2015; Leow et  
120 al. 2017; McDougle and Taylor 2019), thereby unmasking the low-level implicit updating of  
121 internal models.

122 Results revealed that even though adaptation to the two perturbations led to  
123 interference, participants could still successfully compose and decompose them,  
124 demonstrating that the brain is able to segregate the two mappings even when they rely on the  
125 same sensory modality, partially share state variables, and are learned under the same task  
126 goals and context.

127

## 128 **METHOD**

### 129 *Participants*

130 Four groups of right-handed participants took part in this study (Group 1, N=20, Age: 22.8 ±  
131 4.9 yrs., 12 female; Group 2, N=21, Age: 22.7 ± 6.2 yrs., 12 female; Group 3, N=21, Age:  
132 22.3 ± 5.0 yrs., 14 female; Group 4, N=21, Age: 23.1 ± 45.8 yrs., 13 female). Although no  
133 formal a priori power analysis was performed, based on our previous experience using the

134 tracking task (Gouirand et al. 2019; Mathew et al. 2018, 2019a) and pilot testing, we aimed  
135 for a sample size of at least  $n = 20$  per group. We were able to collect 21 participants per  
136 group but had to drop one participant of Group 1. Handedness of participants was verified  
137 using the Oldfield Handedness Inventory with a mean laterality quotient of  $96.0 \pm 6.7\%$ . None  
138 of the participants had neurological or visual disorders. They were naïve as to the  
139 experimental conditions and hypotheses, and had no previous experience with oculo-manual  
140 tracking tasks. The experimental paradigm (2016-02-03-007) was approved by the Ethics  
141 Committee of Aix-Marseille University and complied with the Declaration of Helsinki. All  
142 participants gave written consent prior to participation. Each experimental protocol lasted  
143 about one hour, and participants were compensated 10€ for their participation.

144

#### 145 *Apparatus*

146 The experimental setup is similar to the one used in our previous studies (Gouirand et  
147 al. 2019; Mathew et al. 2018, 2019b), thus we will only report key information. Our setup is  
148 illustrated in Figure 1a. Participants were seated comfortably in a dark room facing a screen  
149 (ACER Predator, 1920×1080, 27" inch, 240Hz) positioned in the frontal plane. Head  
150 movements were restrained by a chin rest and a padded forehead rest. In order to block direct  
151 vision of their hands, a horizontal shield was positioned under the participants' chin.  
152 Participants were required to hold a joystick (Series 812, Megatron, France, with  $\pm 25^\circ$  of  
153 inclination along X-Y axes) with their right hand positioned horizontally on a table in front of  
154 them. Both right and left forearms were resting on the table. The output of the joystick was  
155 fed into a data acquisition system (Keithley ADwin Real Time, Tektronix) and was sampled  
156 at 1000 Hz.

157

#### 158 *Procedure*

159 Throughout the experiment, participants had to perform a tracking task (Figure 1b)  
160 that consisted of moving the joystick with the right hand so as to keep the cursor (red disk,  
161 0.5cm in diameter) as close as possible to a moving target (blue disk, 0.5cm in diameter). The  
162 motion of the target resulted from the combination of sinusoids: two along the X axis (one  
163 fundamental and a second or third harmonic) and two along the Y axis (same procedure; see  
164 Figure 1b for axes). We used the following equations to construct target motion:

$$165 \quad x_t = A_{1x}\cos\omega t + A_{2x}\cos(h_x\omega t - \varphi_x) \quad (1)$$

$$166 \quad y_t = A_{1y}\sin\omega t + A_{2y}\sin(h_y\omega t - \varphi_y) \quad (2)$$

167 This technique was used to generate pseudo-random 2D patterns while preserving  
168 smooth changes in velocity and direction (Danion and Flanagan 2018; Mrotek and Soechting  
169 2007; Soechting et al. 2010). A total of five different patterns with a mean tangential velocity  
170 of 16cm/s were used throughout the experiment (see Table 1 and Figure 1c). The order of  
171 patterns was randomized across trials and participants while ensuring that each pattern was  
172 presented equally often within each experimental condition.

173 Four types of hand-cursor visual mappings were tested: NORMAL, ROTATION,  
174 SPRING, and SPROT. Under the NORMAL mapping the gain of the joystick was such that a  
175 25° change in the inclination of the joystick resulted in a 15cm change on the screen. This  
176 gain prevented the cursor from moving outside the screen. For the NORMAL mapping the  
177 angular relationship between the joystick orientation and its visual consequences on the  
178 screen was one-to-one and thus intuitive: if the joystick was inclined to the left, the cursor on  
179 the screen also moved to the left. Under the ROTATION mapping, the relationship between  
180 the joystick orientation and the position of the cursor was altered by a 90° counter-clockwise  
181 visuomotor rotation (Ogawa and Imamizu 2013). As a result, if the participant moved the  
182 joystick forward, the cursor moved leftward on the screen. Under the SPRING mapping, the  
183 cursor behaved as a mass attached to the hand by means of a spring. We used the following



184 parameters for the simulation: mass = 1 Kg, stiffness = 40 N/m, damping = 1.66 N/m/s,  
185 resting length = 0 m. This parameter setting results in a 1Hz resonance frequency ( $F$ ) as  
186 imposed by the following equation:

187 
$$F = \frac{1}{2\pi} \sqrt{\frac{k}{m}} \quad (3)$$
 with  $m$  accounting for the mass, and  $k$  for the stiffness.

188 This parameter setting is consistent with previous studies investigating the  
189 manipulation of non-rigid objects (Danion et al. 2012, 2017; Dingwell et al. 2002, 2004;  
190 Landelle et al. 2016; Mathew et al. 2019a; Nagengast et al. 2009). Finally the fourth mapping,  
191 SPROT, resulted from the combination of the ROTATION and SPRING mappings, meaning  
192 that the cursor was both rotated and behaving like a mass-spring. Supplemental videos  
193 depicting representative trials of participants in the NORMAL mapping as well as during the  
194 first and last trials of each of the three perturbed mappings can be found here  
195 <https://zenodo.org/record/5138123#.YP75VI5KiUk>.

196 After 4-5 trials of familiarization, each participant began with a baseline block of 10  
197 trials under the NORMAL mapping (see Figure 2). Then they completed one block of 50  
198 trials under each of the 3 experimental conditions: SPRING, ROTATION, and SPROT.  
199 Group 1 and Group 2 were tested for the ability to compose sensorimotor adaptation, with  
200 participants completing SPRING and ROTATION before they were tested on SPROT.  
201 Conversely, Group 3 and Group 4 were tested first on SPROT then on SPRING and  
202 ROTATION, so as to test the ability to decompose sensorimotor adaptation. After completing  
203 these 4 blocks, all participants performed a washout block with 10 trials under the NORMAL  
204 mapping. Overall a total of 170 experimental trials were collected per participant. Each trial  
205 lasted 10 seconds. The total duration of the experiment averaged 60 min.

206

207 At the end of the experiment, there was an informal debriefing. Participants were asked the  
208 following open question: “Please describe the perturbation(s) you experienced”. Our main

209 interest was to evaluate whether participants could report that one perturbation was the  
210 combination of two others.

211

## 212 *Data analysis*

213 Because participants were explicitly instructed to always minimize the cursor-target  
214 distance, our primary dependent variable to characterize performance across all types of  
215 perturbations was hand tracking error. To quantify hand tracking error ( $E$ ) we measured the  
216 distance in cm (in two dimensions;  $x$  and  $y$ ) between the cursor ( $C$ ; moved by the hand) and  
217 the target ( $T$ ) at each instant ( $t$ ) using the following equation:

$$218 \quad E_t = \sqrt{(C_{xt} - T_{xt})^2 + (C_{yt} - T_{yt})^2} \quad (4)$$

219

220 We averaged this error across time for each trial while excluding the first second of  
221 data from each trial.

222 In addition to hand tracking error, two additional metrics were used in an effort to  
223 isolate components of learning that would be specific to either the SPRING or ROTATION  
224 perturbations. The first metric was directional error, which consisted in rotating the cursor  
225 data (around the center) with respect to the target data in each trial, and determining the angle  
226 which minimized hand tracking error (a method inspired from Yang et al. 2020). Here, by  
227 convention, a positive directional error indicates that cursor data had to be rotated clockwise  
228 to match the target data. It was hypothesized that this metric would show strong modulations  
229 during adaptation to the ROTATION and SPROT perturbations, but not during the SPRING  
230 perturbation. The second metric was cursor velocity (i.e., mean tangential velocity in each  
231 trial) because hand/joystick velocity is amplified at the cursor level by the dynamics of the  
232 spring (Landelle et al. 2016; Mathew et al. 2019a). Following this line of reasoning, it was  
233 hypothesized that under initial exposure to the SPRING and SPROT mappings cursor velocity

234 would substantially exceed target velocity (16 cm/s), while this would not be the case under  
235 ROTATION or Baseline. Similar to tracking error, directional error and cursor velocity were  
236 assessed while excluding the first second of data from each trial.

237

### 238 *Statistical analysis*

239 Baseline, as well as washout performance was compared across groups with a 4 Group  
240 x 10 Trial two-way ANOVA with trial as a repeated-measures. Then, to test our main  
241 hypotheses regarding composition/decomposition, we compared adaptation to each of the  
242 three mappings (SPRING, ROTATION, SPROT) across groups. To do so, for each mapping,  
243 adaptation performance was tested with a 4 Group x 2 Phase (Early, Late) two-way ANOVA  
244 with phase as a repeated-measures. Early adaptation consisted of the mean error across the  
245 first 10 trials (1-10), whereas Late adaptation consisted of the mean error across the last 10  
246 trials (41-50). To provide insight regarding the relative complexity of the SPRING and  
247 ROTATION perturbations, we compared performance of naïve participants performing their  
248 first block under each of these mappings, that is Group 1 under SPRING vs. Group 2 under  
249 ROTATION. This was done using a 2 Group x 2 Phase (Early, Late) two-way ANOVA with  
250 phase as a repeated-measures. Finally, to address the possibility of anterograde interference  
251 between ROTATION and SPRING, we compared the performance of participants in each  
252 mapping depending on whether or not learning was immediately preceded by prior exposure  
253 to the other mapping. Namely, we pooled the data of Groups 1 and 3 (in which ROTATION  
254 was immediately preceded by SPRING) as well as those of Groups 2 and 4 (in which  
255 SPRING was immediately preceded by ROTATION) and performed a 2 Order (First vs.  
256 Second) x 2 Phase (Early vs. Late) two-way ANOVA with phase as a repeated measure. This  
257 analysis was done separately for SPRING and ROTATION.

258 Whenever relevant, post-hoc tests were done with two-tailed unpaired t-tests and the  
259 Benjamini-Hochberg procedure [i.e., false discovery rate (FDR); (Benjamini and Hochberg  
260 1995)] was used to correct for multiple comparisons. For ANOVAs, effect sizes are reported  
261 as partial eta squared ( $\eta_p^2$ ; Fritz et al. 2012; Lakens 2013), whereas for targeted comparisons  
262 (i.e., t-tests), effect sizes are reported as Cohen's d. For all analyses, the threshold for  
263 significance was set to  $\alpha = 0.05$ .

264

## 265 **RESULTS**

### 266 ***Baseline tracking***

267 During the first block all participants performed the tracking task under the NORMAL  
268 mapping. The two-way ANOVA (Group by Trial) revealed no systematic difference in  
269 tracking performance between the groups ( $F_{(3,79)} = 0.512, p = 0.675, \eta_p^2 = 0.019$ ). Averaged  
270 across groups, mean hand tracking error during baseline trials was 1.68cm. There was a main  
271 effect of Trial ( $F_{(9,711)} = 5.307, p < 0.001, \eta_p^2 = 0.06$ ) revealing a decrease in tracking error,  
272 however this improvement was similar across groups as revealed by a lack of Group x Trial  
273 interaction ( $F_{(27,711)} = 0.611, p = 0.941, \eta_p^2 = 0.02$ ). Post-hoc analysis of the Trial effect  
274 revealed that while there was a significant decrease in tracking error from trial 1 to 3 ( $p <$   
275  $0.05$ ), there was no significant difference between any of the trials from 3 to 10 (all  $p > 0.22$ ).  
276 This capacity to achieve asymptotic performance after only two trials suggests that  
277 participants were adept at the task and that meta-learning (or mere practice with the tracking  
278 task) is unlikely to account for the learning curves during exposure to perturbations.

279

### 280 ***Adaptation to the SPRING mapping***

281 Figure 3a compares the time course of tracking error for each of the 4 groups under the  
282 SPRING mapping. The two-way ANOVA revealed a main effect of phase ( $F_{(1,79)} = 402.772,$

283  $p < 0.001$ ,  $n_p^2 = 0.836$ ), with a decrease in tracking error as a function of exposure. There was  
284 also a main effect of Group ( $F_{(3,79)} = 3.001$ ,  $p = 0.035$ ,  $n_p^2 = 0.102$ ), as well as a significant  
285 interaction ( $F_{(3,79)} = 10.996$ ,  $p < 0.001$ ,  $n_p^2 = 0.295$ ). Specifically, post-hoc tests revealed that  
286 during Early adaptation, hand tracking error in Group 3 was significantly smaller than in  
287 Groups 1 ( $t_{(39)} = 2.401$ ,  $p = 0.021$ , Cohen's  $d = 0.77$ ), 2 ( $t_{(40)} = 5.317$ ,  $p < 0.001$ , Cohen's  $d =$   
288 1.65) and 4 ( $t_{(40)} = 3.347$ ,  $p = 0.002$ , Cohen's  $d = 1.05$ ; see Figure 3b). Based on these  
289 observations we conclude that Group 3 who experienced the SPRING immediately after the  
290 SPROT mapping is the only group that demonstrated an advantage when adapting to  
291 SPRING. As for Late adaptation, post-hoc tests revealed no difference across groups (all  
292  $p > 0.5$ ; see Figure 3c). This suggests that, irrespective of the previous exposure to other  
293 mappings, all groups were able to adapt to the SPRING to a similar extent.

294

#### 295 ***Adaptation to the ROTATION mapping***

296 Figure 4a compares the time course of tracking error for each of the 4 groups under the  
297 ROTATION mapping. The two-way ANOVA revealed a main effect of phase ( $F_{(1,79)} =$   
298 507.556,  $p < 0.001$ ,  $n_p^2 = 0.865$ ), with a decrease in tracking error as a function of exposure.  
299 There was no main effect of Group ( $F_{(3,79)} = 2.501$ ,  $p = 0.065$ ,  $n_p^2 = 0.087$ ), but a significant  
300 interaction ( $F_{(3,79)} = 21.991$ ,  $p < 0.001$ ,  $n_p^2 = 0.455$ ). Specifically, post-hoc tests revealed that  
301 during Early adaptation, hand tracking error in Group 4 was smaller than in Groups 1  
302 ( $t_{(39)} = 4.672$ ,  $p < 0.001$ , Cohen's  $d = 1.26$ ), 2 ( $t_{(40)} = 3.650$ ,  $p = 0.001$ , Cohen's  $d = 0.91$ ) and  
303 3 ( $t_{(40)} = 2.457$ ,  $p = 0.017$ , Cohen's  $d = 0.75$ ; see Figure 4b). Based on these observations we  
304 conclude that Group 4 who experienced the ROTATION immediately after the SPROT  
305 mapping, is the only group that demonstrated an advantage when adapting to ROTATION. As  
306 for Late adaptation, post-hoc tests revealed no difference across groups (all  $p > 0.3$ ; see

307 Figure 4c). This suggests that, irrespective of the previous exposure to other mappings, all  
308 groups were able to adapt to the ROTATION to a similar extent.

309

### 310 *Adaptation to the COMBINED (SPROT) mapping*

311 Figure 5a compares the time course of tracking error across groups under the SPROT  
312 mapping, which results from the combination of SPRING and ROTATION. The two-way  
313 ANOVA revealed a main effect of phase ( $F_{(1,79)} = 240.580, p < 0.001, n_p^2 = 0.753$ ), with a  
314 decrease in tracking error as a function of exposure. There was a main effect of Group ( $F_{(3,79)}$   
315  $= 18.652, p < 0.001, n_p^2 = 0.415$ ), as well as a significant interaction ( $F_{(3,79)} = 14.882,$   
316  $p < 0.001, n_p^2 = 0.361$ ). Specifically, post-hoc tests revealed that during Early adaptation, hand  
317 tracking error in Groups 3 and 4 was smaller than in Groups 1 and 2 (all  $p < 0.001$ , all  
318 Cohen's  $d > 1.77$ ; see Figure 5b). Based on these observations we conclude that Groups 1 and  
319 2 who had prior experience with the SPRING and ROTATION mappings demonstrated a  
320 clear advantage for the combined mapping. Moreover, it seems that the order in which the  
321 groups experienced the SPRING and ROTATION mappings was not critical for this  
322 composition effect. This benefit was long-lasting, as revealed by the fact that in Late  
323 adaptation, Groups 1 and 2 still presented significantly smaller errors than Groups 3 and 4 (all  
324  $p < 0.05$ , all Cohen's  $d > 0.70$ ; see Figure 5c).

325

### 326 *Washout of adaptation*

327 At the end of the experimental sessions, all groups performed a washout block in  
328 which the NORMAL mapping was restored unexpectedly. A two-way ANOVA (Group x  
329 Trial) revealed no systematic difference in tracking performance across groups during this  
330 block ( $F_{(3,79)} = 0.239, p = 0.869, n_p^2 = 0.009$ ). However, there was a main effect of Trial  
331 ( $F_{(9,711)} = 93.292, p < 0.001, n_p^2 = 0.541$ ) revealing a decrease in tracking error, as well as a

332 significant Group x Trial interaction ( $F_{(27,711)} = 2.744, p < 0.001, n_p^2 = 0.09$ ). Post-hoc  
333 analysis revealed that this effect originated from the fact that during the first washout trial,  
334 tracking was less impaired in Group 4 (who had experienced SPRING just before washout) as  
335 compared to all three other groups (3.06 vs. 4.26cm;  $p < 0.001$ ) which in the latter case were  
336 not different from each other (all  $p > 0.57$ ). Averaged across groups, mean tracking error  
337 during the last washout trial was 1.99cm, a value significantly greater than during Baseline  
338 ( $p < 0.001$ ). Overall these analyses confirm that, no matter the order of the SPRING,  
339 ROTATION, and SPROT mapping, all groups presented potent and long lasting aftereffects  
340 during the washout block.

341

#### 342 *Comparison between SPRING and ROTATION in naïve participants*

343 To assess the relative complexity in adapting to the SPRING and ROTATION  
344 mappings, Figure 6a represents how naïve groups adapted to each perturbation, that is Group  
345 1 under SPRING was compared to Group 2 under ROTATION. As can be seen, initial  
346 tracking error was larger under the ROTATION mapping than SPRING. The two-way  
347 ANOVA revealed a main effect of phase ( $F_{(1,39)} = 291.679, p < 0.001, n_p^2 = 0.882$ ), with a  
348 decrease in tracking error as a function of exposure for both perturbations. There was a main  
349 effect of Group ( $F_{(1,39)} = 6.400, p = 0.016, n_p^2 = 0.141$ ), as well as a significant interaction  
350 ( $F_{(1,39)} = 48.492, p < 0.001, n_p^2 = 0.554$ ). Specifically, in Early adaptation errors were  
351 approximately 40% higher for ROTATION than for SPRING ( $t_{(39)} = 4.309, p < 0.001$ ,  
352 Cohen's  $d = 0.96$ ; see Figure 6b), however in Late adaptation, tracking performance was  
353 similar under both mappings ( $p = 0.922$ ; see Figure 6c). This suggests that although the  
354 ROTATION mapping was initially more challenging than the SPRING mapping, participants  
355 exhibited similar tracking accuracy at the end of exposure.

356

#### 357 *Anterograde interference between SPRING and ROTATION*

358 To test for anterograde interference between ROTATION and SPRING, we compared  
359 adaptation to each mapping depending on whether or not learning was immediately preceded  
360 by prior exposure to the other mapping. Specifically, data from Groups 1 and 3 (in which  
361 ROTATION was immediately preceded by SPRING) were pooled and compared to those of  
362 Groups 2 and 4 (in which SPRING was immediately preceded by ROTATION) using a 2  
363 Order (First vs. Second) x 2 Phase (Early vs. Late) two-way ANOVA with phase as a  
364 repeated measure.

365 For SPRING (Figure 7a), the ANOVA revealed a main effect of Order ( $F_{(1,81)} = 8.121$ ,  
366  $p < 0.006$ ,  $n_p^2 = 0.091$ ), a main effect of Phase ( $F_{(1,81)} = 316.561$ ,  $p < 0.001$ ,  $n_p^2 = 0.796$ ), and  
367 an interaction ( $F_{(1,81)} = 7.513$ ,  $p < 0.008$ ,  $n_p^2 = 0.085$ ). Specifically, in Early adaptation (Figure  
368 7b), errors were lower when SPRING was done before ROTATION (Groups 1 and 3) as  
369 compared to when SPRING was done after ROTATION (Groups 2 and 4) ( $t_{(81)} = 3.732$ ,  
370  $p < 0.001$ , Cohen's  $d = 0.82$ ). However, the influence of Order was temporary, as there was  
371 no difference in Late adaptation ( $t_{(81)} = 1.480$ ,  $p = 0.143$ , Cohen's  $d = 0.33$ ; see Figure 7c).

372 For ROTATION (Figure 7d), the ANOVA revealed a main effect of Order ( $F_{(1,81)} =$   
373  $4.557$ ,  $p < 0.036$ ,  $n_p^2 = 0.053$ ), a main effect of phase ( $F_{(1,81)} = 213.820$ ,  $p < 0.001$ ,  $n_p^2 =$   
374  $0.725$ ), but no interaction ( $F_{(1,81)} = 0.152$ ,  $p < 0.698$ ,  $n_p^2 = 0.002$ ). Specifically, errors were  
375 lower when ROTATION was done before SPRING (Groups 2 and 4) as compared to when  
376 ROTATION was done after SPRING (Groups 1 and 3), an effect that was present both in  
377 Early and Late adaptation (Figure 7e and 7f). Altogether, although SPRING perturbed  
378 ROTATION for a longer period than ROTATION perturbed SPRING, these data provide  
379 clear evidence of anterograde interference between SPRING and ROTATION, in the sense  
380 that prior exposure to one of these two mappings impaired learning of the other mapping.

381

382 *Additional analyses*



383 *Directional errors*

384 In order to provide further insight regarding composition and decomposition of a  
385 component that is specific to the rotational perturbation, directional errors were assessed.  
386 Figure 8 compares the time course of directional errors for the four groups under the three  
387 mappings. As a first qualitative assessment, it can be seen that directional error is near-zero  
388 and similar across groups during Baseline. As expected, directional errors emerge under  
389 ROTATION and SPROT, that is when a rotational perturbation is applied, but tend to  
390 decrease as a function of adaptation. Interestingly, directional errors change polarity during  
391 SPRING in Groups 2, 3 and 4 (which have had previous exposure to the rotation), suggesting  
392 the presence of carry-over effects. The absence of directional errors in Group 1 upon “naïve”  
393 exposure to SPRING is noteworthy, as it demonstrates that this variable is solely influenced  
394 by the rotation perturbation, but not the spring. Composition is exemplified by the fact that  
395 directional errors are lower under SPROT for Groups 1 and 2 (prior experience with rotation)  
396 as compared to Groups 3 and 4 (no prior experience with rotation). Decomposition is  
397 exemplified by the fact that directional errors tend to be lower under ROTATION for Groups  
398 3 and 4 (prior experience with the rotational perturbation under SPROT) as compared Groups  
399 1 and 2 (no prior experience with the rotational perturbation). Hence, these data argue for  
400 composition and decomposition effects that arise from a component of learning that is specific  
401 to the rotational perturbation.

402 Statistical analyses largely confirmed these qualitative assessments. Specifically, for  
403 Baseline, a two-way ANOVA (Group by Trial) revealed no main effect of Group ( $F_{(3,79)} =$   
404  $0.990, p = 0.402, n_p^2 = 0.036$ ), no main effect of Trial ( $F_{(9,711)} = 1.132, p = 0.337, n_p^2 = 0.01$ )  
405 and no interaction ( $F_{(27,711)} = 0.808, p = 0.744, n_p^2 = 0.03$ ).

406 For SPRING, a 4 Group x 2 Phase (Early, Late) two-way ANOVA with phase as a  
407 repeated-measures revealed a main effect of Phase ( $F_{(1,79)} = 198.840, p < 0.001, n_p^2 = 0.716$ ), a

408 main effect of Group ( $F_{(3,79)} = 20.504, p < 0.001, n_p^2 = 0.438$ ), and an interaction ( $F_{(3,79)} =$   
409  $19.922, p < 0.001, n_p^2 = 0.431$ ). Specifically, post-hoc tests revealed that during Early  
410 adaptation, all groups differed ( $p < 0.01$ ) except Groups 2 and 4 ( $p = 0.926$ ). During Late  
411 adaptation, directional errors were smallest in Group 1, being significantly different from both  
412 Groups 2 and 4 ( $p < 0.01$ ). Directional errors were also significantly smaller in Group 3 than  
413 Group 4 ( $p < 0.05$ ). As mentioned earlier, a notable finding here is the null directional errors  
414 for Group 1, which underwent SPRING without having been previously exposed to the  
415 Rotation in any way. This confirms that that this particular metric is specific to the rotation  
416 perturbation.

417 For ROTATION, the ANOVA revealed a main effect of Phase ( $F_{(1,79)} = 32.232,$   
418  $p < 0.001, n_p^2 = 0.290$ ), no effect of Group ( $F_{(3,79)} = 1.327, p = 0.272, n_p^2 = 0.048$ ), but an  
419 interaction ( $F_{(3,79)} = 3.509, p < 0.05, n_p^2 = 0.118$ ). Specifically, post-hoc tests revealed that  
420 during Early adaptation, Group 4, which was exposed to ROTATION immediately after  
421 SPROT, presented significantly lower directional errors than Group 1 ( $p = 0.027$ ), suggesting  
422 decomposition. There were no significant differences during Late adaptation.

423 Concerning SPROT, the ANOVA revealed a main effect of Phase ( $F_{(1,79)} = 66.902,$   
424  $p < 0.001, n_p^2 = 0.459$ ) and a main effect of Group ( $F_{(3,79)} = 4.704, p < 0.01, n_p^2 = 0.152$ ), but  
425 no interaction ( $F_{(3,79)} = 2.573, p = 0.06, n_p^2 = 0.089$ ). Specifically, post-hoc tests revealed that  
426 directional errors in Groups 1 and 2 (which had been previously exposed to the rotation  
427 perturbation), were significantly lower than in Groups 3 and 4 (all  $p < 0.05$ ). This is a potent  
428 demonstration of composition.

429 Finally, during washout directional error changed polarity with respect to ROTATION  
430 and SPROT, an observation consistent with the presence of aftereffects. The two-way  
431 ANOVA (Group by Trial) revealed a main effect of Group ( $F_{(3,79)} = 5.372, p < 0.01, n_p^2 =$   
432  $0.169$ ), a main effect of Trial ( $F_{(9,711)} = 48.453, p < 0.001, n_p^2 = 0.38$ ) and an interaction

433 ( $F_{(27,711)} = 2.352, p < 0.001, \eta_p^2 = 0.08$ ). Specifically, Group 4 presented significantly less  
434 directional error than all other groups during the first 6 trials (all  $p < 0.05$ ), which is consistent  
435 with the fact that this group was tested immediately after SPRING (rather than SPROT or  
436 ROTATION).

437

### 438 *Cursor velocity*

439 In order to provide further insight regarding composition and decomposition of a  
440 component that is specific to the spring perturbation, cursor velocity was assessed. Figure 9  
441 compares the time course of cursor velocity for the four groups under the three mappings. As  
442 a first qualitative assessment, it can be seen that cursor velocity is similar during Baseline  
443 across groups, and that its value is similar to mean target velocity (16 cm/s). As expected,  
444 cursor velocity increased substantially under initial exposure to the SPRING and SPROT  
445 mappings, consistent with the amplificative effect of the spring dynamics. It should be noted,  
446 however, that this variable was not exclusively modulated by the spring perturbation, as an  
447 increase (albeit smaller) was observed in Group 2 during “naïve” exposure to ROTATION.  
448 Nevertheless, composition is reflected by the fact that cursor velocity was lower during the  
449 first ~5 trials of SPROT for Groups 1 and 2 (prior experience with SPRING) as compared to  
450 Groups 3 and 4 (no prior experience with SPRING). Decomposition is exemplified by the fact  
451 that cursor velocity is lower under SPRING for Groups 3 and 4 (prior experience with the  
452 spring perturbation under SPROT) as compared to Groups 1 and 2 (no prior experience with  
453 the spring perturbation). Hence, these data argue for composition and decomposition effects  
454 that arise from a component of learning that is predominantly influenced by the spring  
455 perturbation.

456 Statistical analyses largely confirmed these qualitative assessments. Specifically, for  
457 Baseline, a two-way ANOVA (Group by Trial) revealed no main effect of Group ( $F_{(3,79)} =$

458 0.798,  $p = 0.499$ ,  $n_p^2 = 0.029$ ), no interaction ( $F_{(27,711)} = 1.051$ ,  $p = 0.395$ ,  $n_p^2 = 0.038$ ), but a  
459 main effect of Trial ( $F_{(9,711)} = 2.881$ ,  $p = 0.002$ ,  $n_p^2 = 0.035$ ), revealing that all groups slightly  
460 reduced their cursor velocity over the first 4 trials.

461 For SPRING, a 4 Group x 2 Phase (Early, Late) two-way ANOVA with phase as a  
462 repeated-measures revealed a main effect of Phase ( $F_{(1,79)} = 120.303$ ,  $p < 0.001$ ,  $n_p^2 = 0.604$ ), a  
463 main effect of Group ( $F_{(3,79)} = 11.722$ ,  $p < 0.001$ ,  $n_p^2 = 0.308$ ), and an interaction ( $F_{(3,79)} =$   
464  $10.890$ ,  $p < 0.001$ ,  $n_p^2 = 0.293$ ). Specifically, post-hoc tests revealed that during Early  
465 adaptation, cursor velocity in Groups 3 and 4 was significantly lower than for Groups 1 and 2  
466 (all  $p < 0.01$ ). During Late adaptation, cursor velocity in Group 3 was significantly lower than  
467 for Groups 1 and 2 (both  $p < 0.05$ ), while it was also significantly lower for Group 4 than for  
468 Group 2 ( $p < 0.05$ ). These data reflect decomposition since Groups 3 and 4, which were  
469 exposed to the spring perturbation during SPROT and thus learned to reduce cursor velocity,  
470 carried this effect over to the SPRING condition.

471 For ROTATION, the ANOVA revealed a main effect of Phase ( $F_{(1,79)} = 4.760$ ,  
472  $p < 0.05$ ,  $n_p^2 = 0.057$ ), a main effect of Group ( $F_{(3,79)} = 11.963$ ,  $p < 0.001$ ,  $n_p^2 = 0.312$ ), and an  
473 interaction ( $F_{(3,79)} = 14.291$ ,  $p < 0.001$ ,  $n_p^2 = 0.352$ ). Specifically, post-hoc tests revealed that  
474 during Early adaptation, Group 1 significantly differed from Groups 2 and 3 (both  $p < 0.01$ ),  
475 while Group 2 significantly differed from all other Groups (all  $p < 0.01$ ). During Late  
476 adaptation, Groups 1 and 2 differed from Group 3 (both  $p < 0.05$ ). Here again, the fact that  
477 cursor velocity for Groups 1, 3 and 4 was lower than for “naïve” Group 2 during early  
478 ROTATION (sometimes below baseline levels), suggests the presence of carry-over effects  
479 resulting from prior exposure to the spring perturbation.

480 Concerning SPROT, the ANOVA revealed a main effect of Phase ( $F_{(1,79)} = 102.703$ ,  
481  $p < 0.001$ ,  $n_p^2 = 0.565$ ) no effect of Group ( $F_{(3,79)} = 0.080$ ,  $p = 0.971$ ,  $n_p^2 = 0.003$ ), and a  
482 significant interaction ( $F_{(3,79)} = 5.649$ ,  $p < 0.001$ ,  $n_p^2 = 0.177$ ). Although cursor velocity was

483 lower for Groups 1 and 2 as compared to Groups 3 and 4 during the first ~5 trials of SPROT,  
484 suggesting composition, this effect did not reach statistical significance when considering our  
485 operational definition of Early adaptation (trials 1-10) (all  $p > 0.2$ ). As for Late adaptation,  
486 there was a tendency for cursor velocity to differ between Groups 1 and 2 vs. Group 3, but it  
487 did not reach significant levels (both  $p > 0.07$ ).

488 Finally, during washout cursor velocity was below baseline levels, which is indicative  
489 of aftereffects. The ANOVA revealed no main effect of Group ( $F_{(3,79)} = 2.353$ ,  $p = 0.078$ ,  $n_p^2 =$   
490  $0.082$ ), but a significant main effect of Trial ( $F_{(9,711)} = 17.952$ ,  $p < 0.001$ ,  $n_p^2 = 0.185$ ) and an  
491 interaction ( $F_{(27,711)} = 2.365$ ,  $p < 0.001$ ,  $n_p^2 = 0.082$ ). Specifically, Group 3 presented  
492 significantly less aftereffects than all other groups during the first 4 trials (all  $p < 0.05$ ), which  
493 is consistent with the fact that this group was tested immediately after ROTATION (rather  
494 than SPRING or SPROT).

495

## 496 **DISCUSSION**

497 The main objective of this study was to investigate interference effects as well as  
498 modularity of sensorimotor adaptation in manual tracking under two separate visual  
499 perturbations (SPRING and ROTATION) and their combination (SPROT). First, evidence for  
500 anterograde interference was found whenever participants switched from SPRING to  
501 ROTATION, and vice versa. Second, evidence for modularity was found both in terms of  
502 composition and decomposition. Indeed, irrespective of the order of presentation, prior  
503 exposure to each single mapping clearly benefited to learning the combined mapping.  
504 Conversely, prior exposure to the combined mapping facilitated learning of the single  
505 mapping that immediately followed. More fine-grained analyses revealed that the composition  
506 and decomposition effects were attributable to components of learning that were specifically  
507 acquired through exposure to either the rotational perturbation (i.e., directional error) or the

508 spring perturbation (i.e., cursor velocity), excluding the possibility that these effects be solely  
509 due to task-irrelevant improvements in motor acuity or meta-learning (Braun et al. 2009;  
510 Turnham et al. 2012). Together, these results demonstrate that even though two perturbations  
511 interfere with each other, they can still be composed and decomposed advantageously.

512

### 513 *Interference between SPRING and ROTATION*

514 Our results provide evidence for anterograde interference, in that exposure to either  
515 one of the single mappings (SPRING or ROTATION) impaired subsequent learning of the  
516 other single mapping (see Figure 7). While it is likely that interference arose from a  
517 combination of the previously identified factors (i.e., same sensory modality of the errors,  
518 partially shared state variables, common task goal and context), it suggests that shared neural  
519 populations (or at least neural populations whose dynamics occupy a shared subspace;  
520 Duncker et al. 2020) were involved in adapting to the SPRING and ROTATION mappings.  
521 Nonetheless, as will be discussed in the next sections, interference did not preclude  
522 participants' capacity to compose or decompose these novel sensorimotor representations. In  
523 that sense our results extend the findings of Flanagan et al. (1999) who found evidence for  
524 modularity in the context of force field and visuomotor adaptation (two “orthogonal”  
525 perturbations), in absence of direct evidence of interference between the two. Thanks to our  
526 additional analyses of directional error and cursor velocity (Figures 8 and 9), it could be  
527 confirmed that the interference effects found at the task level (i.e., hand tracking error, see  
528 Figure 7) specifically resulted from carry-over effects inherent to each perturbation. Indeed,  
529 following exposure to the ROTATION and SPROT mappings, participants exhibited a  
530 negative directional bias in cursor motion, which likely accounted for the impairment in  
531 tracking performance under SPRING (and Washout). Similarly, following the SPRING and  
532 SPROT mappings, participants tended to unnecessarily slow down their cursor motion, an

533 effect again likely to have altered tracking performance under ROTATION (and Washout).  
534 Altogether, although anterograde interference is expected when sequentially adapting to  
535 opposite visuomotor rotations (Krakauer et al. 2005; Miall et al. 2004; Wigmore et al. 2002),  
536 we show here that carry-over effects along different dimensions of hand behavior (direction  
537 vs. velocity) can also lead to interference at the task level.

538 No matter their origin, interference effects in our task were not symmetrical, as prior  
539 exposure to the SPRING mapping seems to have had a more detrimental effect on learning of  
540 the ROTATION mapping than the contrary. Indeed, the interference effect from SPRING to  
541 ROTATION was present both in early and late adaptation, whereas the interference effect  
542 from ROTATION to SPRING was only present in early adaptation. This asymmetry may  
543 result from differences in the complexity of the two perturbations, as suggested by distinct  
544 time course of tracking error in naïve participants. Indeed, as shown in Figure 6, the SPRING  
545 mapping appeared less challenging than ROTATION, with lower initial tracking errors and  
546 fewer trials needed to reach asymptotic levels of performance. Given that asymptotic  
547 performance has been shown to initiate consolidation processes and promote anterograde  
548 interference (Leow et al. 2013; Shibata et al. 2017), the more extensive period at asymptote  
549 for SPRING may have led to its stabilization, and ultimately to greater impairment to  
550 ROTATION than the contrary. A second possibility may stem from differences in the state  
551 variables being influenced by each mapping, with ROTATION and SPRING relying on a  
552 common state variable (i.e., position), but SPRING depending upon additional variables (i.e.,  
553 velocity and acceleration). It may be that SPRING had a greater impact on ROTATION  
554 because it interfered with its unique state variable, conversely ROTATION interfered less on  
555 SPRING because many more state variables were involved.

556

557 *Composition and decomposition of visuomotor adaptation*

558 Irrespective of the order of exposure to the SPRING and ROTATION mappings,  
559 participants of Groups 1 and 2 exhibited a strong and reliable advantage for learning the  
560 combined mapping as compared to naïve participants of Groups 3 and 4 (see Figure 5). Not  
561 only was this advantage observed during early exposure, but it persisted throughout the entire  
562 adaptation session. Evidence for composition supports the idea that even though the two  
563 perturbations may have involved partially overlapping neural substrates (thus causing  
564 interference), they were somehow combined advantageously when facing the SPROT  
565 mapping.

566 In addition, following adaptation to the combined mapping, participants of Groups 3  
567 and 4 exhibited an advantage when subsequently tested in either one of the single mappings  
568 (see Figures 3 and 4). This decomposition effect indicates that the SPROT mapping was not  
569 learned as a third entity independent from each single mapping. In contrast, it suggests that  
570 during SPROT the sensorimotor system was seemingly able to pick out error signals  
571 associated with each of the single mappings even though they were superimposed, perhaps  
572 due to the fact that they influenced partly different state variables. Nonetheless, it should be  
573 noted that this effect occurred completely outside of participants' capacity to identify the  
574 perturbations, as none of them was able to report that two mappings were superimposed, let  
575 alone what their underlying nature was. Although these verbal reports do not formally rule out  
576 the use of explicit strategies, they still suggest that cognitive processes, such as re-aiming,  
577 played a negligible role in the gradual improvement in performance observed here. Rather,  
578 they point to the possibility that adaptation was due to the implicit update of an internal  
579 model. This is further supported by the potent and long-lasting aftereffects for each  
580 perturbation during washout, which are generally ascribed to implicit adaptation. Importantly,  
581 these aftereffects were not only observed for tracking error, but also for directional error and  
582 cursor velocity, which respectively pertained to the ROTATION and SPRING mappings. The



583 rotational aftereffects are notable since large perturbations such as the one used here (90°  
584 visuomotor rotation) have been suggested to be mediated to a large extent by strategic/explicit  
585 processes, at least in reaching tasks (Bond and Taylor 2015). Note that even in the case of  
586 reaching movements, the use of stringent (i.e., low) reaction time constraints prevents the  
587 expression of the strategic/explicit component (Leow et al. 2017). This latter observation  
588 echoes with our pursuit tracking task in which participants had to constantly keep track of the  
589 target and update their cursor position, rendering the use of cognitive strategizing and re-  
590 aiming unlikely given that they are time-consuming processes (Fernandez-Ruiz et al. 2011;  
591 Haith et al. 2015; Leow et al. 2017; McDougle and Taylor 2019). In direct support of our  
592 interpretation, recent work has shown that during manual tracking, rotational perturbations of  
593 90° lead to potent directional aftereffects (unlike for a mirror-reversal perturbation), leading  
594 the authors to suggest that it was subtended by genuine adaptive mechanisms rather than de  
595 novo learning (Yang et al. 2020).

596 To some extent, the SPROT mapping can be conceived as a 90° visuomotor rotation  
597 with added noise, given the non-linear hand-cursor spatial relationship incurred by the  
598 SPRING perturbation. In that light, the decomposition effect observed for ROTATION  
599 indicates that despite this increase in noise, participants could reliably extract error signals  
600 specifically pertaining to the visuomotor rotation. This observation is reminiscent of a study  
601 showing that participants could adapt their reaching movements to a visuomotor rotation even  
602 when combined with a 200 ms visual delay (Honda et al. 2012). Moreover, as in our case, that  
603 study revealed that adaptation to the combined perturbation was facilitated by prior exposure  
604 to the visual delay (hence a form of composition). However, that study did not investigate  
605 decomposition of the combined perturbation into each of the two perturbations.

606 An interesting finding is that the decomposition effect was clear for the single  
607 mapping that immediately followed exposure to SPROT but did not extend to the subsequent

608 single mapping. Two non-exclusive reasons may account for this. First, this may have  
609 resulted from two simultaneous effects, namely the enhanced tracking performance in the  
610 individual mappings due to prior practice with the combined perturbation (i.e.,  
611 decomposition), along with anterograde interference. Indeed, given the observed anterograde  
612 interference between SPRING and ROTATION, it is likely that extraction of one of the single  
613 mappings following SPROT counteracted the subsequent extraction of the other single  
614 mapping. Second, as time elapsed, the memory of the combined mapping may have gradually  
615 decayed, favoring the extraction of the first single mapping as compared to the second one.  
616 Future experiments will be needed to clarify the respective contribution of these two  
617 mechanisms.

618 Finally, we observed an asymmetry in the relative strength of the composition and  
619 decomposition effects, with decomposition being more fragile than composition. This effect  
620 may stem from the fact that decomposing a mapping is presumably more complex (from a  
621 computational perspective) than composing two mappings. Indeed although SPROT can  
622 theoretically be decomposable into an infinite set of mappings, combining ROTATION and  
623 SPRING can only lead to a single deterministic outcome. This issue (i.e., inverse problem)  
624 has already been raised in the context of forward/inverse models in conjunction with modular  
625 learning (Miall 2002; Wolpert and Kawato 1998).

626

### 627 *Modularity in continuous and discrete actions*

628 It has been suggested that “the differentiation between discrete and continuous  
629 movements is one of the pillars of motor behavior classification” (Huys et al. 2008). Although  
630 modularity of adaptation was initially uncovered through reaching (Flanagan et al. 1999), a  
631 discrete movement, here we show that manual tracking, a continuous movement, is also prone  
632 to composition and decomposition effects. The extent to which discrete and continuous

633 movements are distinct is a subject of heated debate (Cohen et al. 2019; Howard et al. 2011;  
634 Huys et al. 2008; Ikegami et al. 2010; Schaal et al. 2004; Sternad and Schaal 1999; Yang et al.  
635 2020; Yoo et al. 2021a). On the one hand, continuous and discrete movements are thought to  
636 belong to different movement categories because they seem to rely on different control  
637 processes (Huys et al. 2008; Sternad and Schaal 1999; Yang et al. 2020), as well as neural  
638 structures (Hatsopoulos et al. 2004; Schaal et al. 2004). On the other hand, continuous  
639 movements are sometimes considered as a mere concatenation of discrete actions (Miall et al.  
640 1993; Zimmnik and Churchland 2021), or similarly discrete movements are seen as truncated  
641 continuous movements (Hogan and Sternad 2007). With regard to pointing and tracking  
642 movements, we believe that a key difference lies in how planning and execution processes  
643 operate. During fast pointing movements, planning is essentially performed before hand  
644 movement starts, so that planning and execution operate sequentially. In contrast during  
645 pursuit tracking, planning has to operate while the hand is already moving, so that planning  
646 and execution must operate in concert. Although the current dataset certainly does not settle  
647 the discrete/continuous debate, it suggests that, despite potential key differences between  
648 pointing and tracking movements, both types of movement seem to follow the same general  
649 principles with respect to the modularity of sensorimotor adaptation.

650

### 651 *Concluding comments*

652 To summarize, the present study shows that interference effects can coexist with the  
653 ability to compose/decompose two visuomotor mappings that partially share the same state  
654 variables, and for which the task goals and context are the same. This indicates that the brain  
655 is not only able to flexibly combine multiple visuomotor mappings but is also able to partition  
656 sources of error when dealing with complex visuomotor mappings, allowing participants to  
657 cope efficiently with a fraction of this mapping. More generally this study reinforces the view

658 that modularity is ubiquitous in neuroscience (d'Avella et al. 2015), ranging from cognitive  
659 (Barrett and Kurzban 2006; Coltheart 1999) to sensorimotor processes (d'Avella 2016;  
660 Duncker et al. 2020; Flanagan et al. 1999; Lemke et al. 2019), which in the latter case seems  
661 to encompass both discrete and continuous actions. Finally, we hope that, in addition to its  
662 ecological relevance (Land 1992; Wardill et al. 2017; Yoo et al. 2021b), this study further  
663 demonstrates the relevance of pursuit tracking to address key issues in sensorimotor control  
664 and learning (Engel and Soechting 2000; Mathew et al. 2018; Miall et al. 2001; Yang et al.  
665 2020; Yoo et al. 2021a).

666

667 **BIBLIOGRAPHY**

- 668 **d’Avella A.** Modularity for Motor Control and Motor Learning. In: *Progress in Motor*  
669 *Control: Theories and Translations*, edited by Laczko J, Latash ML. Springer International  
670 Publishing, p. 3–19.
- 671 **d’Avella A, Giese M, Ivanenko YP, Schack T, Flash T.** Editorial: Modularity in motor  
672 control: from muscle synergies to cognitive action representation. *Front Comput Neurosci* 9,  
673 2015.
- 674 **Barrett HC, Kurzban R.** Modularity in cognition: framing the debate. *Psychol Rev* 113: 628,  
675 2006.
- 676 **Benjamini Y, Hochberg Y.** Controlling the False Discovery Rate: A Practical and Powerful  
677 Approach to Multiple Testing. *J R Stat Soc Ser B Methodol* 57: 289–300, 1995.
- 678 **Bond KM, Taylor JA.** Flexible explicit but rigid implicit learning in a visuomotor  
679 adaptation task. *J Neurophysiol* 113: 3836–3849, 2015.
- 680 **Braun DA, Aertsen A, Wolpert DM, Mehring C.** Motor task variation induces structural  
681 learning. *Curr Biol CB* 19: 352–357, 2009.
- 682 **Burgos PI, Mariman JJ, Makeig S, Rivera-Lillo G, Maldonado PE.** Visuomotor  
683 coordination and cortical connectivity of modular motor learning. *Hum Brain Mapp* 39:  
684 3836–3853, 2018.
- 685 **Cohen EJ, Wei K, Minciocchi D.** Visuomotor perturbation in a continuous circle tracing  
686 task: novel approach for quantifying motor adaptation. *Sci Rep* 9: 18679, 2019.
- 687 **Coltheart M.** Modularity and cognition. *Trends Cogn Sci* 3: 115–120, 1999.
- 688 **Danion F, Diamond JS, Flanagan JR.** The role of haptic feedback when manipulating  
689 nonrigid objects. *J Neurophysiol* 107: 433–441, 2012.
- 690 **Danion F, Mathew J, Flanagan JR.** Eye Tracking of Occluded Self-Moved Targets: role of  
691 Haptic Feedback and Hand-Target Dynamics [Online]. *eNeuro* ,  
692 2017<http://www.eneuro.org/content/early/2017/06/26/ENEURO.0101-17.2017> [5 Jul. 2017].
- 693 **Danion FR, Flanagan JR.** Different gaze strategies during eye versus hand tracking of a  
694 moving target. *Sci Rep* 8: 10059, 2018.
- 695 **Davidson PR, Wolpert DM.** Internal models underlying grasp can be additively combined.  
696 *Exp Brain Res Exp Hirnforsch Expérimentation Cérébrale* 155: 334–340, 2004.
- 697 **Dingwell JB, Mah CD, Mussa-Ivaldi FA.** Manipulating objects with internal degrees of  
698 freedom: evidence for model-based control. *J Neurophysiol* 88: 222–235, 2002.
- 699 **Dingwell JB, Mah CD, Mussa-Ivaldi FA.** Experimentally confirmed mathematical model  
700 for human control of a non-rigid object. *J Neurophysiol* 91: 1158–1170, 2004.

- 701 **Duncker L, Driscoll L, Shenoy KV, Sahani M, Sussillo D.** Organizing recurrent network  
702 dynamics by task-computation to enable continual learning. *Adv Neural Inf Process Syst* 33,  
703 2020.
- 704 **Engel KC, Soechting JF.** Manual tracking in two dimensions. *J Neurophysiol* 83: 3483–  
705 3496, 2000.
- 706 **Fernandez-Ruiz J, Wong W, Armstrong IT, Flanagan JR.** Relation between reaction time  
707 and reach errors during visuomotor adaptation. *Behav Brain Res* 219: 8–14, 2011.
- 708 **Flanagan JR, Nakano E, Imamizu H, Osu R, Yoshioka T, Kawato M.** Composition and  
709 decomposition of internal models in motor learning under altered kinematic and dynamic  
710 environments. *J Neurosci* 19: RC34, 1999.
- 711 **Fritz CO, Morris PE, Richler JJ.** Effect size estimates: current use, calculations, and  
712 interpretation. *J Exp Psychol Gen* 141: 2, 2012.
- 713 **Gouirand N, Mathew J, Brenner E, Danion F.** Eye movements do not play an important  
714 role in the adaptation of hand tracking to a visuomotor rotation. *J Neurophysiol* , 2019.  
715 doi:10.1152/jn.00814.2018.
- 716 **Haith AM, Huberdeau DM, Krakauer JW.** The Influence of Movement Preparation Time  
717 on the Expression of Visuomotor Learning and Savings. *J Neurosci* 35: 5109–5117, 2015.
- 718 **Haruno M, Wolpert DM, Kawato M.** Mosaic model for sensorimotor learning and control.  
719 *Neural Comput* 13: 2201–2220, 2001.
- 720 **Hatsopoulos N, Joshi J, O’Leary JG.** Decoding Continuous and Discrete Motor Behaviors  
721 Using Motor and Premotor Cortical Ensembles. *J Neurophysiol* 92: 1165–1174, 2004.
- 722 **Hogan N, Sternad D.** On rhythmic and discrete movements: reflections, definitions and  
723 implications for motor control. *Exp Brain Res Exp Hirnforsch Expérimentation Cérébrale*  
724 181: 13–30, 2007.
- 725 **Honda T, Hirashima M, Nozaki D.** Adaptation to visual feedback delay influences  
726 visuomotor learning. *PLoS One* 7: e37900, 2012.
- 727 **Howard IS, Ingram JN, Franklin DW, Wolpert DM.** Gone in 0.6 Seconds: The Encoding  
728 of Motor Memories Depends on Recent Sensorimotor States. *J Neurosci* 32: 12756–12768,  
729 2012.
- 730 **Howard IS, Ingram JN, Wolpert DM.** Separate representations of dynamics in rhythmic  
731 and discrete movements: evidence from motor learning. *J Neurophysiol* 105: 1722–1731,  
732 2011.
- 733 **Huang FC, Gillespie RB, Kuo AD.** Visual and haptic feedback contribute to tuning and  
734 online control during object manipulation. *J Mot Behav* 39: 179–193, 2007.
- 735 **Huys R, Studenka BE, Rheaume NL, Zelaznik HN, Jirsa VK.** Distinct timing mechanisms  
736 produce discrete and continuous movements. *PLoS Comput Biol* 4: e1000061, 2008.

- 737 **Ikegami T, Hirashima M, Taga G, Nozaki D.** Asymmetric transfer of visuomotor learning  
738 between discrete and rhythmic movements. *J Neurosci Off J Soc Neurosci* 30: 4515–4521,  
739 2010.
- 740 **Imamizu H, Higuchi S, Toda A, Kawato M.** Reorganization of brain activity for multiple  
741 internal models after short but intensive training. *Cortex J Devoted Study Nerv Syst Behav* 43:  
742 338–349, 2007.
- 743 **Krakauer JW, Ghez C, Ghilardi MF.** Adaptation to visuomotor transformations:  
744 consolidation, interference, and forgetting. *J Neurosci Off J Soc Neurosci* 25: 473–478, 2005.
- 745 **Krakauer JW, Ghilardi MF, Ghez C.** Independent learning of internal models for kinematic  
746 and dynamic control of reaching. *Nat Neurosci* 2: 1026–1031, 1999.
- 747 **Krakauer JW, Hadjiosif AM, Xu J, Wong AL, Haith AM.** Motor Learning. *Compr*  
748 *Physiol* 9: 613–663, 2019.
- 749 **Lakens D.** Calculating and reporting effect sizes to facilitate cumulative science: a practical  
750 primer for t-tests and ANOVAs. *Front Psychol* 4, 2013.
- 751 **Land MF.** Visual tracking and pursuit: Humans and arthropods compared. *J Insect Physiol*  
752 38: 939–951, 1992.
- 753 **Landelle C, Montagnini A, Madelain L, Danion F.** Eye tracking a self-moved target with  
754 complex hand-target dynamics. *J Neurophysiol* 116: 1859–1870, 2016.
- 755 **Lemke SM, Ramanathan DS, Guo L, Won SJ, Ganguly K.** Emergent modular neural  
756 control drives coordinated motor actions. *Nat Neurosci* 22: 1122, 2019.
- 757 **Leow L-A, Gunn R, Marinovic W, Carroll TJ.** Estimating the implicit component of  
758 visuomotor rotation learning by constraining movement preparation time. *J Neurophysiol* 118:  
759 666–676, 2017.
- 760 **Leow L-A, de Ruyg A, Loftus AM, Hammond G.** Different mechanisms contributing to  
761 savings and anterograde interference are impaired in Parkinson’s disease. *Front Hum*  
762 *Neurosci* 7, 2013.
- 763 **Lerner G, Albert S, Caffaro PA, Villalta JI, Jacobacci F, Shadmehr R, Della-Maggiore**  
764 **V.** The Origins of Anterograde Interference in Visuomotor Adaptation. *Cereb Cortex* 30:  
765 4000–4010, 2020.
- 766 **Mathew J, Bernier P-M, Danion FR.** Asymmetrical Relationship between Prediction and  
767 Control during Visuomotor Adaptation. *eNeuro* 5, 2018.
- 768 **Mathew J, Flanagan JR, Danion FR.** Gaze behavior during visuomotor tracking with  
769 complex hand-cursor dynamics. *J Vis* 19: 24–24, 2019a.
- 770 **Mathew J, Sarlegna FR, Bernier P-M, Danion FR.** Handedness Matters for Motor Control  
771 But Not for Prediction. *eNeuro* 6, 2019b.
- 772 **McDougle SD, Taylor JA.** Dissociable cognitive strategies for sensorimotor learning. *Nat*  
773 *Commun* 10: 40, 2019.

- 774 **Miall C.** Modular motor learning. *Trends Cogn Sci* 6: 1–3, 2002.
- 775 **Miall RC, Jenkinson N, Kulkarni K.** Adaptation to rotated visual feedback: a re-  
776 examination of motor interference. *Exp Brain Res* 154: 201–210, 2004.
- 777 **Miall RC, Reckess GZ, Imamizu H.** The cerebellum coordinates eye and hand tracking  
778 movements. *Nat Neurosci* 4: 638–644, 2001.
- 779 **Miall RC, Weir DJ, Stein JF.** Intermittency in human manual tracking tasks. *J Mot Behav*  
780 25: 53–63, 1993.
- 781 **Mrotek LA, Soechting JF.** Target interception: hand-eye coordination and strategies. *J*  
782 *Neurosci* 27: 7297–7309, 2007.
- 783 **Nagengast AJ, Braun DA, Wolpert DM.** Optimal control predicts human performance on  
784 objects with internal degrees of freedom. *PLoS Comput Biol* 5: e1000419, 2009.
- 785 **Nagengast AJ, Braun DA, Wolpert DM.** Risk-sensitive optimal feedback control accounts  
786 for sensorimotor behavior under uncertainty. *PLoS Comput Biol* 6: e1000857, 2010.
- 787 **Ogawa K, Imamizu H.** Human sensorimotor cortex represents conflicting visuomotor  
788 mappings. *J Neurosci* 33: 6412–6422, 2013.
- 789 **Pearson TS, Krakauer JW, Mazzoni P.** Learning not to generalize: modular adaptation of  
790 visuomotor gain. *J Neurophysiol* 103: 2938–2952, 2010.
- 791 **Schaal S, Sternad D, Osu R, Kawato M.** Rhythmic arm movement is not discrete. *Nat*  
792 *Neurosci* 7: 1136–1143, 2004.
- 793 **Sheahan HR, Franklin DW, Wolpert DM.** Motor Planning, Not Execution, Separates  
794 Motor Memories. *Neuron* 92: 773–779, 2016.
- 795 **Shibata K, Sasaki Y, Bang JW, Walsh EG, Machizawa MG, Tamaki M, Chang L-H,**  
796 **Watanabe T.** Overlearning hyperstabilizes a skill by rapidly making neurochemical  
797 processing inhibitory-dominant. *Nat Neurosci* 20: 470–475, 2017.
- 798 **Soechting JF, Rao HM, Juveli JZ.** Incorporating prediction in models for two-dimensional  
799 smooth pursuit. *PloS One* 5: e12574, 2010.
- 800 **Sternad D, Schaal S.** Segmentation of endpoint trajectories does not imply segmented  
801 control. *Exp Brain Res Exp Hirnforsch Expérimentation Cérébrale* 124: 118–136, 1999.
- 802 **Tong C, Wolpert DM, Flanagan JR.** Kinematics and dynamics are not represented  
803 independently in motor working memory: evidence from an interference study. *J Neurosci Off*  
804 *J Soc Neurosci* 22: 1108–1113, 2002.
- 805 **Turnham EJA, Braun DA, Wolpert DM.** Facilitation of learning induced by both random  
806 and gradual visuomotor task variation. *J Neurophysiol* 107: 1111–1122, 2012.
- 807 **Wardill TJ, Fabian ST, Pettigrew AC, Stavenga DG, Nordström K, Gonzalez-Bellido**  
808 **PT.** A Novel Interception Strategy in a Miniature Robber Fly with Extreme Visual Acuity.  
809 *Curr Biol CB* 27: 854–859, 2017.



810 **Wigmore V, Tong C, Flanagan JR.** Visuomotor rotations of varying size and direction  
811 compete for a single internal model in motor working memory. *J Exp Psychol Hum Percept*  
812 *Perform* 28: 447–457, 2002.

813 **Wolpert DM, Kawato M.** Multiple paired forward and inverse models for motor control.  
814 *Neural Netw* 11: 1317–1329, 1998.

815 **Yang C, Cowan N, Haith A.** De novo learning versus adaptation of continuous control in a  
816 manual tracking task [Online]. *bioRxiv*  
817 2020. <https://www.biorxiv.org/content/10.1101/2020.01.15.906545v1> [12 Jun. 2020].

818 **Yoo SBM, Hayden BY, Pearson JM.** Continuous decisions. *Philos Trans R Soc B Biol Sci*  
819 376: 20190664, 2021a.

820 **Yoo SBM, Tu JC, Hayden BY.** Multicentric tracking of multiple agents by anterior cingulate  
821 cortex during pursuit and evasion. *Nat Commun* 12: 1985, 2021b.

822 **Zimnik AJ, Churchland MM.** Independent generation of sequence elements by motor  
823 cortex. *Nat Neurosci* 24: 412–424, 2021.

824

825 **FIGURE CAPTIONS**

826 **Figure 1.** *A. Overhead view of the experimental setup. B. Example trajectory of a moving*  
827 *target as well as a hand cursor on the screen. Note that the white trajectory was not presented*  
828 *to participants. C. The five target trajectories employed for pursuit tracking. The blue dot*  
829 *shows the position of the target at the trial start, and the arrow shows its direction (see*  
830 *methods for more details).*

831  
832 **Figure 2.** *Experimental design. Each box represents one block, along with the number of*  
833 *trials in each block.*

834  
835 **Figure 3.** *Tracking error under the SPRING mapping. A. Time course of tracking error as a*  
836 *function of trial and experimental group. B. Comparison of tracking error during early*  
837 *exposure (mean of first 10 trials) across groups. C. Same as B for tracking error during late*  
838 *exposure (mean of last 10 trials). Black dots indicate individual participants, and error bars*  
839 *correspond to SEM. Asterisks indicate significant differences ( $p < 0.05$ ). Note the lower*  
840 *initial tracking error in Group 3 who was exposed to the SPRING mapping immediately after*  
841 *the SPROT mapping.*

842  
843 **Figure 4.** *Tracking error under the ROTATION mapping. A. Time course of tracking error as*  
844 *a function of trial and experimental group. B. Comparison of tracking error during early*  
845 *exposure (mean of first 10 trials) across groups. C. Same as B for tracking error during late*  
846 *exposure (mean of last 10 trials). Black dots indicate individual participants, and error bars*  
847 *correspond to SEM. Asterisks indicate significant differences ( $p < 0.05$ ). Note the lower*  
848 *initial tracking error in Group 4 who was exposed to the ROTATION mapping immediately*  
849 *after the SPROT mapping.*

850  
851 **Figure 5.** *Tracking error under the SPROT mapping. A. Time course of tracking error as a*  
852 *function of trial and experimental group. B. Comparison of tracking error during early*  
853 *exposure (mean of first 10 trials) across groups. C. Same as B for tracking error during late*  
854 *exposure (mean of last 10 trials). Black dots indicate individual participants, and errors bars*  
855 *correspond to SEM. Asterisks indicate significant differences ( $p < 0.05$ ). Note the lower*  
856 *tracking error in Groups 1 and 2 who previously experienced the SPRING and ROTATION*  
857 *mappings separately.*

858  
859 **Figure 6.** *Tracking error under SPRING and ROTATION mappings in naïve participants. A.*  
860 *Time course of tracking error as a function of trial and experimental group. B. Comparison of*  
861 *tracking error during early exposure (mean of first 10 trials) across groups. C. Same as B for*  
862 *tracking error during late exposure (mean of last 10 trials). Black dots indicate individual*  
863 *participants, and errors bars correspond to SEM. Asterisks indicate significant differences*  
864 *( $p < 0.05$ ). Note the larger initial tracking error in ROTATION (G2) than SPRING (G1).*

865  
866 **Figure 7.** *Evidence for anterograde interference. A. Time course of tracking error under the*  
867 *SPRING mapping depending on whether the ROTATION mapping was tested immediately*  
868 *beforehand (G2G4) or not (G1G3). B. Comparison of tracking error during early exposure to*  
869 *SPRING (mean of first 10 trials) across each group pair. C. Same as B for tracking error*  
870 *during late exposure (mean of last 10 trials). D. Time course of tracking error under the*  
871 *ROTATION mapping depending on whether the SPRING mapping was tested immediately*  
872 *beforehand (G1G3) or not (G2G4). E. Comparison of tracking error during early exposure to*  
873 *ROTATION (mean of first 10 trials) across each group pair. F. Same as E for tracking error*

874 during late exposure (mean of last 10 trials). Black dots indicate individual participants, and  
875 errors bars correspond to SEM. Asterisks indicate significant differences ( $p < 0.05$ ). Note in  
876 both cases the detrimental effect of prior exposure on learning of the other mapping.

877

878 **Figure 8.** Time course of directional error as a function of mapping and experimental group.  
879 The table inset provides the order of mapping for each group. Errors bars correspond to  
880 SEM. Under SPROT note the smaller directional error in Groups 1 and 2 who previously  
881 experienced the ROTATION mapping. Note also under SPRING the negative polarity of  
882 directional error in Groups 2, 3 and 4 which previously experienced SPROT, ROTATION, or  
883 both.

884

885 **Figure 9.** Time course of cursor velocity as a function of mapping and experimental group.  
886 The table inset provides the order of mapping for each group. Error bars correspond to SEM.  
887 Early under SPROT (first ~5 trials) note the smaller cursor velocity in Groups 1 and 2 who  
888 previously experienced the SPRING mapping. Note also under SPRING the lower cursor  
889 velocity in Groups 3 and 4 who previously experienced SPROT.

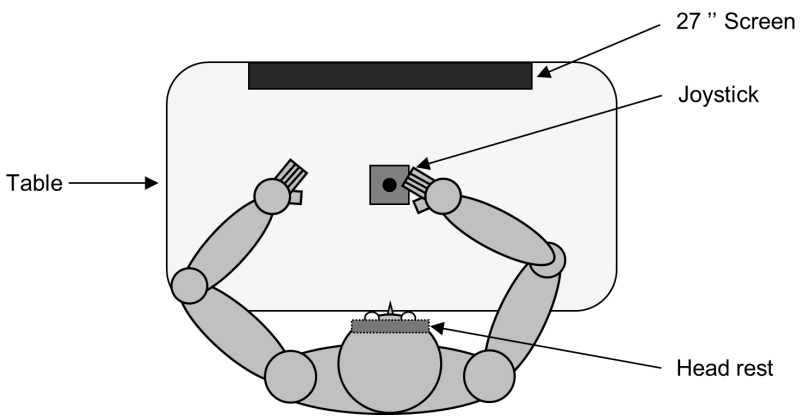
890

891

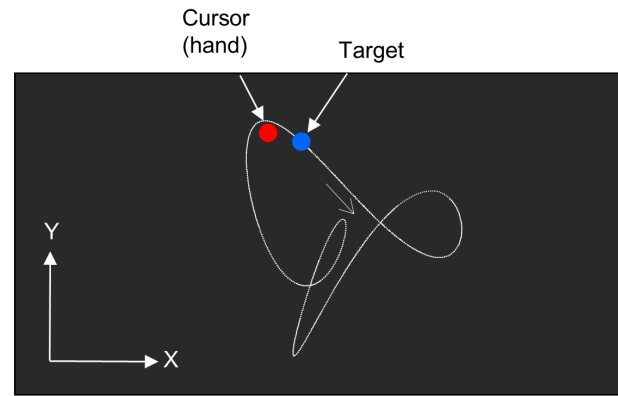
892 **TABLE CAPTION**

893 **Table 1.** Target trajectory parameters.

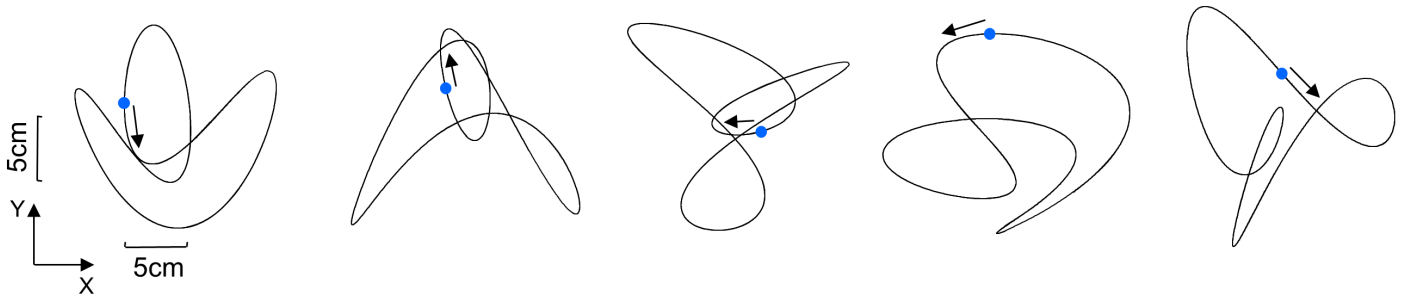
a



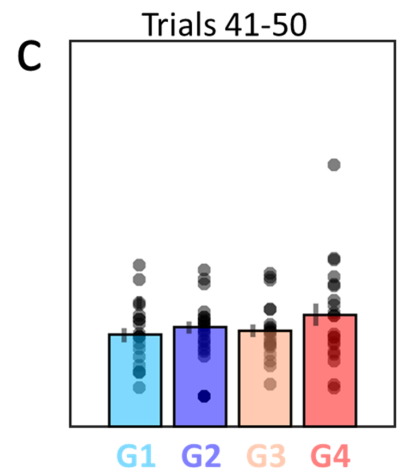
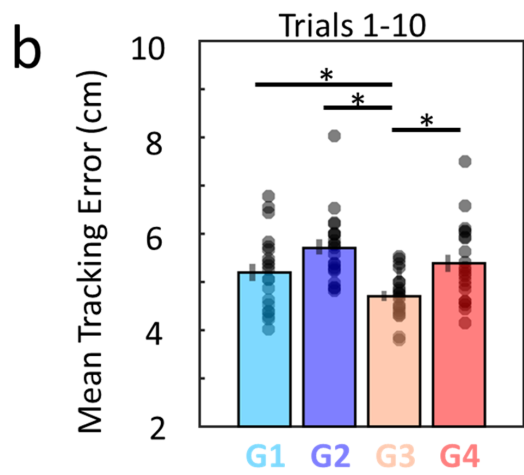
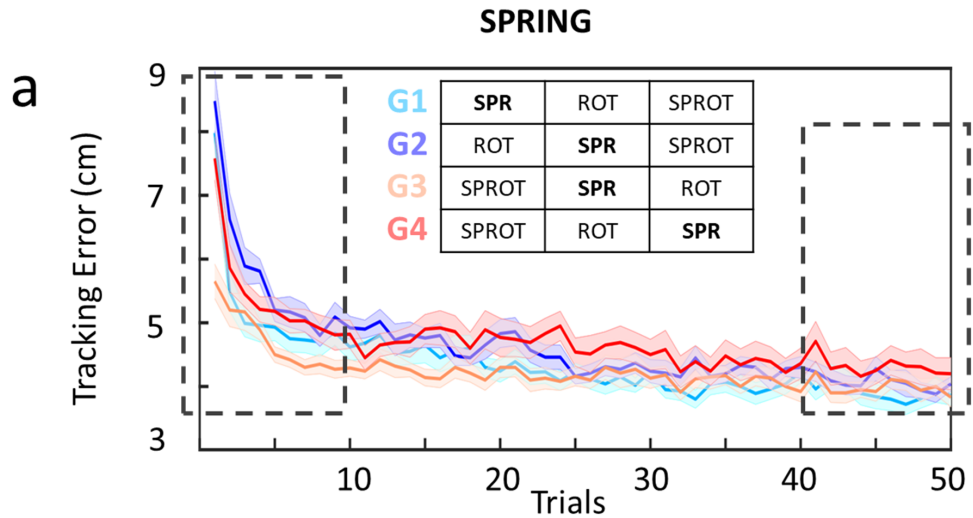
b

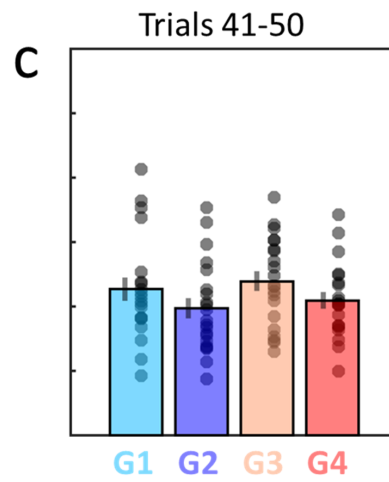
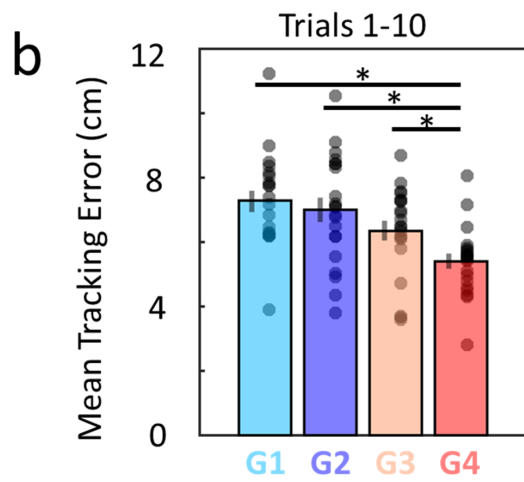
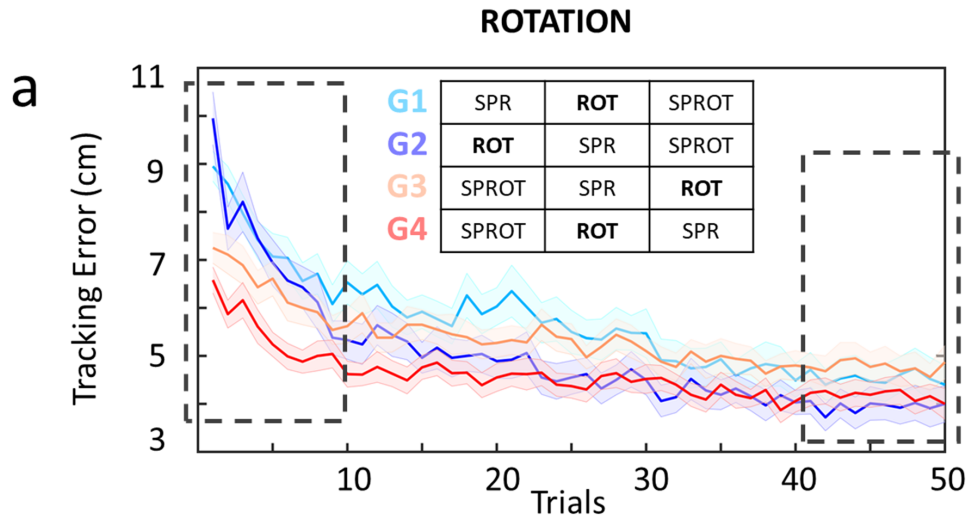


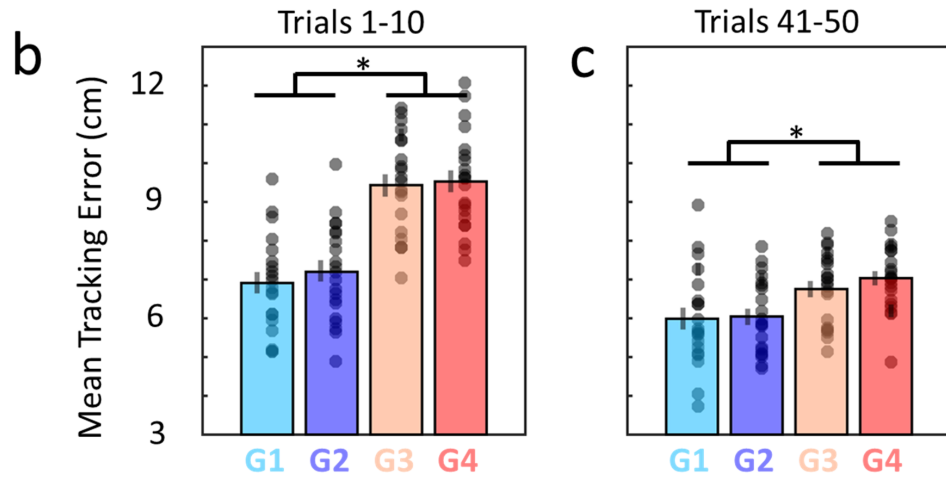
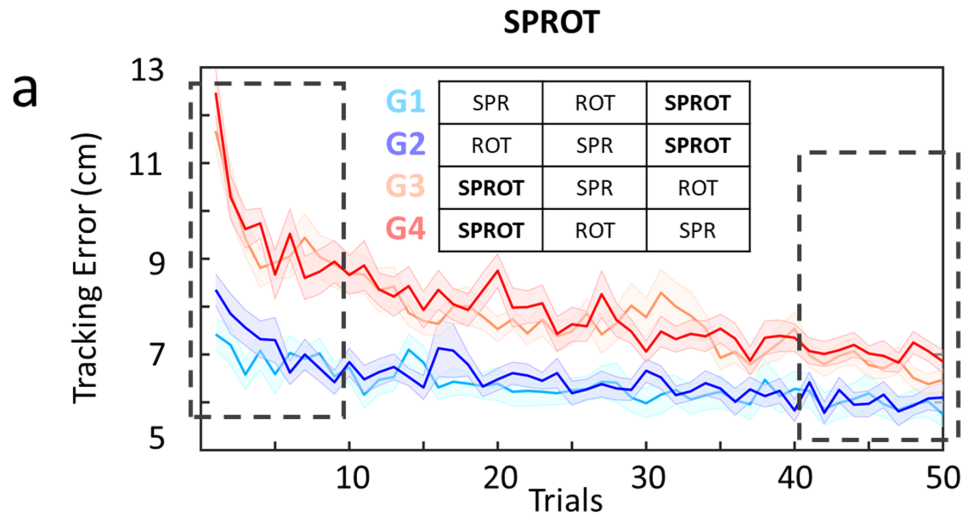
c



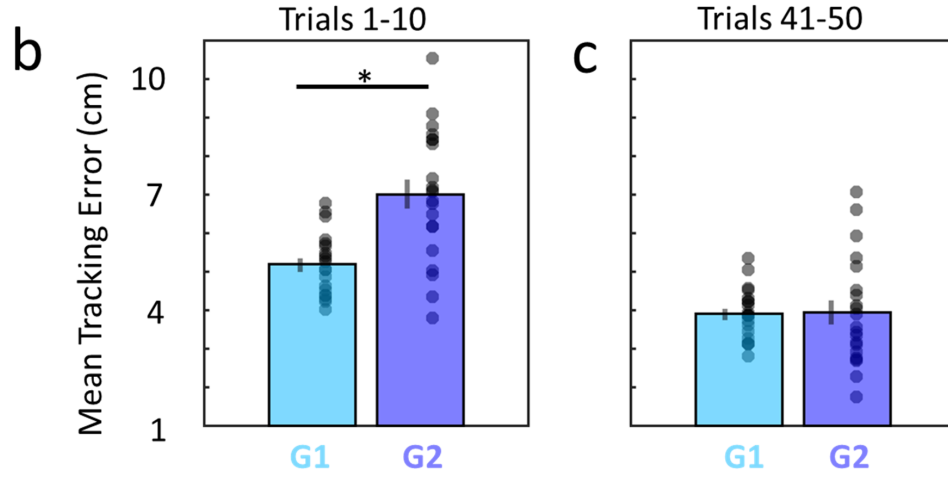
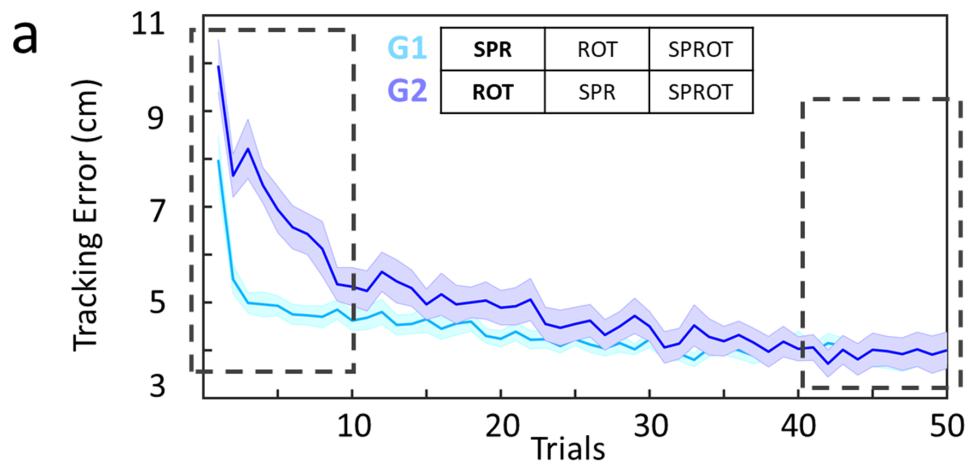
		10 trials	50 trials	50 trials	50 trials	10 trials
Compose	Group 1	Normal	Spring	Rotation	Sprot	Normal
	Group 2	Normal	Rotation	Spring	Sprot	Normal
Decompose	Group 3	Normal	Sprot	Spring	Rotation	Normal
	Group 4	Normal	Sprot	Rotation	Spring	Normal

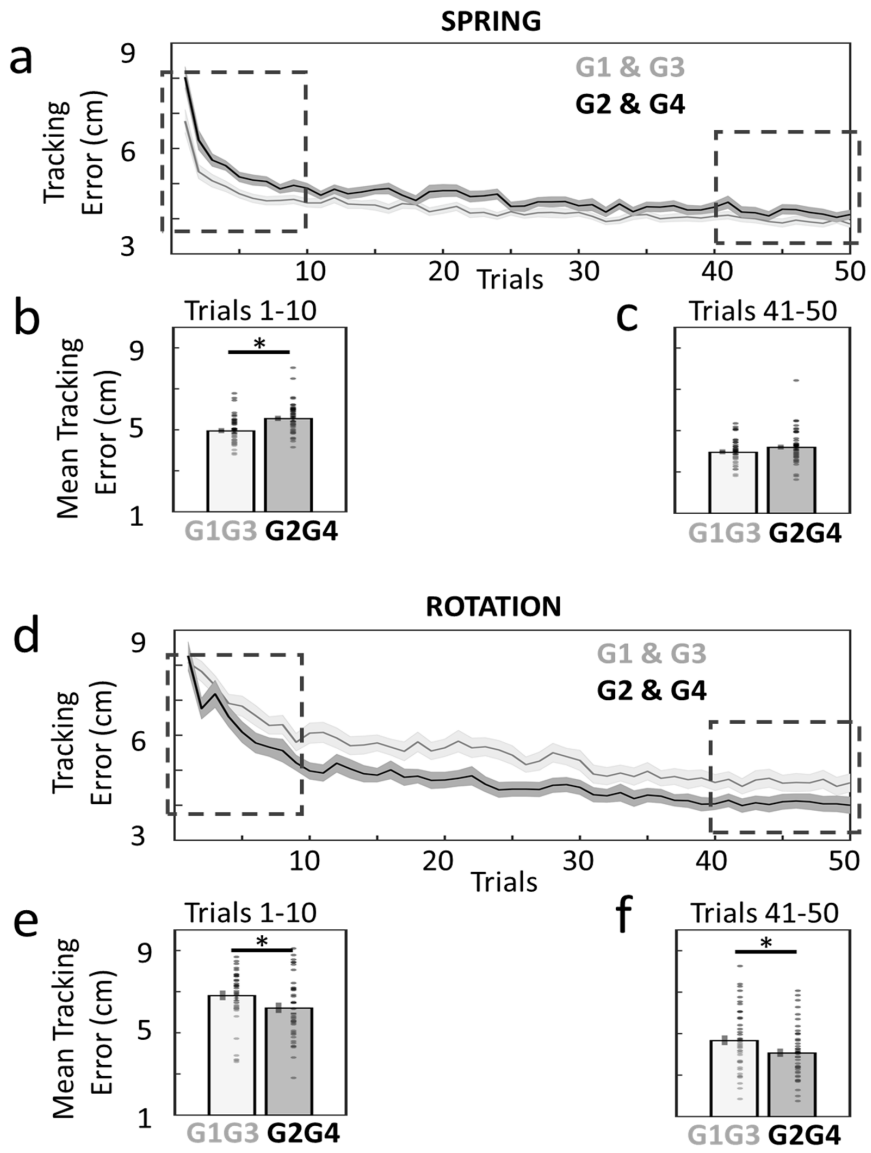


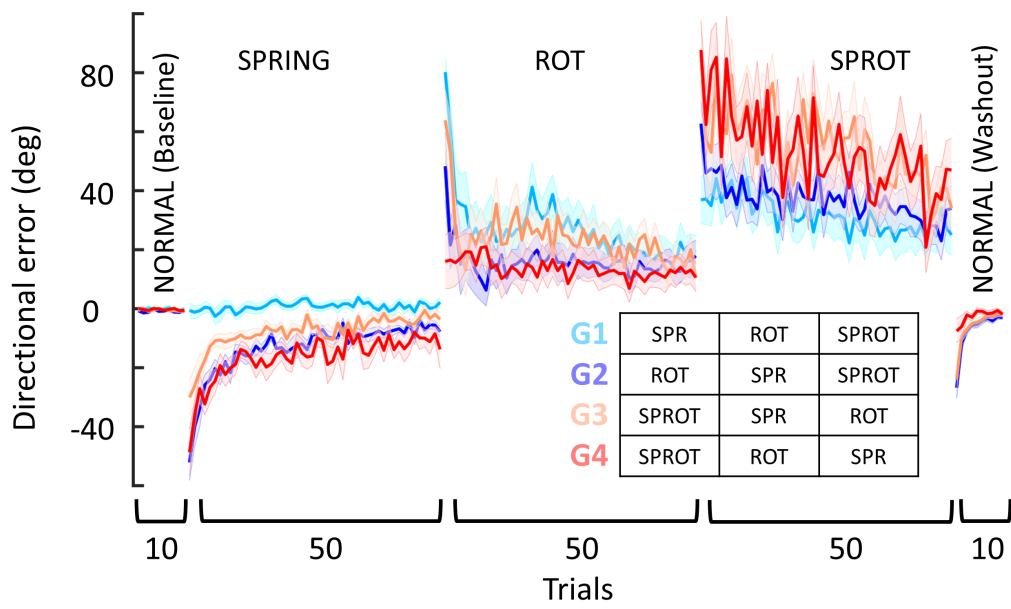


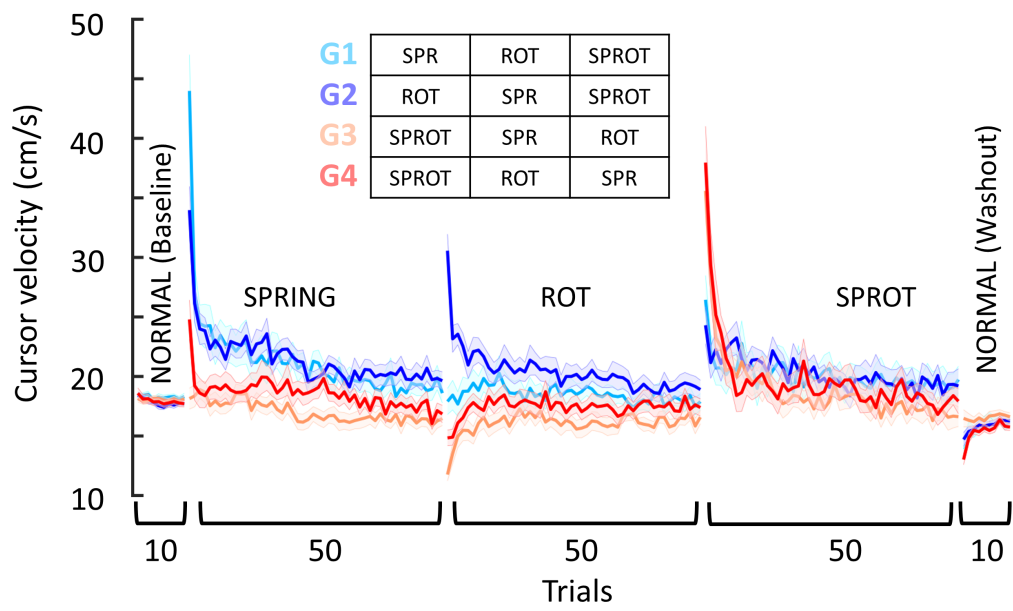






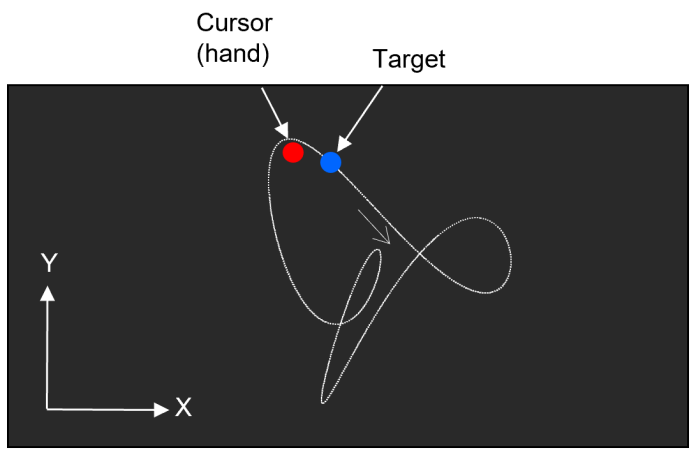
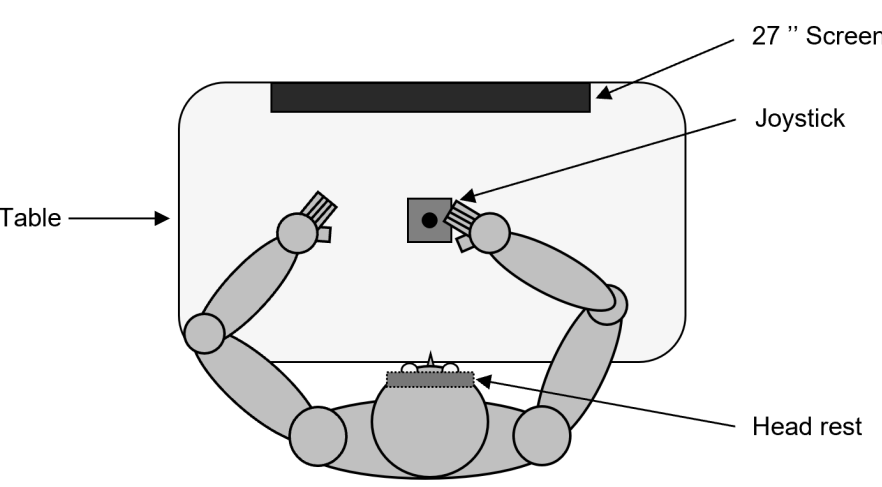






Trajectory	$A_{1x}$ (cm)	$A_{2x}$ (cm)	$h_x$	$\varphi_x$ (°)	$A_{1y}$ (cm)	$A_{2y}$ (cm)	$h_y$	$\varphi_y$ (°)
1	5	5	2	45	5	5	3	-135
2	4	5	2	-60	3	5	3	-135
3	4	5.1	3	-60	4	5.2	2	-135
4	5	5	3	90	3.4	5	2	45
5	5.1	5.2	2	-90	4	5	3	22.5

**Table 1.** Target trajectory parameters.



		10 trials	50 trials	50 trials	50 trials	10 trials
<b>Compose</b>	<b>Group 1</b>	Normal	Spring	Rotation	Sprot	Normal
	<b>Group 2</b>	Normal	Rotation	Spring	Sprot	Normal
<b>Decompose</b>	<b>Group 3</b>	Normal	Sprot	Spring	Rotation	Normal
	<b>Group 4</b>	Normal	Sprot	Rotation	Spring	Normal