



HAL
open science

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

Adrien Coudiere, Enzo Fernandez, Aymar de Ruy, Frederic S Danion

► To cite this version:

Adrien Coudiere, Enzo Fernandez, Aymar de Ruy, Frederic S 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-03795892>

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 Coudière¹, Enzo Fernandez^{1,2}, Aymar de Rugy^{2,3}, and Frederic R. Danion¹

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

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

8
9 ³Centre 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

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°) 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 ± 2.5 yrs, 10 females; Group TR: 20.6 ± 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 ± 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 ± 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 ± 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° 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° 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° 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°

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°) 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→Reach), and Group 2 will be referred
201 as Group RT (Reach→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 ± 2.8 yrs, 8 females, laterality index 79.5 ± 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° for the first one, and 10° 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°) and last tracking trial (6°), 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°). 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 metrics¹, 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

¹ 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**

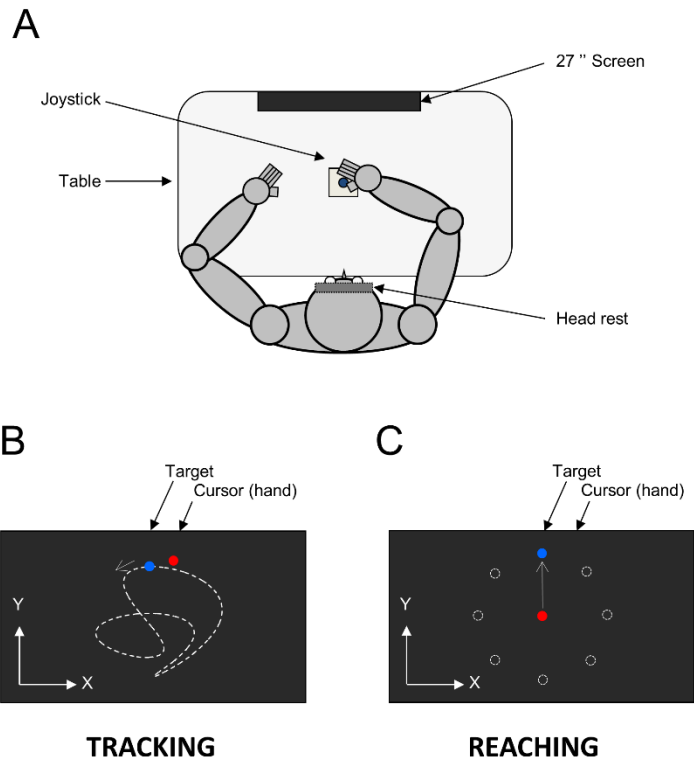
726 We have shown that visuomotor adaptation fully transfers from reaching to tracking,
727 but only modestly transfers from tracking to reaching. At this stage, factors such as the
728 involvement of explicit processes, task complexity, target motion predictability during tracking,
729 and amount of 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.
- 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>.



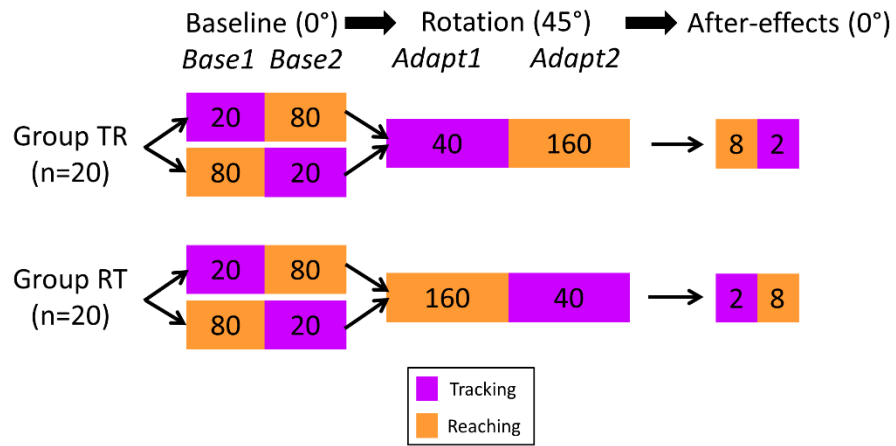
885

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).

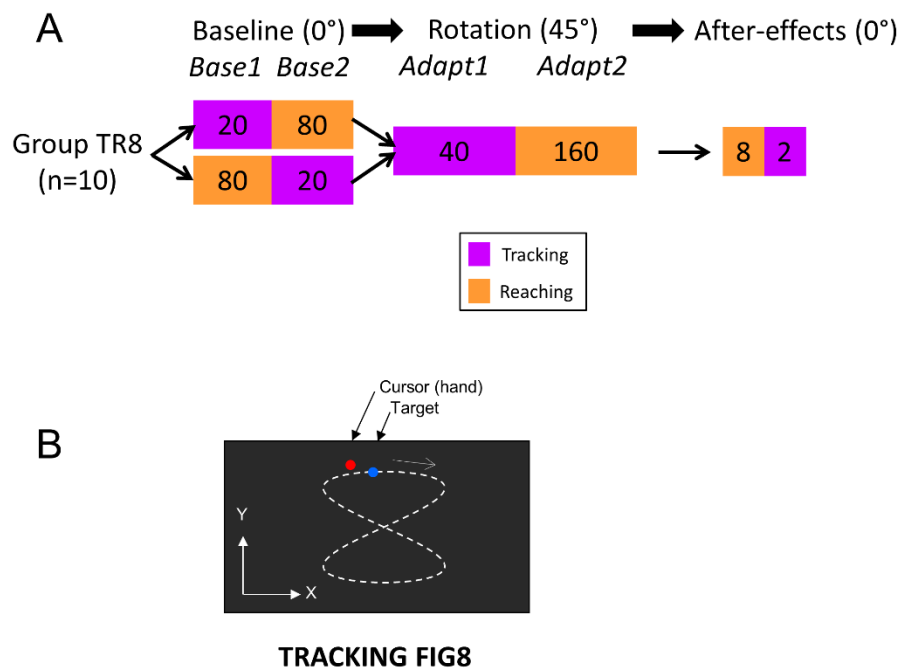
893

894



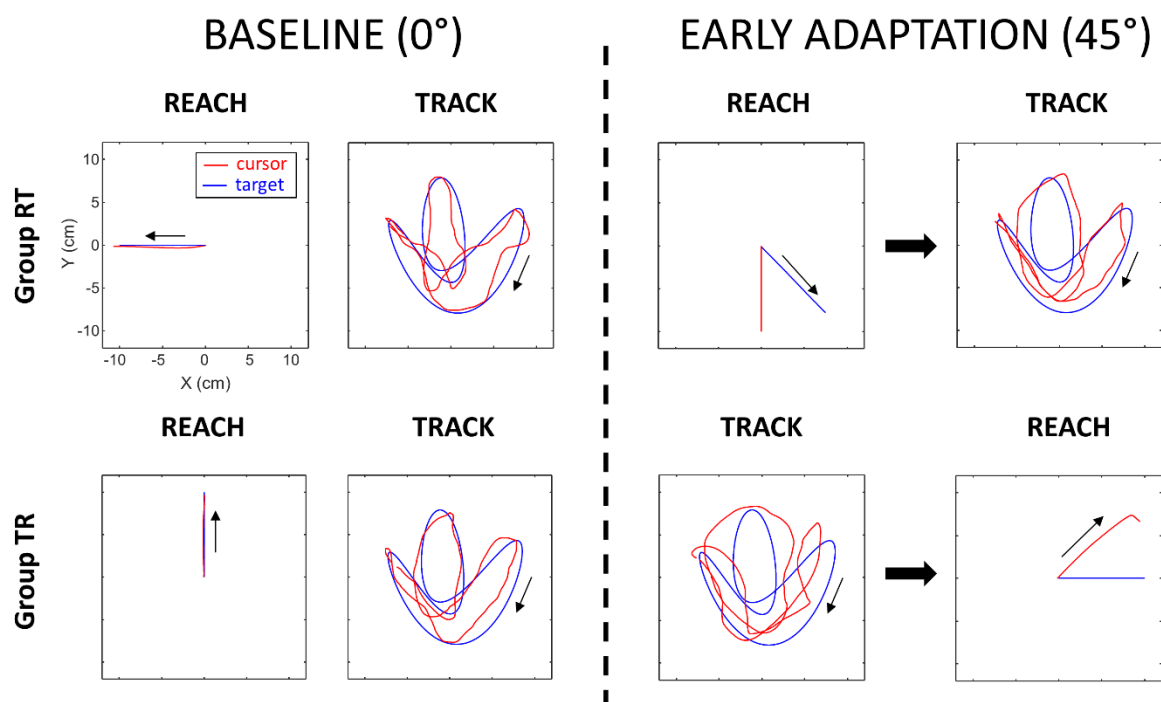
895
 896
 897
 898

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

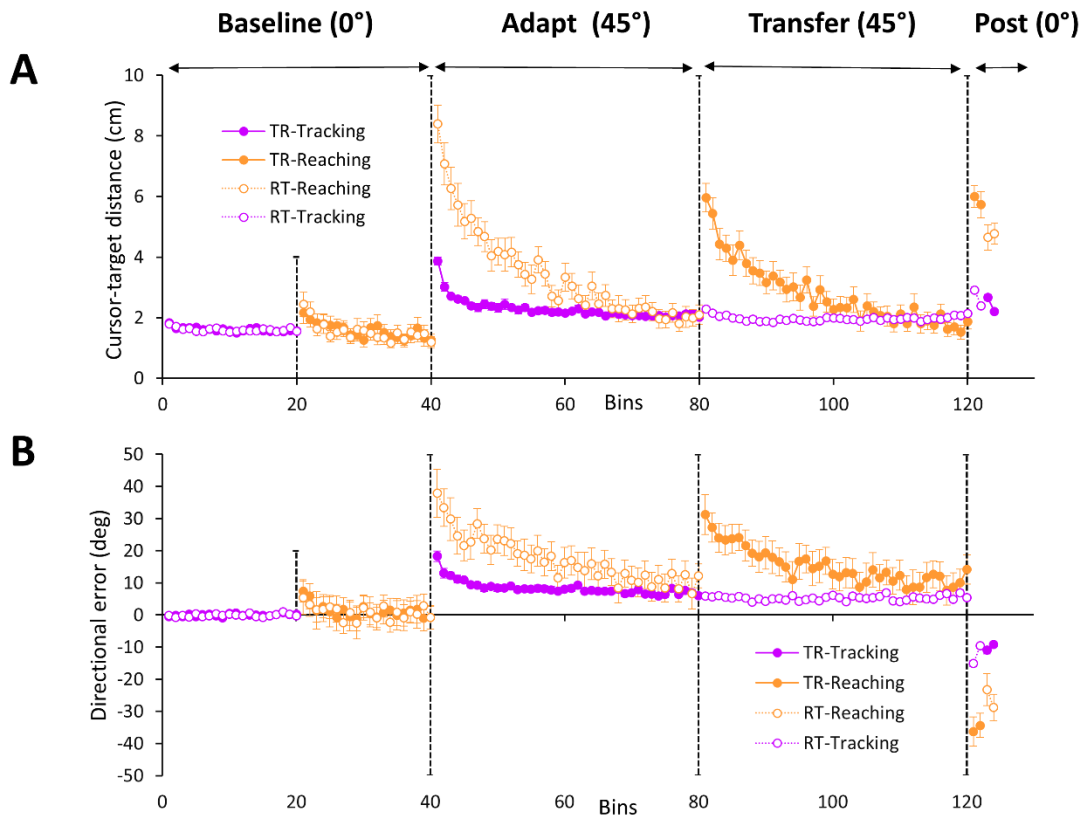


899
 900
 901
 902
 903
 904
 905

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).

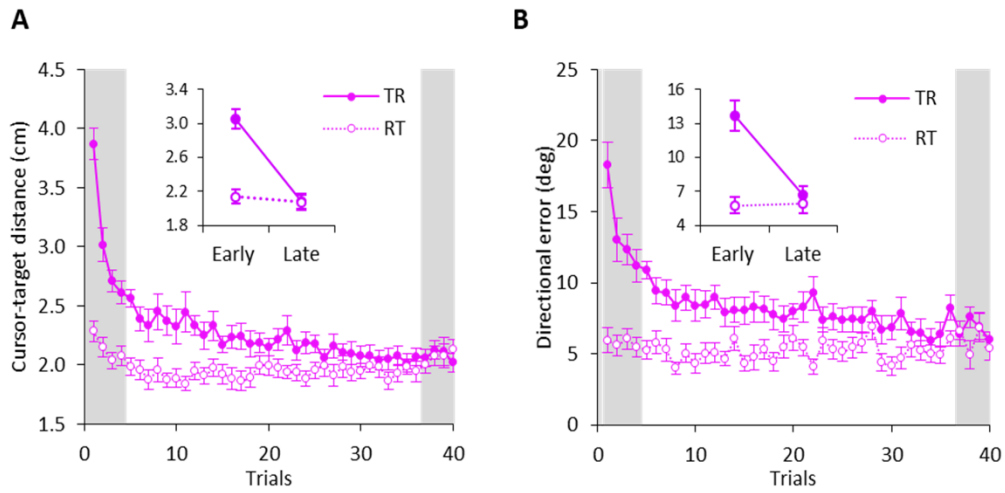


906
 907 **Figure 4:** Typical trials under each experimental condition. Cursor and target signals during
 908 baseline and early exposure to the visuomotor rotation. The top and bottom row show trials
 909 performed respectively by a participant of the RT and TR experimental group. Although each
 910 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

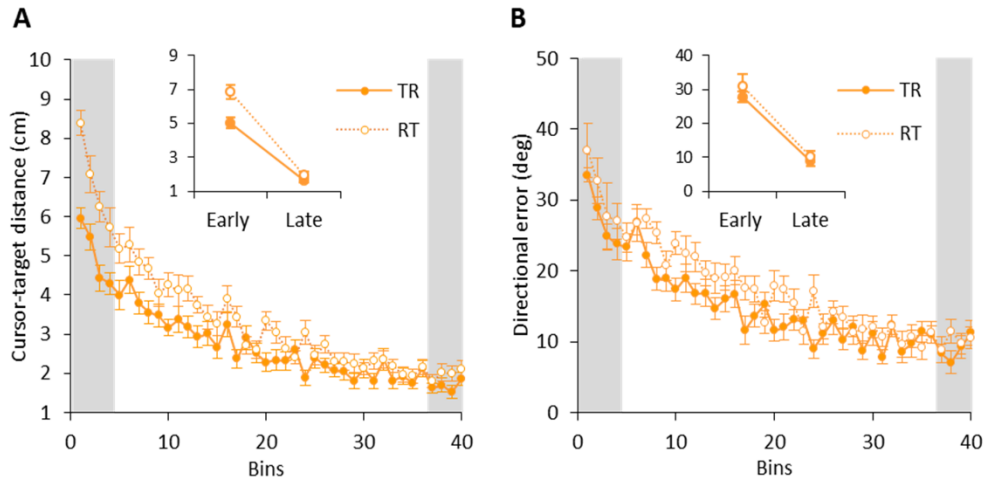


916
917
918
919
920
921
922
923
924

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

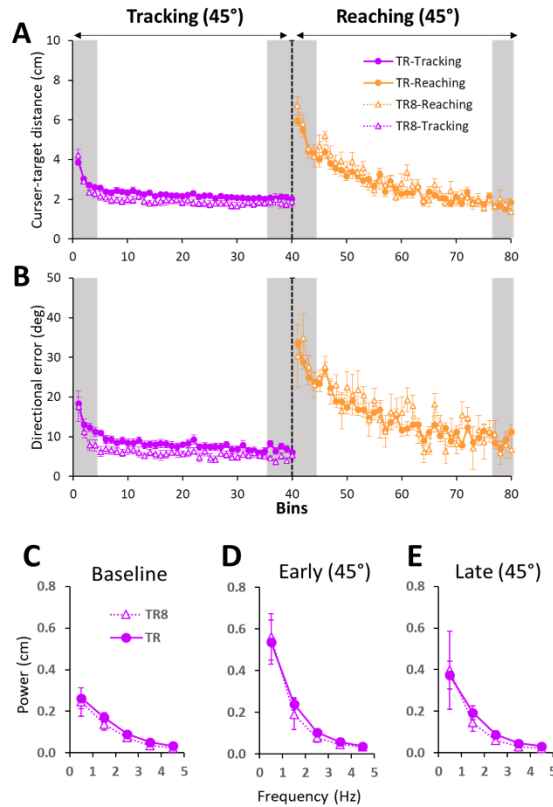


925
 926 **Figure 6.** Tracking performance with and without prior experience with the rotation. A. Time
 927 course of cursor-target distance as a function of trial and experimental group. B. Same as A
 928 for directional error. Error bars correspond to SEM. For both indices, note the substantial
 929 improvement in tracking provided by earlier experience with the rotation during reaching.
 930 Vertical gray zones indicate the four trials that were averaged and displayed in the insert.
 931



932
 933
 934
 935
 936
 937
 938
 939

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



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