Optimal Integration of Gravity in Trajectory Planning of Vertical Pointing Movements

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Abstract

The planning and control of motor actions requires knowledge of the dynamics of the controlled limb in order to generate the appropriate muscular commands and achieve the desired goal. Such planning and control implies that the Central Nervous System must be able to deal with forces and constraints acting on the limb, such as the omnipresent force of gravity. The present study investigates the effect of hypergravity induced by parabolic flights on the trajectory of vertical pointing movements in order to test the hypothesis that motor commands are optimized with respect to the effect of gravity on the limb. Subjects performed vertical pointing movements in normal gravity and hypergravity. We use a model based on optimal control to identify the role played by gravity in the optimal arm trajectory with minimal motor costs. First, the simulations in normal gravity reproduce the asymmetry in the velocity profiles (the velocity reaches its maximum before half of the movement duration), which typically characterizes the vertical pointing movements performed on Earth, whereas the horizontal movements present symmetrical velocity profiles. Second, according to the simulations, the optimal trajectory in hypergravity should present an increase in the peak acceleration and peak velocity despite the increase in the arm weight. In agreement with these predictions, the subjects performed faster movements in hypergravity with significant increases in the peak acceleration and peak velocity, which were accompanied by a significant decrease in the movement duration. This suggests that movement kinematics change in response to an increase in gravity, which is consistent with the hypothesis that motor commands are optimized and the action of gravity on the limb is taken into account. The results provide evidence for an internal representation of gravity in the central planning process and further suggest that an adaptation to altered dynamics can be understood as a re-optimization process.
Introduction

The investigation of the skillful and smooth movements that we achieve so many times a day intends to clarify how movements are controlled by the Central Nervous System. There are an infinite number of feasible trajectories and kinematics that allow individuals to perform a basic movement. However, in general, little variability is observed between repeated movements. Why is this? Is there any reason why one particular movement is realized among an infinite number, and why this movement is stable across repeated executions? To answer this question, one should identify the criteria taken into account when the movements are planned and controlled and how the system responds to a change in the environment.

For this purpose, the concept of optimality has long been associated with mechanical parameter adjustments (Burdet et al. 2001) and with movement planning and control, assuming that motor actions were optimal with respect to a cost defined along the movement. Kinematics and dynamics costs have successfully modeled real movements (Flash and Hogan 1985; Nakano et al. 1999; Uno et al. 1989) as well as the costs related to the movement variability and sensorimotor noise (Harris and Wolpert 1998). Feedback control has also been proposed to rely on optimal strategy, maximizing locally the expected reward related to the next state at minimum cost by taking into account an estimate of the current state (Todorov 2004; Todorov and Jordan 2002). The optimal feedback control framework, supported by the neural basis, finely models the movement strategies, flexibility and learning properties of motor control (Izawa et al. 2008; Liu and Todorov 2007; Scott 2004; Shadmehr and Krakauer 2008).

These models assume that the Central Nervous System has access to the internal representations of the limb dynamics and state (position, velocity, etc.) thanks to internal models (Kawato 1999; Wolpert and Ghahramani 2000) that are necessary for the computation of motor commands in the both feed forward and feedback control schemes (Wagner and Smith 2008). Indeed, the generation of an appropriate motor command must rely on the knowledge of limb dynamics and its interaction with the environment through external
constraints including that omnipresent force field in which we have learned to move from our earliest childhood: the gravity field.

Gravity has multiple implications for motor control. It influences reference frames for body orientation in the environment and for interaction with moving objects (McIntyre et al. 1998; McIntyre et al. 2001; Pozzo et al. 1998). Changes in motor responses following changes in gravity were observed from various contexts such as the synchronization of grasping forces and isometric force production (Augurelle et al. 2003; Crevecoeur et al. 2009; Girgenrath et al. 2005; Mierau et al. 2008; White et al. 2005). In the context of vertical pointing movements, the characteristics of arm kinematics in Earth’s gravity led to the hypothesis that the gravitational constraint is internally represented in the planning process of motor actions (Atkeson and Hollerbach 1985; Papaxanthis et al. 1998). Vertical pointing movements typically exhibit skewness in the velocity profile, with the peak velocity occurring before the middle of the movement. This is in contrast to the horizontal pointing movements, which demonstrate symmetric velocity profiles (Gentili et al. 2007). In addition, simulations of arm trajectories with minimal absolute mechanical work reproduce the skewness in the velocity profiles (Berret et al. 2008), suggesting that the Central Nervous System accounts for the action of the gravitational torque on the limb in order to optimize the motor commands.

In the present paper, we test the hypothesis that motor commands are optimized in the gravity field by investigating how subjects adapt vertical pointing movements in a perturbed environment where the terrestrial gravity was nearly doubled. The analyses combine experimental and modeling approaches with simulations of arm trajectories with minimal control input to theoretically test the effect of an increase in gravity on the optimal trajectory. In particular, the simulations predicted changes in the kinematics profiles in hypergravity as compared to the optimal trajectories computed in normal gravity. The data strongly indicate that the subjects’ behavior in hypergravity was adjusted accordingly, providing further evidence to the theory that the arm motor commands are optimized with respect to the action
of gravity on the limb, and that adaptation can be seen as a re-optimization process (Izawa et al. 2008).
Materials and Methods

Subjects

Ten right-handed volunteers (four males, six females) between the ages of 25 and 52 years with no neurological disorders gave their informed consent to take part in this experiment. They complied with the medical requirements to participate in the parabolic flights (Belgian Center for Aerospace Medicine, class II medical examination). The experimental protocol was approved by the ethical and biomedical requirements for experimentation on human subjects from the European Space Agency (ESA) Medical Board Committee and the French Comité pour la Protection des Personnes, which reviews life science protocols in accordance with French law.

Parabolic Flight

The experiment was performed during the 47th and 48th ESA Parabolic Flight Campaigns. Parabolic maneuvers generate sequences of 20 s of hypergravity (1.8 g), followed by approximately 22 s of weightlessness (0 g) before another period of 20 s of hypergravity. The aircraft ran a sequence of 30 parabolas per flight, which permitted us to evaluate each subject during 15 consecutive parabolas. In the following sections, one block refers to the set of trials performed during one parabola.

Experimental Procedures

The subjects sat in front of three visual targets that were aligned vertically with respect to the aircraft floor and that were separated by 18 cm. The center target was in front of the subject’s shoulder and defined the horizontal arm position. They were asked to grasp a manipulandum (mass 250 g, grip aperture 4.5 cm) with the right hand and to perform visually guided pointing movements towards the current target with arm-straight rotations around the
shoulder. Upward movements (from the center to the top) and downward movements (from the center to the bottom) were randomly interleaved in order to avoid anticipatory movements. All of the subjects performed control experiments in normal gravity conditions (1 g) prior to the in-flight experiment. The subjects performed the task during the 0 g and subsequent 1.8 g phases of each parabola (they did not perform the task under normal gravity conditions during the flight). Each subject performed from 60 to 80 trials in each direction and in each gravitational condition. The analysis reported in the present study focuses on the data acquired during the hypergravity phases. The data collected during the 0 g phases of the flights will be addressed in another study. Indeed, previous studies suggest that the adaptation to other gravity levels do not generalize to zero gravity (Mireau et al. 2008; White et al. 2008), which means that this condition should be considered as a singularity where the adaptation relies on distinct mechanisms.

**Data Acquisition and Post Processing**

Gravity was sampled at 800 Hz with a three-dimensional accelerometer (ADXL330, Analog Devices). This signal was utilized to check that the gravity was stable during the movement executions. The trials performed at the transition phases between 0 g and hypergravity were removed because the gravity was unstable. The three-dimensional positions of the shoulder and the hand held load were acquired at 200Hz (Codamotion, Charnwoods Dynamics, Leicestershire, UK).

The gravity and position signals were digitally low pass filtered with a zero phase-lag Butterworth filter of order four with a cut-off frequency set to 20Hz. The position of the held load and the shoulder permitted us to compute the elevation angle of the arm with respect to the horizontal axis as illustrated in Figure 1-A. The black dots represent the infrared markers placed on the shoulder and the manipulandum for the acquisition of the position signals. Figure 1-B represents a 2D reconstruction of a single upward movement with each line joining the held load and the shoulder marker every 25ms. The angular velocity and angular
acceleration signals were computed from numerical differentiation of the position signals. Figures 1-C to 1-H show the elevation angle, angular velocity and angular acceleration of two trials presenting typical overshoot (Figure 1-C to E) and undershoot (Figure 1-F to H) profiles.

The movement onset and end were computed with the following procedure illustrated in Figure 1-D. The velocity profile was linearized around the intersection with the threshold equal to 10% of the peak velocity (V_T) computed for each trial (linear regressions computed on five time steps). The onset (t_0) and offset (t_f) were then determined by the intersection of the linear regressions with the horizontal axis (red dots). The movement duration was defined as the elapsed time between t_0 and t_f. The procedure to detect the overshoots and undershoots was based on the acceleration profile. For an overshoot, as indicated in Figure 1-E, the acceleration presented a local maximum (red dot) occurring after the movement end (Figure 1-E, t_OSH). We let \( \theta(t) \) be the elevation angle of the arm as a function of time, and defined the overshoot as the percentage of the displacement from t_f to t_OSH with respect to the total displacement from t_0 to t_f:

\[
OSH = 100 \frac{\theta(t_f) - \theta(t_{OSH})}{\theta(t_f) - \theta(t_0)} .
\]  

The elapsed time between t_f and t_OSH was limited to 150 ms in order to exclude corrective movements.

Similarly, an undershoot strategy typically presented a local maximum in the acceleration profile before the end of the movement (t_USH, Figure 1-H). When such a maximum was detected, the undershoots were defined exactly like the overshoot in Equation 1, replacing t_OSH by t_U and t_f by t_USH. With these definitions, the overshoots and undershoots are positive and negative, respectively. Trials presenting an undershoot detected before 150 ms prior to movement end were considered missed trials, given that the amplitude of the correction was not negligible as compared to the total movement amplitude. Such trials must therefore be considered to be composed of at least two distinct movements realized prior to reaching the target. This criterion revealed that one subject actually did not meet the task requirements.
The success rate for this subject was 57% for the upward movements and less than 15% for the downward movements. Accordingly, this subject was removed from the subsequent analysis and the results section reports the data concerning the nine remaining subjects. A direct application of these procedures may provoke the detection of an undershoot and overshoot for the same movement. To avoid this situation, the undershoot strategy was considered to take precedent on the overshoot, which means that the detection of an undershoot implied that no overshoot was recorded for the corresponding trial.

Finally this study analyzes the skewness of the velocity profiles defined as the ratio of the acceleration duration to the total movement duration (AD/MD). Equivalently, this ratio is equal to the relative time from the movement onset to the peak velocity. For a symmetric velocity profile with a peak velocity arising at the middle of the movement, the AD/MD equals 0.5. For the analysis of the AD/MD, the trajectories were interpolated with cubic splines on discretized time intervals of identical size (200 samples) in order to compare the AD/MD ratios measured with identical resolution.

Mechanical and Physiological Model

The model of the arm was composed of three rigid bodies: the arm, the forearm, and the hand. The length and mass of the three bodies were computed for each subject as a fraction of the total body height and mass. The ratio was obtained from classical average anthropometric tables (Winter 1979). The hand length was divided in half in order to mimic the grasp posture. The held load was added to this model as a point mass body located at the same coordinate as the hand center of mass. We assumed that three torques were acting on the limb: the muscular torque \( T(t) \), the gravitational torque, and a viscous friction torque. In addition, the model assumes that the muscular torque is a first-order, low-pass filtered response of the motor command, \( u(t) \), being the control signal. This control can take positive and negative values to model a pair of agonist-antagonist muscles. Let us first consider the unperturbed system in continuous time, the equations for the deterministic case are:
\[
\ddot{\theta} = T - mgl \cos(\theta) - k_v \dot{\theta}, \quad (2)
\]

\[
\dot{T} = \frac{1}{\tau} (k_u u - T). \quad (3)
\]

The explicit dependency on time was omitted for clarity. The viscous constant \(k_v\) was set to 0.63 + 0.095T_M where T_M is the average joint torque across the movement (Nakano et al. 1999), the time constant \(\tau\) was set to 40 ms and g was equal to 9.81 m/s^2 for the 1 g simulations or 17.658 m/s^2 (1.8 g) for the hypergravity simulations. The parameter m is the mass of the whole system, I is its inertia and l is the distance between the center of mass and the shoulder rotation axis. The control gain, \(k_u\), permits us to have consistent units from the physical point of view. Assuming that the control input u represents the motor neuron discharge, then \(k_u\) is the steady state gain relating the torque output to the control input, which can be expressed in spikes density (s). In practice, the control was normalized between -1 and 1, and \(k_u\) was equal to 50 Nm/s (after the simulations, we verified that the bounds were never active).

**Optimal Control Problem and Re-optimization Hypothesis**

The control problem for the unperturbed system is to find an admissible control function, \(u(t)\), which drives the system described in Equations 2 and 3 from its initial to final position in a given amount of time. The minimum control input solution considered in this study is the solution of the control problem that minimizes the following cost:

\[
J(u) = \int_{t_0}^{t_f} |u(t)|^2 dt. \quad (4)
\]

The solutions were computed with Sequential Quadratic Programming (SQP) methods applied to direct multiple shooting (Bock and Plitt 1985). The multiple shooting algorithm works as follows. The time span of the simulation is divided into n intervals \(t_k-t_{k-1}\) where 0 = \(t_0 < t_1 < \ldots < t_n = t_f\). In each interval, the control policy is approximated by a constant value.
In the discretized formulation, the cost function defined in Equation 4 becomes:

$$J(u) = \sum_k u_k^2,$$

and the optimal control problem becomes a discrete constraint optimization problem. We initialize a guess of the state at each point of the time grid, $x_k = x(t_k)$ where $x$ represents the state variables (position, velocity and shoulder torque). Knowing the initial and final positions, the problem to solve is minimization the cost defined in Equation 5 such that the trajectory ends at $x_k$ when the system is integrated from $x_{k-1}$ with control $u_{k-1}$. These are nonlinear constraints (given the nonlinear dynamics) ensuring the continuity of the state at each point $t_k$. The size of the time sub-intervals was equal to 7.5 ms and the system was integrated in each interval with an adaptive step-size Runge-Kutta integrator of order four.

The optimal control sequence $u_k$ constitutes the open loop control policy, which drives the unperturbed system along the optimal trajectory in the absence of noise or unexpected perturbation. However, the Central Nervous System must be able to correct for sensorimotor noise thanks to feedback control. To model this, we now consider a discrete time formulation enabling us to introduce additive and signal dependent noises characterizing the properties of the noise in the sensorimotor system. To this end, the system was linearized around the optimal open loop solutions, which permits us to derive a feedback law as a linear function of the state deviations. The optimal feedback gains were computed at each time step from the local linear approximation of the system dynamics. The stochastic dynamics of the deviations from the optimal trajectories are:

$$(x - x)_{k+1} = A_k(x - x)_k + B_k(1 + \varepsilon_k)(u - \bar{u})_k + \xi_k,$$

where

$$A_k = 1 + \Delta t \left( \frac{\partial f}{\partial x_k} \right), \quad B_k = \Delta t \left( \frac{\partial f}{\partial u_k} \right).$$

and
\( f(x_k, u_k) = \begin{bmatrix} x_k^{(2)} \\ I^{-1}(x_k^{(3)} - mg/l \cos(x_k^{(1)}) - k_u x_k^{(2)}) \\ \tau^{-1}(k_u u_k - x_k^{(3)}) \end{bmatrix} \)  

(8)

defines the system dynamics. The noise terms, \( \epsilon_k \) and \( \xi_k \), are Gaussian random variables with zero mean and variances equal to 0.02 and 0.5 respectively. The cost per step associated to the motor cost and state deviation was:

\[ J_k = r(u - \overline{u})^2 + w^T (x - \overline{x})^2, \]  

(9)

and the optimal feedback gains were computed using the derivation given by Todorov (2005). The weighting factors for the control and state deviation in the cost function were: \( r = 10^{-6} \) and \( w^T = [10, 1, 0.2] \). In summary, the stochastic system is driven by the following control policy:

\[ u_k = \overline{u}_k - L_k (x - \overline{x})_k. \]  

(10)

The first term is the open loop control sequence and the second term is the feedback correction to the local perturbations. This method is a simplified version of optimal control for nonlinear stochastic systems (Li and Todorov 2007). For simplicity, we considered that there was no uncertainty about the state of the system, i.e. the state is fully observable and the feedback correction is computed on the true state. This model still makes the hypothesis that there is a feed forward optimization of the motor plan represented by \( \overline{u}_k \). Indeed, the nonlinear dynamics do not allow computing an optimal control that is a linear function of the state only, and the feed forward component of the control must be added if one desires that the average trajectory of the stochastic system tends to the unperturbed optimal solution.

Under the hypothesis of re-optimization, the feed forward component of the control law cost must be re-computed in hypergravity. Thus, in practice, the same criterion (Equation 4) is applied to the system (Equations 2 and 3) with a distinct value of \( g \).

Non-optimizing strategy
As an alternative, we simulated the following non-optimizing adaptation scheme. The solution of the control problem in normal gravity is primarily added to an offset to compensate for the static postural adjustment, and then corrected to attain the desired final position. That is:

$$\bar{u}^{(1.8g)} = \bar{u}^{(1g)} + \alpha,$$  \hfill (11)

This formulation considers that the open loop component of the control policy ($\bar{u}_k$ in Equation 10) is not re-optimized in hypergravity, but only adjusted in response to the increase in arm weight.

\textit{Comparison between Models and Data}

To compute the optimal trajectory in normal gravity, the simulation duration was adjusted in such a way that, for each individual subject, the durations measured in the data and in the simulation were identical. This adjustment corresponded to about the average movement duration plus 50 ms. To test the effect of hyper gravity on the optimal trajectory, the simulations were computed with all parameters kept constant, except the gravity. Thus, the same simulation duration was employed to compute the optimal trajectory in hypergravity. The simulations were computed for each subject with the inertia, mass, length, movement amplitude and duration adjusted to their individual values. The same procedure was used to measure the ratio AD/MD and the movement duration in the simulations and in the data.
Results

Testing the model

The vertical trajectories performed in the normal gravity condition presented asymmetric velocity profiles. The AD/MD ratio was significantly smaller than 0.5 (t-test, \(P < 0.01\)). Our experiment also confirmed the difference between upward and downward movements: AD/MD was equal to 0.451 ± 0.053 for the upward movements and 0.463 ± 0.060 for the downward movements with a significant effect of the movement direction (all subjects pooled, ANOVA, \(P < 0.01\)). Despite its simplicity, the model captures this property. The asymmetry was computed on simulated trajectories of identical duration for upward and downward movement in normal gravity. The AD/MD ratio was equal to 0.475 ± 0.028 for the upward movements and 0.482 ± 0.027 for the downward movements (mean ± standard deviation computed across the simulations of the model with the parameters fitted to each individual subject). Figure 2 presents the velocity profile for one subject computed from the model simulation (solid black, left) and the velocity profile collected in normal gravity condition averaged across the individual trials (solid grey, right). Both traces present a maximum velocity (vertical line) occurring before the middle of the movement. For comparison, Figure 2 shows the symmetric velocity trace corresponding to the minimum jerk trajectory (dashed black), with an AD/MD ratio equal to 0.5. According to the model, the asymmetry can be directly attributed to the gravitational torque since the simulations for the horizontal movements (with \(g = 0\)) lead to an AD/MD ratio equal to 0.5 without the effect of the movement direction, as observed in the horizontal movements performed in normal gravity.

The effect of hypergravity on the optimal trajectories is illustrated in Figure 3 showing simulations of upwards and downwards movements in both gravitational conditions for the same subject. The red and black traces correspond to the open loop trajectories in the two gravitational conditions. The shaded areas represent the standard deviations from the average
trajectory when the system was simulated with noise (Equations 6, deviations computed on 100 simulations). The difference between the optimal solutions is due to the re-optimization of the feed forward component of the control policy. This difference in optimal trajectories can be directly attributed to the change in gravity since the only difference between the simulations was the value of $g$. Qualitatively, the main effects predicted by the model on the kinematics properties is an increase in the peak angular acceleration and in the peak angular velocity. As a consequence, the velocity profile in hypergravity changes, which leads to a difference in the estimation of the movement end, even for identical simulation durations. Therefore, the measurement of the movement duration applied to the simulations records a decrease in hypergravity. This is emphasized in Figure 3-B, where $\Delta t_f$ illustrates the difference between the estimations of movement's end in normal and hypergravity computed on the simulations.

Learning in Hypergravity

To investigate the effect of hypergravity on unperturbed and uncorrected trajectories, particular attention should be paid to the undershoot strategies, which typically reflect a distinct kind of movement planning and control. The detection of missed trials based on the presence of undershoots occurring 150 ms prior to movement end led to the removal of 5% of the trials for upward movements and 10% for downward movements. This failure rate was comparable to the behavior observed in normal gravity conditions where 8% and 4% of the trials had to be removed for the up and down trials, respectively. The evolution of the percentage of success trials across the blocks and a comparison with the average success rate in normal gravity are shown in Figure 4 (averaged across the subjects ± the standard error). The performance was stable from the beginning for the upward movement, whereas a stable performance for downward movements was observed from the third block. The difference for the downward movements between normal and hypergravity in the first two blocks pooled together was significant (paired t-test, $P < 0.01$, grey rectangle in Figure 4).
Effect of Hypergravity

The elevation angle and angular velocity as a function of time are shown in Figure 5 in the two gravitation conditions. These data are shown for the same subject whose simulations were plotted in Figures 2 and 3. All of the trajectories were aligned with respect to the movement onset in order to compute the average trajectory and standard error at every time step. For the upward movements (Figure 5-A and 5-B), any single trajectory (light grey) rapidly deviates from the average control trajectory (represented in red) and goes faster toward the target. This tendency is further confirmed by the average trajectory in hypergravity (black trace). This logically provokes the change in the speed profile illustrated in Figure 5-B. Similar comments may describe the effect on the downward trajectories (Figures 5-C and 5-D) although the effect of hypergravity seems to have less of an impact on the downward movements than on the upward movements. Clearly, the effect is qualitatively similar to the model predictions shown in Figure 3. The quantitative comparison will be addressed later in this analysis.

The statistical analysis revealed that the tendencies observed qualitatively in Figure 5 were significant. The Wilcoxon Rank Sum test was chosen for testing whether the variations were significant given that the data were not normally distributed. For the upward movements, there was a significant increase in the peak angular acceleration followed by an increase in peak angular velocity and a significant decrease in the movement duration (\( P < 0.01 \)). The same significant effects on the kinematics parameters were observed for the downward movements. In addition, the effect of the movement direction was significant. This was evaluated by comparing the difference between the hypergravity data and the average in normal gravity across the two movement directions. In all of the cases (peak angular acceleration, peak angular velocity and movement duration), the variations in absolute value were larger for upward movements than for downward movements (\( P < 0.01 \)). The magnitude of the effect is illustrated in Figure 6-A for the peak angular acceleration, in Figure
6-B for the peak angular velocity, and in Figure 6-C for the movement duration. All differences across the gravitational conditions were significant (the data of the peak angular acceleration and velocity for the downward movements are presented as absolute values).

The effect of the movement direction revealed that adaptation was not symmetrical for the two movement directions. The analysis of the overshoots and undershoots shown in Figure 7 provides interesting insight on the strategies and enables us to better understand the difference observed between the up and down movements. For the upward movements, the subjects reinforced their tendency to overshoot with 77% of the trials against 73% in normal gravity. In addition, the amplitude of the overshoots was significantly increased in the 1.8 g condition (P < 0.01), as confirmed by the shift in the overshoots histogram of Figure 7-A. In this direction, the undershoots were detected in 6% of the trials in hypergravity as compared to 11% in normal gravity. For the downward movements, there was no difference concerning undershoot trials (6% in hypergravity as compared to 7% in normal gravity without variation in amplitude), whereas the overshoots were observed in only 43% of the trials as compared to 72% in normal gravity (Figure 7-B).

In summary, the subjects’ strategy was to globally reach the target faster in hypergravity and with a significant difference between the up and down variations and a preference for overshooting when going upwards.

Comparison with Model Simulations

For the upward movements, the simulations in hyper gravity predict a relative increase of 25% in the peak acceleration and 8% in the peak velocity. The prediction matched the data for peak acceleration: we observed a relative increase in the peak acceleration of 24% (averaged across subjects). The relative increase in the peak velocity was equal to 19%, which is larger than the prediction. The predictions for the downward movements were similar to the upward movements: the model predicts 28% and 11% of relative increase in the peaks
acceleration and velocity, respectively. Subjects’ behavior varied less: we observed 9% and
3% of increase in peak acceleration and velocity, respectively.

In order to compare the changes in the kinematics profiles across the two gravitational
conditions, we computed the areas between the trajectories performed in the hypergravity
condition and the average 1g trajectory (used as a reference trajectory). As illustrated in
Figure 8-A, the areas $A_1$ and $A_2$ were defined with respect to the sign of the difference
between the reference 1g trajectory (red trace) and the trajectories performed in hypergravity
(black trace, example of one single trajectory taken from data).

Similarly, the areas between the optimal simulations were computed in order to compare
the magnitude of the effect with the experimental data. Figures 8-B and 8-C indicate that the
areas $A_1$ and $A_2$ in the two directions averaged across bins of three movements and across
subjects. The dotted lines in each plot indicate the areas computed on the simulations of an
identical duration as the 1g-reference trajectory and were averaged across the subjects.

As shown in Figure 3, for the upward movements, the optimal trajectory in hypergravity
is “above” the optimal trajectory in the normal gravity condition. Therefore, for simulations
$A_2$ equals 0 (blue dotted line, Figure 8-B), and $A_1$ is a positive constant (black dotted line).
The opposite is observed for the downward movements: Figure 8-C indicates zero for $A_1$ and
a positive value for $A_2$ for the simulations. The tendency observed in the data is clearly
consistent with the simulations. The trajectories performed in hypergravity were neither
strictly above nor under the average trajectory in normal gravity (see example in Figure 8-A,
$A_1$ and $A_2$ are both non-zero), however the general tendency confirms the prediction of the
model. According to the model simulations, for upward movements, the difference between
the predicted and the observed values for $A_1$ demonstrate that the subjects tended to
overcompensate ($A_1$ was larger in data in comparison with the simulations). Similarly, the
effect of movement direction is illustrated in Figures 8-B and 8-C. The downward movements
present more variability although the global tendency is in accordance with the simulations.

To further argue for a re-optimization of the motor commands, we computed the
trajectories obtained when the feed forward component of the control law corresponding to
normal gravity is adjusted to compensate for the increase in the arm weight (Equation 11), but not re-optimized. The simulation of this alternative model predicted that the kinematics of movements in hypergravity are the same as in normal gravity condition, yielding for $A_1$ and $A_2$ values very close to zero in Figure 8. This demonstrates that the model based on the non-optimizing strategy can be rejected.
Our results describe the effect of an increase in gravity on vertical pointing movements and compare the subjects’ behavior with the simulation of arm trajectories utilizing a model based on minimum integrated control input. The proposed model considers a first order low pass filter between the motor neuron discharge and the muscular torque as a physiological model and Newton’s second law for the mechanical equation. The analysis reveals that after an adaptation to hypergravity, the subjects’ behavior was consistent with the model predictions. This was in accordance with the hypothesis that adaptation to altered dynamics is achieved after a re-optimization of the motor plan in the new environment (Izawa et al. 2008).

In addition, data reveal a significant effect of movement direction, which was not predicted by the model simulations. It takes more time to learn the downward movements and upon learning them, the variation in the kinematics parameters was larger for the upward movements. This was accompanied by a clear preference for the overshoot strategy reinforced in hypergravity, despite the increase in the arm weight. The fact that the subject’s behavior is different depending on the direction of the movement may reflect the strategy with respect to the goal of the task, i.e., to stabilize next to the target for which gravity either enables or hinders the braking acceleration. This result suggests that re-optimization is not the only process that ensures an adaptation to altered dynamics. Rather, the goal of the task and the strategies that rely on cognitive factors modulate the adaptation of the motor plan.

The model was kept as simple as possible in order to focus on the effect of a change in gravity and avoid that other factors come into play in the simulations. Several limitations can be easily removed to obtain a better match between the predictions and the data. First, one can introduce a bias in order to account for the effect of the movement direction. Then, more sophisticated mechanical and physiological models can improve the quality of the prediction, by considering more carefully the properties of the musculoskeletal system. Finally, keeping the same simulation duration across the two gravitational conditions was a strong constraint, which can be relaxed to improve the correspondence between the predictions and the data. In
particular, matching the simulation duration with the movement duration in hypergravity yields better predictions for upward movements.

Our modeling approach follows the models proposed by Gentili and colleagues (2007), which consisted of minimal torque changes and minimal commanded torque changes (Nakano, 1999). These models assume that the brain has an access to the joint torque, given that it is the variable being controlled. We added the physiological model (Equation 3) in order to formulate a control variable that is closer to the neural motor command, which is presumably accessible within the Central Nervous System as a corollary discharge. Our results obtained in the normal gravity condition are fully compatible with the results from Gentili and colleagues (2007), despite some differences between the protocols. The main differences were that their subjects performed reaches of various amplitudes and from various starting position, and the movements were performed in darkness without visual feedback. Our protocol was restricted to one movement amplitude from a single starting position in order to collect a sufficient number of trials per subject and per flight. Then, our subjects were provided with continuous visual feedback in order to prevent that they suffer from motion sickness. This was presumably the origin of the high success rate observed early, in particular for the upward movements. However, in normal gravity, we obtained very similar values for the AD/MD ratio. This suggests that asymmetry in the velocity profiles is a robust feature of the vertical movements across various testing conditions. More generally, our model accounts for the difference between vertical and horizontal movements in normal gravity, in addition to the difference between the vertical movements performed in normal and hypergravity.

Our main finding is that an increase in gravity is properly compensated in a feed forward manner in accordance with the hypothesis of minimum control input. In particular, the effect of hypergravity on the peak acceleration (precisely matched by the simulations for upward movements) is in direct support of a change in the central planning process, which must account for the effect of gravity on the limb. In addition, our results suggest that the Central Nervous System utilizes the internal representation of the gravitational torque in order to optimize the motor commands. Our sample does not permit the evaluation of whether the
optimal feedback gains \( (L_k \text{ in Equation 10}) \) are also re-optimized in hypergravity. However, the simulations predict distinct sensitivities to the position and speed errors across the two gravitational conditions. It follows from our result that the Central Nervous System takes into account the effect of external forces on the limb and takes advantage of the dynamic interaction between the body and the environment. White and colleagues reported a similar result in the context of oscillatory movements performed in different gravity conditions (White et al. 2008). They found that the spontaneous movement frequency was driven by gravity as the resonance phenomenon of a pendulum, which is the signature of a system maximizing energy transfer with the environment. The interaction with the environment is emphasized by the changes in the movement frequency in response to the changes in gravity. Altogether, these results provide evidence for an optimal interaction with the environment in both rhythmic and discrete movements depending on the action of gravity on the limb.

Previous studies argued for an optimization of the dynamic forces only (Nishikawa et al. 1999; Soechting et al. 1995), which appears contradictory with the hypothesis of integration of the gravitational torque in the computation of a motor plan. Nishikawa and colleagues showed that the final arm posture after pointing movements depended on the initial position, and these postures were invariant, even for slow movements, where the antigravity component of the joint torque should be dominant in comparison to the peak joint torque. In our study, the initial and final arm postures were prescribed and the movements were constrained to one degree of freedom in the vertical plane. Therefore, for such movements, the minimization of the dynamic variations only (as supported by Nishikawa and colleagues) implies that the gravitational torque is taken into account, as supported by the present study. Other kinds of movement with horizontal components and more degrees of freedom may rely on distinct strategies.

The results of the present study have two main implications. First, the data allow us to reject the hypothesis of an invariant desired trajectory, which assumes that internal models build a new map between a desired trajectory and the motor command, taking the unperturbed trajectory as the desired trajectory. In our experiment, the optimal trajectory in normal gravity
is of course a feasible solution in hypergravity but the simulations reveal that, although possible, this trajectory is no longer optimal. Accordingly, the subjects change the kinematics profile without any tendency to recover the characteristics of the movements performed in normal terrestrial gravity. However, many studies in various contexts do provide evidence for a tendency to return to the performance of the unperturbed condition (Burdet et al. 2001; Lackner and Dizio 1994; Papaxanthis et al. 2005; Shadmehr and Mussa-Ivaldi 1994), whereas other studies, including the present paper, suggest that re-optimization produces definitive changes in the movement kinematics (Izawa et al. 2008). It seems that question of which adaptation process (re-calibration of the internal models or re-optimization) will be observed depending on the experimental conditions remains open to debate.

Second, under the hypothesis that the motor actions are re-optimized in response to a change in the environment, this experiment suggests that the estimation of movement costs can be based on the motor command corollary discharge and proprioceptive feedback. Indeed, gravity acting vertically with respect to the aircraft floor was not a divergent force field for vertical movements. Therefore, it is very unlikely that the re-optimization observed in hypergravity is based solely on visuomotor adjustments. The movements were visually guided and the movement control relied on visual feedback (e.g. corrective adjustments as observed in trials presenting large undershoots). However, visual feedback by itself fails to explain why the subjects changed the kinematics motor plan and performed faster movements. Therefore, the sources of information available for an estimation of the movements’ costs (necessary for optimization) are the motor command corollary discharge, which is represented in the model by \( u(t) \), and the proprioceptive feedback. Such an estimation of movement costs based on these variables compared to an expected cost from prior knowledge can represent a signal that generates the update of the kinematic and dynamic properties of the movement.

A potential region for the generation of this signal is the posterior parietal cortex (PPC), which plays a fundamental role in visuomotor transformations for reaching and in the planning and control of visually guided movements (Buneo and Andersen 2006; Buneo et al.
2002). Downstream to the visuomotor transformation, PPC activity correlates with kinematics parameters such as target location, movement direction, and velocity. The PPC activity further has little effect for various load conditions for a given invariant trajectory (Ashe and Georgopoulos 1994; Hamel-Paquet et al. 2006; Kalaska et al. 1990). In addition, the neural correlates with kinematics errors in reaching were found in the parietal area-5 (Diedrichsen et al. 2005). It was further found that transcranial magnetic stimulations of this region alter the learning of new dynamics (Della-Maggiore et al. 2004). However, the fact that continuous visual feedback was provided suggests that the alteration of learning could be related to visuomotor transformation instead of a kinematics adaptation.

Of course, the neural correlates with kinematics parameters are present in other brain regions such as the premotor areas (Kakei et al. 2003) and the primary motor cortex whose activity is not solely related to force output (Graziano 2006; Scott 2003). However, in addition to the evidence that the PPC codes kinematics features of the movement, the anatomical situation of the PPC is consistent with our hypothesis that internal and proprioceptive feedback are necessary to adapt the kinematics motor plan. Indeed, the PPC receives projection from the somatosensory cortex for proprioceptive feedback, and from the cerebellum via the thalamus (Amino et al. 2001), whose activity relates to state estimation and prediction (Miall et al. 2007; Wolpert et al. 1998), which could contribute to the prior estimate of the movement cost. Altogether, the characteristics of the PPC render it a good candidate as a sensorimotor interface for updating the kinematics motor plans.
Figure Captions

Figure 1. A: Illustration of a subject performing the task. B: 2D reconstruction of an upwards movement. One line joining the shoulder marker and the center of the held load is drawn every 25ms. C, D, E: The elevation angle, angular velocity and angular acceleration as a function of time of a movement presenting a typical overshoot profile. $V_T$ is the threshold of 10% of the peak velocity computed to linearize the speed profile and estimate the movement onset and movement end. F, G, H: The elevation angle, angular velocity and angular acceleration as a function of the time of a movement presenting a typical undershoot profile. The local maxima of the angular acceleration used to compute the overshoot and undershoot are shown in panels E and H, respectively.

Figure 2. The skewness of the velocity profiles of the minimum control input model considered in this study (solid black) and observed in the data for one subject (solid grey). The velocity traces were normalized in time and amplitude. The minimum jerk trajectories with a symmetric velocity profile are shown for comparison (dashed black). The vertical dashed lines are aligned on peak velocity to illustrate the skewness of the corresponding curve.

Figure 3. The plots of the optimal trajectories in normal gravity (red) and hypergravity (black) conditions for upward (left) and downward (right) movements. The dashed traces in panel A represent the optimal control policy and solid traces are the muscular response to the control input. B: The angular velocity of the simulated trajectories as a function of time. C: The optimal trajectories as a function of time. The shaded areas in panels B and C represent the standard deviation of the stochastic system around the optimal trajectories (solid black and red traces). The standard deviation was computed across 100 simulations.
Figure 4. Success rate for hypergravity movements averaged across the subjects (N = 9) in both directions as a function of the block number. The horizontal dashed line is the average success rate in normal gravity for both movement directions. The grey rectangle illustrates the significant difference in the success rate between hyper and normal gravity for downward movements.

Figure 5. The elevation angle and angular velocities for one subject in the two directions. The red traces are the average 1g trajectory plus and minus the standard error computed at each time step. The grey traces show all of the hypergravity trials for this subject, aligned on individual movement onsets. The black trace is the average trajectory in 1.8 g. The top panels indicate the angle as a function of time. The bottom panels indicate the angular velocity as a function of time.

Figure 6. The variation of the kinematics parameters across the two gravitational conditions and in the two movement directions. The means of the peak angular acceleration (A), peak angular velocity (B), and movement duration (C) were averaged across the subjects. The error bars represent the inter-subject standard error of the mean. The data of the peak acceleration and velocity for the downward movements are presented as the absolute value. All of the differences between 1 g and 1.8 g were statistically significant.

Figure 7. The overshoots (OSH) and undershoots (USH) in the normal and hypergravity conditions for the upward (A) and the downward (B) movements. The histograms show the frequency of the observation of trials with the corresponding percentage of displacement. Recall from the methods that the overshoots are positive and the undershoots are negative.

Figure 8. The quantitative analysis of the effect of hypergravity. A: The illustration of the computation procedure, the amplitudes were normalized to the movement amplitude from movement onset to movement end. The time was unchanged. $A_1$ and $A_2$ are the areas between
the hypergravity traces and the reference 1 g trace when the integrated differences were
positive and negative respectively. Panels B (upward) and C (downward) show the areas $A_1$
and $A_2$ averaged across bins of three movements and across the subjects versus the number of
the bin.

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References


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Figure 1
Figure 5
Figure 6
Figure 7
Figure 8