

# **RESEARCH ARTICLE**

Control of Movement

# Distinct adaptation patterns between grip dynamics and arm kinematics when the body is upside-down

# <sup>(D</sup>L. Opsomer,<sup>1,2</sup> <sup>(D</sup>F. Crevecoeur,<sup>1,2</sup> J-L. Thonnard,<sup>1,2</sup> J. McIntyre,<sup>3,4,5</sup> and <sup>(D</sup>P. Lefèvre<sup>1,2</sup>

<sup>1</sup>Institute of Neuroscience, Université catholique de Louvain, Brussels, Belgium; <sup>2</sup>Institute of Information and Communication Technologies, Electronics and Applied Mathematics, Université catholique de Louvain, Louvain-la-Neuve, Belgium; <sup>3</sup>Centre National de la Recherche Scientifique, University of Paris, France; <sup>4</sup>TECNALIA,Basque Research and Technology Alliance (BRTA), Donostia-San Sebastian, Spain; and <sup>5</sup>Ikerbasque Science Foundation, Bilbao, Spain

# Abstract

In humans, practically all movements are learnt and performed in a constant gravitational field. Yet, studies on arm movements and object manipulation in parabolic flight have highlighted very fast sensorimotor adaptations to altered gravity environments. Here, we wondered if the motor adjustments observed in those altered gravity environments could also be observed on Earth in a situation where the body is upside-down. To address this question, we asked participants to perform rhythmic arm movements in two different body postures (right-side-up and upside-down) while holding an object in precision grip. Analyses of grip-load force coordination and of movement kinematics revealed distinct adaptation patterns between grip and arm control. Grip force and load force were tightly synchronized from the first movements performed in upside-down posture, reflecting a malleable allocentric grip control. In contrast, velocity profiles showed a more progressive adaptation to the upside-down posture and reflected an egocentric planning of arm kinematics. In addition to suggesting distinct mechanisms between grip dynamics and arm kinematics for adaptation that can be used for fast sensorimotor coordination across different postures on Earth and, incidentally, across different gravitational conditions in parabolic flights, in human centrifuges, or in Space.

**NEW & NOTEWORTHY** During rhythmic arm movements performed in an upside-down posture, grip control adapted very quickly, but kinematics adaptation was more progressive. Our results suggest that grip control and movement kinematics planning might operate in different reference frames. Moreover, by comparing our results with previous results from parabolic flight studies, we propose that a common mechanism underlies adaptation to unfamiliar body postures and adaptation to altered gravity.

grip force; reference frame; rhythmic arm movements; upside-down posture

# INTRODUCTION

The central nervous system (CNS) develops at an early age the ability to coordinate arm movements and finger forces during object manipulation (1–3). More precisely, to ensure a stable grip the CNS must learn to synchronize grip force (GF), applied perpendicularly to the contact surfaces of the object, with the tangential load force (LF), varying as a function of the object weight and acceleration, so that any self-induced variation of load force is accompanied by a synchronized and finely tuned change of grip force (4, 5). This tight coupling between GF and LF relies on accurate sensory feedback (6–9) and, importantly, on so-called *internal models* that can be used to predict the sensory and physical consequences of motor commands and actions (10–13). These predictive mechanisms, employed by the CNS to program grip force anticipatively, must account for the physical properties of the object such as mass (14–16) and frictional properties (5, 17), as well as for the dynamics of the arm (18–20) and the dynamics of the environment is the omnipresent gravitational force, which combines additively with the inertial forces to generate the tangential



Submitted 16 June 2020 / Revised 11 December 2020 / Accepted 27 January 2021

0022-3077/21 Copyright © 2021 the American Physiological Society

Downloaded from journals.physiology.org/journal/jn at ULB Biblio Fac De Med Erasme (164.015.128.033) on March 24, 2021.

Correspondence: (philippe.lefevre@uclouvain.be).

load at the fingertips. In particular, distinct directions of movement with respect to gravity can yield distinct LF profiles and therefore distinct required GF (27).

In addition to impacting grip control, gravity plays a central role in the planning of movement kinematics. Previous works have shown that the velocity profile of discrete arm movements depends on movement direction (28–31). Furthermore, results from virtual reality experiments (32, 33) and experiments performed in weightlessness (34–37) strongly suggest that this directional asymmetry is preplanned by the CNS. Optimal control models that minimize a weighted sum of movement jerk and absolute work (28, 38, 39) as well as Optimal Feedback Control models (40) have provided a normative explanation for direction-dependent kinematics.

In accordance with the primordial role played by gravity in motor control, various studies reported clear pieces of evidence for the existence of a central internal estimate of the gravitational force that can be used to facilitate perception and control (41-43). On the one hand, an internal estimate of the direction of gravity (which defines the verticality) is constructed by combining vestibular signals from the otolith organs and the semicircular canals of the inner ear (44, 45), visual signals from the retina (46-48), somatosensory signals from mechanoreceptors (49-53), and egocentric cues (30, 48, 48)54, 55). On the other hand, the effects of the gravitational force on objects are learnt for instance by internalizing the trajectory of free-falling objects (56-59) or the forces required to manipulate objects (1, 2, 11). Incongruent visual feedback of motion direction during object manipulation affects the timing of GF (60), providing additional evidence that the *in*ternal model of the effects of gravity that is implicitly employed by the CNS for effective GF control is multimodal and not necessarily precise in all circumstances. All in all, it is reasonable to believe that an internal representation of gravity is used by the brain to plan movement kinematics and to coordinate GF and LF during object manipulation.

Quite remarkably, although the coordination between GF and LF is learnt exclusively in a constant Earth-gravity environment, the CNS has proven to be very swift in its ability to adapt dexterous manipulation control to altered-gravity environments encountered for instance in parabolic flights or in human centrifuges (for a review, see 61). A good temporal synchronization between the two forces is usually observed within seconds of exposure to microgravity (21, 62), partial gravity (63), or hypergravity (21, 22, 62, 64), suggesting flexible predictions of LF that adapt quickly to novel gravitational contexts. In contrast, adaptation of the kinematics of the movement to altered-gravity environments seems to be more progressive (34, 36, 37, 40) which, from the point of view of optimal control, suggests a progressive adjustment of the kinematics to optimize the motor command in terms of dynamic parameters of force, torque, and muscle activation (34, 40). The question arises as to whether the CNS can successfully anticipate load forces and dynamics in all terrestrials conditions or whether mechanisms of sensorimotor adaptation observed in novel gravitational contexts are also required to achieve adequate GF-LF coupling and kinematics planning in unusual circumstances such as when the body is inverted with respect to gravity.

We therefore set out to measure how GF-LF coordination and movement kinematics adapt in a situation where the body is upside-down. In particular, we ask whether the internal estimate of the direction of gravity allows for an allocentric predictive control of finger forces and arm movements, that is to say a control that would use limb motion represented in an Earth-centered reference frame to accurately predict the forces acting on the arm and the fingers, regardless of the body's orientation with respect to gravity; or whether the CNS may have developed predictive mechanisms for load force and limb dynamics based on limb motions expressed in a body-centered reference frame, due to the overwhelming preponderance of movements performed when the body is aligned with gravity.

To answer this question, we asked human participants to perform rhythmic vertical arm movements with a manipulandum held in precision grip in two different body orientations: right-side-up and upside-down. Rhythmic arm movements are especially well suited for investigating sensorimotor coordination, as they generate periodic LF variations that are anticipated by the CNS, as reflected by the synchronized periodic modulation of GF (4). Rhythmic arm movements have been used in the past to test the adaptation of GF control to novel object dynamics such as elastic loads (9, 19) or novel gravitational dynamics (15, 20-22, 62, 63). During vertical arm oscillations performed in a right-side-up posture on Earth and at a moderate pace, LF acts downward on the fingers (toward the feet) and reaches a maximum when object acceleration is maximal upward (toward the head). If one performs the same movement in an upside-down body orientation relative to gravity, from an allocentric point of view the LF profile does not change. But from an egocentric point of view, LF now points toward the head and reaches a maximum when object acceleration is maximal in the direction of the feet.

We hypothesized that, if the GF-LF coupling operates in an allocentric reference frame, the quality of the coordination between the two forces should be high from the first movements performed in the upside-down posture. Indeed, by combining all convergent sensory information indicating a reversal of the body with respect to gravity with flexible predictive mechanisms of movement dynamics, the CNS should theoretically be able to predict accurately the novel sensory consequences of a given motor command sent to the arm. Alternatively, if GF is programmed in an egocentric reference frame, the grip-load force coordination should be seriously impaired in the upside-down posture, at least during initial trials while the system adapts. In addition to the GF-LF coupling, we investigated how the kinematics of the movements adjust when the body is upside-down. Similar to the question of which reference frame is used for GF control, we studied which reference frame is used to plan directiondependent vertical arm movements.

Our results suggest distinct adaptation processes and potentially distinct reference frames between the planning of GF and the planning of kinematics. In the upside-down body orientation, the tight temporal coupling between GF and LF was generally maintained, in agreement with the hypothesis of an allocentric control of GF. In contrast, the kinematics of the arm reflected an egocentric reference frame for trajectory planning, with a more gradual adaptation to this uncommon body posture. Furthermore, kinematics adaptation to upside-down orientation led to aftereffects in the velocity profile of subsequent movements performed in rightside-up orientation, as opposed to the adaptation of GF control. These observations strengthen previous results suggesting distinct adaptation processes underlying trajectory and grip force planning (65, 66). Furthermore, we argue that they support the hypothesis of general mechanisms underlying gravity-dependent motor adjustments that can ensure efficient sensorimotor coordination across different postures on Earth and allow for a rapid sensorimotor adaptation to novel gravitational contexts.

# MATERIALS AND METHODS

#### **Participants**

Thirty-six healthy participants took part in this study. Eighteen participants (aged  $24\pm2.8$ ; 10 males; 17 right-handed) participated in the first experiment and 18 participants (aged  $23.5\pm1.9$ ; 10 males; 16 right-handed) participated in the second experiment. All participants were naïve with respect to the purpose of the study. The experiment was approved by the ethics committee of the Université catholique de Louvain, and all participants provided a written informed consent before the experiment.

## **Experimental Setup**

Participants were installed in a custom-built inversion chair consisting of a bucket seat (Evo XL VTR fiberglass seat, Sparco, Italy) fixed to a rotating frame (Fig. 1A). The rotating frame could be set at two different angles: 0° [the right-sideup (RU) posture] and 180° [the upside-down (UD) posture]. The participants were securely attached to the seat with a 6point harness (Sparco, Italy). Also fixed to the rotating frame was a target mast composed of two LED targets 32 cm apart and aligned to the longitudinal axis of the rotating frame. The position of the target mast could be adjusted along the horizontal and vertical axes to adapt to the participant's size. The participant's feet were held in place with foot straps. During the experiment, the participants held a manipulandum (mass 260g; grip aperture 4.5 cm; Arsalis, Belgium; see Fig. 1B) in precision grip, i.e., between the thumb and the index finger. The cables of the manipulandum were attached to the participant's forearm with straps.

#### **Experimental Task**

Participants were instructed to perform smooth and continuous rhythmic arm movements along the vertical axis, with the arm extended and with the manipulandum held in precision grip. All participants performed the task with the right arm. Movement pace (1Hz) was given by a metronome and movement amplitude (32 cm) was delimited by the two LED targets positioned next to the participant's hand, symmetrically above and below participant's shoulder.

#### **Experiment 1**

In *experiment 1*, participants first performed three training blocks in the right-side-up posture to familiarize with the metronome pace, then performed eight blocks in a row in both the right-side-up (RU) and upside-down (UD) postures. The order of the sequence of the two postures was chosen pseudorandomly for each participant. All blocks were identical and consisted of 25 arm oscillations at a pace of 1Hz. A



**Figure 1.** Experimental setup. A: participants were installed in an inversion chair that could be set in right-side-up (RU) and in upside-down (UD) posture. *B*: the task was performed with a manipulandum held between the right thumb and index finger. The manipulandum allowed measuring the grip force (GF), normal to the contact surface, and the load force (LF), tangential to the contact surface. C: sketches of the vertical velocity, vertical acceleration, and LF profiles during one cycle, expressed in egocentric coordinates. The horizontal lines represent the zero axis.

short break (lasting around 45 s for the RU condition and 90 s for the UD condition) was imposed between two consecutive blocks. The chair was reset back in the right-side-up posture during the break separating two blocks performed in an upside-down posture.

#### Experiment 2

*Experiment 2* was designed to explore changes in arm kinematics over longer practice times in an upside-down posture and to assess the presence of aftereffects in the right-side-up posture after repeated practice in the upside-down posture. The task was identical to *experiment 1*, but the layout of the blocks was different. Participants performed six blocks in the right-side-up posture (RU-PRE) followed by 16 blocks upside-down (UD) and then 10 blocks right-side-up again (RU-POST). All blocks consisted of 22 arm oscillations with the same pace (1Hz) and the same amplitude (32 cm) as in *experiment 1*. Again, the chair was reset back in the right-side-up posture between two blocks performed in an upside-down posture for a short break (~2 min).

J Neurophysiol • doi:10.1152/jn.00357.2020 • www.jn.org

Downloaded from journals.physiology.org/journal/jn at ULB Biblio Fac De Med Erasme (164.015.128.033) on March 24, 2021.

#### **Evaluation of the Slip Force**

In addition to the oscillation task, participants also performed a calibration task to evaluate the slip force (*SF*), i.e., the minimum normal force required to avoid slippage given a specific tangential force applied at the fingertip. This calibration task consisted of three blocks of 25 s during which the participant was instructed to rub the contact surfaces of the manipulandum using different levels of grip force (light, moderate, and firm) and using the same finger configuration as during the oscillation task. This procedure, described in Ref. 67, allows extracting phases during which the finger slides along the surface and the identification of the onset of these phases provides accurate measurements of the static coefficient of friction of the finger-object interface for various levels of normal force. The coefficient of friction was modeled as:

$$\mu_s = k \cdot \left(NF\right)^{n-1},\tag{1}$$

where  $\mu_s$  is the ratio between the tangential force (*TF*) and the normal force (NF) at the time of slip onset and k and nare parameters (67, 68). Because  $TF = \mu_s \cdot SF$  at the time of slip onset, SF can be expressed as  $SF = \left(\frac{TF}{k}\right)^{\overline{n}}$ . The fit parameters k and n in the above formula were computed using standard least-squares regression methods for the thumb and index finger of each participant and for the ulnar and radial directions separately. We also computed  $\mu_s$  for a normal force of 2.25 N (typical value of the peak SF estimated during the oscillation task) using Eq. 1 to compare the coefficient of friction in the ulnar and radial directions for both fingers. In *experiment 1*, the participants performed the three blocks of the calibration task before and after each condition, thus four times in total. In *experiment 2*, the participants performed the three blocks of the calibration task two times, once before and once after the 32 blocks of the oscillation task. Although the coefficient of friction can vary substantially from one subject to another, this method for computing SF can be considered reliable (67) and the median (IQR) R-squared coefficient between the fitted SF and the data was 0.94 (0.09) across all participants, fingers, and load directions (both experiments combined).

#### **Data Collection**

Forces applied by the fingers on the manipulandum were recorded with tridimensional force/torque sensors (Mini 40 F/T transducers, ATI Industrial Automation, North Carolina) located under each finger (see Fig. 1*B*). The manipulandum was also equipped with a tridimensional accelerometer (Analog Devices, ref. ADXL78). Finally, CODA cameras (Codamotion CX-1 units, Charnwood Dynamics, Leicestershire, United Kingdom) tracked the position of four CODA active markers located on the front of the manipulandum shell. The position of the center of mass of the manipulandum was reconstructed from the position of the four markers using custom routines in Matlab.

#### **Data Postprocessing and Analysis**

All analyses were implemented in Matlab R2018a. Data signals were filtered with a dual-pass Butterworth low-pass filter of order 4. For force and accelerometer signals, a cutoff

frequency of 40 Hz was used for the Butterworth filter, whereas for the position signal a cutoff frequency of 5 Hz was used. Signals were measured in an *egocentric* reference frame: The positive direction is always toward the head (Head direction in Fig. 1*B*), whereas the negative direction is always toward the feet (Feet direction).

The velocity of the manipulandum was obtained by numerical differentiation of the position. Arm movements were essentially 1-degree-of-freedom rotations around the shoulder; therefore, the trajectories were slightly curved in the sagittal plane. We focused on the vertical component of the velocity, the horizontal component being on average less than 10 percent of the vertical component. The peaks of the vertical component of the velocity were used to delimit individual cycles of oscillation of the arm (Fig. 1C). We studied the effect of body orientation on the kinematics of the movement by looking at the maxima of the vertical component of the velocity in the two movement directions (Head and Feet), as was done in previous studies for discrete arm movements (29, 36, 39, 69, 70). More precisely, within each cycle we computed the difference between the value of the positive peak velocity  $(\ensuremath{\text{PV}_{\text{Head}}})$  and the absolute value of the negative peak velocity (PV<sub>Feet</sub>). We expressed this difference in velocity peaks ( $\Delta PV$ ) as a percentage of  $PV_{Head}$ .

The first cycle of each block was not included in the analyses of the kinematics of the arm, because we were interested in the kinematics of settled rhythmic movements. Moreover, the first cycle was substantially shorter than the other ones, as the participants had to catch up with the metronome. We nevertheless performed the same analyses after including the first cycle and reached the same conclusions. Note that the first cycle was included in the analysis of the finger forces, because we were particularly interested in the GF-LF coupling during the first movements performed upside-down.

The load force (LF) was defined as the norm of the force applied tangentially on the fingers, computed as the vector sum of the tangential forces measured by the left and right sensors. The grip force (GF) was defined as the force applied by the fingers normally to the contact surfaces and was computed as the average of the normal force measured by the two sensors. We assessed the quality of the GF-LF coupling by computing, for each block, the Pearson correlation coefficient between GF and LF, using a sliding window of five cycles. Within each five-cycle window, we also computed the GF offset and gain, defined as the intercept and slope of the linear regression that best fits the GF-LF relationship in the least-squares sense. The lag of GF with respect to LF was computed as the time delay maximizing the cross-correlation between GF and LF within each five-cycle window. A positive value means that GF lags behind LF. As illustrated on the bottom graph of Fig. 1C, in an egocentric reference frame the LF profiles in the right-side-up and upside-down postures are 180° out-of-phase. A pure egocentric (predictive) control of GF would therefore yield a negative GF-LF correlation, a negative GF gain and a GF lag of half a cycle  $(\sim 500 \text{ ms})$  in the upside-down posture. Finally, we computed the grip safety margin within each cycle. The safety margin was first computed for each finger separately and was defined as the difference between the maximum value of the normal force and the maximum value of the slip force (computed as a function of the tangential force, as explained

in section Evaluation of the Slip Force), divided by the maximum value of the slip force. The minimum between the thumb safety margin and the index safety margin was taken as the final grip safety margin.

The left force sensor was defective for one participant in experiment 2. For this participant, LF was computed using the accelerometer data, and GF was taken as the normal force applied on the right sensor, as the difference between the left and right normal forces was small for the other participants (on average, the mean absolute difference between left and right NF was < 1 N and the correlation between left and right NF was equal to 0.99). This participant was, however, not included in the analysis of the safety margin, as computing the safety margin requires tangential force measurements from both force sensors.

#### **Statistical Analyses**

In experiment 1, we assessed the effect of body posture (RU vs. UD) on the dynamics of precision grip and on the kinematics of the arm by using linear mixed-effect (LME) models with factors Posture (two-level factor) and Block (numeric variable) as fixed effects, and a random intercept that captures interparticipant variability. To test the significance of each fixed-effect term, an F test was used. In experiment 2, we used paired t tests to compare: 1) the average of the six RU-PRE blocks with the average of the first two UD blocks (UD-early); 2) UD-early with the average of the last five UD blocks (UD-late); 3) the average of the first two RU-POST blocks (RU-POST-early) with RU-PRE; and 4) RU-POST-early with the average of the last five RU-POST blocks (RU-POSTlate). For all statistical tests, a significance threshold of 0.05 was used. Kolmogorov-Smirnov tests confirmed the normality of the residuals of the LME model and the normality of the differences between scores for the t tests. All statistical analyses were performed using Matlab Statistical Toolbox.

# RESULTS

## GF Dynamics in Right-Side-Up and Upside-Down Body Orientations

In experiment 1, participants performed eight blocks of vertical arm oscillations in both a right-side-up and an upside-down body orientation. Movement frequency and amplitude were not significantly affected by the condition and were equal to  $1.035 \pm 0.028$  Hz and  $36 \pm 4$  cm in the RU condition (mean  $\pm$  SD), and  $1.031 \pm 0.033$  Hz and  $35 \pm 4$  cm in the UD condition, respectively. Participants were therefore able to follow the metronome pace (1 Hz) in both conditions.

Figure 2 reports the GF and LF data of the first block of oscillations performed in right-side-up and upside-down body orientation by a typical participant. The phase diagram (Fig. 2A) illustrates that the two forces were positively correlated in both conditions. Considering all participants, we found no significant difference in the GF-LF correlation coefficient between the first RU block and the first UD block (paired t test:  $t_{17} = -0.48$ , P = 0.63; see Fig. 2C and Fig. 2F showing the distributions of the correlation coefficient across participants for UD and RU, respectively). This correlation coefficient was equal to 0.61 (0.49, 0.74) for RU movements and 0.64 (0.58, 0.71) for UD movements [mean + 95% confidence interval (CI) of the mean]. The temporal traces of GF and LF during the first 10 s of each condition, depicted in Fig. 2, *B* and *E*, show that the two forces were furthermore tightly synchronized from the first oscillating movements.



Figure 2. Experiment 1: grip dynamics during the first block performed in right-side-up and upside-down body orientations. A: GF versus LF for one typical participant (S9) during the RU (dotted line) and UD (plain line) conditions. The SF curves were averaged across all movement cycles. This participant started with the UD condition. B and E: GF and LF during the first 10 s performed in the UD (B) and in RU (E) conditions for the same participant as in A. Gray vertical lines represent the times of peak LF. C and F: histograms showing the distributions of the GF-LF correlation coefficient across participants during the first block performed in the UD (C) and RU (F) conditions. D and G: histograms showing the distributions of the GF lag (with respect to LF) across participants, during the first block performed in each condition. GF, grip force; LF, load force; RU, right-side-up; SF, slip force; UD, upside-down.

# J Neurophysiol • doi:10.1152/jn.00357.2020 • www.jn.org

Downloaded from journals.physiology.org/journal/jn at ULB Biblio Fac De Med Erasme (164.015.128.033) on March 24, 2021.

We verified that the lag between GF and LF during the first block was not significantly impacted by the posture condition ( $t_{17} = 0.39$ , P = 0.70) and was not significantly different from zero [95% CI of the mean for RU movements: (-19, 40) ms; for UD movements: (-20, 30) ms]. In both conditions, for at least 14 out of 18 participants the GF lag relative to LF was inferior to 25 ms (Fig. 2, *D* and *G*), indicative of an immediate predictive control of GF. This still holds if one considers only the first five cycles of oscillation. A tight GF-LF coupling was therefore established very quickly in the UD condition despite the fact that, from an egocentric perspective, the direction of the load reversed relative to the RU condition and LF was phase-shifted by 180°.

When considering all blocks, the GF-LF correlation was not significantly different in the UD condition with respect to the RU condition (Fig. 3A). There was indeed no effect of Posture on the correlation coefficient ( $F_{1,283} = 0.29$ , P = 0.59), no effect of Block ( $F_{1,283} = 0.0001$ , P = 0.97), and no significant interaction between those two factors ( $F_{1,283} = 2.30$ , P = 0.13). Likewise, the GF lag was not significantly impacted by body orientation (Posture:  $F_{1,283} = 1.16$ , P = 0.28; Posture:Block interaction:  $F_{1,283} = 1.31$ , P = 0.25) but decreased slightly across blocks ( $F_{1,283} = 6.17$ , P = 0.01). In contrast, the *F* test revealed a significant effect of Posture on the GF gain (Fig. 3B; Posture:  $F_{1,283} = 19.4$ , P < 0.001; Block:  $F_{1,283} = 3.42$ , P = 0.07; Posture:Block:  $F_{1,283} = 0.11$ , P = 0.74). The GF gain was indeed more elevated in the UD condition than in the RU condition.

In addition to an increased gain, GF also presented a higher offset in the UD condition relative to the RU condition (main effect of Posture:  $F_{1,283}$  = 100.7, P < 0.001). This offset decreased across blocks in the UD condition but not in the RU condition (Posture:Block interaction: F = 12.9, P < 0.001). The grip safety margin (Fig. 3*C*) was also higher in

the UD condition than in the RU condition (main effect of Posture:  $F_{1,283}$  = 24.5, P < 0.001) and decreased in the UD condition but not in the RU condition (Posture:Block:  $F_{1,283}$  = 10.0, P = 0.002). Importantly, after practice the safety margin was similar in the two body postures (paired t test comparing the last two blocks of each condition:  $t_{17} = -0.12$ , P = 0.90) despite the fact that the GF offset and gain remained more elevated in the UD condition ( $t_{17} = -4.69$ , P < 0.001 and  $t_{17} = -3.65$ , P = 0.002, respectively). This is explained by the fact that the slip force was more elevated in the UD condition than in the RU condition (main effect of Posture: F = 20.0, P < 0.001; see example traces in Fig. 2A), for two reasons. The first reason is that the load force was not distributed equally on the two fingers in the UD condition: it was more elevated on the index finger side than on the thumb side. This was due to a misalignment of the centers of pressure of the two fingers in the upside-down posture. The second reason was that the coefficient of friction of the index finger was smaller in the radial (Head) direction relative to the coefficient of friction in the ulnar (Feet) direction ( $t_{17}$  = 4.97, P < 0.001; see METHODS). These two reasons both tend to increase the slip force, and therefore decrease the safety margin for a given grip force, on the index finger side in the UD condition.

#### Movement Kinematics in Right-Side-Up and Upside-Down Body Orientations

To investigate the impact of body posture on the kinematics of the movement, we looked at the dependence of the velocity profile on movement direction (36) by computing the difference  $\Delta PV$  between the positive velocity peaks ( $PV_{Head}$ ) and the absolute value of the negative peaks ( $PV_{Feet}$ ). We express this difference as a percentage of  $PV_{Head}$ . Note that with such a convention, this asymmetry index is expressed



**Figure 3.** Summary results from *experiment 1* (*n* = 18 participants): GF-LF correlation coefficient (*A*), GF gain (*B*), safety margin (C), and  $\Delta$ PV (*D*) across blocks in the UD and RU conditions (M ± SE). Asterisks show significant main effects of the fixed-effect term Posture in the linear mixed-effects model (see section *Statistical Analyses*). \*\**P* < 0.01; \*\*\**P* < 0.001. GF, grip force; LF, load force; PV, peak velocity; RU, right-side-up; SF, slip force; UD, upside-down.

in an egocentric reference frame. Figure 3D presents the evolution of  $\Delta PV$  across blocks within each condition.  $\Delta PV$  was positive in the right-side-up posture, meaning that PV<sub>Head</sub> was on average greater than  $\ensuremath{\text{PV}_{\text{Feet}}}\xspace$  . In the upside-down posture,  $\Delta PV$  showed a substantial evolution across blocks: it started higher relative to the RU condition, meaning that the difference between PV<sub>Head</sub> (where the Head direction is now the *downward* direction with respect to gravity) and PV<sub>Feet</sub> (where the Feet direction is now the *upward* direction with respect to gravity) was increased. Thus, the asymmetry of the velocity profile was initially in the same direction in both conditions, when seen from an egocentric perspective. Strikingly, with practice this asymmetry progressively decreased in the UD condition. The statistical analysis confirmed those observations. The LME model revealed a significant main effect of Posture ( $F_{1,283}$  = 8.60, P = 0.003) as well as a significant main effect of Block ( $F_{1,281}$  = 4.54, P = 0.03) on  $\Delta PV$ . Importantly, there was a large interaction effect between the Posture and Block factors ( $F_{1,281}$  = 36.8, P <0.001). This interaction confirms that, across blocks,  $\Delta PV$ evolved in opposite directions in the RU and UD conditions. The asymmetry in the velocity profile increased with practice in the right-side-up posture, while it decreased with practice in the upside-down posture. Note that at the end of the eight blocks, the RU and UD asymmetries were not mirror image of each other, as one might expect if the kinematics were planned in a pure gravity-centered reference frame. We stated two hypotheses to explain that 1) the asymmetry is different in the upside-down posture relative to the rightside-up posture because the muscles involved are different; or 2) the practice time was too short for a complete adaptation. The latter hypothesis motivated us to design a second experiment with an increased number of blocks.

### GF Dynamics in Right-Side-Up Orientation after Repeated Practice in Upside-Down Orientation

In *experiment 2*, participants performed six blocks in the right-side-up posture (RU-PRE condition), before performing 16 blocks in the upside-down posture (UD condition). The participants then performed 10 blocks back in the right-side-up posture (RU-POST condition) so that we could probe the presence of aftereffects potentially induced by a motor adaptation to the upside-down posture. We first analyze GF-LF

coupling, compare the results with those of *experiment 1*, and check whether practice in the UD condition led to aftereffects in the control of GF in the subsequent RU-POST condition.

In terms of grip dynamics, most participants reproduced the results observed in experiment 1. More specifically, the GF was positively correlated with LF from the first movements performed in the UD condition (see participant S6 in Fig. 4 and averaged data in Fig. 5A). Interestingly though, in experiment 2 there was an initial decrease in the GF-LF correlation during the first UD block (Fig. 5A). This decrease was not significant (RU-PRE vs. UD-early:  $t_{17}$  = 1.88, P = 0.08), but the correlation coefficient significantly increased with further practice in the UD condition (UD-early vs. UD-late:  $t_{17}$  = -3.45, *P* = 0.003) and regained the baseline value. The GF gain tended to increase across blocks (UD-early vs. UDlate:  $t_{17} = -2.51$ , P = 0.02), which probably contributed to the increase in the GF-LF correlation. For instance, participant S13 displayed a reduced GF gain and an out-of-phase modulation of GF during early blocks in upside-down posture (Fig. 4, bottom row, middle column), two phenomena that tend to decrease the correlation between GF and LF. This participant actually had a negative GF-LF correlation during the first UD block. It is noteworthy that this participant started feeling sick after a few blocks performed in the upside-down posture.

As in *experiment 1*, the GF offset was significantly more elevated in the UD condition than in the preceding RU condition, both at the beginning (RU-PRE vs. UD-early:  $t_{17}$  = -7.33, P < 0.001) and at the end (RU-PRE vs. UD-late:  $t_{17} = -$ 2.47, P = 0.02) of the 16-block sequence. Moreover, it decreased significantly across UD blocks (UD-early vs. UDlate:  $t_{17}$  = 5.55, P < 0.001). However, we found no significant difference between the RU-PRE safety margin and the UD safety margin, although the safety margin decreased significantly across UD blocks (UD-early vs. UD-late:  $t_{17}$  = 2.58, P = 0.02). As in experiment 1, the increased GF offset in the upside-down posture compensated an increased in the peak *SF* (RU vs. UD:  $t_{17} = -2.87$ , *P* = 0.01) that was due to an unequal distribution of the load force on the two fingers and to a smaller coefficient of friction for the index finger in the upside-down posture relative to the right-side-up posture (RU vs. UD:  $t_{17}$  = 4.21, P < 0.01).

**Figure 4.** GF and LF traces for two participants (S6 and S13) displaying different behaviors in terms of GF-LF coupling in the upside-down posture in *experiment* 2. On the left: the last RU-PRE block; in the center: the first UD block; on the right: the first RU-POST block. For clarity, only the first 10 s of each block are plotted. GF, grip force; LF, load force; PRE, prior to UD blocks; POST, posterior to UD blocks; RU, right-side-up; UD, upside-down.





**Figure 5.** *Experiment 2 (n* = 18 participants): arm kinematics, but not grip dynamics, are affected after practice in an upside-down posture. A: GF-LF correlation; *B*: GF gain; *C*: GF safety margin; *D*:  $\Delta$ PV across blocks (M ± SE). Dashed horizontal lines representing the ± SE around the mean of the RU-PRE condition were plotted to facilitate the comparison between the RU-PRE and RU-POST conditions. Asterisks show significant differences between groups of blocks (paired *t* test). \**P* < 0.05; \*\**P* < 0.01. GF, grip force; LF, load force; PRE, prior to UD blocks; POST, posterior to UD blocks; PV, peak velocity; RU, right-side-up; UD, upside-down.

We now compare the RU-PRE condition with the RU-POST condition to test whether repeated practice in an upside-down posture has an impact on the control of grip force in movements performed subsequently in a right-sideup posture. The typical traces in Fig. 4 depict very similar temporal coupling between the first block of the RU-POST condition and the last block of the RU-PRE condition. The averaged data depicted in Fig. 5, A-C, confirm this observation. We found no significant difference between the first blocks of the RU-POST condition and the mean of the RU-PRE blocks in terms of GF-LF correlation (Fig. 5A), GF offset, GF gain (Fig. 5B), safety margin (Fig. 5C), and GF lag (RU-PRE vs. RU-POST-early; P > 0.2 for all comparisons). In terms of GF dynamics, participants were therefore able to switch back rapidly to the "right-side-up" LF model after the 16 blocks in the upside-down posture. We show hereafter that the movement kinematics tell a different story.

### Movement Kinematics in Right-Side-Up Orientation after Repeated Practice in Upside-Down Orientation

The kinematics observed in *experiment 2* were consistent with the results of *experiment 1* (Fig. 5D). In the UD condition,  $\Delta$ PV was initially similar to the RU-PRE condition from an egocentric point of view (RU-PRE vs. UD-early:  $t_{17} = 0.59$ , P = 0.56), but then decreased significantly across blocks (UD-early vs. UD-late:  $t_{17} = 3.52$ , P = 0.003). In contrast to *experiment 1*,  $\Delta$ PV actually reversed with respect to the RU asymmetry after some practice. Importantly, the RU-POST condition allowed us to detect the presence of aftereffects induced by the adaptation to the upside-down posture. Indeed,  $\Delta$ PV at the

beginning of the RU-POST condition was significantly smaller than during the RU-PRE condition (RU-PRE vs. RU-POSTearly:  $t_{17} = -2.76$ , P = 0.01). In contrast, the difference between the first blocks of the RU-POST condition and last blocks of the UD condition was smaller and not significant (UD-late vs. RU-POST-early:  $t_{17} = -1.52$ , P = 0.15).  $\Delta$ PV then increased significantly (decreased in absolute value) with more practice in the right-side-up posture (RU-POST-early vs. RU-POST-late:  $t_{17} = -2.45$ , P = 0.02) and returned to baseline (RU-PRE vs. RU-POST-late:  $t_{17} = 1.31$ , P = 0.21).

# DISCUSSION

In the present study, we challenged the ability of the brain to use an internal estimate of the gravitational force for GF and kinematics programming by asking participants to perform rhythmic arm movements in an upside-down posture, while holding an object in precision grip. Our main goal was to investigate the reference frame in which the control of grip force and arm movement operates in upside-down condition: is it a body-centered (egocentric) reference frame, or an Earth-centered (allocentric) reference frame?

## GF-LF Coupling Reflects an Allocentric Control of Grip Force

A particular attention was given to the quality of the GF-LF coupling, characterized first by the correlation coefficient and the time lag between the two forces (8, 9, 19, 22). For most participants, we found very similar correlation coefficients and time lags in both body orientations, even when focusing on the first cycles performed in each condition. These observations indicate that the mechanism responsible for GF-LF coordination operates in an allocentric reference frame in which gravity defines "up" and "down." If GF was planned in an egocentric reference frame, we would have observed a negative GF-LF correlation coefficient (180° phaseshift) for the first movements performed upside-down, or at least a high time lag between GF and LF reflecting a dominant feedback control. Previous work has emphasized flexible coordination patterns across conditions of loading and movement kinematics (15, 16). Here we provide evidence that this flexibility also enables humans to fine-tune grip-load coupling when the body configuration changes relative to gravity. Because the muscles involved in the generation of single-joint, vertical arm movements in the upside-down body orientation (predominantly the latissimus dorsi, teres major, and posterior deltoid) are very different from those involved in the rightside-up body orientation (predominantly the pectoralis major and anterior deltoid), the hypothesis that GF-LF coupling would stem from an automatic activation of the finger muscles (in particular, the FDI muscle) following activation of the arm muscle is not plausible (20, 71). We suggest instead, as it has been suggested by several authors in the past (10, 20, 21, 23, 24), that the robustness of the GF-LF coupling is due to the existence of a flexible internal model of LF that incorporates an internal estimate of gravity. Alternatively, the CNS could use the constant tangential load acting on the fingers before the movement starts as an estimate of a background force to which the inertial load must be added. We hypothesize that the flexibility of these predictive mechanisms has arisen from the necessity for the CNS to coordinate fingers force and arm movement along various movement directions and in various body postures. This could be accomplished with the help of an Earth-centered parametric forward model (12, 61) where the value of the gravitational force along the movement axis can be adjusted according to movement direction. As a byproduct, such internal parametric model would allow for a fast adaptation of sensorimotor coordination to altered-gravity environments (61). Very fast adaptation of GF control has indeed been observed in parabolic flights in microgravity (21, 23, 62), partial gravity (63), and hypergravity (21, 64), as well as in the hypergravity environment of human centrifuges (22, 26). In contrast, feedforward control of GF needs time to adapt when moving objects with unfamiliar dynamics such as elastic or viscous loads (65, 72-74).

Interestingly, not all participants showed equal grip force adaptation to inverted body orientation. As emphasized in experiment 2, some participants showed in the UD condition a substantial decrease in the GF-LF correlation, mainly due to a decrease in the amplitude of the GF modulation and, in some rare cases, to a substantial increase in the temporal delay between GF and LF. This is a strong indication that sensory feedback informing about the amplitude and direction of the tangential load at the fingertip, already available before the beginning of the movement, is not sufficient in itself to allow for an efficient coupling between GF and LF for these participants. Rather, this sensory feedback must be complemented with accurate predictive mechanisms. Particularly noteworthy is the fact that the GF-LF correlation improved significantly with practice and returned to baseline on average (see Fig. 5A), showing that an initially poor prediction of LF can become rapidly more accurate. Such signs of initial impairment of the GF-LF coupling followed by rapid adaptation were observed during rhythmic and discrete arm movements performed in parabolic flights (21, 63, 75), in short-arm human centrifuges (22), and in rotating chambers (25). The latter is, however, a particular case, as rotating environments induce inertial centrifugal and Coriolis forces that vary as a function of hand position and speed and thus differ greatly from the constant action of gravity. Sensorimotor adaptation to a rotating environment can actually lead to observable aftereffects in the GF-LF coupling (25). The fact that we did not observe any aftereffects in the GF-LF coupling in right-side-up orientation after practice in upside-down orientation (experiment 2) suggests once again that an internal estimate of gravity allows switching from one posture to the next, without the need to activate or generate a new internal model of LF.

Another similarity observed between our results in the inversion chair and parabolic flight results was the greater GF offset observed in the upside-down relatively to the right-side-up condition and the progressive reduction of this offset following practice (21, 23, 63, 75). It has been proposed that increasing the grip force could be a simple strategy to cope with an elevated uncertainty surrounding LF prediction (74, 75), even if the prediction is actually correct. Note that the difference in adaptation times observed between the static component (GF offset) and the dynamic component (GF gain) of the grip force was also observed in some parabolic flights studies (23, 63).

To sum up, the analysis of the grip dynamics strongly indicates that the predictive mechanism used by the CNS to anticipate changes in tangential loads at the fingertips operates in an Earth-centered allocentric reference frame, in agreement with the hypothesis that an internal representation of gravity is used for predictive control. Interestingly, we discuss hereafter the control of the kinematics of the arm that in contrast appears to operate in a more egocentric reference frame.

### Arm Kinematics Reflect an Egocentric Planning of Movement Trajectory

In the right-side-up posture, the vertical velocity of the arm was characterized by a dependency of the velocity peaks on movement direction. More specifically, velocity peaks were more elevated in the upward direction than in the downward direction. Although direction-dependent kinematics have been reported extensively in the literature for discrete arm movements (29–31, 34, to name only a few), we found no previous report documenting this kind of asymmetry for rhythmic arm movements. Model simulations in optimal control theory have shown that selecting different velocity profiles for upward versus downward movements optimizes effort-related motor costs (34, 39, 40, 76). Importantly, the dependency on movement direction has been reported to disappear in the horizontal plane (29, 30)but to persist temporarily in a weightless environment (34, 37), which strongly indicates that the action of gravity is anticipated by the CNS and incorporated into the planning process underlying arm movements. Interestingly, we also observed a persistence of this velocity asymmetry during the first blocks performed in the upside-down posture, from an

egocentric perspective. This is in line with the hypothesis that the orientation of the body with respect to gravity can bias the planning of arm movements (30) and suggests that the kinematics of the arm are preferentially planned in an egocentric reference frame. It is important to stress out, however, that reproducing the same velocity asymmetry as in the right-side-up posture while inverted would still require accurate predictions of gravity's effect, because the muscle groups involved are different in the two body orientations. In other words, to reproduce the kinematics of the right-side-up posture, prediction must precede control (66). Thereby, shoulder dynamics were able to adapt very quickly to the upside-down posture to reproduce the right-side-up kinematics, a result that can be compared to previous results obtained in microgravity (36).

# Arm Kinematics Are Progressively Readjusted in the Upside-Down Posture

Strikingly, with practice in the upside-down posture, the difference in velocity peaks between the Head and Feet directions decreased progressively, and even reversed in experiment 2, tending toward the same difference as in the right-side-up posture from an allocentric perspective. In the same vein, Gaveau and collaborators (34) observed a progressive adaptation of the velocity profile to microgravity toward a new velocity profile that minimizes movement effort in a weightless environment. More generally, a reoptimization process is thought to underlie the kinematic adaptation to novel limbs or environmental dynamics (40, 77). Here, the progressive kinematics tuning observed in the upside-down posture could potentially be explained by a similar reoptimization of the control policy, although model simulations beyond the scope of this paper are required to support this hypothesis. The reproduction of the kinematics of the rightside-up posture during the first block in the upside-down posture, as well as the unimpaired and stable coupling between GF and LF in that same posture, indicate that gravity's effects were predicted accurately. Therefore, the kinematic adaptation does probably not stem from an adaptation of state prediction. Nonetheless, distinct internal models could underlie the control of grip force and the control of arm kinematics (65, 78).

# Kinematic Adaptation to Upside-Down Body Orientation Induces Aftereffects

Importantly, this adaptation to the upside-down body orientation induced significant aftereffects observable in the velocity profile of subsequent movements performed in rightside-up posture (see *experiment 2*). This is very interesting, because all sensory signals indicated to the participants that they were in the right-side-up posture again, long before performing the movements. Once again, these findings suggest that the movement kinematics are planned preferentially in an egocentric reference frame. The transition from one posture to the next would then require an internal rotation of the frame of reference, which took a few trials.

### Verticality Perception in the Upside-Down Posture

Predictive control of grip force and arm trajectory requires an estimate of the movement direction with respect to gravity. Furthermore, transforming sensory signals from different modalities into a common, allocentric reference frame also requires an internal representation of body orientation. Therefore, verticality perception is an important parameter to consider. Verticality perception is built by integrating vestibular, visual, and somatosensory signals as well as prior expectations (48, 50, 79). Vestibular signals are integrated with signals from other sensory modalities already in the vestibular nuclei and in the cerebellum (80, 81) and higher in the thalamus (50, 82). From there, the resulting signals are sent to various cortical areas, including the parieto-insular area often referred to as the vestibular cortex (83-85). Interestingly, fMRI data showed brain activity within that same area to be consistent with a central representation of gravitational motion (86). An estimate of body orientation combined with an internal model of gravity's effect could be used to predict load force changes induced by arm movements. Previous studies have shown that when the body is upside-down, the perceived visual vertical is unbiased but shows greater inter- and intrasubject variability than when the body is upright (54, 87–90). This greater variability in the estimation of the vertical axis when upside-down could be linked to the hypothetical inability of the otolith organs to distinguish between the right-side-up and upside-down head orientations (91, 92). It could be one factor explaining the reduced GF-LF coordination and the increased GF lag observed in some participants, if the perceived orientation of gravity relative to movement direction is used to predict the amplitude and timing of the load force. Future studies investigating the effect of verticality misperception on gripload forces coordination could provide additional support to the hypothesis that the CNS uses of an internal estimate of gravity for predictive grip control.

# Potential Influences of Vestibular Signals and Other Graviceptors on Upper Limb Control

Even though GF control relies on predictive mechanisms, haptic feedback plays a key role in maintaining a stable grip (6, 7, 93, 94). Previous studies have shown that vestibular and tactile inputs can influence reflex responses of motoneurons. Galvanic vestibular stimulations and cutaneous stimulations modulate the monosynaptic reflex in the soleus muscle (95). The monosynaptic reflex of the soleus muscle has also been shown to be influenced by static and dynamic body tilt (96) and by gravity level (97, 98). Vestibular signals also contribute to the control of proximal and distal muscles of the upper limbs, e.g., to increase grasping forces in response to unexpected body sway when holding an earthfixed bar for balance (99) or to correct the trajectory of the arm to compensate for (illusory) body motions (100, 101). Finally, results from parabolic flight experiments suggest that spindle activity in the arm muscles may be influenced by gravitational force level (102). Therefore, it is possible that vestibular signals modulate grip and arm control via the vestibulospinal pathway. We, however, favor the hypothesis that grip and arm control relies on predictive mechanisms that can be adjusted as a function of vestibular inputs, as vestibular signals give valuable information about body orientation relative to gravity and thus about the transformation required to switch from one reference frame to another.

# CONCLUSIONS

This study was performed to investigate whether predictive mechanisms of movement dynamics are flexible enough to allow for accurate predictions of the consequences of arm motor commands when the human body is in the uncommon, upside-down posture. By investigating the coordination between the grip force and the load force during rhythmic arm movements performed in an upside-down posture, we showed that it is generally indeed the case: the predictions of sensory feedback that subserve the tight coupling between the grip force and the movements of the arm is still accurate in an upside-down body posture. In other words, our results indicate that grip-force control is performed in an allocentric (gravity-centered) reference frame. By contrast, time for adaptation was required in the upsidedown posture for the kinematics to retrieve the "right-sideup" profile (as seen from an allocentric perspective) and induced an aftereffect upon return to right-side-up posture, which is consistent with an egocentric (body-centered) planning of movement kinematics. Our results therefore highlight distinct processes underlying the adaptation of grip dynamics and movement kinematics to the unusual upsidedown body orientation with respect to gravity. Moreover, the similarities observed between our study and previous parabolic flight studies suggest that a common mechanism could underlie sensorimotor adaptation to altered gravity environments and sensorimotor adaptation to unfamiliar body orientations.

# GRANTS

This work was supported by ESA PRODEX Grant 400012374 (to P. Lefèvre and J-L. Thonnard) and by grants from the French Space Agency CNES (to J. McIntyre).

# DISCLOSURES

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

#### AUTHOR CONTRIBUTIONS

L.O., F.C., J-L.T., J.M., and P.L. conceived and designed research; L.O. performed experiments; L.O. analyzed data; L.O., F.C., J-L.T., J.M., and P.L. interpreted results of experiments; L.O. prepared figures; L.O. drafted manuscript; L.O., F.C., J-L.T., J.M., and P.L. edited and revised manuscript; L.O., F.C., J-L.T., J.M., and P.L. approved final version of manuscript.

# REFERENCES

- Blank R, Breitenbach A, Nitschke M, Heizer W, Letzgus S, Hermsdörfer J. Human development of grip force modulation relating to cyclic movement-induced inertial loads. *Exp Brain Res* 138: 193–199, 2001. doi:10.1007/s002210000622.
- Forssberg H, Kinoshita H, Eliasson AC, Johansson RS, Westling G, Gordon AM. Development of human precision grip I: basic coordination of force. *Exp Brain Res* 90: 393–398, 1992. doi:10.1007/ BF00227253.
- Forssberg H, Kinoshita H, Eliasson AC, Johansson RS, Westling G, Gordon AM. Development of human precision grip II: anticipatory control of isometric forces targeted for object's weight. *Exp Brain Res* 90: 393–398, 1992. doi:10.1007/bf00227253.

- Flanagan JR, Wing AM. The stability of precision grip forces during cyclic arm movements with a hand-held load. *Exp Brain Res* 105: 455–464, 1995. doi:10.1007/BF00233045.
- Johansson RS, Westling G. Roles of glabrous skin receptors and sensorimotor memory in automatic control of precision grip when lifting rougher or more slippery objects. *Exp Brain Res* 56: 550–564, 1984. doi:10.1007/BF00237997.
- Augurelle A-S, Smith AM, Lejeune T, Thonnard J-L. Importance of cutaneous feedback in maintaining a secure grip during manipulation of hand-held objects. *J Neurophysiol* 89: 665–671, 2003. doi:10.1152/jn.00249.2002.
- Nowak DA, Glasauer S, Hermsdörfer J. How predictive is grip force control in the complete absence of somatosensory feedback? *Brain* 127: 182–192, 2004. doi:10.1093/brain/awh016.
- Sarlegna FR, Baud-Bovy G, Danion FR. Delayed visual feedback affects both manual tracking and grip force control when transporting a handheld object. *J Neurophysiol* 104: 641–653, 2010. doi:10.1152/jn.00174.2010.
- Takamuku S, Gomi H. Better grip force control by attending to the controlled object: evidence for direct force estimation from visual motion. *Sci Rep* 9: 13114, 2019. doi:10.1038/s41598-019-49359-8.
- Blakemore SJ, Goodbody SJ, Wolpert DM. Predicting the consequences of our own actions: the role of sensorimotor context estimation. *J Neurosci* 18: 7511–7518, 1998. doi:10.1523/jneurosci.18-18-07511.1998.
- Johansson RS, Edin BB. Predictive feed-forward sensory control during grasping and manipulation in man. *Biomed Res* 14: 95–106, 1993.
- McNamee D, Wolpert DM. Internal models in biological control. Annu Rev Control Robot Auton Syst 2: 339–364, 2019. doi:10.1146/ annurev-control-060117-105206.
- Miall RC, Wolpert DM. Forward models for physiological motor control. *Neural Netw* 9: 1265–1279, 1996. doi:10.1016/S0893-6080(96) 00035-4.
- Johansson RS, Westling G. Coordinated isometric muscle commands adequately and erroneously programmed for the weight during lifting task with precision grip. *Exp Brain Res* 71: 59–71, 1988. doi:10.1007/BF00247522.
- White O. The brain adjusts grip forces differently according to gravity and inertia: a parabolic flight experiment. *Front Integr Neurosci* 9: 7, 2015. doi:10.3389/fnint.2015.00007.
- Zatsiorsky VM, Gao F, Latash ML. Motor control goes beyond physics: differential effects of gravity and inertia on finger forces during manipulation of hand-held objects. *Exp Brain Res* 162: 300–308, 2005. doi:10.1007/s00221-004-2152-2.
- Edin BB, Westling G, Johansson RS. Independent control of human finger-tip forces at individual digits during precision lifting. *J Physiol* 450: 547–564, 1992. doi:10.1113/jphysiol.1992.sp019142.
- Danion FR. How dependent are grip force and arm actions during holding an object? *Exp Brain Res* 158: 109–119, 2004. doi:10.1007/ s00221-004-1882-5.
- Descoins M, Danion FR, Bootsma RJ. Predictive control of grip force when moving object with an elastic load applied on the arm. *Exp Brain Res* 172: 331–342, 2006. doi:10.1007/s00221-005-0340-3.
- White O, McIntyre J, Augurelle A-S, Thonnard J-L. Do novel gravitational environments alter the grip-force/load-force coupling at the fingertips? *Exp Brain Res* 163: 324–334, 2005. doi:10.1007/s00221-004-2175-8.
- Augurelle A-S, Penta M, White O, Thonnard J-L. The effects of a change in gravity on the dynamics of prehension. *Exp Brain Res* 148: 533–540, 2003. doi:10.1007/s00221-002-1322-3.
- Barbiero M, Rousseau C, Papaxanthis C, White O. Coherent multimodal sensory information allows switching between gravitoinertial contexts. *Front Physiol* 8: 290, 2017. doi:10.3389/fphys.2017.00290.
- Crevecoeur F, Thonnard JL, Lefèvre P. Forward models of inertial loads in weightlessness. *Neuroscience* 161: 589–598, 2009. doi:10.1016/j.neuroscience.2009.03.025.
- Flanagan JR, Wing AM. The role of internal models in motion planning and control: evidence from grip force adjustments during movements of hand-held loads. J Neurosci 17: 1519–1528, 1997. doi:10.1523/jneurosci.17-04-01519.1997.
- Nowak DA, Hermsdörfer J, Schneider E, Glasauer S. Moving objects in a rotating environment: rapid prediction of Coriolis and

*J Neurophysiol* • doi:10.1152/jn.00357.2020 • www.jn.org Downloaded from journals.physiology.org/journal/jn at ULB Biblio Fac De Med Erasme (164.015.128.033) on March 24, 2021. centrifugal force perturbations. *Exp Brain Res* 157: 241–254, 2004. doi:10.1007/s00221-004-1839-8.

- White O, Thonnard J-L, Lefèvre P, Hermsdörfer J. Grip force adjustments reflect prediction of dynamic consequences in varying gravitoinertial fields. *Front Physiol* 9: 131, 2018. doi:10.3389% 2Ffphys.2018.00131.
- Flanagan JR, Wing AM. Modulation of grip force with load force during point-to-point arm movements. *Exp Brain Res* 95: 131–143, 1993. doi:10.1007/BF00229662.
- Gaveau J, Papaxanthis C. The temporal structure of vertical arm movements. *PLoS One* 6: e22045, 2011. doi:10.1371/journal. pone.0022045.
- Gentili R, Cahouet V, Papaxanthis C. Motor planning of arm movements is direction-dependent in the gravity field. *Neuroscience* 145: 20–32, 2007. doi:10.1016/j.neuroscience.2006.11.035.
- Le Seac'h AB, McIntyre J. Multimodal reference frame for the planning of vertical arms movements. *Neurosci Lett* 423: 211–215, 2007. doi:10.1016/j.neulet.2007.07.034.
- Papaxanthis C, Pozzo T, Stapley P. Effects of movement direction upon kinematic characteristics of vertical arm pointing movements in man. *Neurosci Lett* 253: 103–106, 1998. doi:10.1016/S0304-3940 (98)00604-1.
- Sciutti A, Demougeot L, Berret B, Toma S, Sandini G, Papaxanthis C, Pozzo T. Visual gravity influences arm movement planning. J Neurophysiol 107: 3433–3445, 2012. doi:10.1152/jn.00420.2011.
- Toma S, Sciutti A, Papaxanthis C, Pozzo T. Visuomotor adaptation to a visual rotation is gravity dependent. J Neurophysiol 113: 1885– 1895, 2015. doi:10.1152/jn.00369.2014.
- Gaveau J, Berret B, Angelaki DE, Papaxanthis C. Direction-dependent arm kinematics reveal optimal integration of gravity cues. *eLife* 5: e16394, 2016. doi:10.7554/eLife.16394.
- Gaveau J, Paizis C, Berret B, Pozzo T, Papaxanthis C. Sensorimotor adaptation of point-to-point arm movements after spaceflight: the role of internal representation of gravity force in trajectory planning. J Neurophysiol 106: 620–629, 2011. doi:10.1152/jn.00081.2011.
- Papaxanthis C, Pozzo T, McIntyre J. Kinematic and dynamic processes for the control of pointing movements in humans revealed by short-term exposure to microgravity. *Neuroscience* 135: 371–383, 2005. doi:10.1016/j.neuroscience.2005.06.063.
- Papaxanthis C, Pozzo T, Popov KE, McIntyre J. Hand trajectories of vertical arm movements in one-G and zero-G environments. Evidence for a central representation of gravitational force. *Exp Brain Res* 120: 496–502, 1998. doi:10.1007/s002210050423.
- Berret B, Chiovetto E, Nori F, Pozzo T. Evidence for composite cost functions in arm movement planning: an inverse optimal control approach. *PLoS Comput Biol* 7: e1002183, 2011. doi:10.1371/journal. pcbi.1002183.
- Gaveau J, Berret B, Demougeot L, Fadiga L, Pozzo T, Papaxanthis
  C. Energy-related optimal control accounts for gravitational load: comparing shoulder, elbow, and wrist rotations. *J Neurophysiol* 111: 4–16, 2014. doi:10.1152/jn.01029.2012.
- Crevecoeur F, Thonnard J-L, Lefèvre P. Optimal integration of gravity in trajectory planning of vertical pointing movements. *J Neurophysiol* 102: 786–796, 2009. doi:10.1152/jn.00113.2009.
- Jörges B, López-Moliner J. Gravity as a strong prior: implications for perception and action. *Front Hum Neurosci* 11: 203, 2017. doi:10.3389/fnhum.2017.00203.
- Lacquaniti F, Bosco G, Gravano S, Indovina I, La Scaleia B, Maffei V, Zago M. Multisensory integration and internal models for sensing gravity effects in primates. *Biomed Res Int* 2014: 615854, 2014. doi:10.1155/2014/615854.
- Pozzo T, Papaxanthis C, Stapley P, Berthoz A. The sensorimotor and cognitive integration of gravity. *Brain Res Brain Res Rev* 28: 92– 101, 1998. doi:10.1016/s0165-0173(98)00030-7.
- Laurens J, Angelaki DE. The functional significance of velocity storage and its dependence on gravity. *Exp Brain Res* 210: 407–422, 2011. doi:10.1007/s00221-011-2568-4.
- Yakusheva TA, Shaikh AG, Green AM, Blazquez PM, Dickman JD, Angelaki DE. Purkinje cells in posterior cerebellar vermis encode motion in an inertial reference frame. *Neuron* 54: 973–985, 2007. doi:10.1016/j.neuron.2007.06.003.
- Asch SE, Witkin HA. Studies in space orientation. II. Perception of the upright with displaced visual fields and with body tilted. J Exp Psychol 38: 455–477, 1948. doi:10.1037/h0054121.

- 47. Dichgans J, Held R, Young LR, Brandt T. Moving visual scenes influence the apparent direction of gravity. *Science* 178: 1217–1219, 1972. doi:10.1126/science.178.4066.1217.
- Vingerhoets RAA, De Vrijer M, Van Gisbergen JAM, Medendorp WP. Fusion of visual and vestibular tilt cues in the perception of visual vertical. J Neurophysiol 101: 1321–1333, 2009. doi:10.1152/ jn.90725.2008.
- Barbieri G, Gissot A-S, Fouque F, Casillas J-M, Pozzo T, Pérennou D. Does proprioception contribute to the sense of verticality? *Exp Brain Res* 185: 545–552, 2008. doi:10.1007/s00221-007-1177-8.
- Barra J, Marquer A, Joassin R, Reymond C, Metge L, Chauvineau V, Pérennou D. Humans use internal models to construct and update a sense of verticality. *Brain* 133: 3552–3563, 2010. doi:10.1093/brain/awq311.
- Lechner-Steinleitner S, Schöne H, Wade NJ. Perception of the visual vertical: utricular and somatosensory contributions. *Psychol Res* 40: 407–414, 1979. doi:10.1007/BF00309420.
- Mittelstaedt H, Fricke E. The relative effect of saccular and somatosensory information on spatial perception and control. Adv Otorhinolaryngol 42: 24–30, 1988. doi:10.1159/000416072.
- Trousselard M, Cian C, Nougier V, Pla S, Raphel C. Contribution of somesthetic cues to the perception of body orientation and subjective visual vertical. *Percept Psychophys* 65: 1179–1187, 2003. doi:10.3758/BF03194843.
- Kaptein RG, Van Gisbergen JAM. Interpretation of a discontinuity in the sense of verticality at large body tilt. *J Neurophysiol* 91: 2205– 2214, 2004. doi:10.1152/jn.00804.2003.
- Mittelstaedt H. A new solution to the problem of the subjective vertical. *Naturwissenschaften* 70: 272–281,1983. doi:10.1007/ BF00404833.
- Kim IK, Spelke ES. Infants' sensitivity to effects of gravity on visible object motion. J Exp Psychol Hum Percept Perform 18: 385–393, 1992. doi:10.1037/0096-1523.18.2.385.
- Kim IK, Spelke ES. Perception and understanding of effects of gravity and inertia on object motion. *Dev Sci* 2: 339–362, 1999. doi:10.1111/ 1467-7687.00080.
- McIntyre J, Zago M, Berthoz A, Lacquaniti F. Does the brain model Newton's laws? *Nat Neurosci* 4: 693–694, 2001. doi:10.1038/89477.
- Senot P, Zago M, Lacquaniti F, McIntyre J. Anticipating the effects of gravity when intercepting moving objects: differentiating up and down based on nonvisual cues. J Neurophysiol 94: 4471–4480, 2005. doi:10.1152/jn.00527.2005.
- Toma S, Caputo V, Santello M. Visual feedback of object motion direction influences the timing of grip force modulation during object manipulation. *Front Hum Neurosci* 14: 198, 2020. doi:10.3389/ fnhum.2020.00198.
- White O, Gaveau J, Bringoux L, Crevecoeur F. The gravitational imprint on sensorimotor planning and control. *J Neurophysiol* 124: 4–19, 2020. doi:10.1152/jn.00381.2019.
- Hermsdörfer J, Marquardt C, Philipp J, Zierdt A, Nowak DA, Glasauer S, Mai N. Moving weightless objects. Grip force control during microgravity. *Exp Brain Res* 132: 52–64, 2000. doi:10.1007/ s002219900325.
- Opsomer L, Théate V, Lefèvre P, Thonnard J-L. Dexterous manipulation during rhythmic arm movements in Mars, moon, and microgravity. Front Physiol 9: 938, 2018. doi:10.3389/fphys.2018.00938.
- Crevecoeur F, Thonnard J-L, Lefèvre P. Sensorimotor mapping for anticipatory grip force modulation. *J Neurophysiol* 104: 1401–1408, 2010. doi:10.1152/jn.00114.2010.
- Danion FR, Diamond JS, Flanagan JR. Separate contributions of kinematic and kinetic errors to trajectory and grip force adaptation when transporting novel hand-held loads. J Neurosci 33: 2229– 2236, 2013. doi:10.1523/JNEUROSCI.3772-12.2013.
- Flanagan JR, Vetter P, Johansson RS, Wolpert DM. Prediction precedes control in motor learning. *Curr Biol* 13: 146–150, 2003. doi:10.1016/s0960-9822(03)00007-1.
- Barrea A, Bulens DC, Lefèvre P, Thonnard J-L. Simple and reliable method to estimate the fingertip static coefficient of friction in precision grip. *IEEE Trans Haptics* 9: 492–498, 2016. doi:10. 1109/TOH.2016.2609921.
- Adams MJ, Johnson SA, Lefèvre P, Lévesque V, Hayward V, André T, Thonnard J-L. Finger pad friction and its role in grip and touch. J R Soc Interface 10: 20120467, 2013. doi:10.1098/rsif.2012.0467.

- Hondzinski JM, Soebbing CM, French AE, Winges SA. Different damping responses explain vertical endpoint error differences between visual conditions. *Exp Brain Res* 234: 1575–1587, 2016. doi:10.1007/s00221-015-4546-8.
- Papaxanthis C, Pozzo T, Schieppati M. Trajectories of arm pointing movements on the sagittal plane vary with both direction and speed. *Exp Brain Res* 148: 498–503, 2003. doi:10.1007/s00221-002-1327-y.
- Conditt MA, Gandolfo F, Mussa-Ivaldi FA. The motor system does not learn the dynamics of the arm by rote memorization of past experience. *J Neurophysiol* 78: 554–560, 1997. doi:10.1152/jn.1997.78. 1.554.
- Danion FR, Sarlegna FR. Can the human brain predict the consequences of arm movement corrections when transporting an object? Hints from grip force adjustments. *J Neurosci* 27: 12839–12843, 2007. doi:10.1523/JNEUROSCI.3110-07.2007.
- Diamond JS, Nashed JY, Johansson RS, Wolpert DM, Flanagan JR. Rapid visuomotor corrective responses during transport of handheld objects incorporate novel object dynamics. J Neurosci 35: 10572–10580, 2015. doi:10.1523/JNEUROSCI.1376-15.2015.
- Hadjiosif AM, Smith MA. Flexible control of safety margins for action based on environmental variability. *J Neurosci* 35: 9106–9121, 2015. doi:10.1523/JNEUROSCI.1883-14.2015.
- Crevecoeur F, McIntyre J, Thonnard J-L, Lefèvre P. Movement stability under uncertain internal models of dynamics. *J Neurophysiol* 104: 1301–1313, 2010. doi:10.1152/jn.00315.2010.
- Berret B, Darlot C, Jean F, Pozzo T, Papaxanthis C, Gauthier JP. The inactivation principle: mathematical solutions minimizing the absolute work and biological implications for the planning of arm movements. *PLoS Comput Biol* 4: e1000194, 2008. doi:10.1371/ journal.pcbi.1000194.
- Izawa J, Rane T, Donchin O, Shadmehr R. Motor adaptation as a process of reoptimization. J Neurosci 28: 2883–2891, 2008. doi:10.1523/JNEUROSCI.5359-07.2008.
- Flanagan JR, Lolley S. The inertial anisotropy of the arm is accurately predicted during movement planning. J Neurosci 21: 1361–1391, 2001. doi:10.1523/jneurosci.21-04-01361.2001.
- Dakin CJ, Rosenberg A. Gravity estimation and verticality perception. In: *Handbook of Clinical Neurology* (vol. 159), edited by Day BL, Lord SR. Amsterdam: Elsevier, 2018. p. 43–59. https://doi.org/ 10.1016/B978-0-444-63916-5.00003-3
- Angelaki DE, Cullen KE. Vestibular system: the many facets of a multimodal sense. *Annu Rev Neurosci* 31: 125–150, 2008. doi:10.1146/annurev.neuro.31.060407.125555.
- Green AM, Angelaki DE. Internal models and neural computation in the vestibular system. *Exp Brain Res* 200: 197–222, 2010. doi:10.1007/ s00221-009-2054-4.
- Pérennou D, Mazibrada G, Chauvineau V, Greenwood R, Rothwell J, Gresty MA, Bronstein AM. Lateropulsion, pushing and verticality perception in hemisphere stroke: a causal relationship? *Brain* 131: 2401–2413, 2008. doi:10.1093/brain/awn170.
- Brandt T, Dieterich M. The vestibular cortex: its locations, functions, and disorders. Ann N Y Acad Sci 871: 293–312, 1999. doi:10.1111/ j.1749-6632.1999.tb09193.x.
- Frank SM, Greenlee MW. The parieto-insular vestibular cortex in humans: more than a single area? J Neurophysiol 120: 1438–1450, 2018. doi:10.1152/jn.00907.2017.
- Guldin WO, Grüsser OJ. Is there a vestibular cortex? Trends Neurosci 21: 254–259, 1998. doi:10.1016/S0166-2236(97)01211-3.

- Indovina I, Maffei V, Bosco G, Zago M, Macaluso E, Lacquaniti F. Representation of visual gravitational motion in the human vestibular cortex. Science 308: 416–419, 2005. doi:10.1126/science.1107961.
- Kaptein RG, Van Gisbergen JAM. Nature of the transition between two modes of external space perception in tilted subjects. J Neurophysiol 93: 3356–3369, 2005. doi:10.1152/jn.01137.2004.
- Schöne H. On the role of gravity in human spatial orientation. Aerosp Med 35: 764–772, 1964.
- Tarnutzer AA, Bockisch C, Straumann D, Olasagasti I. Gravity dependence of subjective visual vertical variability. *J Neurophysiol* 102: 1657–1671, 2009. doi:10.1152/jn.00007.2008.
- Udo De Haes HA. Stability of apparent vertical and ocular countertorsion as a function of lateral tilt. *Percept Psychophys* 8: 137–142, 1970. doi:10.3758/BF03210192.
- Bortolami SB, Rocca S, Daros S, DiZio P, Lackner JR. Mechanisms of human static spatial orientation. *Exp Brain Res* 173: 374–388, 2006. doi:10.1007/s00221-006-0387-9.
- Graybiel A, Patterson JL Jr. Thresholds of stimulation of the otolith organs as indicated by the oculogravic illusion. J Appl Physiol 7: 666–670, 1955. doi:10.1152/jappl.1955.7.6.666.
- Lima KCA, da Silva Borges S, Hatanaka E, Rolim LC, de Freitas PB. Grip force control and hand dexterity are impaired in individuals with diabetic peripheral neuropathy. *Neurosci Lett* 659: 54–59, 2017. doi:10.1016/j.neulet.2017.08.071.
- Nowak DA, Hermsdörfer J. Digit cooling influences grasp efficiency during manipulative tasks. *Eur J Appl Physiol* 89: 127–133, 2003. doi:10.1007/s00421-002-0759-1.
- Lowrey CR, Bent LR. Modulation of the soleus H-reflex following galvanic vestibular stimulation and cutaneous stimulation in prone human subjects. *Muscle Nerve* 40: 213–220, 2009. doi:10.1002/ mus.21275.
- Knikou M, Rymer WZ. Static and dynamic changes in body orientation modulate spinal reflex excitability in humans. *Exp Brain Res* 152: 466–475, 2003. doi:10.1007/s00221-003-1577-3.
- Miyoshi T, Nozaki D, Sekiguchi H, Kimura T, Sato T, Komeda T, Nakazawa K, Yano H. Somatosensory graviception inhibits the soleus H-reflex in standing man—a parabolic flight experiment. *Exp Brain Res* 150:109–388, 2003. doi:10.1007/s00221-003-1414-8.
- Nomura T, Kawano F, Ishihara A, Sato Y, Mitarai G, Iwase S, Kamiya A, Mano T, Ohira Y. Enhanced Hoffman-reflex in human soleus muscle during exposure to microgravity environment. *Neurosci Lett* 316: 55–57, 2001. doi:10.1016/S0304-3940(01)02367-9.
- Smith CP, Allsop JE, Mistry M, Reynolds RF. Co-ordination of the upper and lower limbs for vestibular control of balance. J Physiol 595: 6771–6782, 2017. doi:10.1113/JP274272.
- Bresciani JP, Blouin J, Popov KE, Bourdin C, Sarlegna FR, Vercher JL, Gauthier GM. Galvanic vestibular stimulation in humans produces online arm movement deviations when reaching towards memorized visual targets. *Neurosci Lett* 318: 34–38, 2002. doi:10.1016/S0304-3940(01)02462-4.
- Keyser J, Medendorp WP, Selen LPJ. Task-dependent vestibular feedback responses in reaching. J Neurophysiol 118: 84–92, 2017. doi:10.1152/jn.00112.2017.
- Lackner JR, DiZio P, Fisk J. Tonic vibration reflexes and background force level. Acta Astronaut 26: 133–136, 1992. doi:10.1016/0094-5765(92)90055-N.