



**HAL**  
open science

# Online corrective responses following target jump in altered gravito-inertial force field point to nested feedforward and feedback control

Loïc Chomienne, Jean Blouin, Lionel Bringoux

## ► To cite this version:

Loïc Chomienne, Jean Blouin, Lionel Bringoux. Online corrective responses following target jump in altered gravito-inertial force field point to nested feedforward and feedback control. *Journal of Neurophysiology*, 2020, 10.1152/jn.00268.2020 . hal-03011323

**HAL Id: hal-03011323**

**<https://amu.hal.science/hal-03011323v1>**

Submitted on 18 Nov 2020

**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.

Motor responses to target jump in altered force field

1 Online corrective responses following target jump in altered gravito-inertial force  
2 field point to nested feedforward and feedback control

3 L. Chomienne<sup>1</sup>, J. Blouin<sup>2</sup>, L. Bringoux<sup>1\*</sup>

4 <sup>1</sup>Aix Marseille Univ, CNRS, ISM, Marseille, France

5 <sup>2</sup>Aix-Marseille Univ, CNRS, LNC, Marseille, France

6 \*Correspondence:

7 Dr. Lionel Bringoux

8 [lionel.bringoux@univ-amu.fr](mailto:lionel.bringoux@univ-amu.fr)

9 UMR 7287 CNRS & Aix-Marseille Université - Faculty of Sport Science

10 163 Avenue de Luminy, CP 910 - 13288 Marseille cedex 9

11

12 **Abstract**

13           Studies on goal-directed arm movements have shown a close link between feedforward  
14 and feedback control in protocols where both planning and online control processes faced a  
15 similar type of perturbation, either mechanical or visual. This particular context might have  
16 facilitated the use of an adapted internal model by feedforward and feedback control. Here we  
17 considered this link in a context where after feedforward control was adapted through  
18 proprioception-based processes, feedback control was tested under visual perturbation. We  
19 analyzed the response of the reaching hand to target displacements following adaptation to an  
20 altered force field induced by rotating participants at constant velocity. Reaching corrections  
21 were assessed through variables related to the accuracy (lateral and longitudinal endpoint  
22 errors) and kinematics (movement time, peak velocity) of the corrective movements. The  
23 electromyographic activity of different arm muscles (pectoralis, deltoid, biceps and triceps  
24 brachii) was analyzed. Statistical analyses revealed that accuracy and kinematics of corrective  
25 movements were strikingly alike between normal and altered gravito-inertial force fields.  
26 However, pectoralis and biceps muscle activities recorded during corrective movements were  
27 significantly modified to counteract the effect of rotation-induced Coriolis and centrifugal  
28 forces on the arm. Remarkably, feedback control was functional from the very first time  
29 participants encountered a target jump in the altered force field. Overall, the present results  
30 demonstrate that feedforward control enables immediate functional feedback control even when  
31 applied to distinct sensorimotor processes.

32

33 **New & Noteworthy**

34           We investigated the link between feedforward and feedback control when applying a  
35 double-step perturbation (visual target jump) during reaching movements performed in  
36 modified gravitoinertial environments. Altogether, kinematics and EMG analyses showed that  
37 movements corrections were highly effective in the different force fields suggesting that,  
38 although feedforward and feedback control were driven by different sensory inputs, feedback  
39 control was remarkably functional, from the very first time participants encountered a target  
40 jump in the altered force field.

41 **Running title:**

42 Motor responses to target jump in altered force field  
43

44 **Keywords:**

45 motor control; reaching movement; force field adaptation; double-step paradigm; internal model

46 **Introduction**

47           Catching an object slipping from our moving hands before it hits the ground reflects the  
48 astonishing ability of feedback control to deal with unpredictable perturbations through online  
49 corrective processes. The question remains as to whether, and if so how, such corrective motor  
50 responses are readily functional after adaptation of the feedforward control responsible for  
51 triggering arm motor commands. We addressed this issue by studying arm-reaching motor  
52 responses to unforeseen changes in target position following sustained exposure to an altered  
53 gravito-inertial force field.

54           Several parameters must be taken into account to produce motor commands for intended  
55 motor actions in stable environments. For instance, the initial position of the hand (Rossetti et  
56 al. 1995; Vindras et al. 1998), movement extent and direction (Messier and Kalaska 2000;  
57 Riehle and Requin 1989; Sarlegna and Blouin 2010), movement velocity (Churchland et al.  
58 2006; Moran and Schwartz 1999) and the effect of gravity on the arm (Gaveau et al. 2016;  
59 Papaxanthis et al. 1998) are key parameters in preparing motor commands. Set before  
60 movement onset, these parameters are thought to be under feedforward control (Desmurget and  
61 Grafton 2000). Importantly, the feedforward control can adapt to internal (e.g., growth) or  
62 external (e.g., force field) changes that persist in time. In the case of a change of the  
63 gravito-inertial force field, this adaptation would rely on internal models updating of arm  
64 dynamics and environmental properties enabled by feedback errors processing (Shadmehr  
65 2004). Thanks to this sensorimotor adaptation, which greatly relies on the cerebellar network  
66 (Donchin et al. 2012; Maschke et al. 2004), the motor actions performed in the new gravitational  
67 environment become comparable to those produced in the normal force field (Coello et al. 1996;  
68 Lackner and Dizio 1994; Sarlegna et al. 2010).

## Motor responses to target jump in altered force field

69           On the other hand, when planning errors occur or when movement planning is no longer  
70 valid due to sudden and unpredictable perturbations, feedback control allows the ongoing  
71 movement to be corrected accordingly. This capacity has been demonstrated by studies showing  
72 that participants could still produce accurate goal-directed arm movements even when targets  
73 suddenly changed position after movement onset (Day and Lyon 2000; Desmurget et al. 1999;  
74 Pélisson et al. 1986; Sarlegna et al. 2003; Soechting and Lacquaniti 1983). The online  
75 movement corrections would notably rely on the posterior parietal cortex (Desmurget et al.  
76 1999; Reichenbach et al. 2014) and would be based on the computed difference between the  
77 motor goal and the current position of the hand during the movement.

78           A critical issue in the field of motor control is to understand the link between  
79 feedforward and feedback control. This relationship has essentially been tackled by  
80 investigating how both types of control respond to perturbations generated in the same domain,  
81 either mechanical or visual. In the mechanical domain, largely associated with upper limb  
82 proprioception, several studies demonstrated that online responses to mechanical perturbations  
83 applied to the moving arm are adapted to the force field in which the movement evolves (Cluff  
84 and Scott 2013; Crevecoeur and Scott 2013; Kimura and Gomi 2009; Maeda et al. 2018;  
85 Wagner and Smith 2008; Wang et al. 2001). For instance, Wagner and Smith (2008) showed  
86 that after learning to move the arm in a velocity-dependent force field, the motor response to  
87 force pulse applied on the arm is immediately scaled to the altered force field. More recent  
88 findings (Maeda et al. 2018) revealed that when participants learn new intersegmental dynamics  
89 involving decreased shoulder muscle activity, the muscle response to unpredictable mechanical  
90 perturbations is also tuned to the adapted feedforward control. In the visual domain, adaptation  
91 to visual feedback rotation was shown to affect visually-based movement corrections. For  
92 instance, responses to sudden visual shifts of hand or target positions were found to be perfectly

93 scaled to the level of adaptation of feedforward control (Dvorkin et al. 2009; Hayashi et al.  
94 2016; Saijo and Gomi 2010; Telgen et al. 2014).

95         In the above studies, the perturbations of the feedforward and feedback control were  
96 likely encoded in a common coordinate system because they both pertain to the same domain  
97 (i.e., intrinsic and extrinsic systems for the mechanical and visual perturbations respectively,  
98 Krakauer et al. 1999). This sensory context most likely reduced the complexity of the  
99 sensorimotor processes involved in online movement corrections. This hypothesis is consistent  
100 with the observations made in several studies that the integration of sensorimotor information  
101 in a same coordinate system leads to smaller noise and bias than when different coordinate  
102 systems are involved (Manson et al. 2019; Sarlegna et al. 2009; Tagliabue and McIntyre 2011;  
103 Tong et al. 2002). As a result, the use of a common sensory modality for encoding target  
104 position and controlling hand trajectory might induce smaller endpoint error and shorter  
105 correction latencies when the motor goal suddenly changes during reaching movements  
106 (Manson et al. 2019; Reichenbach et al. 2009). Then it follows that movement corrections could  
107 be impaired when the feedforward and feedback control involve different coordinate systems,  
108 particularly when the time for implementing these corrections is reduced as is the case with  
109 rapid movements.

110         The question raised, therefore, is whether the strong link between feedforward and  
111 feedback control revealed in studies on goal-directed arm movements holds when both the  
112 sustained and the unpredictable perturbations pertain to different domains. Diamond et al.  
113 (2015) addressed a similar question by assessing the changes of grip and load forces produced  
114 by subjects transporting a hand-held object whose dynamics varied according to its position in  
115 space. After adaptation to the new object dynamics, the visually-indicated location where the  
116 subjects had to bring the object occasionally changed position during the arm movements. The  
117 authors found that the corrections of the load and grip forces were perfectly tuned to the change

## Motor responses to target jump in altered force field

118 of the object's dynamics caused by the new path taken by the hand. They concluded that the  
119 internal models of novel object dynamics were integrated into visually-driven corrective arm  
120 movements (Diamond et al. 2015). However, the spatiotemporal characteristics of online  
121 corrections of the arm trajectory were not addressed in this study. Therefore, while their results  
122 are consistent with a close link between feedforward and feedback control, several key  
123 questions remained unanswered regarding the online control of arm movement when the  
124 perturbations of feedforward and feedback control relate to different domains. Foremost among  
125 these, it remains unclear if the feedback control was readily optimized from the very first time  
126 subjects had to reorient their movements according to the new target position. Moreover, being  
127 a critical function of the feedback control system, the reorganization of the muscular activity  
128 during perturbation trials was not considered in Diamond et al.'s (2015) study.

129 In the present study, we specifically addressed these issues by analyzing the  
130 spatiotemporal dynamics of the arm movements and arm muscle electromyography when  
131 participants corrected their hand trajectories in response to a sudden change of target position  
132 (visual domain) after adaptation of the feedforward control to an altered gravito-inertial force  
133 field (mechanical domain).



134 **Materials and Methods**

135 *Participants*

136 Sixteen right-handed participants (mean age =  $22.8 \pm 2.5$  years, 7 females), all naïve to  
137 the goal of the experiment, participated after giving their informed consent. None reported a  
138 sensorimotor deficit and all had normal or corrected-to-normal vision. The study was approved  
139 by the local ethical committee of the Institute of Movement Sciences and was performed in  
140 accordance with the standards of the Declaration of Helsinki.

141 *Experimental setup*

142 The experiment was carried out in a dark room. Participants were seated in a bucket seat  
143 placed at the center of a motorized rotating platform. A headrest kept their head immobile. In  
144 front of them, a horizontal board was positioned 45 cm above the seat. A micro-switch located  
145 25 cm in front of the participants' mid-trunk, was used to standardize the initial position of the  
146 reaching index finger. Two visual targets (red light-emitting diodes) were located along the  
147 midline body axis at a distance of respectively 25 cm ( $T_{close}$ ) and 35 cm ( $T_{far}$ ) from the micro-  
148 switch (see Fig. 1). Target lighting was controlled by homemade software (Docometre®). The  
149 3D index finger position was recorded at 200 Hz with an optical motion capture system  
150 (Codamotion CXS and ActiveHub; Charnwood Dynamics, Leicestershire, UK) that tracked the  
151 position of an infrared active marker fixed to the tip of the right index finger.

152

-----

153

Insert Fig. 1 about here

154

-----

155 Surface electromyographic activity (EMG) of arm muscles was analyzed to assess  
156 changes in motor commands in response to a target jump in an altered gravito-inertial force field  
157 (BIOPAC Systems, Inc., Santa Barbara, CA, 1000 Hz). We recorded the activity of two agonist

158 muscles (clavicular head of pectoralis; short head of triceps brachii) and two antagonist muscles  
159 (posterior deltoid; lateral head of biceps brachii) involved in the reaching movements. Torques  
160 produced by the pectoralis (arm adductor) and biceps brachii (elbow flexor) muscles can also  
161 help prevent the arm and forearm from being pushed by Coriolis force. Participants' skin was  
162 cleaned with alcohol and rubbed with an abrasive paper before affixing the electrodes (Ag-  
163 AgCl; diameter 1 cm, spacing 2 cm) along a line parallel to their fiber orientation to increase  
164 the signal-to-noise ratio (Brindle et al. 2006; Mills 2005). The motorized platform, the motion  
165 tracking system, and presentation of targets were controlled and synchronized using  
166 Docometre® software interacting with a real-time acquisition system (ADwin-Pro, Jäger,  
167 Germany).

#### 168 ***Procedure***

169 Before each trial, participants positioned their right index finger on the micro-switch,  
170 forearm resting on the board and left hand on left thigh. As soon as the visual target lit up,  
171 participants had to reach it as fast and accurately as possible. The target remained lit until the  
172 release of the micro-switch. In 20% of the trials (pseudo-randomly distributed), a target jump  
173 from  $T_{close}$  to  $T_{far}$  ( $T_{jump}$  condition) occurred on release of the micro-switch, with  $T_{far}$  target  
174 remaining lit for 100ms. Under these conditions, movement corrections are deemed to be  
175 visually-based, even if visual information was withheld during the reaches (see Brouwer and  
176 Knill 2007). For all conditions, participants were instructed to reach towards the target in a  
177 single movement and to avoid corrective movements after their index finger touched the board  
178 (i.e., considered here as offline corrections). An auditory cue provided 1.6 s after movement  
179 onset informed participants to slowly return their forefinger to the starting position.

180 The experimental session consisted of three successive phases (see Fig. 1):

## Motor responses to target jump in altered force field

181           PRE phase (no platform rotation): Participants first performed 10 reaching movements  
182 towards  $T_{close}$  and  $T_{far}$  (5 trials for each randomly-presented target). They were explicitly  
183 informed that there would be no target jump in this set of trials. Then, participants performed  
184 50 reaches towards  $T_{close}$  and  $T_{jump}$  (40  $T_{close}$  and 10  $T_{jump}$  randomly presented). Before  
185 starting this last set of trials, the participants were informed that a change of target position  
186 could occur after movement onset.

187           PER phase (platform rotation): While the participants had their index finger on the  
188 starting position, the velocity of the rotating platform was brought to a  $120 \text{ deg.s}^{-1}$  plateau in 80  
189 s. The counterclockwise rotation generated both Coriolis and centrifugal forces on the moving  
190 arm<sup>1</sup>. According to the laws of physics, the Coriolis force was orthogonal to the movement path  
191 and clockwise (i.e., opposite to the direction of platform rotation). The centrifugal force was in  
192 the direction of the movement path. The series of trials only started 30 s after the platform  
193 reached a constant velocity, i.e. when body rotation was no longer perceived (Benson, 1990;  
194 George et al. 2011). The participants were instructed to remain still until the start of the first  
195 trial. An infrared camera was used to verify their compliance with this instruction. Then,  
196 participants performed 30 reaches towards  $T_{close}$  and  $T_{far}$  (15 trials for each randomly-  
197 presented target: PER-initial phase), a number of trials that has been found sufficient to adapt  
198 feedforward control to Coriolis and centrifugal forces through proprioceptive feedback control  
199 (Coello et al. 1996; Franklin et al. 2007; Lackner and Dizio 1998). After this set of trials,  
200 participants performed 50 reaches towards  $T_{close}$  and  $T_{jump}$  (40  $T_{close}$  and 10  $T_{jump}$   
201 randomly presented: PER-final phase). As in the PRE phase, before both sets of trials  
202 participants were told whether or not target position could change at movement onset.

203           POST phase (no rotation): At the end of the PER phase, the participants remained still  
204 with their forefinger on the starting position until an 80 s deceleration brought the platform to  
205 complete immobilization. For the reason explained regarding the PER phase, the first trial of

## Motor responses to target jump in altered force field

206 the POST phase only started 30 s after the platform became stationary. Participants performed  
207 6 reaches towards  $T_{close}$  and  $T_{far}$  (3 trials for each randomly-presented target: POST-initial  
208 phase), followed by 25 reaches towards  $T_{close}$  and  $T_{jump}$  (20  $T_{close}$  and 5  $T_{jump}$  randomly  
209 presented: POST-final phase). Again, participants were told before both sets of trials whether  
210 or not target position could change at movement onset.

211 Participants familiarized themselves with the reaching task in a preliminary phase by  
212 performing 6 reaching movements towards  $T_{close}$  and  $T_{far}$  (3 trials for each randomly-  
213 presented target) and 15 reaching movements towards  $T_{close}$  and  $T_{jump}$  (12  $T_{close}$  and 3  
214  $T_{jump}$  randomly presented) in a non-altered gravito-inertial force field.

### 215 *Kinematic analyses*

216 Data were analyzed using Matlab (Mathworks, Natick, MA, USA). Raw positional data  
217 of the marker located on the reaching index finger were low-pass filtered with a dual-pass  
218 Butterworth (cut-off frequency: 10 Hz; order: 3). To determine whether participants actually  
219 adapted to the altered gravito-inertial force field, we first compared reaching performance in the  
220 single-step trials (i.e.,  $T_{close}$  and  $T_{far}$ ) from each experimental phase. Following common  
221 procedure for sensorimotor adaptation studies (see Lackner and Dizio 1994; Sarlegna et al.  
222 2010), analyses for each variable of interest (see below) included the mean computed from all  
223 trials of the PRE phase with no target jump possible (baseline), the first and last trials of the  
224 PER phase, and the first and last trials of the POST phase. Note that no target jump was possible  
225 in these PER and POST trials.

226 Several variables were computed to evaluate movement performance. Tangential peak  
227 velocity (PV) of the index finger movement was calculated from the marker x and y coordinates.  
228 Movement time (MT) was calculated as the time between movement onset and offset, identified  
229 as when tangential velocity exceeded and fell below 2 % of PV, respectively.

## Motor responses to target jump in altered force field

230 We computed the lateral endpoint error corresponding to the signed deviation of the  
231 finger at movement offset relative to the target on the x-axis. This mediolateral axis represented  
232 the main direction of the rotation-induced Coriolis force on the reaching arm. Negative and  
233 positive lateral endpoint errors indicated leftward and rightward finger deviations with respect  
234 to the target, respectively. Longitudinal endpoint error corresponded to the signed final  
235 deviation relative to the target on the y-axis. This anteroposterior axis represented the main  
236 direction of centrifugal forces. Negative and positive longitudinal endpoint errors indicated  
237 target undershoot and overshoot, respectively. For both  $T_{close}$  and  $T_{far}$ , endpoint errors were  
238 rebased relative to the mean endpoint positions computed from the first 10 trials of the PRE  
239 phase. For these trials, the participants knew that the targets would remain stationary. Finally,  
240 we measured the angle between the vector connecting starting position and target, and the  
241 vector connecting starting position and finger position to identify the maximum finger angular  
242 deviation from movement onset to time to PV. Because of sensorimotor delays, feedback  
243 control has little influence on movement before PV (Komilis et al. 1993), variables measured  
244 before this kinematics landmark are considered as resulting mainly from feedforward control.

245 The second step consisted in comparing the  $T_{jump}$  trials from the different phases. We  
246 excluded trials exhibiting offline corrective movements, defined as those where, between  
247 movement onset and movement offset, tangential velocity was  $0 \text{ cm}\cdot\text{s}^{-1}$  or the z coordinate of  
248 the index finger equaled the z coordinate of the targets' surface (see Fig. 2C). The remaining  
249 84% of total  $T_{jump}$  trials (with no significant difference in proportion across phases) were  
250 examined to identify whether or not they contained overt online secondary corrections (Fig. 2A  
251 and 2B, respectively). Trials were considered as involving such secondary corrections when  
252 they exhibited a velocity bounce following a first deceleration phase (i.e., after PV, see  
253 Boulinguez et al. 2001). Because secondary corrections are deemed to be under online control,  
254 only  $T_{jump}$  trials with these observable corrections were kept (82% of the  $T_{jump}$  trials showed

## Motor responses to target jump in altered force field

255 secondary corrections with no significant difference in proportion across phases). Note that  
256 trials without such online corrections showed large longitudinal endpoint errors (on average,  
257 5.17 cm undershoot). This observation attests that the secondary corrections, as identified using  
258 the criteria described above, helped preserving movement accuracy. Since 4 participants did  
259 not satisfy the double inclusion criteria (i.e., absence of offline correction and presence of overt  
260 online correction) in at least one phase, the results of 12 out of 16 participants were kept for  
261 this second step of data analyses.

262

-----

263

Insert Fig. 2 about here

264

-----

265 Onset of secondary correction was identified when tangential acceleration exceeded 0  
266  $\text{cm}\cdot\text{s}^{-2}$  after the first acceleration and deceleration phases. From this time, we computed the  
267 secondary correction time (time between movement onset and beginning of secondary  
268 correction), the PV of the secondary correction (maximum tangential velocity between  
269 beginning of secondary correction and movement offset), and relative time to PV of the  
270 secondary correction (TPV), computed in percentage relative to the total duration of the  
271 secondary correction (from the secondary correction time to the movement offset; see Fig. 2A).  
272 For each of these variables, we compared the mean computed from all Tjump trials of the PRE  
273 jump phase, the first and the last Tjump trial of the PER jump phase and the first and the last  
274 Tjump trial of the POST jump phase. Note that splitting the data into different phases (i.e., PER-  
275 initial PER- final and POST-initial POST-final) allowed us to determine 1) if the online  
276 correction observed during the first Tjump after adaptation or re-adaptation was functional and  
277 2) if the online correction in the PER jump phase improved after practice (PER-initial vs PER-  
278 final) as is the case during sensorimotor adaptation and as revealed in the PER phase (without  
279 target jump) of the present study. The exclusion of some trials due to the criteria used to identify

## Motor responses to target jump in altered force field

280 movement correction meant that the Tjump trials analyzed were not always the first or the last  
281 Tjump trial; however, they fell mainly within the first (88%) or last (92%) two trials of the PER  
282 jump and POST jump phases.

### 283 *EMG analyses*

284 Raw EMG data were filtered with a Butterworth type band-pass filter (cut-off  
285 frequency: 20-400 Hz; order: 4) to minimize signals unrelated to the physiological frequency  
286 of muscle activity (van Boxtel 2001). After centering around the mean and rectifying the signal,  
287 a low-pass Butterworth filter was applied twice (forward and backward to remove phase shift)  
288 with a 3 Hz cut-off frequency (order: 3) to create an envelope of the EMG signal. The activity  
289 of each muscle was normalized and expressed as a percentage of their maximum activity  
290 observed during the Tjump trials in the PRE phase.

291 EMG analyses were performed on the Tjump trials of 12 participants (selection  
292 procedure described above). For each muscle (pectoralis, biceps, posterior deltoid, triceps) and  
293 each phase (PRE jump, PER-initial jump, PER-final jump, POST-initial jump, POST-final  
294 jump), activation level was estimated by computing the EMG Root Mean Square (RMS). For  
295 each trial, EMG RMS calculation started 90 ms before the secondary correction (to allow for  
296 'motor time'; Soechting and Lacquaniti 1983) and ended at the PV secondary correction.  
297 Computed over this time window, the EMG RMS can be considered to provide a good  
298 estimation of the motor command during the secondary corrections.

### 299 *Statistical analyses*

300 To determine whether participants adapted to the altered gravitoinertial force field  
301 before the first Tjump trial, for each movement we compared the kinematics variables computed  
302 for the different phases without Tjump trials (PRE, PER-initial, PER-final, POST-initial,  
303 POST-final) using repeated measures ANOVAs. To investigate online corrections following

304 displacements of the visual target, we compared the kinematics and EMG variables computed  
305 for the different phases of the Tjump trials (PRE jump, PER-initial jump, PER-final jump,  
306 POST-initial jump, POST-final jump) using repeated measures ANOVAs.

307 All statistical analyses were performed with Statistica software (StatSoft, Inc., OK,  
308 USA). The normal distribution of data for each variable was confirmed by Kolmogorov-  
309 Smirnov tests. Post-hoc analyses were carried out using Newman-Keuls tests. Significance  
310 threshold was set at  $p < 0.05$  for all analyses.

## 311 **Results**

### 312 *Confirmation of feedforward control adaptation*

313 The reaching trajectories recorded in the different phases prior to the Tjump trials  
314 indicated that participants adapted to the altered gravito-inertial force field (Fig. 3). More  
315 specifically, movements performed before the force field change (PRE phase) showed nearly  
316 rectilinear trajectories and final endpoint positions close to the target. However, in the first trial  
317 performed in the modified force field (PER-initial trial), the subject's reaching finger deviated  
318 to the right and overshoot the target, presumably due to Coriolis and centrifugal forces,  
319 respectively. After several trials in the altered gravito-inertial force field (PER-final trial),  
320 movements became straighter and more accurate. In contrast, the first movements performed  
321 after the gravito-inertial force field returned to normal (POST-initial) deviated widely to the left  
322 of the target. Finally, at the end of the POST phase (POST-final), reaching movements were  
323 almost as rectilinear and as accurate as during the PRE phase.

324 -----

325 Insert Fig. 3 about here

326 -----



## Motor responses to target jump in altered force field

327           The statistical analyses performed on the different kinematics variables revealed how  
328 the exposure phases affected reaching movements. The ANOVA performed on lateral endpoint  
329 errors showed a significant phase effect ( $F_{(4, 56)} = 21.33$ ;  $p < 0.001$ ; Fig. 4A). Post-hoc analysis  
330 showed that reaching movements performed during PER-initial and POST-initial phases were  
331 respectively more deviated to the right and to the left of the target than those performed in the  
332 other phases. Consistent with the adaptation of the feedforward control to the altered force field,  
333 the lateral endpoint errors did not significantly differ between PRE, PER-final and POST-final  
334 phases.

335           The ANOVA also revealed a significant phase effect on longitudinal endpoint errors  
336 ( $F_{(4, 56)} = 7.25$ ;  $p < 0.001$ ; Fig. 4B). Post-hoc analyses revealed that reaching movements  
337 performed in the PER-initial phase overshoot the target and had greater amplitudes than in all  
338 other phases. While the longitudinal endpoint errors did not significantly differ between the  
339 PRE and the POST-initial phases, movements performed during the POST-initial phase had  
340 smaller amplitude than during the PER-final and POST-initial phases. Together, these results  
341 denote some signs of feedforward control adaptation of movement extent in the new force field.

342

-----

343

Insert Fig. 4 about here

344

-----

345           Maximum finger angular deviation before PV was also impacted by phase ( $F_{(4, 56)} =$   
346  $12.43$ ;  $p < 0.001$ ; Fig. 5). Post-hoc analyses showed that the reaching movements performed in  
347 the PER-initial and POST-initial phases were significantly more deviated to the right and to the  
348 left than movements in the PRE and PER-final phases, respectively. On the other hand, before  
349 PV, movements in the POST-initial phase was more deviated to the left than those in the PRE  
350 phase ( $p < 0.001$ ). Kinematic landmarks falling before peak velocity are considered to mainly  
351 illustrate feedforward control (Komilis et al. 1993). Therefore, these results confirm that

352 feedforward control was adapted to the altered gravito-inertial force field, consistent with  
353 findings from previous studies that used similar types of paradigms (Lackner and Dizio 1994;  
354 Sarlegna et al. 2010).

355 -----  
356 Insert Fig. 5 about here

357 -----

### 358 *Comparison of Tfar and Tjump trials*

359 The presence of a target jump during reaching fundamentally changed the  
360 spatiotemporal organization of the movement. This can be seen in Fig. 6, which shows the  
361 respective mean tangential velocities of all Tfar and valid Tjump trials, where the same spatial  
362 goal had to be reached with or without a change of target position. Compared to Tfar trials,  
363 Tjump trials had a smaller peak velocity and showed a secondary PV after a first deceleration  
364 phase. Movement times were also longer in Tjump trials than in Tfar trials (mean: 490 ms  $\pm$  63  
365 ms vs 336 ms  $\pm$  56 ms respectively), as confirmed by a paired t-test ( $t_{(11)} = 9.73$ ;  $p < 0.001$ ).  
366 These modified kinematics show that visually extracted information on the new target position  
367 was integrated into the control of the ongoing reaching movement. Moreover, for Tjump trials,  
368 the secondary correction time was much shorter than the reaction time of the primary movement  
369 (mean: 278 ms  $\pm$  53 ms vs 411 ms  $\pm$  58 ms respectively;  $t_{(11)} = 6.82$ ;  $p < 0.0001$ ). This result  
370 concurs with the findings from several studies using double step reaching paradigm which  
371 showed that the modification of motor commands under feedback control is faster than the time  
372 necessary to produce new motor commands under feedforward control (Day and Lyon 2000;  
373 Fautrelle et al. 2010; Kadota and Gomi 2010; Prablanc and Martin 1992; Reichenbach et al.  
374 2009; Saunders and Knill 2003; Smeets et al. 2016).

375

376

-----

377

Insert Fig. 6 about here

378

-----

379 ***Comparison of Tjump trials from the different jump phases***

380

381

382

383

384

385

386

387

388

389

390

The main goal of the present study was to determine whether the movement corrections observed in a normal gravito-inertial force field remain effective after adaptation to a new force field. Remarkably, none of the temporal and spatial variables pertaining to Tjump trials differed significantly between the different experimental phases (PRE jump, PER-initial jump, PER-final jump, POST-initial jump, POST-final jump). ANOVAs did not reveal significant phase effects on mean MT ( $F_{(4, 44)} = 1.16$ ;  $p = 0.34$ , overall mean ( $\bar{x}$ ):  $489 \text{ ms} \pm 54 \text{ ms}$ ), lateral endpoint errors ( $F_{(4, 44)} = 1.19$ ;  $p = 0.33$ ,  $\bar{x}$ :  $0.60 \text{ cm} \pm 0.81 \text{ cm}$ ; Fig. 7A) or longitudinal endpoint errors ( $F_{(4, 44)} = 2.19$ ;  $p = 0.09$ ,  $\bar{x}$ :  $0.85 \text{ cm} \pm 3.21 \text{ cm}$ ; Fig. 7B), PV secondary correction ( $F_{(4, 44)} = 1.36$ ;  $p = 0.26$ ;  $\bar{x}$ :  $97 \text{ cm}\cdot\text{s}^{-1} \pm 45 \text{ cm}\cdot\text{s}^{-1}$ ; Fig. 7C), TPV secondary correction ( $F_{(4, 44)} = 0.97$ ;  $p = 0.43$ ;  $\bar{x}$ :  $35\% \pm 11\%$ ; Fig. 7D), and secondary correction time ( $F_{(4, 44)} = 0.88$ ;  $p = 0.48$ ;  $\bar{x}$ :  $278 \text{ ms} \pm 53 \text{ ms}$ ).

391

-----

392

Insert Fig. 7 about here

393

-----

394

395

396

397

398

399

400

However, the EMG RMS analyses showed that muscle activities recorded during movement corrections differed between phases (see Fig. 8 for comparison between PRE jump and PER-initial jump phases). Notably, the ANOVA revealed a significant phase effect on the EMG RMS for the biceps brachii ( $F_{(4, 44)} = 7.4$ ;  $p < 0.001$ ; Fig. 9A). Post-hoc analysis showed higher EMG RMS values in the PER-initial jump and PER-final jump phases than in the other phases. The ANOVA also indicated a significant phase effect on the pectoralis ( $F_{(4, 44)} = 4.26$ ;  $p$

## Motor responses to target jump in altered force field

401 < 0.01; Fig. 9B) and posterior deltoid ( $F_{(4, 44)} = 3.5$ ;  $p < 0.05$ ; Fig.9C) EMG RMS. For the  
402 posterior deltoid, EMG RMS was greater in the PER-initial jump phase than in POST-initial  
403 jump and POST-final jump phases. For the pectoralis, EMG RMS was greater in the PER-initial  
404 jump phase than in all the other phases.

405

-----

406

Insert Fig. 8 about here

407

-----

408

Finally, the ANOVA performed on the EMG RMS of triceps brachii ( $F_{(4,44)} = 1.7$ ;  $p =$

409

0.16; Fig. 9D) did not show a significant phase effect.

410

-----

411

Insert Fig. 9 about here

412

-----

413

414 **Discussion**

415         The present study explored the link between feedback and feedforward control by  
416 looking at whether, when motor commands are adapted to a new force field, online control of  
417 arm movement remains effective under a perturbation of a different nature. In a two-step  
418 experimental protocol, participants first adapted feedforward control to the mechanical  
419 perturbation of an altered gravito-inertial force field by reaching towards visual targets while  
420 seated in a rotating environment. Then, we assessed whether online control mechanisms were  
421 readily functional in this altered force field by examining the participants' arm responses to  
422 unpredictable changes in target position (i.e., visual perturbation) at movement onset. Together,  
423 kinematics and EMG analyses showed for the first time that although feedforward and feedback  
424 control were driven by different sensory inputs, feedback control was remarkably functional,  
425 from the very first time participants encountered a target jump in the altered force field.

426 *Validation of adaptation to an altered gravito-inertial force field*

427         The first reaching movement performed by the participants after being re-exposed to a  
428 normal gravito-inertial force field (i.e., in POST-initial phase) showed wide trajectory deviation.  
429 The deviation was in the opposite direction to the Coriolis force exerted on the arm during the  
430 preceding series of reaches in the altered force field. This so-called post-effect confirmed that  
431 the feedforward control responsible for triggering the movements was adapted to the force field  
432 change induced by platform rotation (Coello et al. 1996; Franklin et al. 2007; Lackner and Dizio  
433 1998). According to prevailing theories of motor control, this adaptation reflects the updating  
434 of internal models of reaching, based on the new environment dynamics detected through  
435 proprioceptive information processing (Wolpert et al. 2011).

436         Adaptation to externally-induced centrifugal forces has received little attention in  
437 previous studies. Those using a paradigm in which participants were seated on-axis of a rotating

## Motor responses to target jump in altered force field

438 platform (Coello et al. 1996; Lackner and Dizio 1994), or off-axis (Bourdin et al. 2001; Kurtzer  
439 et al. 2005; Lackner and Dizio 1998), showed that centrifugal force had no significant effects  
440 on movement accuracy, and that exposure to this force did not lead to post-effects. On the  
441 contrary, our participants widely overshoot the target during their first reach under externally-  
442 induced centrifugal force. The smaller longitudinal errors reported in previous studies may stem  
443 from the fact that, prior to reaching, the hand position appeared to be farther from the rotation  
444 axis, even when participants were seated above this axis (see Coello et al. 1996; Lackner and  
445 Dizio 1994). This gave participants the opportunity to perceive the centrifugal force applied to  
446 their body before reaching, and to take it into account when planning their movements. Similar  
447 integration of the gravitoinertial context prior to movement execution has been reported in  
448 several studies (Blouin et al. 2015; Bockisch and Haslwanter 2007; Cohn et al. 2000; Macaluso  
449 et al. 2017). In our study, however, before initiating their movements, participants' hands were  
450 positioned very close to the rotation axis, a position that prevented detection of the centrifugal  
451 force and anticipation of its effects on the arm during the movement.

452         Although longitudinal endpoint errors returned to baseline level after ~3 trials  
453 performed in the altered gravitoinertial force field, the post-effect observed for this variable  
454 greatly differed from that revealed for the directional errors. Indeed, the participants'  
455 longitudinal errors when first re-exposed to a normal force field did not significantly differ from  
456 those produced prior to the force field alteration (PRE phase). However, the amplitude of the  
457 first post-rotation movement was significantly smaller than the last movement performed  
458 during the rotation (PER-final) and the last movement performed after being re-exposed to a  
459 normal force field (POST-final). This pattern of results suggests that participants had begun to  
460 adapt their movement amplitude by the end of exposure to the altered gravitoinertial force field,  
461 but to a lesser extent compared to the adaptation shown for movement direction (assessed here  
462 using lateral endpoint errors).

463           These differing capacities to adapt movement amplitude and direction could be  
464 explained with reference to the vectorial coding model of movements. According to this model,  
465 motor commands are planned according to the direction and the amplitude of a hand-target  
466 vector computed by the brain (Davare et al. 2012; Favilla et al. 1990; Krakauer et al. 1999,  
467 2000; Messier and Kalaska 2000; Rossetti et al. 1995). Importantly, the fact that movement  
468 direction has to be specified before movement onset (Fleury et al. 1994; Ghez et al. 1989;  
469 Paulignan et al. 1991; van Sonderen et al. 1988), unlike movement amplitude (Favilla et al.  
470 1990; Ghez et al. 1989; Sarlegna et al. 2010) might place greater stress on planning movement  
471 direction than movement amplitude. This could be responsible for the observation made here  
472 and in previous studies (Bourdin et al. 2001; Coello et al. 1996; Kurtzer et al. 2005; Lackner  
473 and Dizio 1994, 1998) that adaptation to Coriolis force is faster than adaptation to centrifugal  
474 force.

475 ***The strong relationship between feedforward and feedback control is not context-dependent***

476           To our knowledge, the link between feedforward and feedback control in different  
477 domains has only been assessed by Diamond et al. (2015). In their study, the feedforward  
478 control was first adapted by having participants transport several times a hand-held object  
479 whose load force depended on its position within the working space. Then, the experimenter  
480 changed the (visual) location where the participants had to bring the object while they were  
481 moving it. The authors showed that participants could remarkably scale grip and load forces  
482 according to the change of object load force associated with the movement correction.  
483 However, no analyses related to reaching corrections were reported. The authors simply  
484 indicated that the reaching errors were greater than 0.5 cm in only 17% of the trials but without  
485 specifying whether these trials were gathered within the first attempts to reach the new target  
486 location. In the present study, the thorough investigation of movement corrections revealed that  
487 the spatiotemporal characteristics of the corrective movements were strikingly similar between

## Motor responses to target jump in altered force field

488 normal and altered gravito-inertial force fields. This strong similarity was observed even when  
489 participants experienced their first target jump in the altered gravito-inertial force field (PER-  
490 initial jump phase), and for all movement parameters (e.g., lateral and longitudinal endpoint  
491 errors, movement duration, correction latency). Even the fine kinematics variables, such as the  
492 peak velocity of the corrective movement and its relative time of occurrence, were not impacted  
493 by the change in gravito-inertial forces. The remarkable spatiotemporal stability of online  
494 corrective responses, including during the first experience of a target jump in the new force  
495 field, supports the hypothesis that the adaptation of feedforward control readily transferred to  
496 feedback control.

497         Because rotating the environment in which individuals moved their arm created Coriolis  
498 and centrifugal forces, similar movement corrections could be expected to require different  
499 muscle torques in normal and altered gravito-inertial force fields. This was confirmed by our  
500 EMG analyses, which showed greater activity of the biceps (PER-initial jump and PER-final  
501 jump phases), pectoralis (PER-initial jump phase) and posterior deltoid (PER-initial jump  
502 compared to POST-initial jump and POST-final jump phases) muscles during the movement  
503 corrections observed in the altered gravito-inertial force field.

504         When participants reached towards the targets while being rotated in the  
505 counterclockwise direction, Coriolis force pushed the arm to the right. The increased activities  
506 of the right biceps (elbow flexor) and pectoralis (arm adductor) muscles may therefore have  
507 helped to offset Coriolis force and maintain a rectilinear hand trajectory during movement  
508 corrections. On the other hand, because it was in the same direction as the movement trajectory,  
509 centrifugal force facilitated reaching movements during platform rotation. Thus, the increased  
510 activation of the biceps and posterior deltoid muscles may also have slowed down the hand  
511 being pushed by centrifugal force as it moved away from the center of rotation. Importantly,  
512 this fine-tuning of biceps and pectoralis muscle activities was also effective from the first time



## Motor responses to target jump in altered force field

513 the target changed its position during the reaching movements. These results, which corroborate  
514 the kinematic analyses, suggest readily functional online control when feedforward control is  
515 adapted to new gravito-inertial constraints.

516         Increasing muscle activity when learning new arm dynamics is known to reduce  
517 movement errors and to accelerate the adaptation process (Heald et al. 2018). This raises the  
518 possibility that the greater activity observed here in the pectoralis, biceps brachii and posterior  
519 deltoid muscles during movement corrections may have improved the efficiency of feedback  
520 control. This hypothesis requires further testing, but it is in line with the suggestion that  
521 increasing the activity of arm muscles enhances visuomotor feedback gain and improves arm  
522 responses to sudden and unpredictable visual perturbations (Franklin et al. 2012). Because  
523 pectoralis muscle was less active on the last Tjump trial, co-contraction or muscle stiffness may  
524 not be the motor strategies developed by the brain to counter the forces, at least in the longer  
525 term. The decrease of pectoralis muscle activity observed here over time could be explained by  
526 the optimal control theory (Diedrichsen et al. 2010; Todorov 2004). An optimization of motor  
527 command over Tjump trials may be based on a reorganization of muscular synergies (d'Avella  
528 et al. 2006) to minimize energy cost while maintaining spatial accuracy. The fact that pectoralis  
529 muscle was the main agonist muscle in the present reaching task, and therefore the most energy  
530 costing, could explain why the diminution of EMG activity was only effective in this muscle.

531         The question of whether feedback control is linked to feedforward control has  
532 essentially been investigated by testing both types of control under perturbations pertaining to  
533 a common domain, e.g., mechanical or visual. Thus, these studies found feedforward and  
534 feedback control to be driven either by proprioceptive (Cluff and Scott 2013; Crevecoeur and  
535 Scott 2013; Kimura and Gomi 2009; Maeda et al. 2018; Wagner and Smith 2008; Wang et al.  
536 2001) or by visual (Dvorkin et al. 2009; Hayashi et al. 2016; Saijo and Gomi 2010; Telgen et  
537 al. 2014) feedback. They showed effective corrections from the first movement perturbation,

538 confirming that in this context, feedforward and feedback controls are closely linked (Telgen  
539 et al. 2014; Wagner and Smith 2008). The present study demonstrates that the changes resulting  
540 from feedforward control adaptation are readily available to feedback-based processes in  
541 contexts where the two modes of control are facing different types of perturbation. While force  
542 field and visuomotor adaptations have been found to involve distinct neural networks (Donchin  
543 et al. 2012; Rabe et al. 2009), our findings suggest that these networks are functionally (directly  
544 or indirectly) interconnected, thereby allowing greater flexibility in the control of arm  
545 movements.

546 In conclusion, we demonstrated that after adapting feedforward control to the  
547 mechanical perturbation of a sustained altered gravito-inertial force field, the internal model  
548 based on arm dynamics and environmental properties led to functional feedback control driven  
549 by visual information about the new target position. Thus, when feedforward control provides  
550 a state estimate of arm dynamics under mechanical perturbation, feedback control processes  
551 may be able to use visual information to produce adapted motor commands that also take into  
552 account the mechanical changes and their consequences on the upper limb.

553

554 **Acknowledgments**

555       The authors wish to thank F. Buloup for technical support and assistance with  
556 experiments. The authors are also grateful to the participants in this study.

557 **Grants**

558       This work was supported by APR Grants (“FLEXMOVE” Grants 884 & 944) from the  
559 French National Space Research Centre (CNES), and grants from the French Research Council  
560 (ANR Motion - 14-CE30-0007).

561 **Disclosures**

562       The authors declare that the research was conducted in the absence of any commercial or  
563 financial relationships that could be construed as a potential conflict of interest.

564 **Author contributions**

565       LC designed and performed the experiment, analyzed data and wrote the paper; LB and  
566 JB designed the experiment and wrote the paper.

567

568 **References**

- 569 **d'Avella A, Portone A, Fernandez L, Lacquaniti F.** Control of Fast-Reaching Movements  
570 by Muscle Synergy Combinations. *J Neurosci* 26: 7791–7810, 2006.
- 571 **Benson AJ.** Sensory Functions and Limitations of the Vestibular System. In: *The Perception*  
572 *and Control of Self-Motion*, edited by Warren R. & Wertheim AH. Hillsdale, NJ: Lawrence  
573 Erlbaum Associates, Inc., 1990, p. 145-170.
- 574 **Blouin J, Bresciani J-P, Guillaud E, Simoneau M.** Prediction in the vestibular control of arm  
575 movements. *Multisensory Res* 28: 487–505, 2015.
- 576 **Bockisch CJ, Haslwanter T.** Vestibular contribution to the planning of reach trajectories. *Exp*  
577 *Brain Res* 182: 387–397, 2007.
- 578 **Boulinguez P, Nougier V, Velay JL.** Manual asymmetries in reaching movement control. I:  
579 Study of right-handers. *Cortex* 37: 101–122, 2001.
- 580 **Bourdin C, Gauthier G, Blouin J, Vercher JL.** Visual feedback of the moving arm allows  
581 complete adaptation of pointing movements to centrifugal and Coriolis forces in human  
582 subjects. *Neurosci Lett* 301: 25–28, 2001.
- 583 **van Boxtel A.** Optimal signal bandwidth for the recording of surface EMG activity of facial,  
584 jaw, oral, and neck muscles. *Psychophysiology* 38: 22–34, 2001.
- 585 **Brindle TJ, Nitz AJ, Uhl TL, Kifer E, Shapiro R.** Kinematic and EMG characteristics of  
586 simple shoulder movements with proprioception and visual feedback. *J Electromyogr Kinesiol*  
587 16: 236–249, 2006.
- 588 **Brouwer A-M, Knill DC.** The role of memory in visually guided reaching. *J Vis* 7: 6.1-12,  
589 2007.
- 590 **Churchland MM, Santhanam G, Shenoy KV.** Preparatory activity in premotor and motor  
591 cortex reflects the speed of the upcoming reach. *J Neurophysiol* 96: 3130–3146, 2006.
- 592 **Cluff T, Scott SH.** Rapid feedback responses correlate with reach adaptation and properties of  
593 novel upper limb loads. *J Neurosci* 33: 15903–15914, 2013.
- 594 **Coello Y, Orliaguet JP, Prablanc C.** Pointing movement in an artificial perturbing inertial  
595 field: a prospective paradigm for motor control study. *Neuropsychologia* 34: 879–892, 1996.
- 596 **Cohn JV, DiZio P, Lackner JR.** Reaching during virtual rotation: context specific  
597 compensations for expected coriolis forces. *J Neurophysiol* 83: 3230–3240, 2000.
- 598 **Crevecoeur F, Scott SH.** Priors engaged in long-latency responses to mechanical perturbations  
599 suggest a rapid update in state estimation. *PLoS Comput Biol* 9: e1003177, 2013.
- 600 **Davare M, Zénon A, Pourtois G, Desmurget M, Olivier E.** Role of the medial part of the  
601 intraparietal sulcus in implementing movement direction. *Cereb Cortex* 22: 1382–1394, 2012.
- 602 **Day BL, Lyon IN.** Voluntary modification of automatic arm movements evoked by motion of  
603 a visual target. *Exp Brain Res* 130: 159–168, 2000.

- 604 **Desmurget M, Epstein CM, Turner RS, Prablanc C, Alexander GE, Grafton ST.** Role of  
605 the posterior parietal cortex in updating reaching movements to a visual target. *Nat Neurosci* 2:  
606 563–567, 1999.
- 607 **Desmurget M, Grafton ST.** Forward modeling allows feedback control for fast reaching  
608 movements. *Trends Cogn Sci* 4: 423–431, 2000.
- 609 **Diamond JS, Nashed JY, Johansson RS, Wolpert DM, Flanagan JR.** Rapid Visuomotor  
610 Corrective Responses during Transport of Hand-Held Objects Incorporate Novel Object  
611 Dynamics. *J Neurosci Off J Soc Neurosci* 35: 10572–10580, 2015.
- 612 **Diedrichsen J, Shadmehr R, Ivry RB.** The coordination of movement: optimal feedback  
613 control and beyond. *Trends Cogn Sci* 14: 31–39, 2010.
- 614 **Donchin O, Rabe K, Diedrichsen J, Lally N, Schoch B, Gizewski ER, Timmann D.**  
615 Cerebellar regions involved in adaptation to force field and visuomotor perturbation. *J*  
616 *Neurophysiol* 107: 134–147, 2012.
- 617 **Dvorkin AY, Kenyon RV, Keshner EA.** Effects of roll visual motion on online control of arm  
618 movement: reaching within a dynamic virtual environment. *Exp Brain Res* 193: 95–107, 2009.
- 619 **Fautrelle L, Prablanc C, Berret B, Ballay Y, Bonnetblanc F.** Pointing to double-step visual  
620 stimuli from a standing position: very short latency (express) corrections are observed in upper  
621 and lower limbs and may not require cortical involvement. *Neuroscience* 169: 697–705, 2010.
- 622 **Favilla M, Gordon J, Hening W, Ghez C.** Trajectory control in targeted force impulses. VII.  
623 Independent setting of amplitude and direction in response preparation. *Exp Brain Res* 79: 530–  
624 538, 1990.
- 625 **Fleury M, Bard C, Auddifren M, Teasdale N, Blouin J.** The attentional cost of amplitude  
626 and directional requirements when pointing to targets. *Q J Exp Psychol: Hum Exp Psychol* 47A:  
627 481–495, 1994.
- 628 **Franklin DW, Liaw G, Milner TE, Osu R, Burdet E, Kawato M.** Endpoint stiffness of the  
629 arm is directionally tuned to instability in the environment. *J Neurosci* 27: 7705–7716, 2007.
- 630 **Franklin S, Wolpert DM, Franklin DW.** Visuomotor feedback gains upregulate during the  
631 learning of novel dynamics. *J Neurophysiol* 108: 467–478, 2012.
- 632 **Gaveau J, Berret B, Angelaki DE, Papaxanthis C.** Direction-dependent arm kinematics  
633 reveal optimal integration of gravity cues. *eLife* 5, 2016.
- 634 **George RJS, Day BL, Fitzpatrick RC.** Adaptation of vestibular signals for self-motion  
635 perception. *J Physiol* 589: 843–853, 2011.
- 636 **Ghez C, Hening W, Favilla M.** Gradual specification of response amplitude in human tracking  
637 performance. *Brain Behav Evol* 33: 69–74, 1989.
- 638 **Hayashi T, Yokoi A, Hirashima M, Nozaki D.** Visuomotor map determines how visually  
639 guided reaching movements are corrected within and across trials. *eNeuro* 3, 2016.

- 640 **Heald JB, Franklin DW, Wolpert DM.** Increasing muscle co-contraction speeds up internal  
641 model acquisition during dynamic motor learning. *Sci Rep* 8: 16355, 2018.
- 642 **Kadota K, Gomi H.** Implicit visuomotor processing for quick online reactions is robust against  
643 aging. *J Neurosci Off J Soc Neurosci* 30: 205–209, 2010.
- 644 **Kimura T, Gomi H.** Temporal development of anticipatory reflex modulation to dynamical  
645 interactions during arm movement. *J Neurophysiol* 102: 2220–2231, 2009.
- 646 **Komilis E, Pélisson D, Prablanc C.** Error processing in pointing at randomly feedback-  
647 induced double-step stimuli. *J Mot Behav* 25: 299–308, 1993.
- 648 **Krakauer JW, Ghilardi MF, Ghez C.** Independent learning of internal models for kinematic  
649 and dynamic control of reaching. *Nat Neurosci* 2: 1026–1031, 1999.
- 650 **Krakauer JW, Pine ZM, Ghilardi MF, Ghez C.** Learning of visuomotor transformations for  
651 vectorial planning of reaching trajectories. *J Neurosci* 20: 8916–8924, 2000.
- 652 **Kurtzer I, DiZio PA, Lackner JR.** Adaptation to a novel multi-force environment. *Exp Brain*  
653 *Res* 164: 120–132, 2005.
- 654 **Lackner JR, Dizio P.** Rapid adaptation to Coriolis force perturbations of arm trajectory. *J*  
655 *Neurophysiol* 72: 299–313, 1994.
- 656 **Lackner JR, Dizio P.** Gravito-inertial force background level affects adaptation to coriolis force  
657 perturbations of reaching movements. *J Neurophysiol* 80: 546–553, 1998.
- 658 **Macaluso T, Bourdin C, Buloup F, Mille M-L, Sainton P, Sarlegna FR, Vercher J-L,**  
659 **Bringoux L.** Sensorimotor reorganizations of arm kinematics and postural strategy for  
660 functional whole-body reaching movements in microgravity. *Front Physiol* 8: 821, 2017.
- 661 **Maeda RS, Cluff T, Gribble PL, Pruszynski JA.** Feedforward and feedback control share an  
662 internal model of the arm's dynamics. *J Neurosci* 38: 10505–10514, 2018.
- 663 **Manson GA, Blouin J, Kumawat AS, Crainic VA, Tremblay L.** Rapid online corrections  
664 for upper limb reaches to perturbed somatosensory targets: evidence for non-visual  
665 sensorimotor transformation processes. *Exp Brain Res* 237: 839–853, 2019.
- 666 **Maschke M, Gomez CM, Ebner TJ, Konczak J.** Hereditary cerebellar ataxia progressively  
667 impairs force adaptation during goal-directed arm movements. *J Neurophysiol* 91: 230–238,  
668 2004.
- 669 **Messier J, Kalaska JF.** Covariation of primate dorsal premotor cell activity with direction and  
670 amplitude during a memorized-delay reaching task. *J Neurophysiol* 84: 152–165, 2000.
- 671 **Mills KR.** The basics of electromyography. *J Neurol Neurosurg Psychiatry* 76 Suppl 2: ii32-  
672 35, 2005.
- 673 **Moran DW, Schwartz AB.** Motor cortical representation of speed and direction during  
674 reaching. *J Neurophysiol* 82: 2676–2692, 1999.

- 675 **Papaxanthis C, Pozzo T, McIntyre J.** Arm end-point trajectories under normal and micro-  
676 gravity environments. *Acta Astronaut* 43: 153–161, 1998.
- 677 **Paulignan Y, MacKenzie C, Marteniuk R, Jeannerod M.** Selective perturbation of visual  
678 input during prehension movements. 1. The effects of changing object position. *Exp Brain Res*  
679 83: 502–512, 1991.
- 680 **Pélisson D, Prablanc C, Goodale MA, Jeannerod M.** Visual control of reaching movements  
681 without vision of the limb. II. Evidence of fast unconscious processes correcting the trajectory  
682 of the hand to the final position of a double-step stimulus. *Exp Brain Res* 62: 303–311, 1986.
- 683 **Prablanc C, Martin O.** Automatic control during hand reaching at undetected two-  
684 dimensional target displacements. *J Neurophysiol* 67: 455–469, 1992.
- 685 **Rabe K, Livne O, Gizewski ER, Aurich V, Beck A, Timmann D, Donchin O.** Adaptation to  
686 visuomotor rotation and force field perturbation is correlated to different brain areas in patients  
687 with cerebellar degeneration. *J Neurophysiol* 101: 1961–1971, 2009.
- 688 **Reichenbach A, Thielscher A, Peer A, Bühlhoff HH, Bresciani J-P.** Seeing the hand while  
689 reaching speeds up on-line responses to a sudden change in target position. *J Physiol* 587: 4605–  
690 4616, 2009.
- 691 **Reichenbach A, Thielscher A, Peer A, Bühlhoff HH, Bresciani J-P.** A key region in the  
692 human parietal cortex for processing proprioceptive hand feedback during reaching  
693 movements. *NeuroImage* 84: 615–625, 2014.
- 694 **Riehle A, Requin J.** Monkey primary motor and premotor cortex: single-cell activity related  
695 to prior information about direction and extent of an intended movement. *J Neurophysiol* 61:  
696 534–549, 1989.
- 697 **Rossetti Y, Desmurget M, Prablanc C.** Vectorial coding of movement: vision, proprioception,  
698 or both? *J Neurophysiol* 74: 457–463, 1995.
- 699 **Saijo N, Gomi H.** Multiple motor learning strategies in visuomotor rotation. *PLoS One* 5: e9399,  
700 2010.
- 701 **Sarlegna FR, Blouin J.** Visual guidance of arm reaching: online adjustments of movement  
702 direction are impaired by amplitude control. *J Vis* 10: 24, 2010.
- 703 **Sarlegna FR, Blouin J, Bresciani J-P, Bourdin C, Vercher J-L, Gauthier GM.** Target and  
704 hand position information in the online control of goal-directed arm movements. *Exp Brain Res*  
705 151: 524–535, 2003.
- 706 **Sarlegna FR, Malfait N, Bringoux L, Bourdin C, Vercher J-L.** Force-field adaptation  
707 without proprioception: can vision be used to model limb dynamics? *Neuropsychologia* 48: 60–  
708 67, 2010.
- 709 **Sarlegna FR, Przybyla A, Sainburg RL.** The influence of target sensory modality on motor  
710 planning may reflect errors in sensori-motor transformations. *Neuroscience* 164: 597–610,  
711 2009.

## Motor responses to target jump in altered force field

- 712 **Saunders JA, Knill DC.** Humans use continuous visual feedback from the hand to control fast  
713 reaching movements. *Exp Brain Res* 152: 341–352, 2003.
- 714 **Shadmehr R.** Generalization as a behavioral window to the neural mechanisms of learning  
715 internal models. *Hum Mov Sci* 23: 543–568, 2004.
- 716 **Smeets JB, Oostwoud Wijdenes L, Brenner E.** Movement Adjustments Have Short Latencies  
717 Because There is No Need to Detect Anything. *Motor Control* 20: 137–148, 2016.
- 718 **Soechting JF, Lacquaniti F.** Modification of trajectory of a pointing movement in response to  
719 a change in target location. *J Neurophysiol* 49: 548–564, 1983.
- 720 **van Sonderen JF, Denier van der Gon JJ, Gielen CC.** Conditions determining early  
721 modification of motor programmes in response to changes in target location. *Exp Brain Res* 71:  
722 320–328, 1988.
- 723 **Tagliabue M, McIntyre J.** Necessity is the mother of invention: reconstructing missing  
724 sensory information in multiple, concurrent reference frames for eye-hand coordination. *J*  
725 *Neurosci* 31: 1397–1409, 2011.
- 726 **Telgen S, Parvin D, Diedrichsen J.** Mirror reversal and visual rotation are learned and  
727 consolidated via separate mechanisms: recalibrating or learning de novo? *J Neurosci* 34:  
728 13768–13779, 2014.
- 729 **Todorov E.** Optimality principles in sensorimotor control. *Nat Neurosci* 7: 907–915, 2004.
- 730 **Tong C, Wolpert DM, Flanagan JR.** Kinematics and dynamics are not represented  
731 independently in motor working memory: evidence from an interference study. *J Neurosci* 22:  
732 1108–1113, 2002.
- 733 **Vindras P, Desmurget M, Prablanc C, Viviani P.** Pointing errors reflect biases in the  
734 perception of the initial hand position. *J Neurophysiol* 79: 3290–3294, 1998.
- 735 **Wagner MJ, Smith MA.** Shared internal models for feedforward and feedback control. *J*  
736 *Neurosci* 28: 10663–10673, 2008.
- 737 **Wang T, Dordevic GS, Shadmehr R.** Learning the dynamics of reaching movements results  
738 in the modification of arm impedance and long-latency perturbation responses. *Biol Cybern* 85:  
739 437–448, 2001.
- 740 **Wolpert DM, Diedrichsen J, Flanagan JR.** Principles of sensorimotor learning. *Nat Rev*  
741 *Neurosci* 12: 739–751, 2011.



742 **Figure captions**

743 Fig. 1: Experimental setup and temporal organization of the protocol. The first step consisted  
 744 in validating sensorimotor adaptation using trials without Tjump. For this validation, the  
 745 statistical analyses were performed using only unperturbed trials of the PRE phase (before  
 746 rotation), of the PER-initial and PER-final phases (first and last unperturbed trial during  
 747 rotation), and of the POST-initial and POST-final phases (first and last unperturbed trial after  
 748 rotation). Note that for all these trials without target jumps, the participants knew that no target  
 749 jump would occur during their movements. The second step consisted in comparing Tjump  
 750 trials between the same phases (PRE, PER-initial, PER-final, POST-initial, POST-final). These  
 751 trials were randomly distributed in a new series of trials including target jump.

752 Fig. 2: Reaching index finger position in Z axis (left column) and finger tangential velocity in  
 753 the sagittal plane (right column) of representative trials showing (A) online secondary  
 754 correction, (B) absence of online secondary correction and (C) offline secondary correction.  
 755 Note that B and C types of trials were rejected from the analyses.

756 Fig. 3: Mean index finger trajectories of all participants (top view) computed in each phase in  
 757 Tclose trials.

758 Fig. 4: Means of (A) lateral and (B) longitudinal endpoint errors compared between phases in  
 759 Tclose and Tfar trials. \*:  $p < 0.05$ ; \*\*:  $p < 0.01$ ; \*\*\*:  $p < 0.001$ .

760 Fig. 5: Maximum angular deviation before PV for the different phases in Tclose and Tfar trials.  
 761 \*:  $p < 0.05$ ; \*\*:  $p < 0.01$ ; \*\*\*:  $p < 0.001$ .

762 Fig. 6: Mean endpoint tangential velocity in the sagittal plane for Tfar (blue line) and Tjump  
 763 (red line) in all phases. Shaded areas represent positive and negative standard deviations.

764 Fig. 7: Mean (A) lateral and (B) longitudinal endpoint errors compared between jump phases  
 765 in Tjump trials. Mean (C) finger peak velocity and (D) relative time to peak velocity during  
 766 secondary correction compared between phases in Tjump trials. None of these variables were  
 767 significantly impacted by experimental phases.

768 Fig. 8: Mean EMG activity of the four recorded muscles for Tjump trials in PRE (blue trace)  
 769 and PER-initial (red trace) jump phases. The vertical dotted line represents movement onset  
 770 and the yellow area the time window used to compute EMG RMS during movement  
 771 corrections.

772 Fig. 9: Mean EMG RMS of the four recorded muscles computed during the temporal window  
 773 of secondary correction and compared between phases in Tjump trials. \*:  $p < 0.05$ . \*\*:  $p < 0.01$ .

774

775 **Footnotes**

776 <sup>1</sup> Coriolis force is a pseudo force applied on the whole body in movement in a rotating  
777 referential. It increases according to the mass of the segment (m), the rotation velocity ( $\omega$ ), the  
778 segment velocity (v) and the trajectory angle of the displacement ( $\theta$ ). Formula:  $F_{Cor} = 2m \cdot \omega \cdot v / \theta$

779 Centrifugal force is a force applied in a rotating referential. It increases according to the mass  
780 of the segment (m), the linear velocity on the tangent to the trajectory (v), the radius of the curve  
781 (r). Formula:  $F_{Cen} = m \cdot v^2 / r$