

RESEARCH ARTICLE

Control of Movement

## 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 end point errors) and kinematics (movement time, peak velocity) of the corrective movements. The electromyographic activity of different arm muscles (pectoralis, posterior deltoid, biceps brachii, 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.

**NEW & NOTEWORTHY** We investigated the link between feedforward and feedback control when applying a double-step perturbation (visual target jump) during reaching movements performed in modified gravito-inertial environments. Altogether, kinematics and EMG analyses showed that movement corrections were highly effective in the different force fields, suggesting 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.

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

### 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 (1, 2), movement extent and direction (3–5), movement velocity (6, 7), and the effect of gravity on the arm (8, 9) are key parameters in preparing motor commands. Set before movement onset, these parameters are thought to be under feedforward control (10). 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 error processing (11). Thanks to



this sensorimotor adaptation, which greatly relies on the cerebellar network (12, 13), the motor actions performed in the new gravitational environment become comparable to those produced in the normal force field (14–16).

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 (17–21). The online movement corrections would notably rely on the posterior parietal cortex (18, 22) 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 have demonstrated that online responses to mechanical perturbations applied to the moving arm are adapted to the force field in which the movement evolves (23–28). For instance, Wagner and Smith (27) 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 (26) 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 (29–32).

In the above-mentioned 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 (33)]. 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 (34–37). As a result, the use of a common sensory modality for encoding target position and controlling hand trajectory might induce smaller end point error and shorter correction latencies when the motor goal suddenly changes during reaching movements (34, 38). 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. (39) 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 (39). However, the spatiotemporal characteristics of online corrections of the arm trajectory were not addressed in this study. Therefore, although 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 related to different domains. Foremost among these, it remains unclear whether the feedback control was readily optimized from the very first time that 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 that 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 yr, 7 females), all naïve to the goal of the experiment, participated after giving their written, informed consent. None reported a sensorimotor deficit, and all had normal or corrected-to-normal vision. The study was approved by the local ethics 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 heads immobile. In front of them, a horizontal board was positioned 45 cm above the seat. A microswitch located 25 cm in front of the participants' midtrunk 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 microswitch (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.

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 (1,000 Hz; BIOPAC Systems, Inc., Santa Barbara, CA). We recorded the activity of two agonist muscles (clavicular head of pectoralis and short head of triceps brachii) and two antagonist muscles (posterior deltoid and 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 the electrodes were affixed (Ag-AgCl; diameter 1 cm, spacing 2 cm) along a line parallel to their fiber orientation to increase the signal-to-noise ratio (40, 41). The motorized platform, 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 microswitch, 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 microswitch. In 20% of the trials (pseudorandomly distributed), a target jump from T<sub>close</sub> to T<sub>far</sub> (T<sub>jump</sub> condition) occurred on release of the microswitch, with T<sub>far</sub> target remaining lit for 100 ms. Under these conditions, movement corrections are deemed to be visually based, even if visual information was withheld during the reaches (see Ref. 42). For all conditions, participants were instructed to reach toward 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).

#### PRE phase (no platform rotation).

Participants first performed 10 reaching movements prior to platform rotation (i.e., PRE phase) toward T<sub>close</sub> and T<sub>far</sub> (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 toward T<sub>close</sub> and T<sub>jump</sub> (40 T<sub>close</sub> and 10 T<sub>jump</sub> 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°/s plateau in 80 s. The counterclockwise rotation generated both Coriolis and centrifugal forces on the moving arm<sup>1</sup>. 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 started only 30 s after the platform reached a constant velocity, i.e., when body rotation was no longer perceived (43, 44). The participants were instructed to remain still until the start of the first trial during rotation (i.e., PER phase). An infrared camera was used to verify their compliance with this instruction. Then, participants performed 30 reaches toward T<sub>close</sub> and T<sub>far</sub> (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 (14, 45, 46). After this set of trials, participants performed 50 reaches toward T<sub>close</sub> and T<sub>jump</sub> (40 T<sub>close</sub> and 10 T<sub>jump</sub> 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 platform rotation).

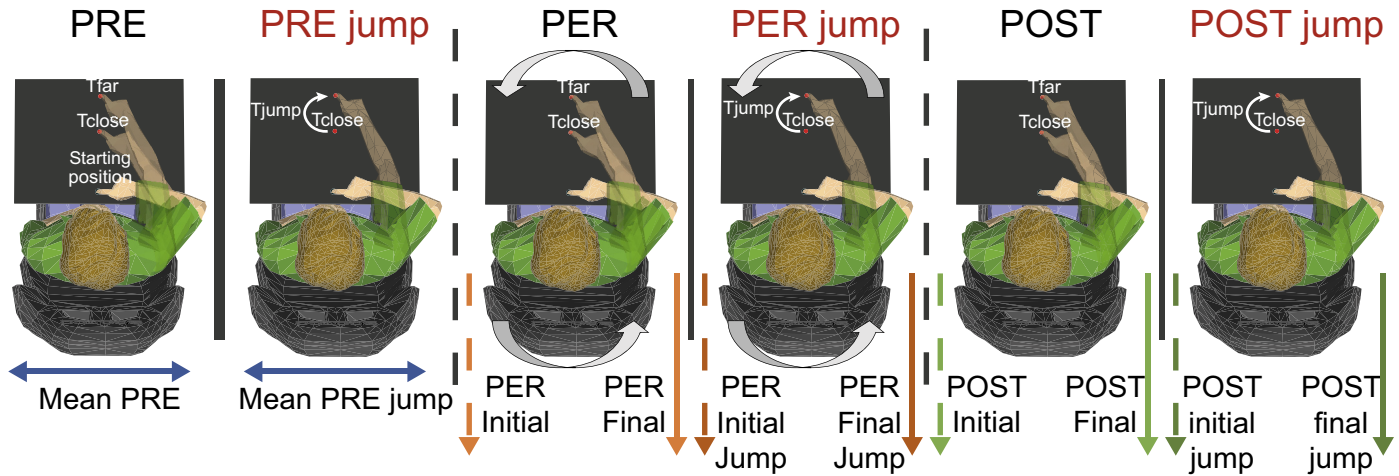
At the end of the PER phase, the participants remained still with their forefinger on the starting position until an 80-s deceleration brought the platform to complete immobilization. For the reason explained regarding the PER phase, the first trial following rotation (i.e., POST phase) started only 30 s after the platform became stationary. Participants performed 6 reaches toward T<sub>close</sub> and T<sub>far</sub> (3 trials for each randomly presented target: POST-initial phase), followed by 25 reaches toward T<sub>close</sub> and T<sub>jump</sub> (20 T<sub>close</sub> and 5 T<sub>jump</sub> 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 toward T<sub>close</sub> and T<sub>far</sub> (3 trials for each randomly presented target) and 15 reaching movements toward T<sub>close</sub> and T<sub>jump</sub> (12 T<sub>close</sub> and 3 T<sub>jump</sub> randomly presented) in a nonaltered gravito-inertial force field.

#### Kinematic Analyses

Data were analyzed using MATLAB (MathWorks, Natick, MA). 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., T<sub>close</sub> and T<sub>far</sub>) from each experimental phase. Following common procedure for

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



**Figure 1.** Experimental setup and temporal organization of the protocol. The first step consisted in validating sensorimotor adaptation using trials without target jumps (Tjump), that is, including reachings to the close target (Tclose) or to the far target (Tfar). For this validation, the statistical analyses were performed using only unperturbed trials of the PRE phase (before rotation), of the PER-initial and PER-final phases (first and last unperturbed trial during rotation), and of the POST-initial and POST-final phases (first and last unperturbed trial after rotation). Note that for all these trials without target jumps the participants knew that no target jump would occur during their movements. The second step consisted in comparing Tjump trials (i.e., reachings during target jump from the close to the far target) between the same phases (PRE, PER-initial, PER-final, POST-initial, POST-final). These trials were randomly distributed in a new series of trials including target jump.

sensorimotor adaptation studies (see Refs. 15 and 16), 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.

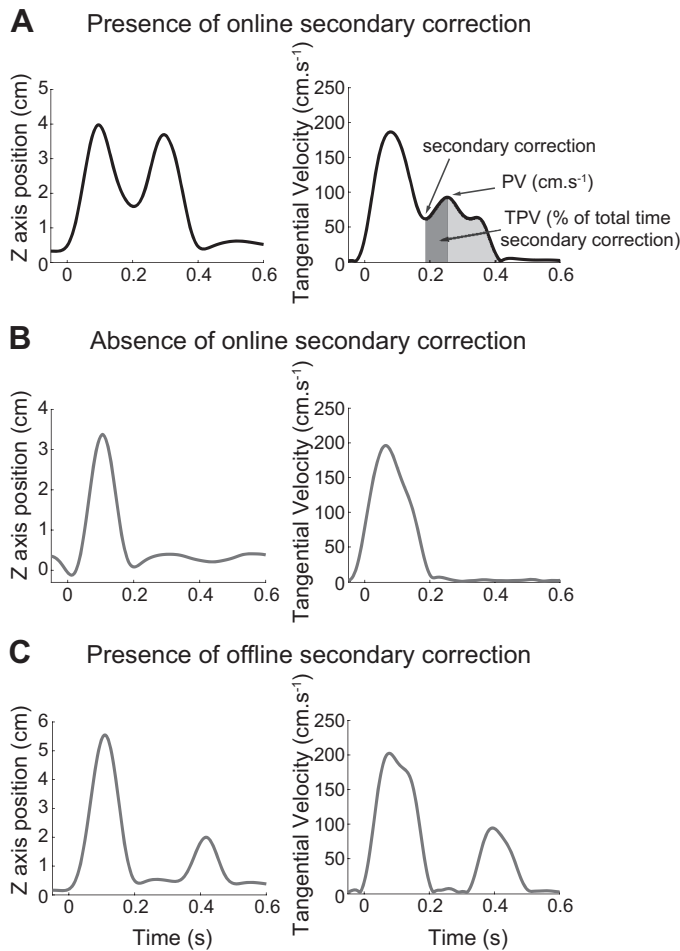
Several variables were computed to evaluate movement performance. Tangential peak velocity (PV) of the index finger movement was calculated from the marker *x* and *y* coordinates. Movement time (MT) was calculated as the time between movement onset and offset, identified as when tangential velocity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

We computed the lateral end point 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 end point errors indicated leftward and rightward finger deviations, respectively, with respect to the target. Longitudinal end point 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 end point errors indicated target undershoot and overshoot, respectively. For both Tclose and Tfar, end point errors were rebased relative to the mean end point 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

(47); variables measured before this kinematics landmark are considered as resulting mainly from feedforward control.

The second step consisted in comparing the Tjump trials from the different phases. We excluded trials exhibiting off-line corrective movements, defined as those where, between movement onset and movement offset, tangential velocity was 0 cm/s or the *z* coordinate of the index finger equaled the *z* coordinate of the target's surface (see Fig. 2C). The remaining 84% of total Tjump trials (with no significant difference in proportion across phases) were examined to identify whether or not they contained overt online secondary corrections (Fig. 2, A and B, 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 Ref. 48). Because secondary corrections are deemed to be under online control, only Tjump trials with these observable corrections were kept (82% of the Tjump trials showed secondary corrections with no significant difference in proportion across phases). Note that trials without such online corrections showed large longitudinal end point 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 four 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 of 16 participants were kept for this second step of data analyses.

Onset of secondary correction was identified when tangential acceleration exceeded 0 cm/s<sup>2</sup> after the first acceleration and deceleration phases. From that 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),



**Figure 2.** Reaching index finger position in z-axis (*left*) and finger tangential velocity in the sagittal plane (*right*) of representative Tjump trials (i.e., including a target jump from the close to the far target) showing online correction illustrated by a secondary peak velocity (PV) and time-to-peak velocity (TPV) (A), absence of online correction (B), and offline secondary correction (C). Note that B and C types of trials were rejected from the analyses.

computed in percentages 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 whether 1) the online correction observed during the first Tjump after adaptation or readaptation was functional, and 2) the online correction in the PER jump phase improved after practice (PER-initial vs PER-final), as was 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 (49). After centering around the mean and rectifying of 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” (21)] 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

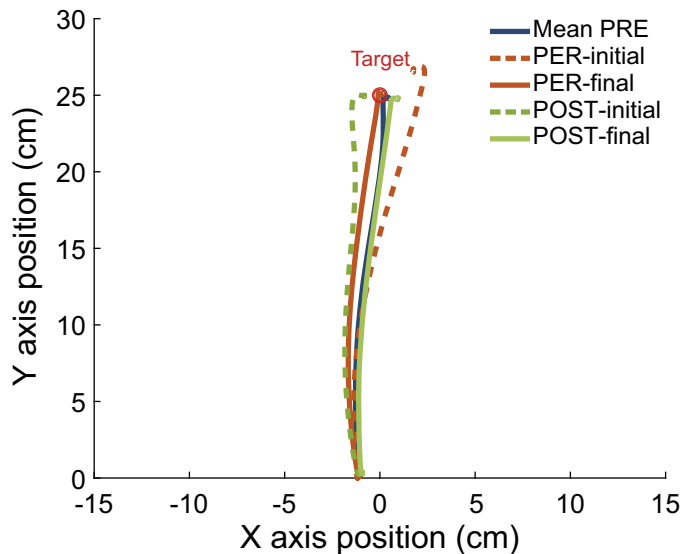
To determine whether participants adapted to the altered gravito-inertial force field before the first Tjump trial, for each movement we compared the kinematics variables computed for the different phases without Tjump trials (PRE, PER-initial, PER-final, POST-initial, POST-final), using repeated-measures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



**Figure 3.** Mean index finger trajectories of all participants (*top*) computed in each phase in Tclose trials (i.e., reachings to the close target). PRE phase, before rotation; PER-initial and PER-final phases, first and last unperturbed trial during rotation; POST-initial and POST-final phases, first and last unperturbed trial after rotation.

reaching movements were almost as rectilinear and as accurate as during the PRE phase.

The statistical analyses performed on the different kinematics variables revealed how the exposure phases affected reaching movements. The ANOVA performed on lateral end point 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 end point errors did not significantly differ between PRE, PER-final, and POST-final phases.

The ANOVA also revealed a significant phase effect on longitudinal end point 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. Whereas the longitudinal end point 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-final phases. Together, these results denote some signs of feedforward control adaptation of movement extent in the new force field.

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 were more deviated to the left than those in the PRE phase ( $P < 0.001$ ). Kinematic landmarks falling before peak velocity are

considered to illustrate mainly feedforward control (47). 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 (15, 16).

### Comparison of Tfar and Tjump Trials

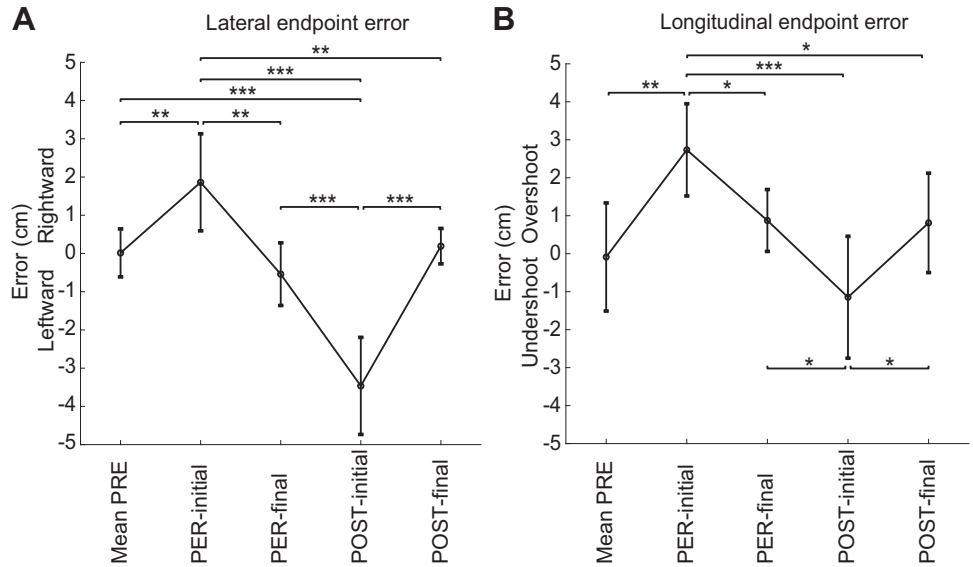
The presence of a target jump during reaching fundamentally changed the spatiotemporal organization of the movement. This can be seen in Fig. 6, which shows the respective mean tangential velocities of all Tfar and valid Tjump trials, where the same spatial goal had to be reached with or without a change of target position. Compared with Tfar trials, Tjump trials had a smaller PV and showed a secondary PV after a first deceleration phase. Movement times were also longer in Tjump trials than in Tfar trials (mean:  $490 \pm 63$  ms vs.  $336 \pm 56$  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:  $278 \pm 53$  ms vs.  $411 \pm 58$  ms respectively;  $t_{(11)} = 6.82$ ;  $P < 0.0001$ ). This result concurs with the findings from several studies using a double-step reaching paradigm that showed that the modification of motor commands under feedback control was faster than the time necessary to produce new motor commands under feedforward control (17, 38, 50–54).

### 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 ( $\bar{x}$ ):  $489 \pm 54$  ms), lateral end point errors ( $F_{(4,44)} = 1.19$ ;  $P = 0.33$ ,  $\bar{x}$ :  $0.60 \pm 0.81$  cm; Fig. 7A), or longitudinal end point errors ( $F_{(4,44)} = 2.19$ ;  $P = 0.09$ ,  $\bar{x}$ :  $0.85 \pm 3.21$  cm; Fig. 7B), PV secondary correction ( $F_{(4,44)} = 1.36$ ;  $P = 0.26$ ;  $\bar{x}$ :  $97 \pm 45$  cm/s; Fig. 7C), TPV secondary correction ( $F_{(4,44)} = 0.97$ ;  $P = 0.43$ ;  $\bar{x}$ :  $35 \pm 11\%$ ; Fig. 7D), and secondary correction time ( $F_{(4,44)} = 0.88$ ;  $P = 0.48$ ;  $\bar{x}$ :  $278 \pm 53$  ms).

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 ( $F_{(4,44)} = 4.26$ ;  $P < 0.01$ ; Fig. 9B) and posterior deltoid ( $F_{(4,44)} = 3.5$ ;  $P < 0.05$ ; Fig. 9C) EMG RMS. For the posterior deltoid, EMG RMS was greater in the PER-initial jump phase than in POST-initial jump and POST-final jump phases. For

**Figure 4.** Means of lateral (A) and longitudinal (B) end point errors compared between phases in Tclose (i.e., reachings to the close target) and Tfar (i.e., reachings to the far target) trials. PRE phase, before rotation; PER-initial and PER-final phases, first and last unperturbed trial during rotation; POST-initial and POST-final phases, first and last unperturbed trial after rotation. \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .



the pectoralis, EMG RMS was greater in the PER-initial jump phase than in all the other phases.

Finally, the ANOVA performed on the EMG RMS of triceps brachii ( $F_{(4,44)} = 1.7$ ;  $P = 0.16$ ; Fig. 9D) did not show a significant phase effect.

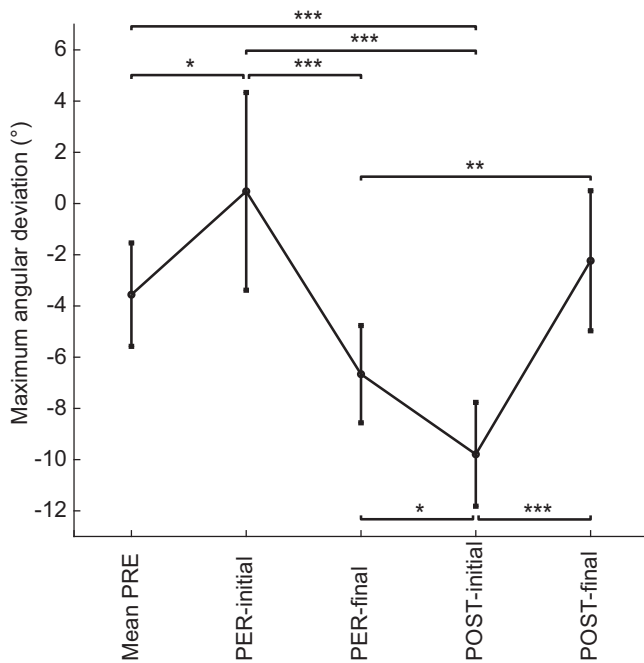
## DISCUSSION

The present study explored the link between feedback and feedforward control by looking at whether, when

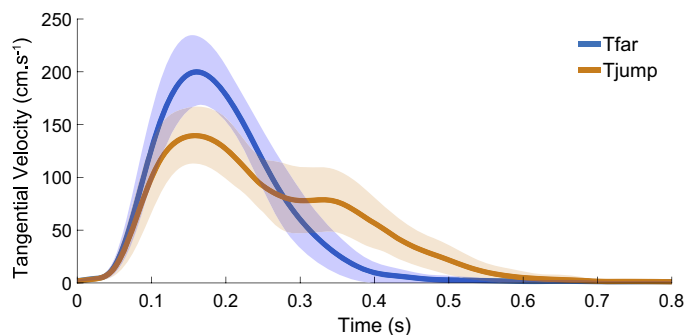
motor commands are adapted to a new force field, online control of arm movement remains effective under a perturbation of a different nature. In a two-step experimental protocol, participants first adapted feedforward control to the mechanical perturbation of an altered gravito-inertial force field by reaching toward 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 that participants encountered a target jump in the altered force field.

### Validation of Adaptation to an Altered Gravito-inertial Force Field

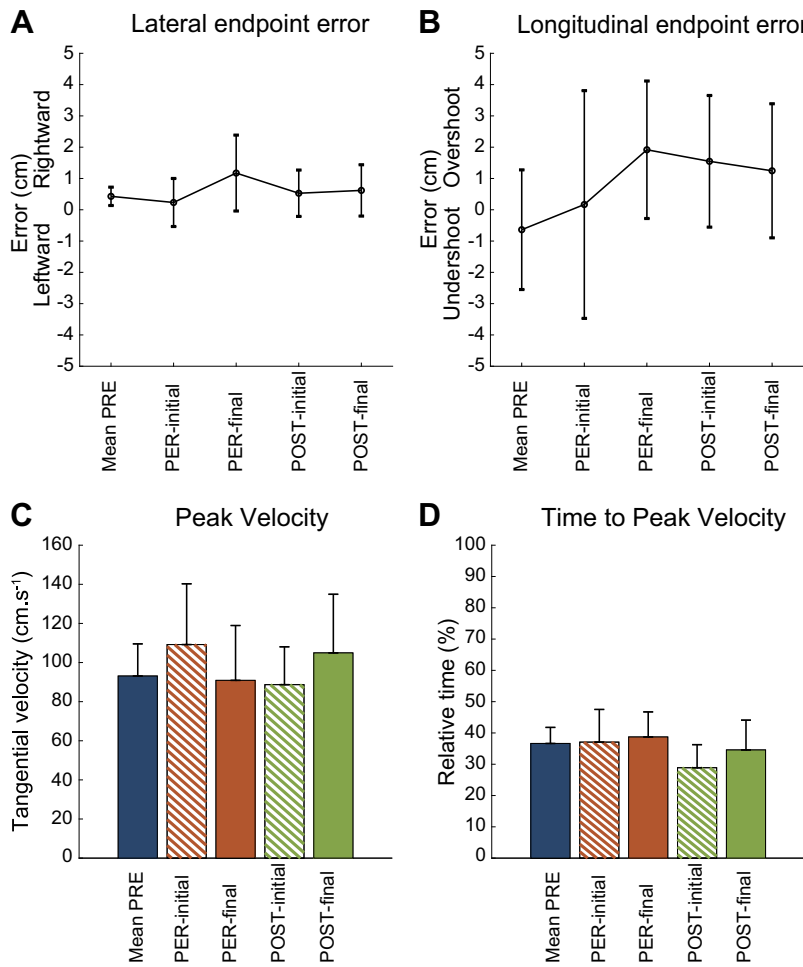
The first reaching movement performed by the participants after being reexposed to a normal gravito-inertial force field (i.e., in POST-initial phase) showed wide trajec-



**Figure 5.** Maximum angular deviation before peak velocity (PV) for the different phases in Tclose (i.e., reachings to the close target) and Tfar (i.e., reachings to the far target) trials. PRE phase, before rotation; PER-initial and PER-final phases, first and last unperturbed trial during rotation; POST-initial and POST-final phases, first and last unperturbed trial after rotation. \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .



**Figure 6.** Mean end point tangential velocity in the sagittal plane for Tfar (i.e., reachings to the far target; blue line) and Tjump (i.e., reachings during target jump from the close to the far target; red line) in all phases. Shaded areas represent positive and negative standard deviations.



**Figure 7.** Mean lateral (A) and longitudinal (B) end point errors compared between jump phases in Tjump trials (i.e., reachings during target jump from the close to the far target). Mean finger peak velocity (C) and relative time to peak velocity (D) during secondary correction compared between phases in Tjump trials. None of these variables were significantly impacted by experimental phases. PRE phase, Tjump trials before rotation; PER-initial and PER-final phases, first and last Tjump trials during rotation; POST-initial and POST-final phases, first and last Tjump trials after rotation.

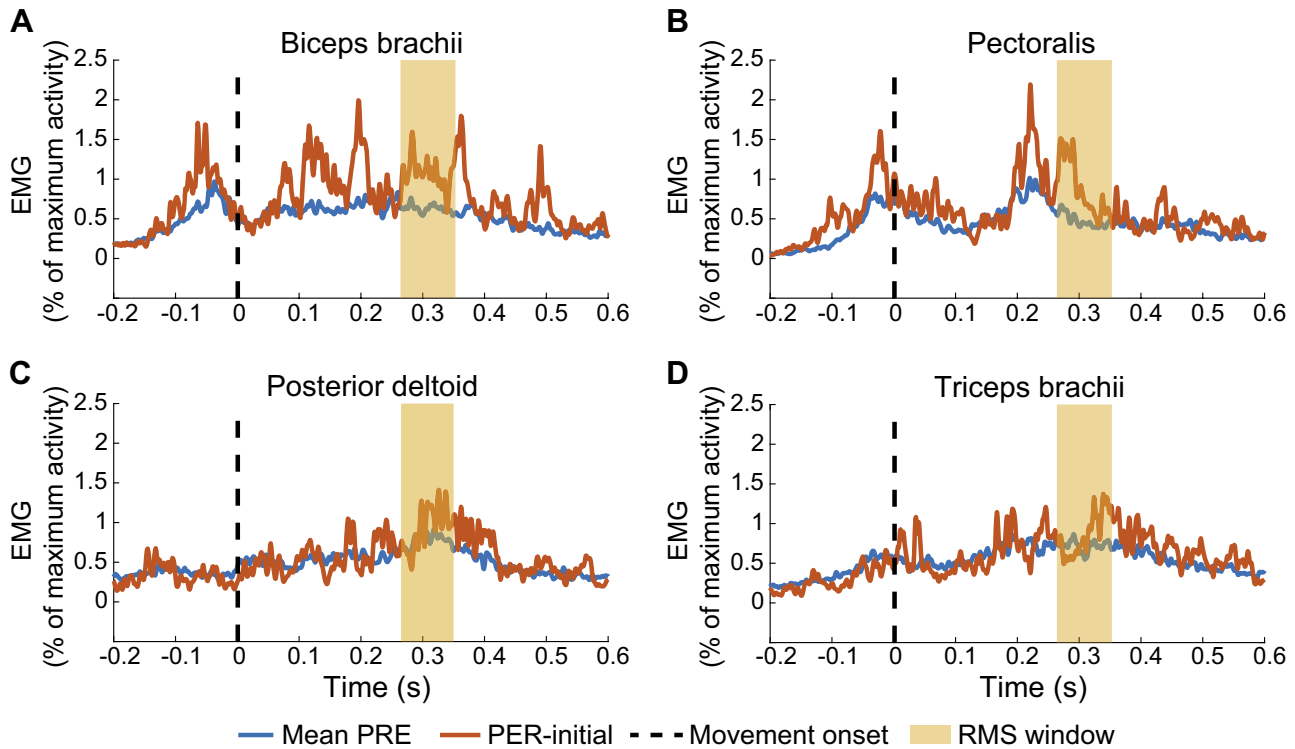
ory deviation. The deviation was in the opposite direction to the Coriolis force exerted on the arm during the preceding series of reaches in the altered force field. This so-called posteffect confirmed that the feedforward control responsible for triggering the movements was adapted to the force field change induced by platform rotation (14, 45, 46). 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 (55).

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 (14, 15), or off-axis (46, 56, 57), showed that centrifugal force had no significant effects on movement accuracy and that exposure to this force did not lead to posteffects. 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, before reaching, the hand position appeared to be farther from the rotation axis, even when participants were seated above this axis (14, 15). 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 before movement execution has been reported in several studies (58–61). 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 end point errors returned to baseline level after around three trials performed in the altered gravito-inertial force field, the posteffect observed for this variable greatly differed from that revealed for the directional errors. Indeed, the participants' longitudinal errors when first reexposed to a normal force field did not significantly differ from those produced before the force field alteration (PRE phase). However, the amplitude of the first postrotation movement was significantly smaller than the last movement performed during the rotation (PER-final) and the last movement performed after being reexposed 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 with the adaptation shown for movement direction (assessed here using lateral end point errors).





**Figure 8.** Mean EMG activity of the biceps brachii (A), pectoralis (B), posterior deltoid (C), and triceps brachii (D) for Tjump (i.e., reachings during target jump from the close to the far target) trials in PRE (before rotation; blue trace) and PER-initial (first Tjump trial during rotation; red trace) phases. Vertical dotted line represents movement onset and yellow area the time window used to compute EMG root mean squares (RMS) during movement corrections.

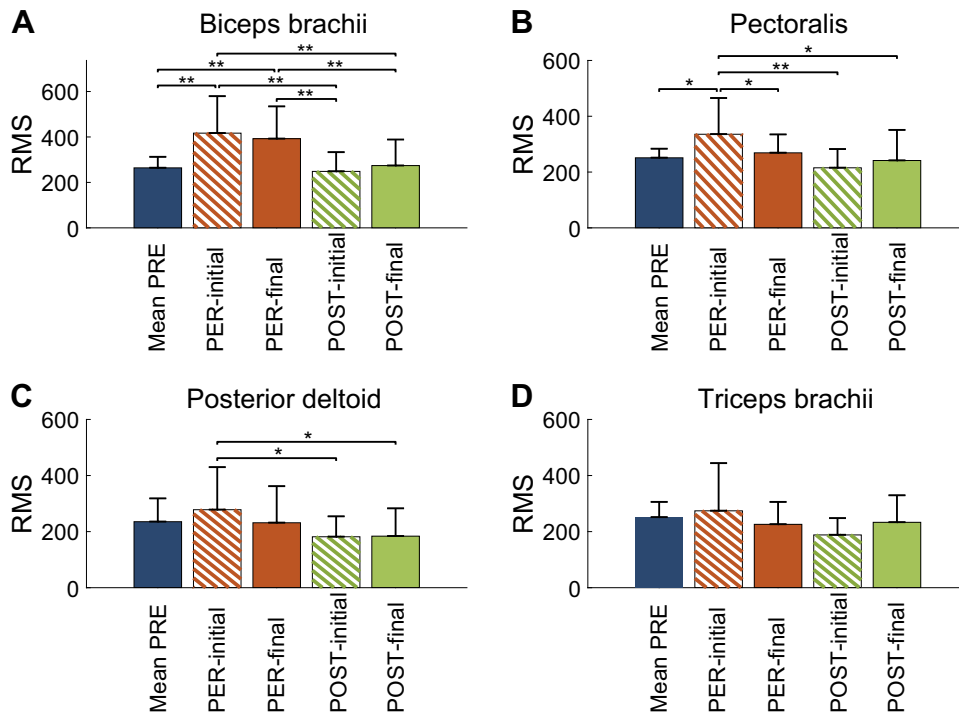
These differing capacities to adapt movement amplitude and direction could be explained with reference to the vectorial coding model of movements. According to this model, motor commands are planned according to the direction and the amplitude of a hand-target vector computed by the brain (1, 3, 33, 62–64). Importantly, the fact that movement direction has to be specified before movement onset (65–68), unlike movement amplitude (16, 63, 66), might place greater stress on planning movement direction than movement amplitude. This could be responsible for the observation made here and in previous studies (14, 15, 46, 56, 57) 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 been assessed only by Diamond et al. (39). In their study, the feedforward control was first adapted by having participants transport several times a handheld 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 end point 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 vs. POST-initial jump and POST-final jump phases) muscles during the movement corrections observed in the altered gravito-inertial force field.



**Figure 9.** Mean EMG root mean squares (RMS) of the biceps brachii (A), pectoralis (B), posterior deltoid (C), and triceps brachii (D) computed during the temporal window of secondary correction and compared between phases in Tjump trials (i.e., reachings during target jump from the close to the far target). PRE phase, Tjump trials before rotation; PER-initial and PER-final phases, first and last Tjump trials during rotation; POST-initial and POST-final phases, first and last Tjump trials after rotation. \* $P < 0.05$ , \*\* $P < 0.01$ .

When participants reached toward 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 kinematics 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 (69). 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 (70). Because pectoralis muscle was less active on the last Tjump trial, cocontraction 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 (71, 72). An optimization of motor command over Tjump trials may be based on a reorganization of muscular synergies (73) 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 effective only 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 (23–28) or by visual (29–32) feedback. They showed effective corrections from the first movement perturbation, confirming that, in this context, feedforward and feedback controls are closely linked (27, 32). 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. Although force field and visuomotor adaptations have been found to involve distinct neural networks (12, 74), 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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## DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

## AUTHOR CONTRIBUTIONS

L.C., J.B., and L.B. conceived and designed research; L.C. performed experiments; L.C. analyzed data; L.C., J.B., and L.B. interpreted results of experiments; L.C. prepared figures; L.C., J.B., and L.B. drafted manuscript; L.C., J.B., and L.B. edited and revised manuscript; L.C., J.B., and L.B. approved final version of manuscript.

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