

Gravity-dependent estimates of object mass underlie the generation of motor commands for horizontal limb movements

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Crevecoeur F, McIntyre J, Thonnard JL, Lefèvre P. Gravity-dependent estimates of object mass underlie the generation of motor commands for horizontal limb movements. *J Neurophysiol* 112: 000–000, 2014. First published April 30, 2014; doi:10.1152/jn.00061.2014.—Moving requires handling gravitational and inertial constraints pulling on our body and on the objects that we manipulate. Although previous work emphasized that the brain uses internal models of each type of mechanical loads, little is known about their interaction during motor planning and execution. In this report, we examine visually guided reaching movements in the horizontal plane performed by naive participants exposed to changes in vertical gravity during parabolic flight. This approach allowed us to isolate the effect of gravity because the environmental dynamics along the horizontal axis remained unchanged. We show that vertical gravity has a direct effect on movement kinematics, with faster movements observed after transitions from normal gravity to hypergravity (1.8g), followed by significant movement slowing after the transition from hypergravity to zero gravity. We recorded finger forces applied on an object held in precision grip and found that the coupling between grip force and inertial loads displayed a similar effect, with an increase in grip force modulation gain under hypergravity followed by a reduction of modulation gain after entering the zero-gravity environment. We present a computational model to illustrate that these effects are compatible with the hypothesis that participants partially attribute changes in weight to changes in mass and scale incorrectly their motor commands with changes in gravity. These results highlight a rather direct internal mapping between the force generated during stationary holding against gravity and the estimation of inertial loads that limb and hand motor commands must overcome.

reaching control; object manipulation; altered gravity; feedback control; motor adaptation; horizontal movements

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ANY MOVEMENT, from the mundane lift of a coffee cup to the skillful performance of elite athletes or musicians, requires accurate knowledge of both gravitational constraints pulling on our limbs and on the objects that we manipulate and inertial loads arising when we move the objects around. To achieve this, building internal models of the effect of gravito-inertial constraints is likely a fundamental feature of sensorimotor control (Angelaki et al. 2004; Bock 1998; Lackner and DiZio 1996; McIntyre et al. 2001; Senot et al. 2012). However, the interaction between gravitational forces and the neural mech-

anisms underlying movement planning and control is not yet fully understood.

Different theories have been suggested to explain how the brain handles gravitational forces during motor control. Previous work has suggested that the brain calibrates motor commands in a gravity-dependent way so as to adjust movement kinematics or reoptimize motor commands with respect to the environmental gravity field (Berret et al. 2008; Crevecoeur et al. 2009b; Gaveau et al. 2011; Gaveau and Papaxanthi 2011; Gentili et al. 2007; Papaxanthi et al. 2005; Pozzo et al. 1998). While these studies provide important insight on how the CNS handles gravitational constraints, the effect of internal errors in the estimated mass of the limb or manipulated objects has not been thoroughly investigated. This is striking because body and object weights directly vary with gravity, which is known to induce errors in the internal encoding of their properties (Ross et al. 1984). To date, the influence of gravity on the encoding of objects' mass has been clearly documented (Bock 1998; Ross et al. 1984), but the impact of this effect on visually guided reaching and object manipulation has remained largely unexplored, despite known effects of changes in gravity on parameters unaffected by the change in environmental dynamics such as horizontal movements (Fisk et al. 1993; Mechtch-eriakov et al. 2002). However, a mismatch between the actual and estimated masses may directly affect internal predictions about inertial loads.

More specifically, attributing changes in weight to a change in mass under altered gravity, even partially, induces a mismatch between the actual and expected movement dynamics. For instance, an increase in weight experienced on Earth always results from a doubled mass, which requires an adjustment of the muscle activity to overcome greater inertial constraints. However, under hypergravity conditions the inertia is unchanged. Thus changes in muscle activity are also needed, but only to compensate for the increase in weight, as inertial constraints remain unchanged. Therefore, if the motor system responds to the increase in weight by expecting an increased mass, we predict that participants' behavior will exhibit an overcompensation of inertial loads. The opposite reasoning predicts that undercompensation will be observed after a decrease in gravity.

In this study, we show that this hypothesis partially captures the effect of hyper- and microgravity on the control of reaching and finger forces applied on manipulated objects. We use a

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computational model to show theoretically that a mismatch between the estimated and actual mass of the system induces systematic motor errors. These results of our computational model were compared to horizontal reaching movements performed by healthy humans during different phases of parabolic flights with an object held in precision grip. In agreement with the model, our results indicate that the brain may rely on an internal mapping between weights and loads at movement initiation that scales motor commands and internal predictions with the force developed during stationary holding against the effector's weight. Our data further suggest that this mechanism may be common to the limb and hand motor systems.

METHODS

Subjects. A total of 12 subjects participated in the experiments presented below, and the data were collected during the 51st and 52nd Parabolic Flight Campaigns of the European Space Agency (ESA; 2010) and during a parabolic flight campaign sponsored by the French Centre National d'Études Spatiales (CNES; October 2011). The experimental protocol was approved by the ESA Medical Board, by the French Committee for Persons Protection (CPP, Université de Caen), and by the local Ethics Committee at the Université catholique de Louvain. All participants were given scopolamine to prevent motion sickness. One subject was excluded from the sample, as he experienced motion sickness during the flight and was not able to perform the task.

Experimental procedures. Participants were seated in front of three visual targets (green LEDs) mounted on a horizontal support located above the shoulder height. The structure allowed movements directly under the horizontal support equipped with the visual targets. The targets were placed 18 cm apart, and the center target was approximately in front of the shoulder rotation axis (Fig. 1A). Participants were instructed to grasp a manipulandum with a precision grip (grip aperture 4.5 cm, mass 0.25 kg) and align it with the lit target with

shoulder abduction or adduction. Thus movements mostly involved monoarticular arm movements around the shoulder joint. They were asked to align the grip axis with the axis parallel to their arm in such a way that the direction of the center-out movements was orthogonal to the grip axis (Fig. 1A). The target sequence generated movements from the center to the left or right target with probability 0.5, followed by movements returning to the center target. The target changed every second. Participants performed 10 blocks of 20 center-out trials under the normal gravity condition (1g) before performing the task in flight. Only six blocks were collected under normal gravity for one subject because of technical difficulties.

During the flights, each participant performed the task through a series of 15 consecutive parabolic maneuvers generating changes in gravity as illustrated in Fig. 1C. Two subjects were tested per flight: one participant performed the task during *parabolas 1–15*, and the second participant performed the task during *parabolas 16–30*. The task started 10 to 5 s before the first hypergravity phase of each parabola (Fig. 1C, 1.8g) and was performed until the end of each zero-gravity phase as announced by the pilot (Fig. 1C, 0g). Participants released the manipulandum at the end of the zero-gravity phase. Because the acquisition under the 1g condition was not performed on the same day as the flight, we initiated the task prior to the hypergravity phase to verify that participants' behavior in this condition was similar across ground and flight environments.

Data collection. We recorded the position of the manipulandum and the position of the shoulder with a Codamotion tracking system at 200 Hz (Charnwood Dynamics, Leicester, UK). Tangential and normal forces at the interface between the participants' fingertip and the manipulandum were collected at 800 Hz (40-mm diameter, Mini 40 F/T transducers; ATI Industrial Automation, Apex, NC). Position and force signals were digitally low-pass filtered with a dual-pass, 4th-order Butterworth filter with 25-Hz and 50-Hz cutoff frequencies, respectively. We used three-axis accelerometers attached to the aircraft floor (ADXL330; Analog Devices) to measure the vertical gravity during each parabola. Trials in hypergravity were considered valid when the gravity averaged across the movement was $>1.6g$. Zero-gravity trials were validated when the absolute average gravity was $<0.05g$. These validation criteria are illustrated for one typical parabola in Fig. 1D. The number of valid trials varied across participants, as it depended on the gravity levels of each parabola. These numbers were between 91 and 124 trials in hypergravity (median 104) and between 98 and 142 trials in zero gravity (median 133).

Data analysis. The linear coordinate of the held object was measured along the axis aligned with the visual targets (x -axis, Fig. 1A). The analysis of movement kinematics was based on the peak acceleration, peak velocity, and movement duration and followed procedures fully described in our earlier study (Crevecoeur et al. 2009b). We also measured the average absolute vertical deviations throughout the movement as well as the shape of the velocity profile characterized as the ratio between the acceleration duration and the total movement duration. This ratio is equivalent to the relative time to peak velocity. The movement onset and movement end were determined based on linear approximation of the velocity around the time when it crossed 10% of its peak value computed for each individual trial. The grip force was defined as the force component normal to the force sensors. The grip force was decomposed into two components according to procedures described previously (Crevecoeur et al. 2009a): the static component is the average of the grip force in a 100-ms time window following the target onset, and the dynamic component is the difference between the grip force during the movement and the static component. The load force was defined as the force component tangent to the force sensors. We define the change in load force (ΔLF) as the scalar difference between the norm of the total load force and the object weight (Fig. 1B). Observe that ΔLF is not equal to the inertial load because the movement vector is not aligned with gravity.

Statistical comparisons of trials across gravitational conditions were based on nonparametric Wilcoxon rank sum tests for each

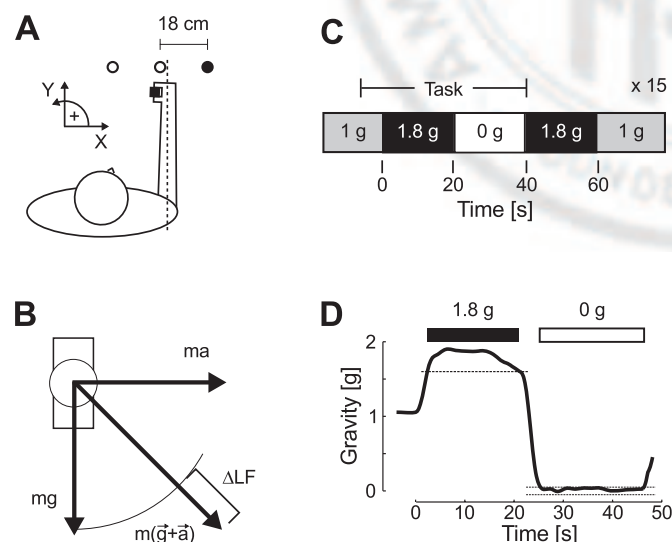


Fig. 1. A: overhead representation of a subject performing the task. The visual targets were placed 18 cm apart, and the center target was approximately in front of the shoulder rotation axis. B: gravitational (mg) and inertial (ma) force vectors projected onto the vertical plane. The actual increase in tangential load resulting from the object acceleration is represented (ΔLF). C: illustration of gravity levels during a parabolic maneuver with a schematic representation of the period during which participants performed the task. D: exemplar trace of vertical gravity as a function of time. The dashed horizontal lines illustrate the thresholds used to validate the trials (see METHODS: hypergravity $> 1.6g$; $-0.05g < \text{zero gravity} < 0.05g$).

individual subject. Nonparametric tests were preferred because some samples displayed non-Gaussian distribution (9/33 samples of peak acceleration, 11 participants $\times$ 3 gravitational condition, Kolmogorov-Smirnov test, $P < 0.05$). Kinematic parameters used to characterize the reaching movements were then averaged for each individual, as we did not find any significant variation across or within parabolas [$F_{(13,136)} < 0.41$, $P > 0.05$]. Group comparisons of individuals' means across conditions were based on paired t -tests in order to mitigate the impact of interparticipant variability on statistical comparisons. The relationship between the grip force and the load force was characterized with least-square linear regressions.

Model. The model is based on the translation of a point mass along a one-dimensional axis. Although it is simplified, this approximation captures many features of the experimental effects. The motion of the point mass is described by Newton's laws of motion:

$$m\ddot{x} = -k\dot{x} + F \quad (1)$$

where x is the mass coordinate, m is the mass, k is a viscous constant, and F is the force applied by the controller on the mass. This model considers a single point mass for simplicity, although in reality the brain must clearly estimate the resultant mass of the whole limb in addition to the manipulated object. Single and double dots represent the first and second time derivative, respectively. This equation was coupled with a linear, first-order low-pass filter model of muscle dynamics relating the control variable, u , to the force production:

$$\tau\dot{F} = u - F \quad (2)$$

The time constant was set to $\tau = 66$ ms, compatible with a first-order approximation of the muscle dynamics (Brown et al. 1999). We used normalized parameters for simplicity: $m = 1$ kg and $k = 0.1$ Ns/m.

Equations 1 and 2 were transformed into discrete time in the form

$$x_{t+1} = Ax_t + Bu_t + \zeta_t \quad (3)$$

The noise disturbance represented by ζ_t only affected Eq. 2. Equation 3 expresses the state of the system and the location of the goal target and allows handling of feedback delays from system augmentation according to procedures fully described previously (Crevecoeur et al. 2011). We consider that the feedback available is a delayed and noisy measurement of the true state as follows:

$$y_t = x_{t-h} + w_t \quad (4)$$

where h is the feedback delay expressed in number of sample times and w_t is the noise affecting sensory signals. The feedback delay was set to 100 ms, and the motor and sensory noise covariance matrices were set to 10^{-6} . The model parameters (mass, viscosity, and muscle time constants) as well as the variance of motor and sensory noise had qualitatively no impact on the simulation results.

The control problem consisted of 18-cm reaching movements as described by a cost function penalizing the end-point location and velocity. The movement duration was set to 0.5 s, corresponding to the average movement duration measured under the 1g condition, followed by a stabilization duration of 0.5 s. With these definitions, we derived the optimal controller and the optimal state estimator (Kalman filter), following standard procedures (Astrom 1970; Todorov 2005). We chose a model based on optimal feedback control to illustrate that internal model errors impact the whole movement trajectory even when motor commands are based on online state estimation. In other words, internal model errors can alter the whole movement kinematics even when sensory feedback indicates a difference between actual and expected movement trajectory.

Simulations. We hypothesize that changes in object weight are partially attributed to changes in mass, in agreement with participants' life-long experience acquired on Earth. This hypothesis can be formulated with one single parameter, $0 \leq w \leq 1$, which quantifies how much participants believe that the mass changed. The value $w = 0$ indicates that the controller considers that the mass did not change. In

contrast, $w = 1$ indicates that the controller believes that gravity did not change. In other words, the controller believes that it manipulates a mass defined as follows (the "hat" designates the estimation, and Δg is the change in gravity relative to the normal gravity condition):

$$\hat{m} = m(1 + w\Delta g) \quad (5)$$

If the mass remains constant but $w > 0$, the difference between the estimated and actual mass induces an error in the internal models of dynamics, which impacts the trajectory control as well as the prediction of inertial loads as presented below.

RESULTS

Model predictions. Attributing the weight increase to a change in mass has a direct effect on the movement kinematics presented in Fig. 2A. These simulations were computed with $w = 0.3$. Under the hypergravity condition, the controller generates an initial force to overcome inertial constraints that are lower than expected. As a consequence, the initial peak acceleration increases, followed by an increased peak velocity (Fig. 2A, red). The opposite effect is observed under the zero-gravity condition, where the mass underestimation results in movement slowing with decreased peak acceleration and peak velocity (Fig. 2A, blue). Importantly, the change in tangential loads does not vary linearly with the gravity because the acceleration and gravity vectors are not aligned (see Fig. 1B). Figure 2B shows in black the nonlinear change in load force across gravitational conditions for a given value of peak acceleration. If the mass is not well estimated ($w > 0$), the predicted inertial load for the same peak acceleration will vary according to the gray profiles corresponding to distinct values of w . Observe that the expected changes in load force decrease

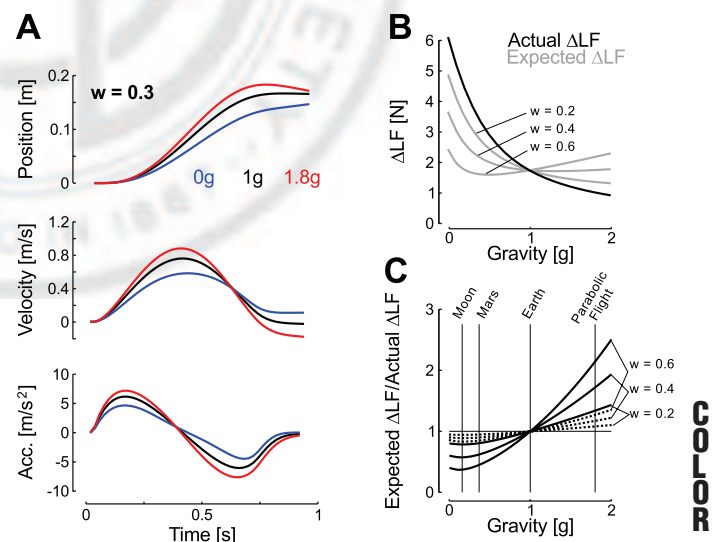


Fig. 2. Model simulations. A: effect of biased mass estimation on the position (top), velocity (middle), and acceleration (bottom) profiles of reaching movements. Attributing 30% of the change in weight to a change in mass ($w = 0.3$, see METHODS) generates faster (red) or slower (blue) movements when gravity increases or decreases, respectively. The black trace corresponds to the baseline simulation (normal gravity). B: actual (black) and expected (gray) changes in load force for a constant peak acceleration as a function of changes in gravity. The effect of the internal prior about changes in mass is illustrated for different values of the parameter w . C: ratio between expected and actual changes in load force illustrating the under- and overestimation expected under hypo- and hypergravity conditions. The dashed traces in C were computed based on the actual peak acceleration obtained from the simulated trajectories.

or increase depending on whether gravity is below or above Earth gravity (1g). Figure 2C presents the ratio between the actual and expected load force computed directly from Fig. 2B. We should also take into account that these values are based on the same peak acceleration value, which may be inaccurate because changes in movement kinematics partially counterbalance the error in load estimation. Figure 2C presents the ratio between actual and expected load force with the actual peak acceleration obtained from the simulations with values of $w > 0$ (dashed trace). Observe that the effect is qualitatively similar when taking the actual kinematics into account. Hence, the model predicts that changes in peak acceleration and peak velocity, as well as load force prediction errors, should correlate with the change in gravity.

Experimental data. Overall, movements were smooth with bell-shaped velocity profiles. Movements were also mostly planar, despite significant effects of changes in gravity on the vertical components of the reaching path. Figure 3A illustrates the main effects of changes in gravity on the movement trajectories. Movements performed in flight presented greater peak-to-peak vertical deviations compared with normal gravity [Fig. 3B; $t_{(10)} = 6.7$, $P < 0.001$], but these deviations remained $< 10\%$ of the reaching amplitude on average (Fig. 3B). We observed a consistent tendency for upward deviations under hypergravity. This tendency was also apparent after extracting the ratio between the vertical load and the total change in load, which significantly increased under hypergravity [Fig. 3B; $t_{(10)} = 3.04$, $P < 0.05$], although its magnitude represented $6 \pm 4\%$ of the total change in load force. Thus although the change in gravity induced greater vertical deviations, movements remained mostly planar, allowing us to perform one-dimensional analysis of the movement kinematics along the x -axis. Along this dimension, the movement shape captured by the ratio between acceleration duration and the total movement duration indicated asymmetric velocity profiles (0.45 ± 0.026 , mean $\pm$ SD across participants). This ratio was statistically similar across gravitational conditions (1-way ANOVA, $F = 0.98$, $P = 0.4$).

Changes in gravity had a direct impact on the movement kinematics as illustrated in Fig. 4A. After the increase in gravity (Fig. 4A, left, 1g to 1.8g), participants tended to perform faster movements. This tendency was captured by an increase in initial acceleration peak [paired t -test across sub-

jects, $t_{(10)} = 3.58$, $P < 0.01$], an increase in peak velocity [$t_{(10)} = 2.7$, $P < 0.05$], and a decrease in movement duration [$t_{(10)} = -2.97$, $P < 0.05$]. The same effect was observed across individual trials for 8 of 11 participants (Fig. 4B, left; Wilcoxon rank sum test, $P < 0.05$). The transition from hypergravity to zero gravity also induced systematic changes in movement kinematics with an opposite effect (Fig. 4, A and B, right): participants reduced the initial peak acceleration [$t_{(10)} = -6.13$, $P < 0.001$] and the peak velocity [$t_{(10)} = -4.7$, $P < 0.001$] and increased the movement duration [$t_{(10)} = 5.2$, $P < 0.001$]. Average values and standard deviations across participants are summarized in Table 1. The analysis of individual trials across subjects revealed that the initial acceleration peak and movement duration significantly varied for 10 of 11 participants, while the peak velocity significantly varied for 9 of 11 participants (Fig. 4B, right). In summary, although the changes in vertical gravity do not affect the environmental dynamics along the horizontal axis, the transitions between gravitational conditions induced systematic changes in movement parameters. The general tendency to speed up and then slow down while entering the hypergravity and zero-gravity phases is in agreement with the model predictions (Fig. 2A). The analysis of the angular motion at the shoulder joint revealed exactly the same effects of changes in gravity on the angular velocity and acceleration peaks. The three participants displaying opposite effects in hypergravity were the same for all kinematics parameters. These three participants were all experiencing changes in gravity for the first time, and there was no systematic order effect that could explain this difference. The opposite tendency observed with these participants likely reflects natural idiosyncrasy.

We extracted the movements performed in flight under 1g prior to the hypergravity phases to verify that participants' behavior was similar across ground and flight environments (Fig. 1C). We found that the average peak acceleration significantly increased by $\sim 26\%$ during the flight [$t_{(10)} = 2.43$, $P < 0.05$]; however, the peak acceleration under hypergravity was still significantly greater [$t_{(10)} = 2.43$, $P < 0.05$]. The peak velocity and movement durations were statistically similar across ground and flight 1g conditions [$t_{(10)} > 1.3$, $P > 0.2$]. Thus, although there was an effect of the flight on the peak acceleration, the results are similar regardless of whether 1g data collected on the ground or in flight are considered.

In theory, mistakenly attributing the change in weight to a change in mass should also have an effect on the load force prediction (Fig. 2, B and C), with a consistent tendency to over- or underestimate the change in load force as gravity increases or decreases, respectively. The grip/load force coupling directly supports this theoretical prediction. Typical force traces are represented in Fig. 5A (data from 1 subject). The static component of the grip force was quickly adjusted to the change in object weight and displayed only limited changes across parabolas as illustrated in Fig. 5C. We observed a tendency for a decrease in static grip force within each 0g phase of the parabolas [first and last trials average static grip force: $t_{(10)} = 5$, $P < 0.01$], suggesting the presence of washout between the blocks of trials due to the execution of the task across different gravitational phases within parabolas.

Regarding the dynamic modulation of the grip force, ΔGF was generally well correlated with ΔLF . We measured 73% of significant regressions under normal gravity conditions, 77%

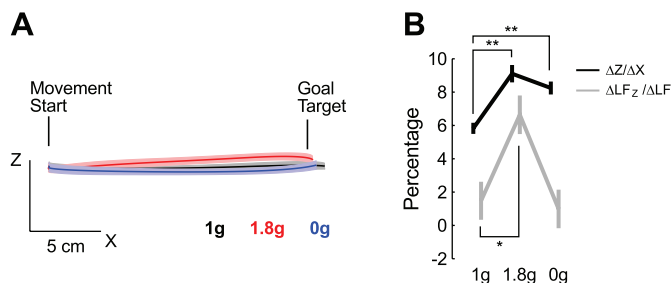


Fig. 3. A: illustration of 2-dimensional reaching movements toward the right target in the 3 distinct gravitational conditions. Traces represent the average x - and z -coordinates, and the shaded areas represent 1 standard deviation of the vertical component across participants. B: black: peak-to-peak vertical deviations averaged across trials for each participant and then across participants. Vertical bars represent 1 standard error; values are displayed as % of the reaching amplitude along the horizontal axis. Gray: ratio between the vertical load force and the total change in load force in each gravitational condition. Significant difference compared with data collected under normal gravity conditions: $*P < 0.05$, $**P < 0.01$.

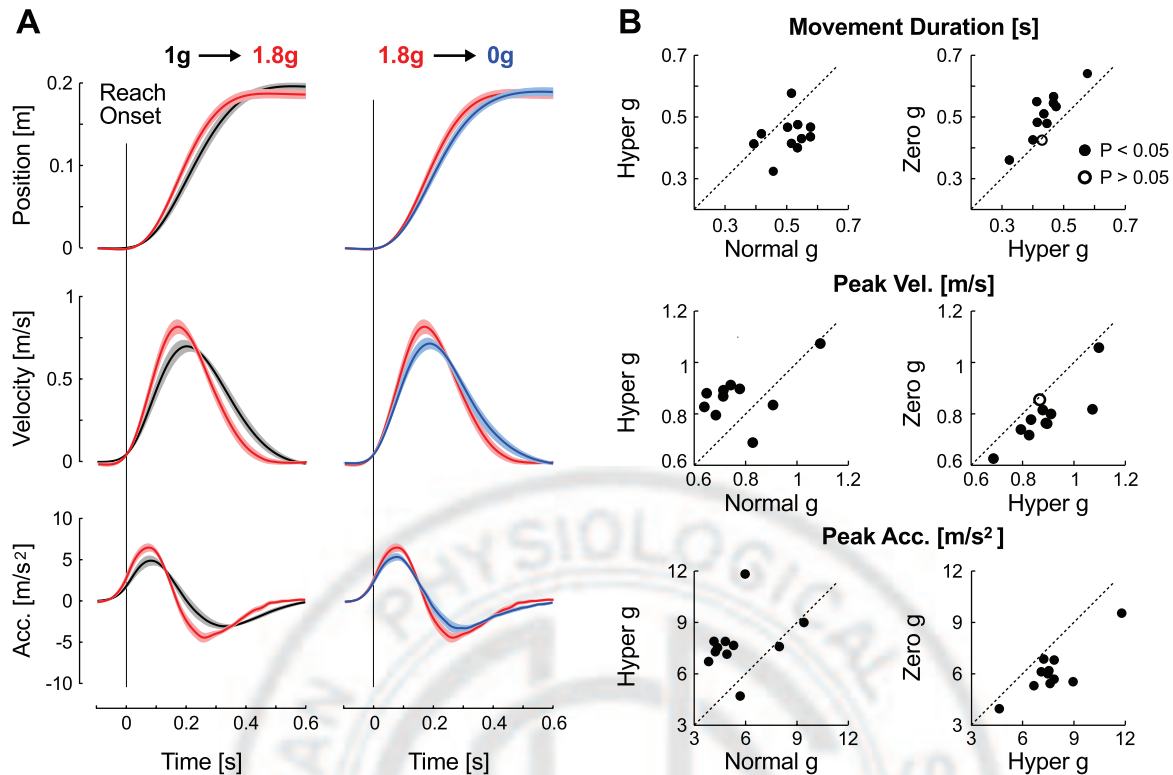


Fig. 4. A: position (top), velocity (middle), and acceleration (bottom) of the manipulandum in the 3 gravitational conditions averaged across subjects: zero gravity (blue), hypergravity (red), and normal gravity (black). Shaded areas correspond to 1 standard error. Only rightward movements (positive x-coordinate) are represented. Leftward movements display the same effect. Traces were aligned on the reach onset (vertical line). B: effect of changes in gravity on movement duration (top), peak velocity (middle), and peak acceleration (bottom). Displays are participants' individual means in each gravitational condition plotted against their values in the gravitational condition experienced just before. Filled (open) dots represent the subjects who exhibited a (non)significant change in the corresponding parameter after comparing individual trials across conditions (Wilcoxon rank sum test, $P < 0.05$).

under the hypergravity condition, and 86% under the zero-gravity condition (11 subjects $\times$ 2 movement directions). The correlations were $R = 0.34 \pm 0.21$ (1g, mean $\pm$ SD), 0.43 ± 0.23 (1.8g), and 0.41 ± 0.19 (0g). Hence, participants were able to anticipate the change in load force in each gravitational context, and the correlations between anticipatory grip force adjustments and changes in load force were similar. However, the regression slopes clearly varied with the gravitational context. The effect is shown in Fig. 5B for one participant who best illustrates the general tendency: although ΔLF overlapped in each gravitational condition, the slopes of the regressions between ΔGF and ΔLF were higher in hypergravity and lower in zero gravity. Group data are reported in Fig. 5D with the results of pairwise comparisons performed across conditions (paired t -tests).

We investigated the temporal coordination between grip and load force by extracting the timing of peak grip force rate occurring prior to the load force peak. We chose this parameter because grip force modulation profiles do not systematically

present a single peak, as a consequence of the biphasic load profile. As well, the peak grip force sometimes coincides in time with the first or second load force peak, making the coordination more difficult to characterize than for vertical movements presenting a single grip/load force peak (see also Flanagan and Wing 1993). The trials with a peak in grip force rate prior to the load force peak represented $72 \pm 18\%$ under normal gravity, $29 \pm 6\%$ under microgravity, and $26 \pm 3\%$ under hypergravity. For those trials, there was no main effect of gravity on the correlations and regression slopes between the timing of load/grip force rates [1-way ANOVA, $F_{(2,30)} > 2.3$, $P > 0.11$]. The regression slopes were close to unity, as expected for synchronized signals (slopes: 0.95 ± 0.14 ; correlations: $R^2 = 0.51 \pm 0.14$, mean $\pm$ SD across participants). Thus, although a smaller proportion of trials displayed stereotyped grip/load force rate, the synchronization between grip and load force was generally preserved across gravitational conditions.

We used the average relative changes in regression slopes to fit the parameter w and estimate how much participants responded to changes in weight as if the mass had changed. Interestingly, we found that the value of w corresponding to hypergravity ($w = 0.29$) was smaller than the value corresponding to microgravity ($w = 0.58$). The values of w were computed using the peak acceleration obtained in the baseline case ($w = 0$).

We based the foregoing analysis on the assumption that the nervous system anticipates the load force increments (ΔLF in

Table 1. Summary of kinematics parameters across gravitational conditions

	Movement Duration, s	Peak Acceleration, m/s ²	Peak Velocity, m/s
1g	0.49 ± 0.06	5.51 ± 1.73	0.77 ± 0.13
1.8g	0.44 ± 0.06	7.73 ± 1.7	0.89 ± 0.12
0g	0.5 ± 0.08	6.13 ± 1.37	0.79 ± 0.1

Values represent means $\pm$ SD across participants.

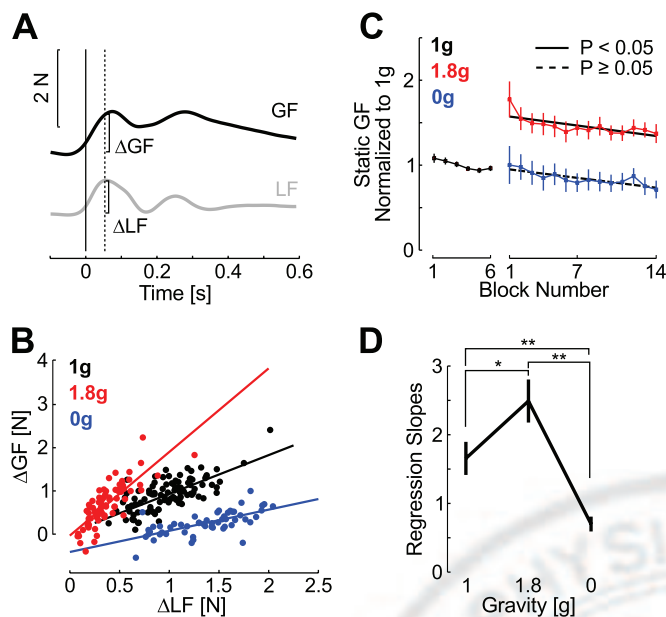


Fig. 5. A: average grip force and load force traces from 1 representative subject. Traces were aligned on reach onset (solid vertical line). The dashed vertical line illustrates the time of the first load force peak, used to extract ΔLF as shown in Fig. 1B, as well as ΔGF (see METHODS). B: effect of changes in gravity on the relationship between ΔGF and ΔLF for the same subject. Each dot is 1 trial. Observe the change in the gain of the modulation despite a clear overlap in ΔLF distribution across gravitational conditions. C: evolution of the static grip force across the blocks or parabolas (mean $\pm$ SE across subjects). Participants' data were normalized to their average static grip force measured under the normal gravity condition. Significant decrease across blocks was observed under hypergravity. The decrease in static grip force across blocks under zero gravity was marginally significant ($P = 0.054$). D: effect of changes in gravity on the regression slopes. Displays are means $\pm$ SE across subjects. Significant differences in regression slopes or intercept across conditions: * $P < 0.05$, ** $P < 0.01$ (paired t -tests).

Fig. 1B), which vary with the inertial load in a nonlinear way. However, we verified that the results are similar under the assumption that the brain scales the grip force with the inertial load only (Fig. 1B, $m \times a$), yet the effect was statistically weaker and observed after the transition between gravitational phases similar to the changes in movement kinematics reported above. We computed the regressions between the increments of grip force and the inertial load and found a significant increase in the regression slopes under hypergravity compared with normal gravity [paired t -test, $t_{(11)} = 2.34$, $P < 0.05$], followed by a decrease in the regression slope under zero gravity [paired t -test, $t_{(11)} = 2.92$, $P < 0.05$]. The variation in regression intercept did not display any significant variation across gravitational conditions. Thus the interpretation of our results remains the same: we suggest that the mass is underestimated in 0g and overestimated in 2g, whether the net change in load force or the inertial load only is taken into account in the modulation of the grip force.

DISCUSSION

We examined one particular mechanism that potentially plays an important role in motor planning and execution during altered gravity levels: a possible mismatch in internal models of dynamics resulting from inaccurate estimate of the object mass. We used predictions from a computational model to show that this hypothesis predicts over- and undercompensa-

tion for inertial loads, which was directly supported by the data. Indeed, movement profiles and grip/load force modulation reflected up-/downregulation of the motor gains following changes in gravity, despite the fact that the environmental dynamics in the horizontal plane was unchanged. The similarity between changes in reaching movement profiles and grip force modulation suggests that the mechanism underlying prediction of inertial loads may be common to the hand and the limb motor systems. Indeed, the brain must estimate the mass both of the limb and of the manipulated object, and we observed a scaling of motor gains with gravity levels in the movement kinematics as well as in the modulation of the grip force. This observation suggests that a similar mechanism underlies movement generation and fingertip force control.

Two potential limitations of our study should be emphasized. The first is the alternation between gravitational phases imposed by the parabolic maneuvers (Fig. 1D). This aspect of our parabolic flight conditions was partially advantageous because it may have hindered the short-term adaptation across parabola and magnified the changes in motor behavior following the transition between gravitational phases. However, alternating gravitational phases do not allow extraction of the effect of each condition independently. Instead, we concentrated on the changes in movement kinematics following the transitions between the different gravitational phases. The shortcoming of this approach is that a direct comparison between 1g and 0g conditions is partially inconclusive, because we do not know how much the behavior under 0g was influenced by the hypergravity condition experienced prior to the 0g phase. However, the change in grip force modulation gain predicted by the model was well emphasized by comparing participants' data under zero gravity directly with their data collected under normal gravity. In addition, movement slowing and overall reduction in motor gains under zero gravity have been reported previously (Crevecoeur et al. 2010a; Mechtch-eriakov et al. 2002; Papaxanthis et al. 2005), which suggests that the decrease in movement acceleration and velocity following the transition from 2g to 0g generally reflected the effect expected under the 0g condition.

The second limitation is the fact that gravity altered the vertical component of movements. Variable gravity levels within each movement induced parts of these deviations. As leaving the arm unconstrained was critical to addressing the question of gravity-dependent motor planning, we could not provide any support to the arm in order to control for these vertical deviations. Vertical peak-to-peak deviations and vertical acceleration represented $<10\%$ of the reaching amplitude or change in load force, respectively. This result suggests that movements were generally planar and that the change in the vertical component is not the source of the observations obtained in 0g.

We did not observe any clear change in kinematic parameters occurring across parabolas. Evidence for short-term adaptation was observed with a reduction in static grip force under hypergravity along with a similar trend under microgravity compatible with previous reports (Augurelle et al. 2003; Crevecoeur et al. 2010a; Hermsdorfer et al. 1999; Nowak et al. 2001). The mechanisms underlying short-term adaptation are not fully understood, and it is unclear why short-term adaptation was not more apparent in the present data set. It is known that participants with extensive experience of an altered gravity

environment fully adapt to altered gravitational contexts (Augurelle et al. 2003; White et al. 2005). We expect that future studies performed under longer-term and stable exposure will provide critical insight on this important question.

It is difficult to explain our data under current models for motor learning and adaptation. Indeed, current theories suggest that motor commands adjust after errors caused by novel environmental dynamics (Shadmehr et al. 2010; Wolpert et al. 2011). This approach makes the prediction that there should be no effect of gravity on horizontal movements, because the usual motor plans and predictions corresponding to an Earth gravity environment would have generated movements that followed the expected path without any substantial motor error. The main difference is that most learning studies use dynamic perturbations experienced during the movement (Flanagan and Wing 1997; Franklin et al. 2008; Krakauer et al. 1999; Lackner and DiZio 1994; Shadmehr and Mussa-Ivaldi 1994; Singh and Scott 2003; Smith et al. 2006), and consequently trial-by-trial changes in movement control follow from execution errors. In contrast, our data emphasize a direct effect of vertical gravity on horizontal movements and highlight the fact that initial conditions prior to the reaching movement also play a central role in the generation of the motor commands. Observe that our results also differ from previously reported scaling of grip force with internal expectations about objects' weight acquired from experience and learning (Flanagan et al. 2008; Johansson and Flanagan 2009). In our study, the normal weight could be fully known, as participants lifted the manipulandum and initiated a series of movements under normal gravity conditions before each parabola (see Fig. 1). Thus the effects that we report indicate that the transformation of weight signals into motor commands uses sensory information available just before each individual movement.

Our hypothesis is that the generation of motor commands is based on a direct mapping of body and object weight into inertial loads. Such a mapping could simply reflect that changes in weight experienced on Earth are always induced by changes in mass, and as a consequence, inertial loads always vary proportionally to the change in weight multiplied by the movement acceleration relative to gravity. In this framework, varying the gravity induces a mismatch between the expected and actual inertial constraints, with the consequences for reaching control and object manipulation presented above. We previously suggested this mechanism to explain the increases in the gain of grip force modulation with load force experienced during vertical reaching movements (Crevecoeur et al. 2010b). However, this interpretation was subject to caution because this previous study could not dissociate possible effects of mass estimation errors from a possible influence of changes in the environmental dynamics (Crevecoeur et al. 2009b).

Under the assumption of errors in the internal encoding of arm and object mass, we attempted to quantify the magnitude of the error by estimating the parameter w (Eq. 5). We found asymmetric changes, with a more profound impact of micro-gravity, which may reflect the informally reported highly unusual sensation experienced in this condition. We should emphasize that such estimates did not take into account the actual change in movement acceleration that partially reduces the mismatch between the predicted and actual inertial loads (Fig. 2C). This somewhat limits the interpretations that can be

made about the numerical value, but it is also important to consider that the model does not capture possible online feedback modulation of grip force gain following unexpected variation in movement acceleration that can be perceived prior to the load force peak. Thus our estimate of the parameter w can be considered, with caution, as a first approximation.

Previous work suggested that hand curvature of reaching movements in the sagittal plane was explained by motor commands being reoptimized for an overestimated level of gravity (Gaveau et al. 2011). This conclusion was partially supported by the observation that loading participants' mass had no effect on the movement curvature [see the control experiment performed by Gaveau and colleagues (Gaveau et al. 2011)]. In general, our conclusions agree in the sense that gravity-dependent effects on movement profiles may result from mismatch in model parameters. However, we propose to nuance the interpretations. Our hypothesis predicts that loading the arm under normal gravity should not influence the movement, because weight and inertia vary according to participants' expectations. Instead, we believe that the effect of changes in vertical gravity reported in this article is not due to a simple loading of the arm but to a mismatch between actual and expected loads. Such a mismatch could be captured by errors in the estimation of gravity levels, but this hypothesis does not easily explain our data because, contrary to the study by Gaveau and colleagues (2011), our movements were mostly confined to the transversal plane. These observations indicate that a mismatch in gravity estimates alone is not sufficient to explain our experimental effects, and we proposed that gravity-dependent estimates of limbs' and objects' masses may explain the effect of vertical gravity on horizontal movements. However, our simulations are compatible with the hypothesis that participants partially accounted for the change in gravity ($w < 1$ in Eq. 5), which may also be prone to errors impacting some features of movement including a vertical component (Gaveau et al. 2011). In addition, the study by Gaveau and colleagues addressed sensorimotor adaptation after a spaceflight. It is possible that for acute changes in gravitational level the changes in movement parameters result from a misperception of the object's mass, while after longer-term exposure to 0g movement characteristics are more affected by misperception of gravity's influence itself. An important question for future studies is to clarify under which circumstances the brain relies on estimates of environmental (gravity) or body parameters to generate the motor commands, and how these processes are sensitive to changes in gravity.

Our conclusions regarding the 0g condition also appear compatible with our previous report in which we suggested that the implicit movement objective is dynamically adjusted to reduce the feedback gains and preserve smooth movements in the presence of internal model errors (Crevecoeur et al. 2010a). In fact, a mismatch in mass/inertia estimates predicts large end-point errors, in particular for the end-point velocity (Fig. 2). End-point velocity errors mean that the movement does not stop at the target within the prescribed movement time. Such large end-point velocity errors were not observed in our data set, which suggests that participants were able to stabilize the movement despite initial motor errors highlighted by changes in peak acceleration and peak velocity. Compatible with our previous report (Crevecoeur et al. 2010a), simulations confirm that stabilizing the hand at the target in the presence of internal

model errors and feedback delays is necessary to perform such corrections without altering the movement profile (simulations not shown).

Our hypothesis, therefore, is that the brain uses the sensation of weight to anticipate inertial loads, and that this mechanism is shared across the arm and hand motor systems. In contrast to this idea, Fisk and colleagues (Fisk et al. 1993) previously suggested that such gravity-dependent scaling of motor commands originates from changes in muscle spindle activations or from descending influences of vestibular inputs on the tonic activation of motor neurons. Each of these two mechanisms could explain the slowing of movements in 0g in terms of muscle tone and limb impedance. In this context, the fact that we observed gravity-dependent modulation of motor gains in the finger forces applied on the held object is telling. Since finger muscles do not directly participate in the generation of the limb movement, it is unlikely that the changes in muscle tone or spindle activation underlie the gravity-dependent modulation of grip force/load force coupling that we observed. Rather, since grip force/load force coupling is often considered to reflect predictive mechanisms (Flanagan and Wing 1997; Johansson and Westling 1988; Witney et al. 1999), the gravity-dependent effects on this coupling are more readily explained by a misestimation of the inertial parameters of the limb and load during motor planning. Of course, we do not reject the possibility that the mapping between gravity and motor planning might be heavily influenced by the background muscle tone, and the question of whether (and how much) the effects of gravity originate from peripheral or central mechanisms is of fundamental importance. Unfortunately, our experiments do not permit us to quantify the influence of each of these mechanisms. However, we do emphasize that, in theory, misestimating the system mass may account for both the effects on limb kinematics and grip force/load force coupling that we observed. We therefore suggest that transformations of sensory signals into motor commands via weight-dependent estimates of mass provides a parsimonious explanation as to why the CNS modulates motor programs in the face of modulations of the gravitational environment.

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DISCLOSURES

AQ: 6 No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: F.C., J.M., J.-L.T., and P.L. conception and design of research; F.C., J.M., J.-L.T., and P.L. performed experiments; F.C. analyzed data; F.C., J.M., J.-L.T., and P.L. interpreted results of experiments; F.C., J.M.,

J.-L.T., and P.L. prepared figures; F.C. drafted manuscript; F.C., J.M., J.-L.T., and P.L. edited and revised manuscript; F.C., J.M., J.-L.T., and P.L. approved final version of manuscript.

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