



**HAL**  
open science

# Asymmetrical transfer of adaptation between reaching and tracking: implications for feedforward and feedback processes

Adrien Coudière, Enzo Fernandez, Aymar de Rugy, Frédéric Danion

## ► To cite this version:

Adrien Coudière, Enzo Fernandez, Aymar de Rugy, Frédéric Danion. Asymmetrical transfer of adaptation between reaching and tracking: implications for feedforward and feedback processes. *Journal of Neurophysiology*, 2022, 128 (3), pp.480-493. 10.1152/jn.00547.2021 . hal-03795892

**HAL Id: hal-03795892**

**<https://hal.science/hal-03795892v1>**

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           **Asymmetrical transfer of adaptation between reaching and** 2           **tracking: implications for feedforward and feedback processes**

3           Adrien Coudière<sup>1</sup>, Enzo Fernandez<sup>1,2</sup>, Aymar de Rugy<sup>2,3</sup>, and Frederic R. Danion<sup>1</sup>

4           <sup>1</sup>University of Poitiers, CNRS, Center for Research on Cognition and Learning (CERCA)  
5           UMR 7295, Poitiers, France

6           <sup>2</sup>Université de Bordeaux, Centre National de la Recherche Scientifique, Institut de  
7           Neurosciences Cognitives et Intégratives d'Aquitaine, UMR 5287, Bordeaux, France

8  
9           <sup>3</sup>Centre for Sensorimotor Performance, School of Human Movement and Nutrition Sciences,  
10          The University of Queensland, Brisbane, Queensland, Australia

11  
12          *Running Head:* Asymmetrical transfer between reaching and tracking

13          *Keywords:* visuomotor rotation; humans; manual tracking; reaching movements; transfer of  
14          adaptation

15          *Corresponding author:*

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

17          Address: Centre de Recherches sur la Cognition et l'Apprentissage (UMR 7295)  
18          MSHS -Bâtiment A5  
19          5, rue T. Lefebvre - TSA 21103  
20          F - 86073 Poitiers Cedex 9

21          *Number of pages:* 34            *Number of figures:* 8

22  
23          *Acknowledgement:*

24          We thank Cedric Goulon and Franck Buloup for technical support and providing respectively  
25          their ICE and Docometre software (courtesy of Institut des Sciences du Mouvement, Marseille,  
26          France). We also thank Otmar Bock for helpful discussion regarding a closely related study  
27          performed in his lab. Our experiments were performed using the human behaviour analysis  
28          facilities of the Maison des Sciences de l'Homme et de la Société (MSHS) of Poitiers (UAR  
29          3565 CNRS—Université de Poitiers).

30  
31          *Conflict of interest:*

32          The authors state they have no conflict of interest.

33  
34          *Contributions:*

35          AC and EF collected the data. AC and FD analysed the data and draw figures. FD and ADR  
36          conceived the experiment and drafted manuscript. AC, FD and ADR edited and revised  
37          manuscript.

38  
39

40 **ABSTRACT**

41 Reaching and manual tracking are two very common tasks for studying human sensorimotor  
42 processes. Although these motor tasks rely both on feedforward and feedback processes,  
43 emphasis is more on feedforward processes for reaching, and more on feedback processes for  
44 tracking. The extent to which feedforward and feedback processes are interrelated when being  
45 updated is not settled yet. Here, using reaching and tracking as proxies, we examined the  
46 bidirectional relationship between the update of feedforward and feedback processes. Forty  
47 right-handed participants were asked to move a joystick so as to either track a target moving  
48 rather unpredictably (pursuit tracking) or to make fast pointing movements toward a static target  
49 (center-out reaching task). Visuomotor adaptation was elicited by introducing a 45° rotation  
50 between the joystick motion and the cursor motion. Half of the participants adapted to rotation  
51 first via reaching movements, and then with pursuit tracking, while the other half performed  
52 both tasks in opposite order. Group comparisons revealed a strong asymmetrical transfer of  
53 adaptation between tasks. Namely, although nearly complete transfer of adaptation was  
54 observed from reaching to tracking, only modest transfer was found from tracking to reaching.  
55 A control experiment (N=10) revealed that making target motion fully predictable did not  
56 impact the latter finding. One possible interpretation is that the update of feedforward processes  
57 contributes directly to feedback processes, but the update of feedback processes engaged in  
58 tracking can be performed in isolation. These results suggest that reaching movements are  
59 supported by broader (i.e. more universal) mechanisms than tracking ones.

60

61 **New and Noteworthy**

62

63 Reaching and manual tracking are thought to rely differently on feedforward and feedback  
64 processes. Here we show that, although nearly complete transfer of visuomotor adaptation  
65 occurs from reaching to tracking, only minimal transfer is found from tracking to reaching.  
66 Even though the update of feedforward processes (key for reaching) proved directly useful to  
67 feedback processes (key for tracking), the strong asymmetrical transfer suggests that feedback  
68 control can be updated independently from feedforward adaptation.

69

## 70 INTRODUCTION

71 In behavioral neuroscience, reductionism forces us to focus only on a small fraction of  
72 the human repertoire. As a result one may wonder to what extent results found using one motor  
73 task applies to another motor task, in other words « *how interchangeable are these tasks with*  
74 *respect to general insights* » [1]. Reaching and tracking/pursuit are two key motor tasks when  
75 trying to decipher the computational principles driving voluntary hand movements [2–5]. In the  
76 former one, with the arm being at rest, the participant is required to perform a pointing  
77 movement so as to bring a cursor (or the hand) as fast as possible toward a static target. In the  
78 second one, the participant is asked to bring/maintain a cursor (or the hand) as close as possible  
79 to a moving target, which typically follows a pseudo random trajectory. Although reaching and  
80 tracking rely both on feedforward and feedback processes [6–9], this is apparently done with  
81 different extent [4]. Fast hand reaching movements (especially the initiation) are thought to rely  
82 mainly on feedforward processes, whereby hand motor command is essentially programmed  
83 before movement initiation (such that feedback loops have minimal impact on hand movement).  
84 In contrast, when tracking a target that follows an unpredictable path, on-line adjustments of  
85 the hand motor command are a constant requirement, and feedback loops are key to ensure  
86 proper hand positioning. Here we propose to capitalize on these differences between reaching  
87 and tracking to explore the relationship between feedback and feedforward processes.

88 How dependent are the update of feedforward and feedback processes is key in motor  
89 control and thus has led to numerous studies. Let us start with a body of studies that investigated  
90 whether the update of feedforward processes engaged in hand reaching movements also lead to  
91 the update of feedback processes involved in reaching. To address this issue a neat way is to  
92 introduce unexpected target jumps following the adaptation phase. Although this protocol  
93 demonstrated that participants were able to trigger adequate online corrections (reflexes)  
94 following adaptation to force field [10–14] or to visuomotor rotation [15–17], contrasting

95 results were observed following adaptation to visual feedback inversion [18–20]. Surprisingly,  
96 the possibility that the update of feedback mechanisms could reciprocally drive the update of  
97 feedforward mechanisms is much less documented, presumably because setting the adequate  
98 experimental conditions to address this issue is challenging. To our knowledge, only two studies  
99 have met this challenge, but they provide rather contrasting results. In the first one, training of  
100 reflex responses by means of short mechanical perturbations was shown to transfer to  
101 feedforward control of reaching [21]. In contrast, a recent study using an arc-pointing task under  
102 various conditions suggests that on-line feedback training could actually suppresses  
103 improvement in feedforward control during motor learning [22].

104         To further explore this issue, we propose to assess the transfer of visuomotor adaptation  
105 between reaching and tracking, considering respectively these tasks as a proxy for feedforward  
106 and feedback control. We reason that if the update of feedforward and feedback processes are  
107 tightly linked [13–15,21], substantial and reciprocal transfer should occur between reaching  
108 and tracking. Alternatively, if the update of feedforward and feedback processes are largely  
109 independent [20], limited transfer should be expected between reaching and tracking  
110 movements.

111         To our knowledge, the issue of whether visuomotor adaptation could transfer between  
112 reaching and tracking has been only examined in three papers. In Abeele and Bock [23], using  
113 full arm movements and a 60° rotation, the authors found significant transfer between center-  
114 out reaching and pursuit tracking, albeit more extensively from reaching to tracking than the  
115 other way around. More recently, while also using full arm movements and a 90° rotation, Yang  
116 et al [4] reported clear benefits from point-to-point reaching to tracking, but the experimental  
117 design did not allow to assess transfer in the reverse direction. Finally, using another type of  
118 protocol and full arm movements, Tong and Flanagan [24] found no sign of interference when  
119 adapting successively center-out-and-back movements to a 30° rotation, and tracking

120 movements to an opposite ( $-30^\circ$ ) rotation, thereby leading to the conclusion that adaptation to  
121 visuomotor rotation is task specific. Altogether, given the diversity of the findings, we felt the  
122 need for further examination.

123 In contrast to previous studies which all employed full arm movements, here we propose  
124 to re-examine the issue of visuomotor transfer in the context of a center-out reaching task and  
125 a pursuit tracking task using a joystick. We reason that, because fast reaching movements  
126 performed with a joystick are likely of shorter duration, they might offer a better proxy of  
127 feedforward processes. Furthermore, by using a target that follows a pseudo random motion,  
128 we reason that our pursuit tracking task becomes more suitable to monitor feedback processes  
129 [25,26]. As an aside we also test transfer of adaptation when tracking training is performed with  
130 a fully predictable motion thereby presumably emphasizing the feedforward component.  
131 Irrespective of target motion predictability, results show a strong asymmetrical transfer of  
132 adaptation between tasks. Namely although nearly complete transfer of adaptation is observed  
133 from reaching to tracking, only modest transfer is found from tracking to reaching.

134

## 135 **METHODS**

### 136 *Participants*

137 Two groups of twenty healthy right-handed volunteers were recruited (Group RT:  $20.5$   
138  $\pm 2.5$  yrs, 10 females; Group TR:  $20.6 \pm 2.8$  yrs, 10 females). Handedness of participants was  
139 verified using the Oldfield Handedness Inventory [27] with a mean laterality index of  $74.0 \pm$   
140  $15.4$  for Group RT, and  $80.5 \pm 15.0$  for Group TR. All participants gave written consent prior  
141 to participation. The experimental paradigm (IRB00012476-2021-11-02-88) was approved by  
142 the local ethics committee (CERSTAPS) and complied with the Declaration of Helsinki.

143

### 144 *Data Acquisition*

145 Figure 1A shows the experimental set up. Participants were seated comfortably in a dark  
146 room facing a screen (ACER predator, 1920×1080, 27 inch, 240Hz) positioned on the frontal  
147 plane 57 cm away from the participant's eye. Participants' head movements were restrained by  
148 a chin rest and a padded forehead rest so that the eyes in primary position were directed toward  
149 the center of the screen. In order to block the vision of their hands, a mask was positioned under  
150 the participants' chin. They were required to hold with the right hand a joystick (Serie 812,  
151 Megatron, France, with  $\pm 25$  degrees of rotation along X-Y axes) positioned horizontally on a  
152 table in front of the participant, in line with central sagittal plane. Note that, in contrast to our  
153 previous experiments [28–30], here the joystick was spring loaded with a restoring force that  
154 was low but sufficient to bring back the joystick at its central position when the participant  
155 releases it. Both right and left forearms were resting on the table. The output of the joystick was  
156 recorded at 1000 Hz. In contrast to some of our previous studies [28–30], eye movements were  
157 not recorded in the current study. No explicit instruction was given regarding the point of gaze.

158 (Please insert Figure 1 about here)

159

### 160 ***Experimental Design***

161 Participants had to perform either a tracking task or a reaching task with their right hand.  
162 All technical details about the tracking task can be found in our previous studies [28,29].  
163 Briefly, during the tracking task, participants were instructed to minimize the distance between  
164 a red cursor (driven by the joystick) and a blue target (see Figure 1B). The motion of the target  
165 was rather unpredictable as it resulted from the combination of sinusoids: two sinusoids along  
166 the frontal axis, and two sinusoids along the sagittal axis. Mean tangential velocity was  $16 \pm$   
167  $5.9$  cm/s with values ranging from 0 to 27 cm/s, mean target eccentricity was  $6.0 \pm 2.7$  cm, with  
168 values ranging from 0.4 up to 11.8 cm. A total of 5 patterns was tested. The order of these  
169 patterns was randomized across trials and participants. Each tracking trial had a duration of 10

170 s. Given that the time necessary to complete a full revolution was 5s, each movement pattern  
171 was repeated twice per trial.

172 During the reaching task, participants were instructed to perform fast and accurate  
173 center-out pointing movements (see Figure 1C). At the beginning of each trial the participant  
174 was instructed to release the joystick in order to allow the red cursor to move at the center of  
175 the screen. Then after a fixed delay (2 s), a blue target appeared at the periphery. As soon as  
176 this peripheral target was visible, participants were required to make a fast and accurate pointing  
177 movement toward it. The target appeared at 1 of 8 possible locations ( $45^\circ$  apart) that were  
178 spread 10 cm around the start position. Participants were encouraged to produce a quick  
179 uncorrected movement toward the target and were specifically instructed to refrain the release  
180 of final adjustments. After hand movement stops, participants had to release the joystick so that  
181 a new trial could start (3s after the target was presented). The position of the target was  
182 randomized, but after every block of 8 trials, each of the 8 possible targets was presented once.  
183 The order of targets was randomized across blocks and participants.

184 Under baseline condition, the relation between the joystick motion and its visual  
185 consequences on the screen was intuitive, mimicking the behavior of a computer mouse, with  
186 forward/backward joystick movements eliciting up/down cursor movements on the screen, and  
187 left/right joystick movements eliciting left/right cursor movements. Under adaptive condition,  
188 the previous mapping was rotated by  $45^\circ$  counterclockwise. Subjects were not informed about  
189 the rotation provided during the exposure session.

190 Participants were split into two groups that both performed the tracking and reaching  
191 task under the regular and rotated mapping, albeit in different orders. The experimental session  
192 consisted of 3 phases (see Figure 2). During the initial phase (Baseline,  $0^\circ$  rotation), the first  
193 group of participants (Group 1) performed one block of 20 tracking trials and one block 80  
194 reaching trials under the regular mapping. Subsequently, during the adaptation phase ( $45^\circ$



195 rotation), this group performed one block of 40 tracking trials followed by one block of 160  
196 reaching trials, both under the rotated mapping. During the final phase, the initial mapping was  
197 restored ( $0^\circ$ ) allowing to test for after-effects with 8 reaching trials followed by 2 tracking trials.  
198 The second group of participants (Group 2) followed the same protocol (baseline, adaptation to  
199 rotation, and after-effects) except that the order of tasks was reversed for each phase. For  
200 simplicity Group 1 will be referred as Group TR (Track $\rightarrow$ Reach), and Group 2 will be referred  
201 as Group RT (Reach $\rightarrow$ Track). Note that for the baseline phase, half of the participants in each  
202 group ( $n=10$ ), started by the tracking task, while the other half started by the reaching task. This  
203 procedure was used to ensure homogeneity of baseline data across our groups. Altogether, each  
204 participant performed a total 62 tracking trials and 248 reaching trials. This experimental design  
205 used a  $\frac{1}{4}$  ratio between tracking and reaching trials (i.e., 1 tracking trial for 4 reaching trials),  
206 in order to elicit comparable level of adaptation (thanks to pilot testing). Comparisons between  
207 groups were used to assess transfer of adaptation. To assess transfer of adaptation from reaching  
208 to tracking, tracking movements from Group RT (that could have benefited from previous  
209 adaptation in reaching movements) were compared to that of Group TR (that could not have  
210 benefited from previous adaptation). The opposite assignment was used to assess transfer from  
211 tracking to reaching movements.

212 (Please insert Figure 2 about here)

### 213 ***Control experiment***

214 As will be shown later, we observed a lack of transfer from the tracking to the reaching  
215 task. As an aside we tested whether target motion predictability during tracking could influence  
216 this finding. To achieve this goal, we tested another group of ten healthy right-handed  
217 volunteers (Group TR8:  $20.6 \pm 2.8$  yrs, 8 females, laterality index  $79.5 \pm 13.9$ ) that followed  
218 the very same protocol of GROUP TR (see Figure 3A) except that this time, all tracking trials

219 were performed with a fully predictable target motion. Specifically, the target motion  
220 consistently followed a figure 8 (see Figure 3B) determined by the following equations:

$$221 \quad x_t = A \cos \left( 4\pi Ft + \frac{\pi}{2} \right) \quad (1)$$

$$222 \quad y_t = A \sin (2\pi Ft) \quad (2)$$

223 We used the following parameter settings,  $A=8.47\text{cm}$  and  $F=0.2\text{ Hz}$  to keep both mean  
224 tangential velocity ( $16 \pm 5.3\text{ cm/s}$ ) and target eccentricity ( $5.4 \pm 2.6\text{ cm}$ , with values ranging  
225 from 0 up to 8.47 cm) in the vicinity of values associated with our unpredictable target patterns.  
226 Finally, as previously set, the target completed two revolutions during each 10s trial.

227 (Please insert Figure 3 about here)

## 228 ***Data Analysis***

229 Cursor position time series were low-pass filtered with a Butterworth (fourth order)  
230 using a cutoff frequency of 25 Hz. The resultant signals were differentiated to obtain cursor  
231 tangential velocity. To quantify tracking error ( $E$ ), we measured the Euclidian distance in cm  
232 (in two dimensions;  $x$  and  $y$ ) between the cursor ( $C$ ; moved by the hand) and the target ( $T$ ) at  
233 each instant ( $t$ ) using the following equation:

$$234 \quad E_t = \sqrt{(C_{xt} - T_{xt})^2 + (C_{yt} - T_{yt})^2} \quad (3)$$

235

236 We averaged this error across time for each trial while excluding the first second of data  
237 from each trial to minimize transients due to initial cursor positioning [30–32]. To assess the  
238 presence of a possible bias in hand movement direction, we rotated the cursor data (while also  
239 excluding the first sec of data) around the center and determined which angle allowed to  
240 minimize the Euclidian distance [32]. This angle was called directional error. We expected  
241 minimal directional error during baseline tracking.

242 To assess reaching performance in each trial, we measured the directional error, the  
243 Euclidian distance at the end of the movement, as well as reaction time and movement time.

244 These variables were extracted as follows. Beginning and end of movement were estimated  
245 based on cursor tangential velocity, using a threshold at 8% of maximal peak velocity [33].  
246 Determining those instants allowed to compute reaction time and movement duration. Final  
247 position error (i.e. Euclidian cursor-target distance at the end of movement) was evaluated using  
248 the same equation as presented earlier (see also [34]). Cursor-path directional error was  
249 evaluated both at maximal tangential velocity and at maximal tangential acceleration [35]. It  
250 was calculated as the angle between the vector going from initial starting cursor position to  
251 cursor position at maximal velocity (or maximal acceleration), and the vector going from the  
252 start position to target location. Because both types of directional error led to similar pattern of  
253 results, we only report directional error at maximal velocity. A few reaching trials (less than 1  
254 %) were excluded because reaction time did not fall within the 150-700 ms interval.

255 For the sake of comparison between reaching and tracking, reaching data was down  
256 sampled and averaged every 4 trials into bins. This procedure allowed to present a similar  
257 number of bins for the reaching and tracking tasks in the baseline, adaptation, transfer, and post  
258 effect sessions (thus for tracking, bin and trial are equivalent terms). Repeated measures  
259 ANOVAs were used as the main tool for statistical analyses. To assess the homogeneity of  
260 groups during baseline, we examined the effect of GROUP (RT vs. TR) on average errors over  
261 the last 4 bins. To assess transfer of adaptation, we examined the effect of GROUP (RT vs. TR),  
262 and BIN (4 first vs. 4 last bins). Regarding the control experiment and the effect of target  
263 predictability, we focused on the comparison between GROUP TR and TR8. Newman-Keuls  
264 corrections were used for post hoc t-tests to correct for multiple comparisons. A conventional  
265 0.05 significance threshold was used for all analyses.

266

## 267 **RESULTS**

268 *Typical trials*

269 Figure 4 plots representative trials performed by one participant in each group during  
270 baseline performance and early exposure to the visuomotor rotation during both the reaching  
271 and tracking task. As can be seen on the left side of the right panel (early adaptation), tracking  
272 and reaching performance were both substantially altered when the rotation was first  
273 introduced. However, the first row suggests that when prior experience with the rotation was  
274 offered under reaching (Group RT), the detrimental effect of the rotation on tracking was  
275 strongly reduced. In contrast, the second row shows that prior experience with the rotation under  
276 tracking (Group TR) did not alleviate the detrimental effect of the rotation on reaching, thereby  
277 arguing for asymmetrical transfer effect between reaching and tracking. In the next sections,  
278 we analyze in more details these preliminary observations.

279 (Please insert Figure 4 about here)

#### 280 *General overview*

281 In Figure 5 we present the timeline of spatial accuracy (panel A) and directional error  
282 (panel B) over the whole experiment, for each group separately. As can be seen, transfer of  
283 adaptation is more striking when switching from reaching to tracking (Group RT) than the other  
284 way around (Group TR). Below we examine transfer in more details and separately for these  
285 two cases, but first we assess possible differences across groups in baseline condition. Finally,  
286 we examine post-effects.

287 (Please insert Figure 5 about here)

#### 288 *Baseline trials*

289 During the baseline block, all participants performed the tracking and reaching task  
290 under the NORMAL mapping. The one-way ANOVA revealed no systematic difference in  
291 tracking performance between the groups, neither in terms of tracking error (TR=1.56 vs.  
292 RT=1.58 cm;  $F(1,38)=0.205$ ;  $p=0.65$ ) nor in directional error (TR=0.3° vs. RT=0°;  
293  $F(1,38)=0.87$ ;  $p=0.35$ ). Regarding the reaching task, the ANOVA also led to a lack of group

294 difference when examining spatial accuracy of reach (TR=1.41 vs. RT=1.40 cm;  
295  $F(1,38)=0.007$ ;  $p=0.93$ ), and eventual directional bias (TR=2.3° vs. RT=2.7°;  $F(1,38)=0.44$ ;  
296  $p=0.51$ ). Other dependent variables related to the reach such as reaction time (TR=310 vs.  
297 RT=320 ms;  $F(1,38)=0.58$ ;  $p=0.45$ ), and movement duration (TR=212 vs. RT=216 ms;  
298  $F(1,38)=0.124$ ;  $p=0.73$ ), also revealed a lack of group difference. Finally, when examining the  
299 relation between cursor-target distance in the tracking and reaching task across our 40  
300 participants, we found virtually no correlation ( $R=0.13$ ,  $p=0.41$ ). Overall, these analyses  
301 suggest that our two groups were homogeneous in terms of their baseline performance, and that  
302 tracking and reaching rely on (at least partly) different visuomotor processes.

303

#### 304 *Examining transfer from reaching to tracking movements*

305 To assess whether adaptation to the rotation transferred from reaching to tracking we  
306 compared the time course of tracking performance across groups, with Group TR serving as  
307 control group (i.e. with no prior experience with the rotation), and Group RT serving as test  
308 group (i.e. with prior adaptation to rotation by means of reaching). In Figure 6A, we present the  
309 time course of tracking error in both groups as a function of trial. As can be seen, initial tracking  
310 error is substantially reduced in Group RT compared to Group TR. The two-way ANOVA  
311 showed a main effect of GROUP ( $F(1,38)=20.68$ ,  $p<0.001$ ), BIN ( $F(1,38)=161.38$ ,  $p<0.001$ ),  
312 and GROUP by BIN interaction ( $F(1,38)=123.17$ ,  $p<0.001$ ). Post hoc of the interaction reveals  
313 that although there was a significant difference across groups early in the adaptation (TR=3.05  
314 vs. RT=2.14 cm,  $p<0.001$ ), there was no difference late in the adaptation (TR=2.08 vs. RT=2.07  
315 cm,  $p=0.95$ ). Moreover, not only we observed that tracking error remained stable for  
316 experienced participants in Group RT (2.14 vs. 2.07 cm,  $p=0.50$ ), but also that their initial  
317 tracking error was comparable to final tracking error of naïve participants (2.14 vs. 2.08 cm,

318 p=0.59). Altogether, these results demonstrate that visuomotor adaptation acquired under  
319 reaching movements fully transferred to tracking ones.

320 (Please insert Figure 6 about here)

321 Similar findings were obtained when examining the directional error associated with  
322 tracking movements (see Figure 6B). Indeed, directional error was substantially reduced when  
323 earlier practice with the rotation was offered with reaching (Group RT). The ANOVA revealed  
324 a main effect of GROUP ( $F(1,38)=21.64$ ,  $p<0.001$ ), BIN ( $F(1,38)=40.71$ ,  $p<0.001$ ), and an  
325 interaction ( $F(1,38)=45.33$ ,  $p<0.001$ ). Post hoc of the interaction reveals that although there was  
326 a significant difference across groups early in the adaptation (TR=13.7 vs. RT=5.8 deg,  
327  $p<0.001$ ), there was no difference late in the adaptation (TR=6.7 vs. RT=6.0 deg,  $p=0.48$ ).  
328 Besides, not only we observed that directional error remained lower and stable for experienced  
329 participants in Group RT (5.8 vs. 6.0 deg,  $p=0.80$ ), but also that their initial bias was comparable  
330 to final bias of naïve participants (5.8 vs. 6.7 deg,  $p=0.65$ ). Altogether, the analysis of  
331 directional error reinforces the view of a complete transfer of adaptation from reaching to  
332 tracking movements.

333

#### 334 *Examining transfer from tracking to reaching movements*

335 To assess whether visuomotor adaptation could transfer from tracking to reaching,  
336 reaching performance was compared across groups, but this time with Group RT serving as  
337 control group (i.e. with no prior experience with the rotation), and Group TR serving as test  
338 group (i.e. with prior adaptation by means of tracking). In Figure 7A we compare the time  
339 course of cursor-target distance at the end of each reach across groups. The two-way ANOVA  
340 showed a main effect of GROUP ( $F(1,38)=15.50$ ,  $p<0.001$ ), BIN ( $F(1,38)=631.01$ ,  $p<0.001$ ),  
341 and a GROUP by BIN interaction ( $F(1,38)=21.35$ ,  $p<0.001$ ). The post hoc of the interaction  
342 revealed a significant difference across groups during the early phase of adaptation (RT=6.86

343 vs. TR=5.04 cm,  $p<0.001$ ), but not during the late one (RT=1.98 vs. TR=1.67 cm,  $p=0.34$ ).  
344 Altogether, prior experience with the rotation under tracking allowed a reduction of initial error  
345 by about 27% (5.04 vs 6.86 cm). In contrast to the nearly complete transfer of adaptation found  
346 from reaching to tracking, this analysis suggests a rather modest transfer of adaptation from  
347 tracking to reaching.

348 The analysis of directional error in reaching movements further reinforces the view of a  
349 rather limited transfer from tracking to reaching (see Figure 7B). The ANOVA showed a main  
350 effect of BIN ( $F(1,38)=230.3$ ,  $p<0.001$ ), but no main effect of GROUP ( $F(1,38)=1.67$ ,  $p=0.20$ ),  
351 nor GROUP by BIN interaction ( $F(1,38)=0.68$ ,  $p=0.41$ ), supporting a lack of difference across  
352 groups in both the initial and final directional error. Altogether these analyses suggest that prior  
353 adaptation of tracking provided only scarce benefit for the adaptation of reaching.

354 (Please insert Figure 7 about here)

355

### 356 *Aftereffects*

357 As expected, when the perturbation was removed, reliable aftereffects were observed  
358 for each of the 8 reaching trials and 2 tracking trials that we collected (see right side of Figure  
359 5). Not only those aftereffects were visible using spatial and directional error, but they  
360 concerned both reaching and tracking, no matter the order in which these tasks were tested.  
361 Still, it appears that aftereffects were typically greater when being measured firsthand. Namely  
362 aftereffects on reaching were greater when assessed immediately after reaching than after  
363 tracking; note that for statistical analyses we only considered aftereffects pooled across the two  
364 bins. Indeed, the magnitude of aftereffects in reaching was greater in Group TR compared to  
365 Group RT, both in terms of spatial error (5.88 vs. 4.71 cm;  $F(1,38)=23.04$ ,  $p<0.001$ ) and  
366 directional bias (-35.3 vs. -24.8 deg;  $F(1,38)=44.5$ ,  $p<0.001$ ). Similarly, aftereffects on tracking  
367 performance were more obvious when assessed immediately after tracking than after reaching.

368 Indeed the magnitude of tracking aftereffects was greater in Group RT compared to Group TR,  
369 both in terms of spatial error (2.65 vs. 2.43 cm;  $F(1,38)=4.32$ ,  $p=0.04$ ) and directional bias (-  
370 12.4 vs. -10.1 deg;  $F(1,38)=3.99$ ,  $p=0.05$ ). These rather long-lasting aftereffects are consistent  
371 with the implication of implicit adaptation.

372

### 373 *Effect of target motion predictability*

374 Limited transfer of adaptation was found from tracking to reaching when training was  
375 performed with a rather unpredictable target motion. To determine whether target motion  
376 predictability could influence this finding, we assessed transfer of adaptation in another group  
377 of participants (GROUP TR8) that was trained with a target that repeatedly followed a figure  
378 8, making its motion fully predictable. Before exploring the outcome of this new protocol, we  
379 propose first to compare baseline tracking in GROUP TR and GROUP TR8. As expected, we  
380 found that tracking performance was facilitated under the figure 8 pattern as revealed by both  
381 a smaller tracking error (TR8=1.38 vs. TR=1.58 cm;  $F(1,28)=5.20$ ;  $p=0.03$ ) and a smaller  
382 cursor-target lag (TR8=34 vs. TR=51 ms;  $F(1,28)=5.31$ ;  $p=0.028$ ), suggesting that participants  
383 did take advantage of target motion predictability when made available. Moreover, we found a  
384 positive correlation between spatial error in this new version of the tracking task and the  
385 reaching task ( $R=0.70$ ,  $p<0.05$ ). The fact that TR8 participants with better performance in one  
386 task were also better at the other task suggests that more common mechanisms might be  
387 involved here than in the main experiment (for which no such correlation was observed).

388 Next, we compared the time course of tracking adaptation under predictable and  
389 unpredictable target motion (see left side of Figure 8). Two-way ANOVA of cursor target  
390 distance showed a main effect BIN ( $F(1,28)=109.87$ ;  $p<0.001$ ), but no main effect of GROUP  
391 ( $F(1,28)=0.44$ ;  $p=0.51$ ) nor an interaction ( $F(1,28)=1.53$ ;  $p=0.23$ ). Similar results were obtained  
392 for the directional error, namely we found a main effect of BIN ( $F(1,28)=68.79$ ;  $p<0.001$ ), but



393 no main effect of GROUP ( $F(1,28)=2.99$ ;  $p=0.09$ ) nor GROUP by BIN interaction  
394 ( $F(1,28)=0.07$ ;  $p=0.79$ ). Overall, we conclude that predictability of target motion had rather  
395 limited influence on the time course of tracking adaptation.

396 Now a key issue is whether prior adaptation to tracking under predictable and  
397 unpredictable target motion benefit differently to reaching adaptation. To assess this point, in  
398 the right side of Figure 8, we compare the time course of spatial (panel A) and directional error  
399 (panel B) of reaching movements in GROUP TR and TR8. Regarding spatial accuracy, the two-  
400 way ANOVA showed a main effect of BIN ( $F(1,28)=491.22$ ,  $p<0.001$ ), consistent with an  
401 improvement of reaching across trials, but no main effect of GROUP ( $F(1,28)=0.38$ ,  $p=0.54$ ),  
402 nor a GROUP by BIN interaction ( $F(1,28)=0.59$ ,  $p=0.45$ ). The analysis of directional error led  
403 to similar results, namely with a main effect of BIN ( $F(1,28)=209.1$ ,  $p<0.001$ ), but no main  
404 effect of GROUP ( $F(1,38)=0.0003$ ,  $p=0.987$ ), nor GROUP by BIN interaction ( $F(1,28)=0.71$ ,  
405  $p=0.40$ ). Altogether these analyses suggest that prior adaptation elicited by tracking a fully  
406 predictable target motion does not alleviate the limited transfer from tracking to reaching  
407 movements.

408 (Please insert Figure 8 about here)

409 Finally, although we provided evidence that target motion predictability influences  
410 tracking performance but not the transfer from tracking to reaching, we wished to examine its  
411 possible impact on the contribution of feedback/feedforward processes during both baseline  
412 and adaptation trials. To achieve this objective, we analyzed the dynamics of ongoing tracking  
413 error by means of power spectral density functions [36]. Specifically, in the bottom part of  
414 Figure 8, we compare the power spectra of cursor-target distance (over the last 9 sec of each  
415 trial) in GROUP TR and TR8. This analysis was run separately for the last 4 baseline trials, the  
416 first 4 and the last 4 adaptation trials (presented respectively in panel C, D, and E). As can be  
417 seen, in each case, the power spectra of GROUP TR and GROUP TR8 have very similar profile.

418 Concerning baseline trials, two-way ANOVA showed a main effect of GROUP ( $F(1,28)=8.21$ ,  
419  $p<0.01$ ) and FREQ ( $F(4,112)=348.08$ ,  $p<0.001$ ), but no GROUP by FREQ interaction  
420 ( $F(4,112)=0.67$ ,  $p=0.61$ ). Average across frequencies, the power of ongoing tracking error was  
421 15% smaller when the target motion was made predictable, a value that matches well the  
422 associated 13% reduction in mean tracking error. Regarding the adaptation trials, for both early  
423 (first 4) and late (last 4) adaptation trials, we found no main effect of GROUP ( $F(1,28)<1.86$ ,  
424  $p>0.18$ ), as well as no GROUP by FREQ interaction ( $F(4,112)<1.99$ ,  $p>0.10$ ), still here the  
425 amplitude of mean tracking error was comparable in TR and TR8 groups. Overall, apart from  
426 an occasional scaling difference (that matches with a signal-dependent-noise effect), the  
427 dynamics of tracking error was rather similar under predictable and unpredictable conditions,  
428 thereby suggesting that feedback/feedforward processes were similarly at play under both  
429 conditions.

430

#### 431 *Extra analyses*

432 Following adaptation of reaching movements, we found a massive transfer for tracking  
433 movements. Still during reach training, participants only performed center-out movements. In  
434 contrast, during tracking participants had to face both situations in which the target could get  
435 closer or move away from the center of the screen. As a result, we decided to examine whether  
436 transfer of adaptation was as large for centripetal (center-in) than for centrifugal (center-out)  
437 movements. Practically each tracking trial was partitioned into a succession of centripetal and  
438 centrifugal episodes based on target motion. We propose to focus first on centripetal tracking  
439 movements that match with the direction of reaching during training. As expected, evidence for  
440 transfer was obvious in that case. Two-way ANOVA of cursor-target distance showed an  
441 interaction between GROUP and BIN ( $F(1,38)=114.06$ ,  $p<0.001$ ). Post hoc showed that initial  
442 tracking error was 31% smaller in experienced participants compared to naïve ones (2.39 vs.

443 3.45 cm;  $p < 0.001$ ). In addition, tracking error remained stable between early and late trials in  
444 experienced participants (Group RT, 2.39 vs. 2.37 cm,  $p = 0.97$ ), while their initial tracking error  
445 was comparable to final tracking error in naïve participants (2.39 vs. 2.37 cm,  $p = 0.90$ ). When  
446 repeating this analysis for centripetal movements that did not match with the direction of center  
447 out reaching movements, evidence for massive transfer was still found. Indeed, not only the  
448 ANOVA showed a significant GROUP by BIN interaction ( $F(1,38) = 74.46$ ,  $p < 0.001$ ), but the  
449 post hoc showed that initial tracking error was 29% smaller in experienced participants  
450 compared to naïve ones (1.83 vs. 2.58 cm;  $p < 0.001$ ), that this error remained stable between  
451 early and late trials in experienced participants (Group RT, 1.83 vs. 1.72 cm,  $p = 0.14$ ), and that  
452 their initial tracking error was comparable to final tracking error in naïve participants (1.83 vs.  
453 1.73 cm,  $p = 0.32$ ). Altogether, these results demonstrate that visuomotor adaptation acquired  
454 exclusively under center-out reaching movements generalized well to both centripetal and  
455 centrifugal tracking movements.

456       Feedforward control is a key attribute of fast reaching movements. Although we have  
457 provided evidence that movement durations were minimal during baseline trials (about 210-  
458 220 ms), we have not ensured that movement were similarly rapid under the rotated trials. To  
459 achieve this goal, using a two-way ANOVA (GROUP by COND), we have compared mean  
460 movement durations under baseline and rotated trials. Results showed no effect of GROUP  
461 ( $F(1,38) = 0.199$ ,  $p = 0.66$ ), COND ( $F(1,38) = 2.205$ ,  $p = 0.14$ ), as well as no interaction  
462 ( $F(1,38) = 0.07$ ,  $p = 0.79$ ). Mean movement times (MT) during rotated trials were 217 and 223 ms  
463 respectively for TR and RT groups. Altogether reaching movements performed under the  
464 visuomotor rotation were as fast as those performed under baseline, and thus as prone to  
465 feedforward control. We also investigated whether transfer from tracking to reaching would be  
466 facilitated in our slowest participants under the assumption that longer reaching movements are  
467 more prone for feedback processes to kick in. Using mean individual MT during the adaptation

468 phase, each group of participants was split in two subgroups (10 faster mean MT=190 ms vs.  
469 10 slower mean MT=250 ms). In line with our hypothesis, we found traces of better transfer in  
470 slower participants. Indeed, although prior tracking training allowed a reduction in reach spatial  
471 error of 2.0 cm (-29%) for slow participants, this reduction reached 1.6 cm for fast participants  
472 (-24%). However, two-way ANOVA with SPEED (FAST vs. SLOW) and GROUP as between  
473 subject-factors failed to provide a significant interaction ( $p=0.65$ ), possibly suggesting that  
474 greater disparity in MT between SLOW and FAST participants (here 60ms) is needed to  
475 observe a reliable impact of MT on transfer.

476 The possibility that participants implemented an explicit strategy (re-aiming) when  
477 adapting their reaching movements was investigated by comparing their reaction times during  
478 baseline and rotated trials. A two-way ANOVA (GROUP by COND) showed an effect of  
479 COND ( $F(1,38)=12.012$ ,  $p<0.01$ ) consistent with an increase in reaction time under the rotated  
480 trials (baseline=315 vs. rotated=326 ms). However, there was no effect of GROUP  
481 ( $F(1,38)=0.336$ ,  $p=0.56$ ), nor GROUP by COND interaction ( $F(1,38)=0.718$ ,  $p=0.40$ ). Given  
482 that re-aiming is typically associated with lengthenings in reaction time ranging from +200 to  
483 +400ms [16,37,38], the much lower increase in reaction time observed in our study (+11ms)  
484 does not match with the implementation of an explicit re-aiming strategy.

485 When first exposed to the rotation, Figure 5 suggests that initial error is smaller during  
486 tracking than reaching, whereas terminal errors are rather comparable, giving the impression  
487 that reduction of error extends further for reaching than tracking. Because an asymmetry in the  
488 extent of adaptation could be the source of our asymmetrical transfer between reaching and  
489 tracking, additional analyses were performed to examine this possibility. When analyzing  
490 directional error of reaching trial by trial, we found  $42^\circ$  for the first one, and  $10^\circ$  for the last  
491 one, suggesting an extent adaptation of 76%. When the extent of adaptation was computed  
492 using directional error between the first ( $18^\circ$ ) and last tracking trial ( $6^\circ$ ), we obtain 67%, a

493 supposedly smaller value. However, we reasoned that, given the duration of our tracking trial  
494 (10s), we may have underestimated the initial detrimental effect of the rotation. Indeed, when  
495 directional error was restricted to the first second considered in the analysis (i.e. from  $t=1s$  to  
496  $t=2s$ , as the very first second was discarded) of the first tracking trial, we found a greater initial  
497 error ( $26^\circ$ ). When that initial tracking error was taken into account, the extent of adaptation in  
498 tracking and reaching appeared very similar (77 vs. 76%). Altogether, it is unlikely that the  
499 asymmetrical transfer found between our reaching and tracking task originates from differences  
500 in the extent of adaptation.

501 Finally, we wished to examine whether the smoothness of tracking movements was  
502 influenced by prior reach training. Specifically, we wished to examine whether massive transfer  
503 from reaching to tracking could simply result from RT participants who would persist in using  
504 discrete/intermittent movements during tracking. To achieve this goal, we analyzed fluctuations  
505 in cursor tangential velocity and acceleration, and tested whether those fluctuations were greater  
506 in RT participants compared to TR participants. We reasoned that more intermittent movement  
507 during tracking should be associated with larger standard deviations (SD) in cursor velocity and  
508 acceleration. Two-way ANOVAs conducted on these fluctuations led to similar results for  
509 velocity and acceleration, namely we found no effect of GROUP ( $F(1,38) < 3.42$ ,  $p > 0.05$ ), but  
510 an effect of BIN ( $F(1,38) > 9.36$ ,  $p < 0.01$ ) as well as a GROUP by BIN interaction ( $F(1,38) > 4.88$ ,  
511  $p < 0.05$ ). In both cases the post-hoc of the interaction revealed that during early practice,  
512 experienced participants (Group RT) exhibited smaller fluctuations in cursor velocity (-9%;  
513 9.72 vs. 10.71 cm/s) and acceleration (-12%; 226.7 vs. 256.2  $cm/s^2$ ) than naïve participants  
514 (Group TR). Altogether these analyses rule out the possibility that massive transfer from  
515 reaching to tracking originates from a persistence in using fractionated (point-to-point)  
516 movements. The increased jerkiness exhibited by TR participants during tracking is probably  
517 consecutive to the fact that they triggered more corrective movements than RT participants.

518

519

520

## 521 **DISCUSSION**

522       The goal of this study was to investigate to which extent prior adaptation to visuomotor  
523 rotation acquired during discrete reaching might transfer to continuous tracking, and vice versa.  
524 So far, our study brought several main findings. Concerning the effect of prior training of  
525 reaching, the analyses of tracking in terms of spatial accuracy and directional bias showed  
526 nearly full transfer of adaptation, thereby indicating excellent generalization from reaching to  
527 tracking movements. Regarding the effect of prior training of tracking, the same analyses  
528 conducted on reaching movements revealed contrasting results, with very limited generalization  
529 from tracking to reaching movements. Importantly, a control experiment indicated that this very  
530 limited transfer was similarly observed whether prior training of tracking was conducted with  
531 a predictable or an unpredictable target motion. We propose now to discuss these observations,  
532 as well as the possible mechanisms that led to this strong asymmetrical transfer between  
533 reaching and tracking movements.

534

### 535 **Full transfer from reaching to tracking**

536       When participants had prior training with the rotation under reaching movements, we  
537 found that they subsequently exhibited better tracking performance under the rotation compared  
538 to naïve participants. Specifically, experienced participants exhibited initial tracking  
539 performance that was comparable to that of naïve participants at the end of training. These  
540 results were confirmed by both the analyses of cursor-target distance and directional bias.  
541 Altogether those results speak for (nearly) full transfer of adaptation from reaching to tracking,  
542 as tracking performance was similar no matter participants were trained via the reaching or the

543 tracking task. These results are consistent with the study of Abeele and Bock [23] in which  
544 large transfer (about 80%) was observed from reaching to tracking. They are also consistent  
545 with the study of Ikegami et al [39] in which nearly full transfer was found from discrete out-  
546 and-back movement toward rhythmic movement. However, these results contrast with those of  
547 Tong and Flanagan [24] in which previous adaptation of reaching to visual feedback rotated in  
548 one direction did not impair subsequent adaptation of tracking to visual feedback rotated in the  
549 opposite direction. Yet, our results are consistent with the view that adaptation of  
550 reaching/pointing movements generalizes well to other movement types, as previously found  
551 when testing for generalization to circular movements during force field adaptation [40], or to  
552 ocular saccades following target jump adaptation [41].

553         Our extra analyses showed that this generalization from reaching to tracking extended  
554 beyond the context in which reaching movements were performed. Indeed, we found that both  
555 centrifugal and centripetal tracking movements benefited from previous adaptation of reaching.  
556 Altogether these analyses speak for massive generalization from well characterized 10 cm  
557 center-out reaching movements to a much wider variety of movements, allowing accurate  
558 tracking even for out-to-center movements and in possibly unvisited workspace areas.  
559 Furthermore, the fact that tracking movement smoothness was better in experienced participants  
560 rules out the possibility that the benefit provided by reaching practice follows from relying on  
561 a point-to-point strategy during subsequent tracking.

562

### 563 **Limited transfer from tracking to reaching**

564         Prior experience with the rotation through tracking movements did not benefit much to  
565 subsequent reaching movements performed under the rotation. Indeed, when comparing initial  
566 performance of experienced participants and late performance of naïve ones, we found virtually  
567 no transfer for directional error, and only rather modest transfer for spatial error (27%). This

568 slight difference might stem from the fact that spatial error is measured at the end of movement  
569 whereas directional error is measured near the onset of movement. As a result, spatial error is  
570 more likely to be influenced by feedback mechanisms than directional error, which is too early  
571 for a possible intervention of any feedback processes. In this context, it makes sense that we  
572 observed no transfer for directional error, but slight transfer for spatial error as it might have  
573 allowed feedback processes (presumably updated by tracking training) to kick in at the end of  
574 the reach.

575         Still, our results contrast with those obtained by Abeele and Bock [23], in which a larger  
576 transfer (about 60%) was observed from tracking to reaching movements. The larger sample  
577 size used here (20 participants per group, as compared to 10 in [23]), and the consistency of our  
578 results over several metrics<sup>1</sup>, provide confidence over the observed effects. However, another  
579 possibly important methodological difference is the use of a joystick here, as opposed to real  
580 arm movement in Abeele and Bock [23]. First, it is possible that proprioceptive information is  
581 more pregnant when using full arm movements as compared to hand movements with a  
582 joystick, offering the possibility to estimate and predict more accurately hand position,  
583 especially during tracking. Altogether it is possible that the feedforward component was more  
584 involved during tracking with full arm movements than with the joystick, thereby favoring  
585 larger transfer across tasks as observed by Abeele and Bock [23]. Second, given the differences  
586 in limb inertia, movement duration is likely to be shorter with the use of a joystick. Although  
587 no explicit information was reported in Abeele and Bock [23] with respect to movement  
588 duration and related instruction given to participants (regarding movement speed, and  
589 possibility to correct), we expect movement duration to be greater for full arm movements  
590 (typically 300-350ms) as compared to movements performed with the joystick (here 210-  
591 230ms). If correct, this longer duration of arm reaching movements (about +100ms) may have

---

<sup>1</sup> In Abeele and Bock (2003) performance was assessed with separate metrics for tracking (spatial error) and reaching (directional error), whereas here we used both metrics in each task.



592 been less restrictive regarding the intervention of feedback processes, thereby reducing the  
593 asymmetry in feedback/feedforward processes between their tracking and reaching task. As an  
594 attempt to address this issue in more details, we reanalyzed our data while separating fast and  
595 slow participants in the reaching task, and observed that transfer from tracking to reaching was  
596 somewhat improved in slow participants. Although the possible implication of movement  
597 duration remains speculative, it is worth noting that our results are consistent with two other  
598 studies conducted on real arm movements: the study of Tong and Flanagan [24], in which the  
599 adaptation of tracking movements did not interfere with previous adaptation on reaching  
600 movements, and the study Ikegami et al [39], in which minimal transfer was found from  
601 continuous rhythmic to discrete movement.

602 To further investigate the critical role of feedback and feedforward processes in our  
603 asymmetrical transfer, we subsequently tested whether transfer from tracking to reaching would  
604 benefit from training with a fully predictable target motion, assuming that predictability should  
605 increase the contribution of feedforward processes [25,26] that might transfer to the reaching  
606 task. Unexpectedly, the results of that control study did not match with this hypothesis since  
607 transfer of adaptation from tracking to reaching remained scarce. How to reconcile this  
608 observation with our initial line of reasoning? In this respect, we believe that our spectral  
609 analyses of cursor-target distance offer key information. Indeed, no key changes were found in  
610 the dynamics of tracking error under predictable and unpredictable target motion. Altogether,  
611 one may argue that in the context of our study, the relative contribution of feedback/feedforward  
612 processes was not dramatically changed by using a predictable target motion.

613

#### 614 **Asymmetrical transfer between reaching and tracking**

615 So far, we have shown that transfer of learning was nearly complete from reaching to  
616 tracking, but much scarcer from tracking to reaching. How can we account for this asymmetrical

617 transfer across tasks? Let us state first that our study is not the first one to report an asymmetrical  
618 transfer in the context of visuomotor adaptation [29,39,42,43], including Abeele and Bock  
619 (2003) who also found an asymmetrical transfer between reaching and tracking (albeit smaller  
620 than our). After reviewing possible methodological concerns that might have impacted our  
621 results, we discuss mechanisms that may underlie this strong asymmetrical transfer.

622 A first concern may lie in the extent to which naïve participants were exposed to rotation  
623 training. Indeed, one may argue that the number of training trials was greater for reaching than  
624 for tracking (160 vs. 40), which may incidentally have favored transfer from reaching to  
625 tracking. However, we do not think this is a fair argument. Indeed, each tracking trial had a  
626 duration of 10s, meaning that overall, participants benefited from 400s of exposure to the  
627 rotation. In contrast, even when considering an average movement time of 250ms per reach  
628 (real MT was 230ms), the total duration of exposure to the rotation during reach training would  
629 not exceed 40s. Altogether, duration of exposure to the visuomotor rotation was about 10 times  
630 longer during tracking than during reaching. If duration of training was critical, we should have  
631 observed the opposite effect, namely a larger transfer from tracking to reaching. We conclude  
632 that the amount of training with the rotation is not a key factor to account for the greater transfer  
633 from reaching to tracking. A similar conclusion was drawn by Ikegami et al [39] when trying  
634 to account for the greater transfer from discrete to rhythmic movements.

635 A second possibility may lie in differential contribution of explicit/implicit processes into  
636 the adaptation of reaching and tracking. Abeele and Bock [23] suggested that, because “*pointing*  
637 *provided much more compelling cognitive cues about the nature of the imposed distortion*”,  
638 tracking may benefit more extensively from explicit strategies developed under reaching than  
639 the other way around. Still, they showed that if participants had to simultaneously perform the  
640 reaching task and a concurrent letter-naming task (as an attempt to minimize the contribution  
641 of explicit processes in adaptation), transfer from reaching to tracking was not impaired.

642 Therefore, the authors concluded “*that the advantage of pointing is not strongly related to a*  
643 *deeper cognitive processing during the pointing than during the tracking task*”. Here the current  
644 experiment was not designed to assess the respective contribution of explicit and implicit  
645 processes. However, although not investigated in Abeele and Bock [23], our protocol included  
646 a few trials testing for after-effects. Not only clear after-effects were found (see Figure 5), but  
647 their persistence through several trials of tracking and reaching speak for the implication of  
648 implicit processes. Moreover, it is unclear how an explicit strategy could be implemented  
649 during tracking given that the target position is changing constantly. Finally, strategic re-aiming  
650 has been evoked during the adaptation of reaching movements, but the fact that our reaction  
651 times remained low (320ms) and rather unaffected by the rotation does not support this  
652 possibility [16,37,38].

653 A third issue may reside in task difficulty. One may argue that transfer should be easier  
654 from a simple to a more difficult task than the other way around [44], and that our tracking task  
655 might be more difficult than the reaching one. In both tasks our participants were explicitly  
656 required to minimize the cursor-target distance. The fact that during baseline trials, spatial error  
657 was slightly greater (+12%) during tracking in comparison to reaching (1.57 vs. 1.40 cm) could  
658 be viewed as a sign that tracking might be a more difficult task than reaching. However, this  
659 difference was no longer observed when tracking was performed with a predictable target  
660 motion (respectively 1.40 vs. 1.38 cm), and yet, the same limited transfer was observed from  
661 tracking to reaching. Task difficulty does not appear therefore as a critical factor to account for  
662 the asymmetrical transfer between reaching and tracking.

663 Let us now discuss the current results in the context of our initial hypothesis, namely that  
664 fast reaching movements are more concerned by feedforward processes, whereas tracking a  
665 moving target is more concerned by feedback processes [4]. In the context of adaptation to  
666 novel arm dynamics, the finding that feedforward adaptation directly translates into functional

667 feedback responses to unanticipated perturbations has been interpreted as evidence that  
668 feedforward and feedback controls share the same internal models [13,14]. Closely related  
669 findings and interpretations were found with rotated visual feedback. Indeed, rapid feedback  
670 responses to visual displacement were also found directly functional after feedforward  
671 adaptation to a rotated feedback [15,17], and interpreted in terms of a shared visuomotor map  
672 for both feedforward and feedback controls [15]. Although the latter were obtained in the  
673 context of fast feedback response to a perturbation (whether mechanical or visual), shared  
674 internal models or visuomotor map, adapted through feedforward control involved in reaching  
675 and used directly for online feedback corrections involved in tracking, could very well explain  
676 the almost complete transfer we observed from reaching to our tracking task.

677       The much-reduced transfer observed in the other direction, however, demonstrates that  
678 adaptation encountered first in tracking was not achieved through the same visuomotor map or  
679 models as developed and used for feedforward control in reaching. Otherwise, an almost  
680 complete transfer would similarly be observed from tracking to reaching. At least partly distinct  
681 mechanisms for feedforward and feedback control are needed to reconcile the asymmetrical  
682 transfer found in our study. Such possibility is put forward in several other studies. First,  
683 inconsistent force fields were found to elicit systematic changes in feedback responses without  
684 equivalent changes in feedforward adaptation [45]. Second, when reaching under mirror  
685 reversal condition, feedback control was not adaptively changed when participants were trained  
686 without online corrections [19,20]. Third, recent findings show that when people learn to  
687 produce a circle-shaped movement, improvements in feedforward and feedback do not always  
688 work in concert [22]. Indeed, although training without online feedback improved both  
689 feedforward and feedback control, training with online feedback benefited only to feedback  
690 control. Considering that the first form of training was targeted to elicit improvements in  
691 feedforward control, whereas the latter was intended to initiate improvements in feedback

692 control, those results match well with our main hypothesis. Namely, improvements in  
693 feedforward control lead to improvements in feedback control, but improvements in feedback  
694 control can be performed in isolation.

695 In the context of feedback and feedforward processes, error representation and processing  
696 are also key ingredients of sensorimotor adaptation [46] that probably differ between reaching  
697 and tracking. In contrast to task performance error (represented here by the cursor-target  
698 distance) that should be similarly available in our reaching and tracking tasks, access to sensory  
699 prediction error (difference between the planned and actual action outcomes) may be more  
700 challenging during tracking. In the case of an unpredictable target, the impossibility to predict  
701 where the target is going to be next prevents *de facto* any planning to be there, and in turn may  
702 impede potential access to sensory prediction error. In the case of a fully predictable target,  
703 however, such planning should in principle be possible, thereby granting possible access to  
704 sensory prediction error. The fact that our main results were unaffected by target predictability  
705 may indicate that continuous involvement of participants in always aligning the cursor with the  
706 moving target is sufficient to impair sensory prediction error. If correct, given the importance  
707 of sensory prediction error in sensorimotor adaptation [3,47–51], it would make sense that the  
708 update of visuomotor maps extends further following reaching movements than tracking ones.

709 To account for asymmetrical transfers found elsewhere in the literature, authors typically  
710 evoke the fact that motor processes and/or adaptation occur at different hierarchical levels  
711 [39,43]. For instance, to account for the observation that prism adaptation transfers from  
712 walking to reaching but not the other way around, Morton and Bastian [43] proposed that  
713 walking “*invokes a more general system for visuomotor remapping, involving recalibration of*  
714 *higher order*”. Similarly, to account for the observation that adaptation to rotated feedback  
715 transfers from discrete to rhythmic arm movement but not vice versa, Ikegami et al [39]  
716 proposed that “*the brain areas specific to discrete process involved higher-level*”. Following

717 our initial line of reasoning (emphasis on feedforward processes in reaching vs. on feedback  
718 processes in tracking), it is tempting to envisage here that the adaptation of feedforward  
719 processes occurs at a higher level in the neural circuitry than feedback processes. This position  
720 resonates with brain imaging studies suggesting separate neural substrate for feedback and  
721 feedforward control [8,52,53]. Although this scheme remains largely speculative, our results  
722 indicate that fast center-out reaching movements are supported by broader (i.e. more  
723 widespread/universal) mechanisms than those engaged in tracking a moving target.

724

## 725 **Conclusion**

726 We have shown that visuomotor adaptation fully transfers from reaching to tracking,  
727 but only modestly transfers from tracking to reaching. At this stage, factors such as the  
728 involvement of explicit processes, task complexity, target motion predictability during tracking,  
729 and amount of training, do not appear as key factors to explain this asymmetrical transfer. In  
730 contrast, the differences between reaching and tracking in terms of separate contributions of  
731 feedforward and feedback processes [4], and their associated differences in error representation  
732 and processing, appear as more promising routes. More generally, this study further documents  
733 the possibility that sensorimotor generalization across tasks is not necessarily a reciprocal  
734 process [29,31,39,42,43], thereby stressing the need for protocols that assess transfer in both  
735 directions.

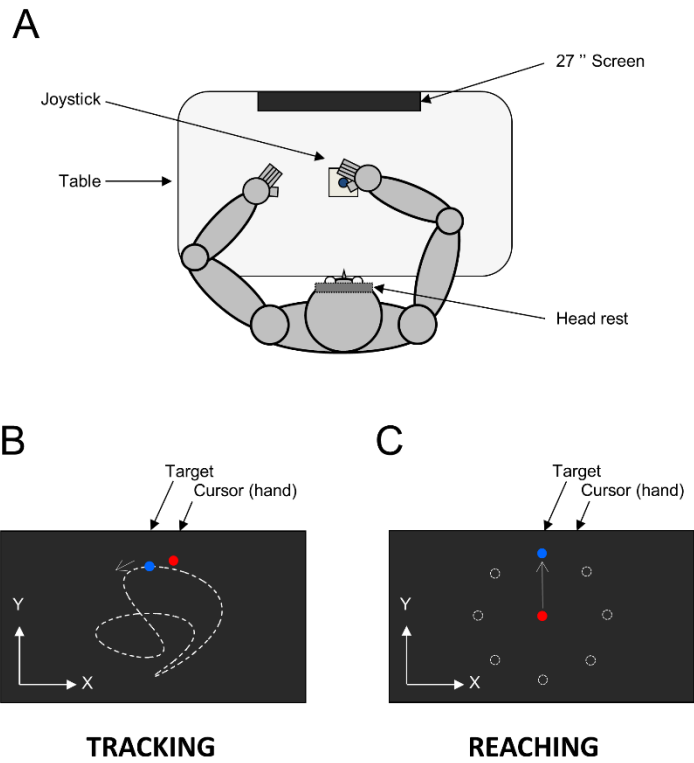
736

- 738 [1] J.W. Krakauer, P. Mazzoni, Human sensorimotor learning: adaptation, skill, and beyond,  
739 *Curr. Opin. Neurobiol.* 21 (2011) 636–644. <https://doi.org/10.1016/j.conb.2011.06.012>.
- 740 [2] R.C. Miall, G.Z. Reckess, H. Imamizu, The cerebellum coordinates eye and hand  
741 tracking movements, *Nat. Neurosci.* 4 (2001) 638–644. <https://doi.org/10.1038/88465>.
- 742 [3] R. Shadmehr, M.A. Smith, J.W. Krakauer, Error correction, sensory prediction, and  
743 adaptation in motor control, *Annu. Rev. Neurosci.* 33 (2010) 89–108.  
744 <https://doi.org/10.1146/annurev-neuro-060909-153135>.
- 745 [4] C.S. Yang, N.J. Cowan, A.M. Haith, De novo learning versus adaptation of continuous  
746 control in a manual tracking task, *ELife.* 10 (2021) e62578.  
747 <https://doi.org/10.7554/eLife.62578>.
- 748 [5] S.B.M. Yoo, J.C. Tu, S.T. Piantadosi, B.Y. Hayden, The neural basis of predictive  
749 pursuit, *Nat. Neurosci.* 23 (2020) 252–259. <https://doi.org/10.1038/s41593-019-0561-6>.
- 750 [6] M. Mulder, D.M. Pool, D.A. Abbink, E.R. Boer, P.M.T. Zaal, F.M. Drop, K. van der El,  
751 M.M. van Paassen, Manual Control Cybernetics: State-of-the-Art and Current Trends,  
752 *IEEE Trans. Hum.-Mach. Syst.* 48 (2018) 468–485.  
753 <https://doi.org/10.1109/THMS.2017.2761342>.
- 754 [7] S.H. Scott, Optimal feedback control and the neural basis of volitional motor control,  
755 *Nat. Rev. Neurosci.* 5 (2004) 532–546. <https://doi.org/10.1038/nrn1427>.
- 756 [8] R.D. Seidler, D.C. Noll, G. Thiers, Feedforward and feedback processes in motor  
757 control, *NeuroImage.* 22 (2004) 1775–1783.  
758 <https://doi.org/10.1016/j.neuroimage.2004.05.003>.
- 759 [9] X. Zhang, S. Wang, J.B. Hoagg, T.M. Seigler, The Roles of Feedback and Feedforward  
760 as Humans Learn to Control Unknown Dynamic Systems, *IEEE Trans. Cybern.* 48  
761 (2018) 543–555. <https://doi.org/10.1109/TCYB.2016.2646483>.
- 762 [10] M.A. Ahmadi-Pajouh, F. Towhidkhal, R. Shadmehr, Preparing to Reach: Selecting an  
763 Adaptive Long-Latency Feedback Controller, *J. Neurosci.* 32 (2012) 9537–9545.
- 764 [11] L. Chomienne, J. Blouin, L. Bringoux, Online corrective responses following target  
765 jump in altered gravito-inertial force field point to nested feedforward and feedback  
766 control, *J. Neurophysiol.* 125 (2020) 154–165. <https://doi.org/10.1152/jn.00268.2020>.
- 767 [12] J.S. Diamond, J.Y. Nashed, R.S. Johansson, D.M. Wolpert, J.R. Flanagan, Rapid  
768 Visuomotor Corrective Responses during Transport of Hand-Held Objects Incorporate  
769 Novel Object Dynamics, *J. Neurosci. Off. J. Soc. Neurosci.* 35 (2015) 10572–10580.  
770 <https://doi.org/10.1523/JNEUROSCI.1376-15.2015>.
- 771 [13] R.S. Maeda, T. Cluff, P.L. Gribble, J.A. Pruszynski, Feedforward and Feedback Control  
772 Share an Internal Model of the Arm’s Dynamics, *J. Neurosci. Off. J. Soc. Neurosci.* 38  
773 (2018) 10505–10514. <https://doi.org/10.1523/JNEUROSCI.1709-18.2018>.
- 774 [14] M.J. Wagner, M.A. Smith, Shared internal models for feedforward and feedback control,  
775 *J. Neurosci. Off. J. Soc. Neurosci.* 28 (2008) 10663–10673.  
776 <https://doi.org/10.1523/JNEUROSCI.5479-07.2008>.
- 777 [15] T. Hayashi, A. Yokoi, M. Hirashima, D. Nozaki, Visuomotor Map Determines How  
778 Visually Guided Reaching Movements are Corrected Within and Across Trials, *ENeuro.*  
779 3 (2016) ENEURO.0032-16.2016. <https://doi.org/10.1523/ENeuro.0032-16.2016>.
- 780 [16] N. Saijo, H. Gomi, Multiple Motor Learning Strategies in Visuomotor Rotation, *PLoS*  
781 *ONE.* 5 (2010) e9399. <https://doi.org/10.1371/journal.pone.0009399>.
- 782 [17] S. Telgen, D. Parvin, J. Diedrichsen, Mirror Reversal and Visual Rotation Are Learned  
783 and Consolidated via Separate Mechanisms: Recalibrating or Learning De Novo?, *J.*  
784 *Neurosci.* 34 (2014) 13768–13779. <https://doi.org/10.1523/JNEUROSCI.5306-13.2014>.

- 785 [18] M.N. Abdelghani, D.B. Tweed, Learning course adjustments during arm movements  
786 with reversed sensitivity derivatives, *BMC Neurosci.* 11 (2010) 150.  
787 <https://doi.org/10.1186/1471-2202-11-150>.
- 788 [19] V. Gritsenko, J.F. Kalaska, Rapid online correction is selectively suppressed during  
789 movement with a visuomotor transformation, *J. Neurophysiol.* 104 (2010) 3084–3104.  
790 <https://doi.org/10.1152/jn.00909.2009>.
- 791 [20] S. Kasuga, S. Telgen, J. Ushiba, D. Nozaki, J. Diedrichsen, Learning feedback and  
792 feedforward control in a mirror-reversed visual environment, *J. Neurophysiol.* 114  
793 (2015) 2187–2193. <https://doi.org/10.1152/jn.00096.2015>.
- 794 [21] R.S. Maeda, P.L. Gribble, J.A. Pruszynski, Learning New Feedforward Motor  
795 Commands Based on Feedback Responses, *Curr. Biol.* 30 (2020) 1941–1948.e3.  
796 <https://doi.org/10.1016/j.cub.2020.03.005>.
- 797 [22] A. Raichin, A. Shkedy Rabani, L. Shmuelof, Motor skill training without online visual  
798 feedback enhances feedforward control, *J. Neurophysiol.* 126 (2021) 1604–1613.  
799 <https://doi.org/10.1152/jn.00145.2021>.
- 800 [23] S. Abeele, O. Bock, Transfer of sensorimotor adaptation between different movement  
801 categories, *Exp. Brain Res.* 148 (2003) 128–132. [https://doi.org/10.1007/s00221-002-](https://doi.org/10.1007/s00221-002-1317-0)  
802 [1317-0](https://doi.org/10.1007/s00221-002-1317-0).
- 803 [24] C. Tong, J.R. Flanagan, Task-specific internal models for kinematic transformations, *J.*  
804 *Neurophysiol.* 90 (2003) 578–585. <https://doi.org/10.1152/jn.01087.2002>.
- 805 [25] F.M. Drop, R. de Vries, M. Mulder, H.H. Bühlhoff, The Predictability of a Target Signal  
806 Affects Manual Feedforward Control, *IFAC-Pap.* 49 (2016) 177–182.  
807 <https://doi.org/10.1016/j.ifacol.2016.10.482>.
- 808 [26] S.-Y. Lam, A. Zénon, Information Rate in Humans during Visuomotor Tracking,  
809 *Entropy.* 23 (2021) 228. <https://doi.org/10.3390/e23020228>.
- 810 [27] R.C. Oldfield, The assessment and analysis of handedness: the Edinburgh inventory,  
811 *Neuropsychologia.* 9 (1971) 97–113.
- 812 [28] N. Gouirand, J. Mathew, E. Brenner, F. Danion, Eye movements do not play an  
813 important role in the adaptation of hand tracking to a visuomotor rotation, *J.*  
814 *Neurophysiol.* (2019). <https://doi.org/10.1152/jn.00814.2018>.
- 815 [29] J. Mathew, P.-M. Bernier, F.R. Danion, Asymmetrical Relationship between Prediction  
816 and Control during Visuomotor Adaptation, *ENeuro.* 5 (2018).  
817 <https://doi.org/10.1523/ENEURO.0280-18.2018>.
- 818 [30] J. Mathew, F.R. Sarlegna, P.-M. Bernier, F.R. Danion, Handedness Matters for Motor  
819 Control But Not for Prediction, *ENeuro.* 6 (2019).  
820 <https://doi.org/10.1523/ENEURO.0136-19.2019>.
- 821 [31] S. Abeele, O. Bock, Transfer of sensorimotor adaptation between different movement  
822 categories, *Exp. Brain Res.* 148 (2003) 128–132.
- 823 [32] P.-M. Bernier, J. Mathew, F.R. Danion, Composition and decomposition of visuomotor  
824 maps during manual tracking, *J. Neurophysiol.* 126 (2021) 1685–1697.  
825 <https://doi.org/10.1152/jn.00058.2021>.
- 826 [33] P.K. Mutha, K.Y. Haaland, R.L. Sainburg, Rethinking Motor Lateralization: Specialized  
827 but Complementary Mechanisms for Motor Control of Each Arm, *PLOS ONE.* 8 (2013)  
828 e58582. <https://doi.org/10.1371/journal.pone.0058582>.
- 829 [34] J. Wang, R.L. Sainburg, Limitations in interlimb transfer of visuomotor rotations, *Exp.*  
830 *Brain Res.* 155 (2004) 1–8. <https://doi.org/10.1007/s00221-003-1691-2>.
- 831 [35] J. Wang, R.L. Sainburg, Generalization of Visuomotor Learning Between Bilateral and  
832 Unilateral Conditions, *J. Neurophysiol.* 102 (2009) 2790–2799.  
833 <https://doi.org/10.1152/jn.00444.2009>.



- 834 [36] R.C. Miall, J.K. Jackson, Adaptation to visual feedback delays in manual tracking:  
835 evidence against the Smith Predictor model of human visually guided action, *Exp. Brain*  
836 *Res.* 172 (2006) 77–84. <https://doi.org/10.1007/s00221-005-0306-5>.
- 837 [37] J. Fernandez-Ruiz, W. Wong, I.T. Armstrong, J.R. Flanagan, Relation between reaction  
838 time and reach errors during visuomotor adaptation, *Behav. Brain Res.* 219 (2011) 8–14.  
839 <https://doi.org/10.1016/j.bbr.2010.11.060>.
- 840 [38] M.K. Rand, S. Rentsch, Eye-Hand Coordination during Visuomotor Adaptation with  
841 Different Rotation Angles: Effects of Terminal Visual Feedback, *PloS One.* 11 (2016)  
842 e0164602. <https://doi.org/10.1371/journal.pone.0164602>.
- 843 [39] T. Ikegami, M. Hirashima, G. Taga, D. Nozaki, Asymmetric transfer of visuomotor  
844 learning between discrete and rhythmic movements, *J. Neurosci. Off. J. Soc. Neurosci.*  
845 30 (2010) 4515–4521. <https://doi.org/10.1523/JNEUROSCI.3066-09.2010>.
- 846 [40] M.A. Conditt, F. Gandolfo, F.A. Mussa-Ivaldi, The motor system does not learn the  
847 dynamics of the arm by rote memorization of past experience, *J. Neurophysiol.* 78  
848 (1997) 554–560.
- 849 [41] O. Bock, G. Schmitz, V. Grigorova, Transfer of adaptation between ocular saccades and  
850 arm movements, *Hum. Mov. Sci.* 27 (2008) 383–395.
- 851 [42] J.W. Krakauer, P. Mazzoni, A. Ghazizadeh, R. Ravindran, R. Shadmehr, Generalization  
852 of motor learning depends on the history of prior action, *PLoS Biol.* 4 (2006) e316.  
853 <https://doi.org/10.1371/journal.pbio.0040316>.
- 854 [43] S.M. Morton, A.J. Bastian, Prism adaptation during walking generalizes to reaching and  
855 requires the cerebellum, *J. Neurophysiol.* 92 (2004) 2497–2509.  
856 <https://doi.org/10.1152/jn.00129.2004>.
- 857 [44] J. Wang, R.L. Sainburg, Interlimb transfer of novel inertial dynamics is asymmetrical, *J.*  
858 *Neurophysiol.* 92 (2004) 349–360. <https://doi.org/10.1152/jn.00960.2003>.
- 859 [45] N. Yousif, J. Diedrichsen, Structural learning in feedforward and feedback control, *J.*  
860 *Neurophysiol.* 108 (2012) 2373–2382. <https://doi.org/10.1152/jn.00315.2012>.
- 861 [46] J.R. Morehead, J.-J.O. de Xivry, A Synthesis of the Many Errors and Learning Processes  
862 of Visuomotor Adaptation, *BioRxiv.* (2021) 2021.03.14.435278.  
863 <https://doi.org/10.1101/2021.03.14.435278>.
- 864 [47] P.A. Butcher, J.A. Taylor, Decomposition of a sensory prediction error signal for  
865 visuomotor adaptation, *J. Exp. Psychol. Hum. Percept. Perform.* 44 (2018) 176–194.  
866 <https://doi.org/10.1037/xhp0000440>.
- 867 [48] J.W. Krakauer, Motor learning and consolidation: the case of visuomotor rotation, *Adv.*  
868 *Exp. Med. Biol.* 629 (2009) 405–421. [https://doi.org/10.1007/978-0-387-77064-2\\_21](https://doi.org/10.1007/978-0-387-77064-2_21).
- 869 [49] K. Lee, Y. Oh, J. Izawa, N. Schweighofer, Sensory prediction errors, not performance  
870 errors, update memories in visuomotor adaptation, *Sci. Rep.* 8 (2018) 16483.  
871 <https://doi.org/10.1038/s41598-018-34598-y>.
- 872 [50] P. Mazzoni, J.W. Krakauer, An implicit plan overrides an explicit strategy during  
873 visuomotor adaptation, *J. Neurosci. Off. J. Soc. Neurosci.* 26 (2006) 3642–3645.  
874 <https://doi.org/10.1523/JNEUROSCI.5317-05.2006>.
- 875 [51] Y.-W. Tseng, J. Diedrichsen, J.W. Krakauer, R. Shadmehr, A.J. Bastian, Sensory  
876 prediction errors drive cerebellum-dependent adaptation of reaching, *J. Neurophysiol.* 98  
877 (2007) 54–62. <https://doi.org/10.1152/jn.00266.2007>.
- 878 [52] S.T. Grafton, P. Schmitt, J. Van Horn, J. Diedrichsen, Neural substrates of visuomotor  
879 learning based on improved feedback control and prediction, *NeuroImage.* 39 (2008)  
880 1383–1395. <https://doi.org/10.1016/j.neuroimage.2007.09.062>.
- 881 [53] K.L. Macuga, S.H. Frey, Differential contributions of the superior and inferior parietal  
882 cortex to feedback versus feedforward control of tools, *NeuroImage.* 92 (2014) 36–45.  
883 <https://doi.org/10.1016/j.neuroimage.2014.01.024>.



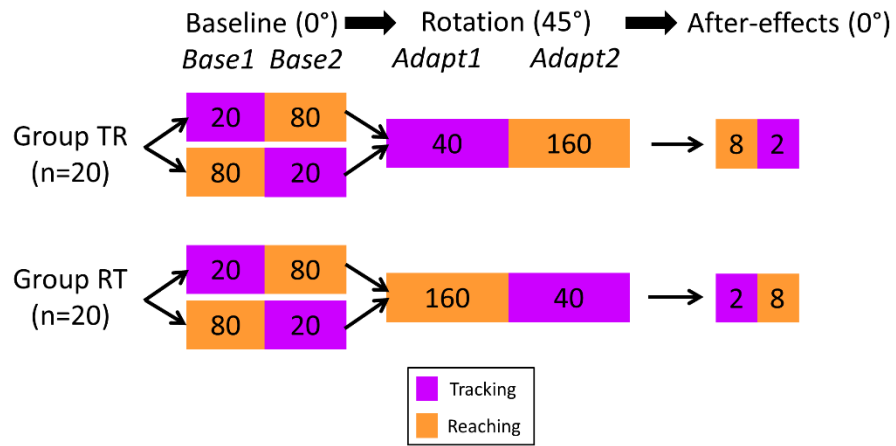
885

886

887 **Figure 1.** Schematic drawing of the experimental setup. A. Top view of the participant sitting  
 888 in the experimental setup. B. Schematic view of the screen during the tracking task. The target  
 889 trajectory (white dotted line) is displayed for illustration purposes (i.e. not visible during the  
 890 actual task) C. Schematic view of the screen during the reaching task (see method for more  
 891 details). Hollow white targets are displayed for illustration purposes (i.e. not visible during the  
 892 actual task).

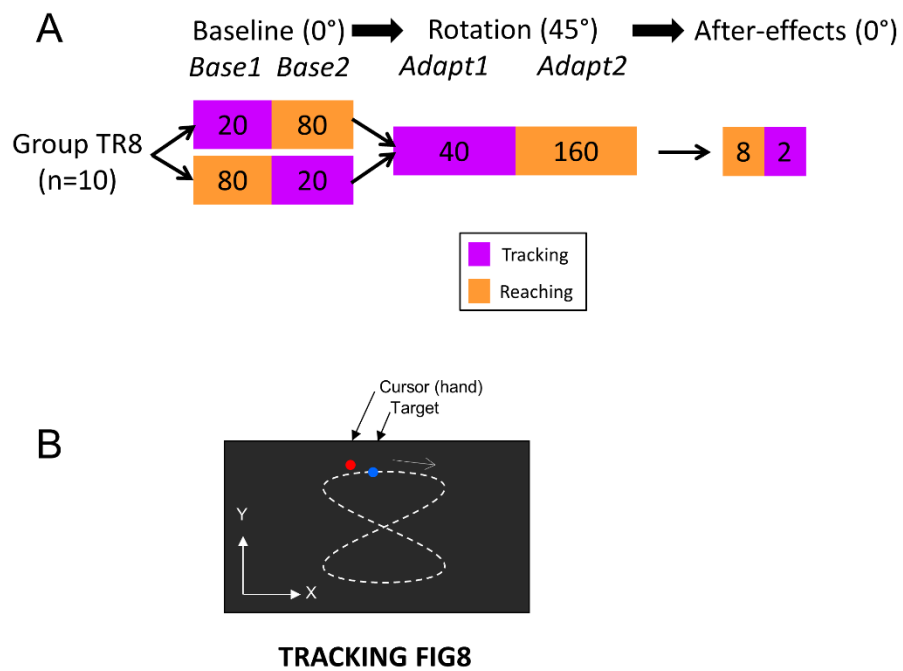
893

894



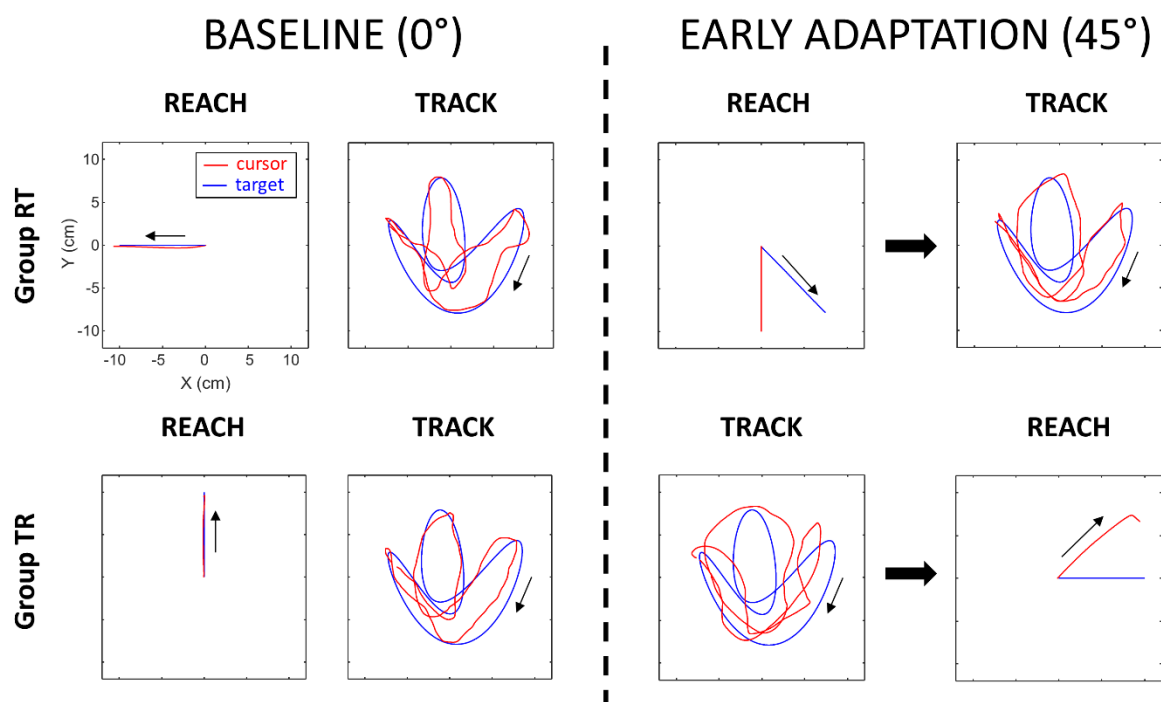
895  
 896  
 897  
 898

**Figure 2.** Experimental design for each group of participants (see Materials and Methods for further information)

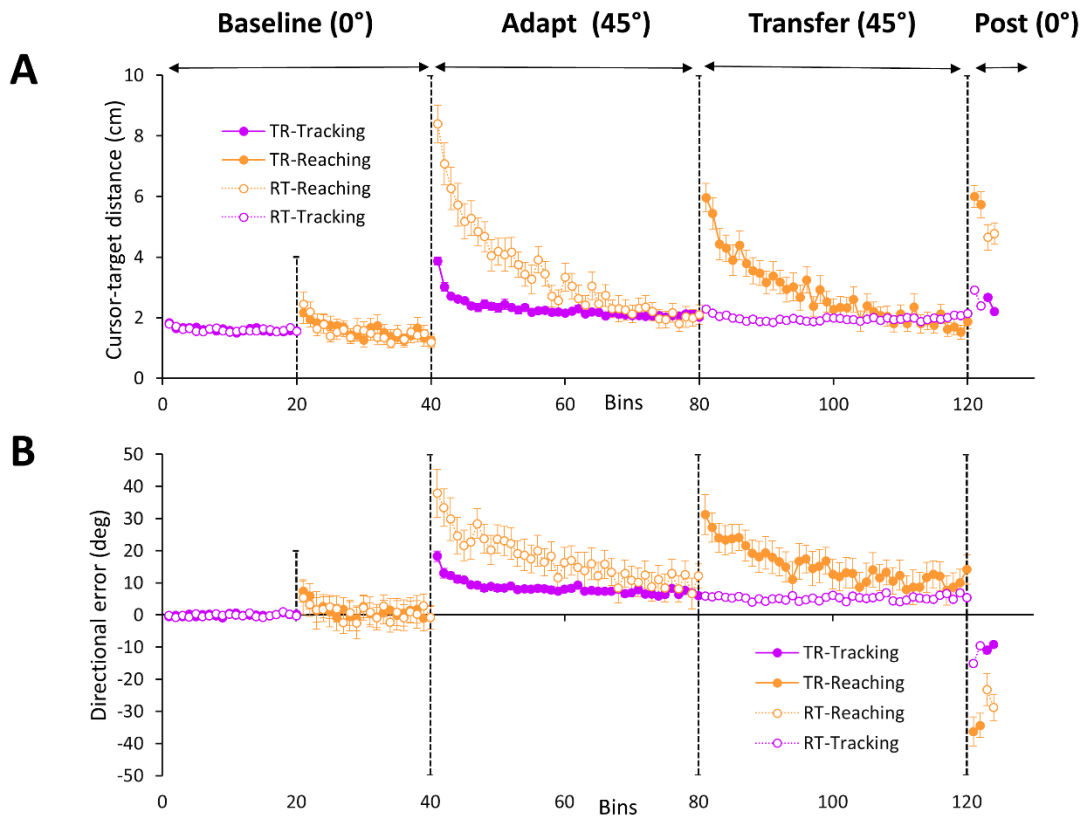


899  
 900  
 901  
 902  
 903  
 904  
 905

**Figure 3.** Control experiment. A. Experimental design B. Schematic view of the screen when tracking the target along the figure 8 pattern. The target trajectory (white dotted line) is displayed for illustration purposes only (i.e. not visible during the actual task, see Materials and Methods for further information).

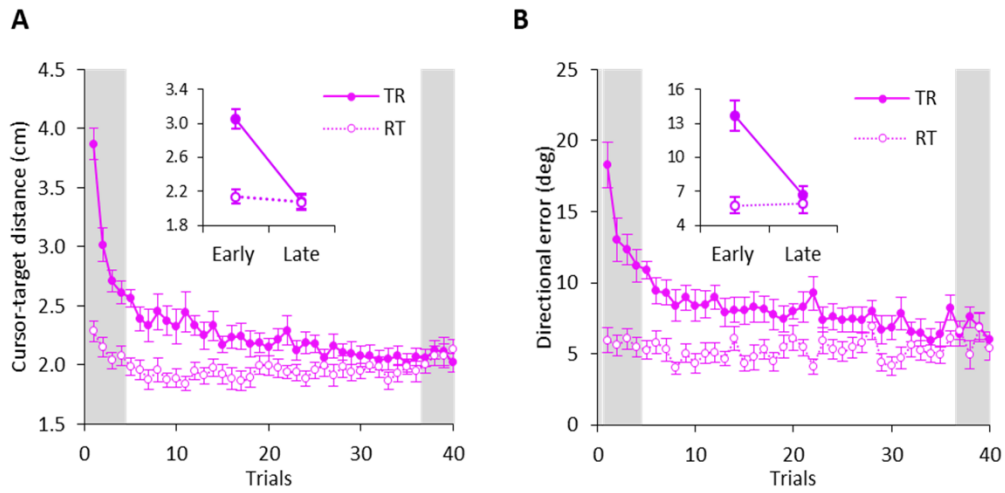


906  
 907 **Figure 4:** Typical trials under each experimental condition. Cursor and target signals during  
 908 baseline and early exposure to the visuomotor rotation. The top and bottom row show trials  
 909 performed respectively by a participant of the RT and TR experimental group. Although each  
 910 tracking trial was 10 s long, only 5 s of signals are displayed for clarity. To make the  
 911 comparison easier, we display trials with the same target trajectory. Note the smaller  
 912 detrimental effect of the rotation when switching from reaching to tracking than from tracking  
 913 to reaching.  
 914  
 915



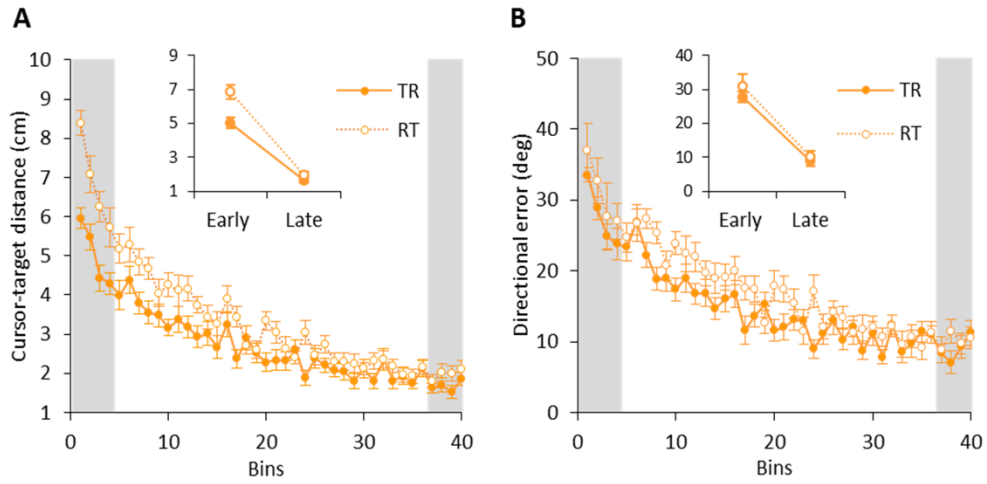
916  
 917 **Figure 5.** Timeline of reaching and tracking performance across all experimental conditions  
 918 and groups. A. Spatial accuracy of reaching and tracking movements. Error bars correspond  
 919 to the standard error of the mean (SEM). B. Same as A for directional error. For both indices,  
 920 note the smoother transition under visuomotor rotation from reaching to tracking than the other  
 921 way around. The order of reaching/tracking during baseline was adjusted for visualization  
 922 purposes.

923  
 924



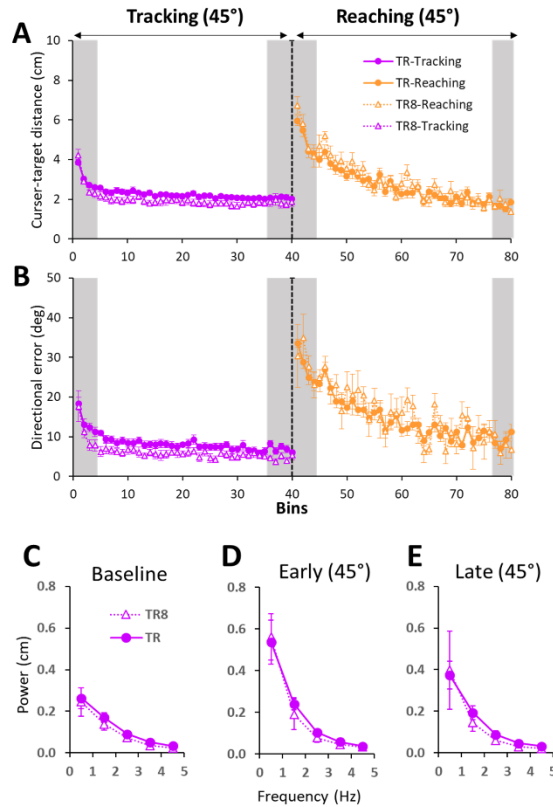
925  
 926  
 927  
 928  
 929  
 930  
 931

**Figure 6.** Tracking performance with and without prior experience with the rotation. *A.* Time course of cursor-target distance as a function of trial and experimental group. *B.* Same as *A* for directional error. Error bars correspond to SEM. For both indices, note the substantial improvement in tracking provided by earlier experience with the rotation during reaching. Vertical gray zones indicate the four trials that were averaged and displayed in the insert.



932  
 933 **Figure 7.** Reaching performance with and without prior experience with the rotation. A. Time  
 934 course of cursor-target distance as a function of bin and experimental group. B. Same as A  
 935 for directional error. Error bars correspond to SEM. For both indices, note the rather modest  
 936 improvement in reaching provided by earlier experience with the rotation during tracking.  
 937 Vertical gray zones indicate the four bins that were averaged and displayed in the insert.  
 938  
 939





940  
 941 **Figure 8.** Effect of target motion predictability. A. Timeline of spatial accuracy of tracking  
 942 during the adaptation phase and of reaching movements during the transfer phase in both TR  
 943 and TR8 groups. Error bars correspond to the standard error of the mean (SEM). Vertical gray  
 944 zones indicate the four bins/trials that were kept and averaged for analysis. B. Same as A for  
 945 directional error. For both indices note the lack of group difference in reaching movements,  
 946 thereby arguing for a lack of transfer in both groups. C. Power spectra of ongoing tracking  
 947 error during baseline trials in TR and TR8 groups. D, and E. Same as C for early and late  
 948 adaptation trials. Error bars correspond to the standard deviation of the mean (SD). Apart  
 949 from a possible scaling difference between groups during baseline trials, note the similarity in  
 950 the dynamics of tracking error.  
 951