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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

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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).

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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

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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 ± 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

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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):

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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 deg.s^{-1} plateau in 80
189 s. The counterclockwise rotation generated both Coriolis and centrifugal forces on the moving
190 arm¹. 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

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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.

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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

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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.

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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

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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.

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Insert Fig. 3 about here

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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.

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Insert Fig. 4 about here

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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).

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356 Insert Fig. 5 about here

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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).

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Insert Fig. 6 about here

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

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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} : $278 \text{ ms} \pm 53 \text{ ms}$).

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Insert Fig. 7 about here

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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

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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.

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Insert Fig. 8 about here

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

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

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Insert Fig. 9 about here

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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

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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

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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

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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

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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

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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 ¹ 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 (ω), the
778 segment velocity (v) and the trajectory angle of the displacement (θ). 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: $F_{Cen} = m \cdot v^2 / r$