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

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Abstract

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

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 gravito-inertial 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

Introduction

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

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

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

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

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

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

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

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

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

Materials and Methods

Participants

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

Experimental setup

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

Insert Fig. 1 about here

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

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

Procedure

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

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

Motor responses to target jump in altered force field

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

PER phase (platform rotation): While the participants had their index finger on the starting position, the velocity of the rotating platform was brought to a 120 deg.s^{-1} plateau in 80 s. The counterclockwise rotation generated both Coriolis and centrifugal forces on the moving arm¹. According to the laws of physics, the Coriolis force was orthogonal to the movement path and clockwise (i.e., opposite to the direction of platform rotation). The centrifugal force was in the direction of the movement path. The series of trials only started 30 s after the platform reached a constant velocity, i.e. when body rotation was no longer perceived (Benson, 1990; George et al. 2011). The participants were instructed to remain still until the start of the first trial. An infrared camera was used to verify their compliance with this instruction. Then, participants performed 30 reaches towards T_{close} and T_{far} (15 trials for each randomly-presented target: PER-initial phase), a number of trials that has been found sufficient to adapt feedforward control to Coriolis and centrifugal forces through proprioceptive feedback control (Coello et al. 1996; Franklin et al. 2007; Lackner and Dizio 1998). After this set of trials, participants performed 50 reaches towards T_{close} and T_{jump} (40 T_{close} and 10 T_{jump} randomly presented: PER-final phase). As in the PRE phase, before both sets of trials participants were told whether or not target position could change at movement onset.

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

the POST phase only started 30 s after the platform became stationary. Participants performed 6 reaches towards Tclose and Tfar (3 trials for each randomly-presented target: POST-initial phase), followed by 25 reaches towards Tclose and Tjump (20 Tclose and 5 Tjump randomly presented: POST-final phase). Again, participants were told before both sets of trials whether or not target position could change at movement onset.

Participants familiarized themselves with the reaching task in a preliminary phase by performing 6 reaching movements towards Tclose and Tfar (3 trials for each randomly-presented target) and 15 reaching movements towards Tclose and Tjump (12 Tclose and 3 Tjump randomly presented) in a non-altered gravito-inertial force field.

Kinematic analyses

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

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

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

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

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

Insert Fig. 2 about here

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

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

EMG analyses

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

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

Statistical analyses

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

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

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

Results

Confirmation of feedforward control adaptation

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

Insert Fig. 3 about here

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

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

Insert Fig. 4 about here

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

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

Insert Fig. 5 about here

Comparison of Tfar and Tjump trials

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

Insert Fig. 6 about here

Comparison of Tjump trials from the different jump phases

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} : $97 \text{ cm.s}^{-1} \pm 45 \text{ cm.s}^{-1}$; 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} : $278 \text{ ms} \pm 53 \text{ ms}$).

Insert Fig. 7 about here

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.

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406 Insert Fig. 8 about here

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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.

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411 Insert Fig. 9 about here

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Discussion

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

Validation of adaptation to an altered gravito-inertial force field

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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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: $FCor = 2m.\omega.v/\theta$
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: $FCen = m.v^2/r$