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Optimal Integration of Gravity in Trajectory Planning of Vertical Pointing Movements

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Crevecoeur F, Thonnard J-L, Lefèvre P. Optimal integration of gravity in trajectory planning of vertical pointing movements. *J Neurophysiol* 102: 786–796, 2009. First published May 20, 2009; doi:10.1152/jn.00113.2009. The planning and control of motor actions requires knowledge of the dynamics of the controlled limb to generate the appropriate muscular commands and achieve the desired goal. Such planning and control imply that the CNS 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 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 reoptimization 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 CNS. There are infinite numbers 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 these questions, 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 CNS has access to the internal representations of the limb dynamics and state (position, velocity, etc.), as a result of internal models (Kawato 1999; Wolpert and Ghahramani 2000), that are necessary for the computation of motor commands in the both feedforward 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, 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; Papaxanthi 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

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CNS accounts for the action of the gravitational torque on the limb to optimize the motor commands.

In the present study, 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 compared with 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 reoptimization process (Izawa et al. 2008).

METHODS

Subjects

Ten right-handed volunteers (four males, six females) between the ages of 25 and 52 yr 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 about 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 toward 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 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 does 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 postprocessing

Gravity was sampled at 800 Hz with a three-dimensional (3D) accelerometer (ADXL330, Analog Devices). This signal was used 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 3D positions of the shoulder and the hand held load were acquired at 200 Hz (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 cutoff frequency set to 20 Hz. 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 Fig. 1A. The black dots represent the infrared markers placed on the shoulder and the manipulandum for the acquisition of the position signals. Figure 1B represents a two-dimensional reconstruction of a single upward movement, with each line joining the held load and the shoulder marker every 25 ms. The angular velocity and angular acceleration signals were computed from numerical differentiation of the position signals. Figure 1, C–H shows the elevation angle, angular velocity, and angular acceleration of two trials presenting typical overshoot (Fig. 1, C–E) and undershoot (Fig. 1, F–H) profiles.

The movement onset and end were computed with the following procedure illustrated in Fig. 1D. 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 Fig. 1E, the acceleration presented a local maximum (red dot) occurring after the movement end (Fig. 1E, 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 .

$$OSH = \frac{\theta(t_f) - \theta(t_{OSH})}{\theta(t_f) - \theta(t_0)} \times 100 \quad (1)$$

The elapsed time between t_f and t_{OSH} was limited to 150 ms 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} , Fig. 1H). When such a maximum was detected, the undershoots were defined exactly like the overshoot in Eq. 1, replacing t_{OSH} by t_f 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 compared with 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 <15% for the downward movements. Accordingly, this subject was removed from the subsequent analysis and in the RESULTS the data are reported 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 precedence over the overshoot, which means that the detection of an undershoot implied that no overshoot was recorded for the corresponding trial.

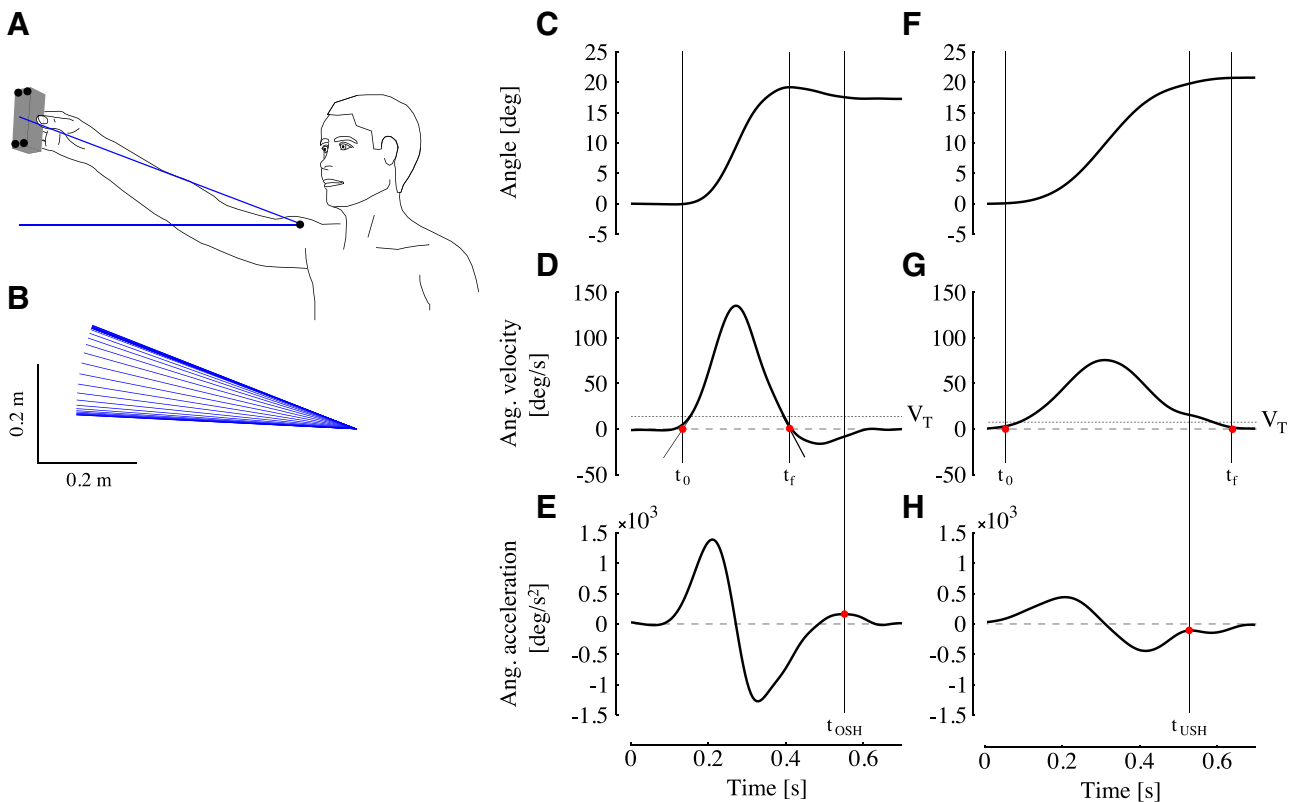


FIG. 1. A: illustration of a subject performing the task. B: 2-dimensional reconstruction of an upward movement. One line joining the shoulder marker and the center of the held load is drawn every 25 ms. C, D, and E: the elevation angle, angular velocity, and angular acceleration as a function of time 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, and 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 E and H, respectively.

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 = 0.5. For analysis of the AD/MD, the trajectories were interpolated with cubic splines on discretized time intervals of identical size (200 samples) 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 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

$$I\ddot{\theta} = T - mgl \cos(\theta) - k_v \dot{\theta} \quad (2)$$

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

The explicit dependence 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 τ 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 perspective. 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 spike 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 reoptimization hypothesis

The control problem for the unperturbed system is to find an admissible control function $u(t)$, which drives the system described in Eqs. 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 $0 = t_0 < t_1 < \dots < t_n = t_f$. In each interval, the control policy is

approximated by a constant value (say $\bar{u}_k$). In the discretized formulation, the cost function defined in Eq. 4 becomes

$$J(u) = \sum_k \bar{u}_k^2 \quad (5)$$

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 $\bar{x}_k = \bar{x}(t_k)$, where $\bar{x}$ represents the state variables (position, velocity, and shoulder torque). Knowing the initial and final positions, the problem to solve is minimization of the cost defined in Eq. 5 such that the trajectory ends at $\bar{x}_k$ when the system is integrated from $\bar{x}_{k-1}$ with control $\bar{u}_{k-1}$. These are nonlinear constraints (given the nonlinear dynamics) ensuring the continuity of the state at each point t_k . The size of the time subintervals 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 $\bar{u}_k$ 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 CNS must be able to correct for sensorimotor noise as a result of 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

$$(x - \bar{x})_{k+1} = A_k(x - \bar{x})_k + B_k(1 + \varepsilon_k)(u - \bar{u})_k + \xi_k \quad (6)$$

where

$$A_k = 1 + \Delta t \left(\frac{\partial f}{\partial \bar{x}_k} \right) \quad B_k = \Delta t \left(\frac{\partial f}{\partial \bar{u}_k} \right) \quad (7)$$

and

$$f(x_k, u_k) = \left\langle \begin{matrix} x_k^{(2)} \\ I^{-1} \{x_k^{(3)} - mgl \cos[x_k^{(1)}] - k_v x_k^{(2)}\} \\ \tau^{-1}[k_u u_k - x_k^{(3)}] \end{matrix} \right\rangle \quad (8)$$

defines the system dynamics. The noise terms ε_k and ξ_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

$$J_k = r(u - \bar{u})_k^2 + w^T(x - \bar{x})_k^2 \quad (9)$$

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 the second term, the square is computed component-wise. In summary, the stochastic system is driven by the following control policy

$$u_k = \bar{u}_k - L_k(x - \bar{x})_k \quad (10)$$

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 feedforward optimization of the motor plan represented by $\bar{u}_k$. Indeed, the nonlinear dynamics do not allow computing an optimal control that is a linear function of the state only and the feedforward 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 reoptimization, the feedforward component of the control law cost must be recomputed in hypergravity. Thus in practice, the same criterion (Eq. 4) is applied to the system (Eqs. 2 and 3) with a distinct value of g .

Nonoptimizing strategy

As an alternative, we simulated the following nonoptimizing 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

$$\bar{u}^{(1.8g)} = \bar{u}^{(1.0g)} + \alpha \quad (11)$$

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

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 hypergravity on the optimal trajectory, the simulations were computed with all parameters kept constant, except the gravity. Thus the same simulation duration was used 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 < 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 movements 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 $\pm$ SD 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 gray, right). Both traces present a maximum velocity (vertical line) occurring before the middle of the movement. For comparison, Fig. 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

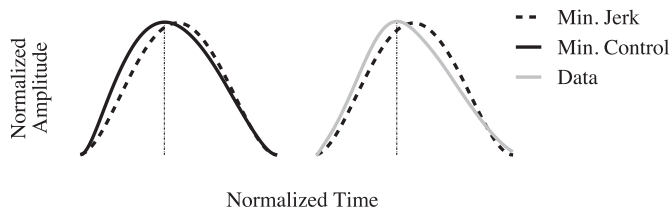


FIG. 2. The skewness of the velocity profiles of the minimum control input model considered in this study (solid black) and observed in the data for one subject (solid gray). The velocity traces were normalized in time and amplitude. The minimum jerk trajectories with a symmetric velocity profile are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

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 Fig. 3 showing simulations of upward and downward 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 SDs from the average trajectory when the system was simulated with noise (Eq. 6, deviations computed on 100 simulations). The difference between the optimal solutions is due to the reoptimization of the feedforward 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 Fig. 3B, where Δt_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 Fig. 4 (averaged across the subjects $\pm$ SE). 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, $P < 0.01$, gray rectangle in Fig. 4).

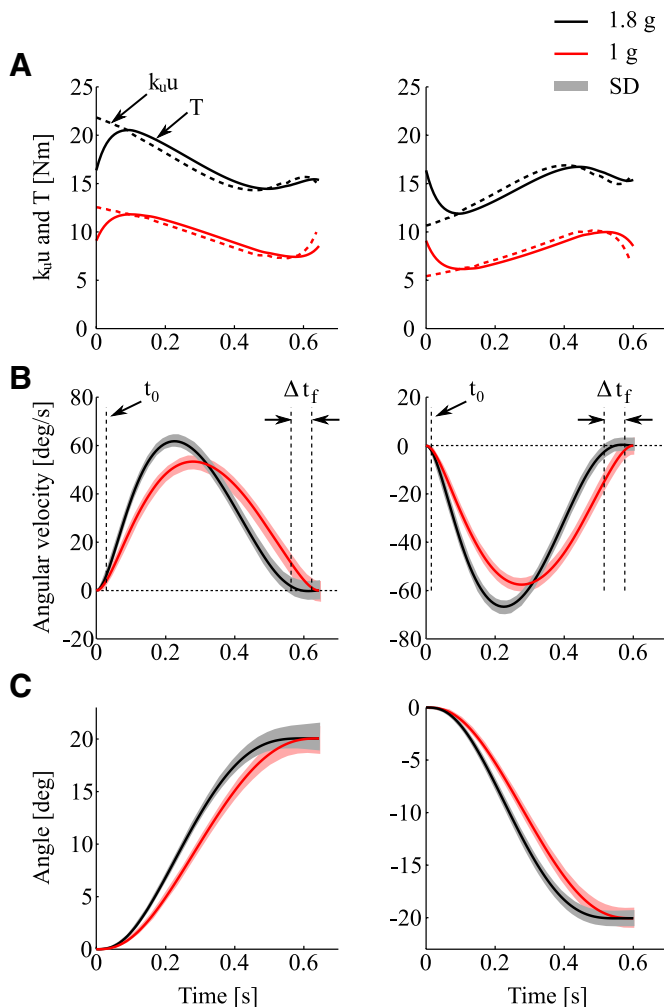


FIG. 3. The plots of the optimal trajectories in normal gravity (red) and hypergravity (black) conditions for upward (left) and downward (right) movements. The dashed traces in A represent the optimal control policy and solid traces are the muscular response to the control input. B: the angular velocity of the simulated trajectories as a function of time. C: the optimal trajectories as a function of time. The shaded areas in B and C represent the SD of the stochastic system around the optimal trajectories (solid black and red traces). The SD was computed across 100 simulations.

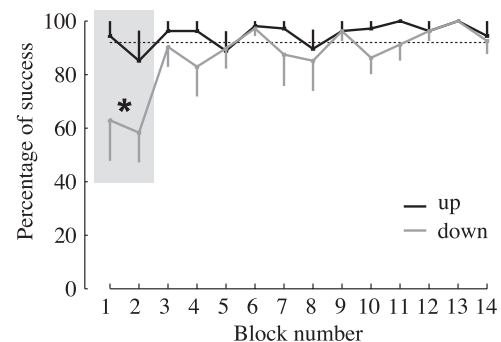


FIG. 4. Success rate for hypergravity movements averaged across the subjects ($n = 9$) in both directions as a function of the block number. The horizontal dashed line is the average success rate in normal gravity for both movement directions. The gray rectangle illustrates the significant difference in the success rate between hyper and normal gravity for downward movements.

Effect of hypergravity

The elevation angle and angular velocity as a function of time are shown in Fig. 5 in the two gravitation conditions. These data are shown for the same subject whose simulations were plotted in Figs. 2 and 3. All of the trajectories were aligned with respect to the movement onset to compute the average trajectory and SE at every time step. For the upward movements (Fig. 5, *A* and *B*), any single trajectory (light gray) 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 Fig. 5*B*. Similar comments may describe the effect on the downward trajectories (Fig. 5, *C* and *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 Fig. 3. The quantitative comparison will be addressed later in this analysis.

The statistical analysis revealed that the tendencies observed qualitatively in Fig. 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 those for downward movements ($P < 0.01$). The magnitude of the effect is illustrated in Fig. 6*A* for the peak angular acceleration, in Fig. 6*B* for the peak angular velocity, and in Fig. 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. Analysis of the overshoots and undershoots shown in Fig. 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 Fig. 7*A*. In this direction, the undershoots were detected in 6% of the trials in hypergravity compared with 11% in normal gravity. For the downward movements, there was no difference concerning undershoot trials (6% in hypergravity compared with 7% in normal gravity without variation in amplitude), whereas the overshoots were observed in only 43% of the trials compared with 72% in normal gravity (Fig. 7*B*).

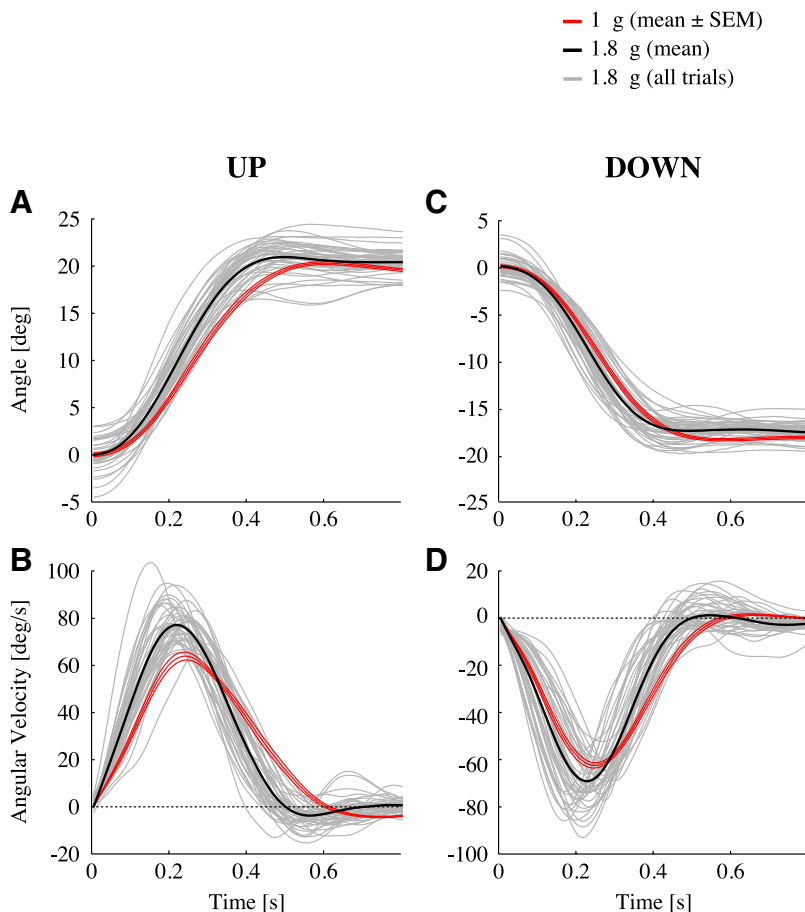


FIG. 5. The elevation angle and angular velocities for one subject in the 2 directions. The red traces are the average 1-*g* trajectory plus and minus the SE computed at each time step. The gray traces show all of the hypergravity trials for this subject, aligned on individual movement onsets. The black 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.

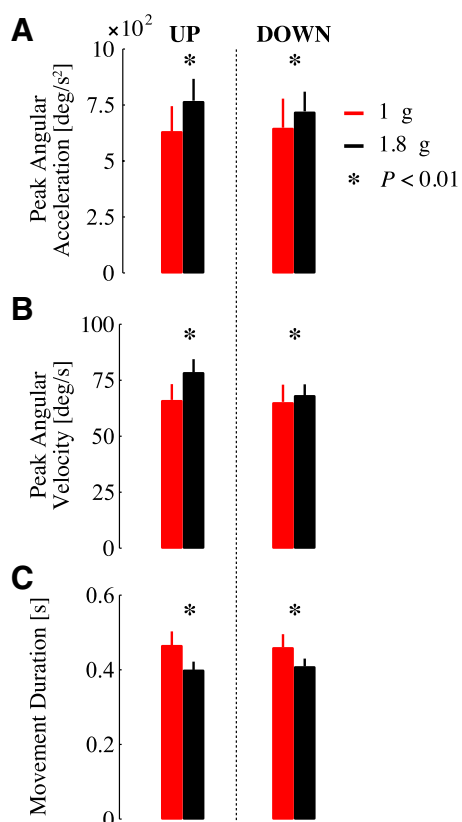


FIG. 6. The variation of the kinematics parameters across the 2 gravitational conditions and in the 2 movement directions. The means of the peak angular acceleration (A), peak angular velocity (B), and movement duration (C) were averaged across the subjects. The error bars represent the intersubject SE. The data of the peak acceleration and velocity for the downward movements are presented as the absolute value. All of the differences between 1 and 1.8 g were statistically significant.

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 upward.

Comparison with model simulations

For the upward movements, the simulations in hypergravity 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. Predictions for the downward movements were similar to the upward movements: the model predicts 28 and 11% of relative increase in the peak acceleration and velocity, respectively. Subjects' behavior varied less: we observed 9 and 3% of increase in peak acceleration and velocity, respectively.

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 1 g trajectory (used as a reference trajectory). As illustrated in Fig. 8A, the areas A_1 and A_2 were defined with respect to the sign of the difference between the reference 1 g 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 to compare the magnitude of the effect with the experimental data. Figure 8, B and C indicates 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 1 g reference trajectory and were averaged across the subjects.

As shown in Fig. 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, Fig. 8B) and A_1 is a positive constant (black dotted line). The opposite is observed for the downward movements: Fig. 8C 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 Fig. 8A; A_1 and A_2 are both nonzero), although 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 demonstrates that the subjects tended to overcompensate (A_1 was larger in data compared with the simulations). Similarly, the effect of movement direction is illustrated in Fig. 8, B and C. The downward movements present more variability, although the global tendency is in accordance with the simulations.

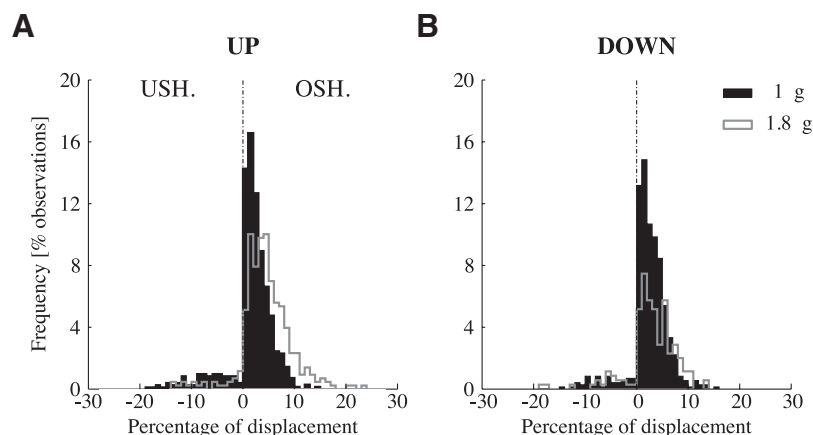


FIG. 7. The overshoots (OSH) and undershoots (USH) in the normal and hypergravity conditions for the upward (A) and the downward (B) movements. The histograms show the frequency of the observation of trials with the corresponding percentage of displacement. Recall from METHODS that the overshoots are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

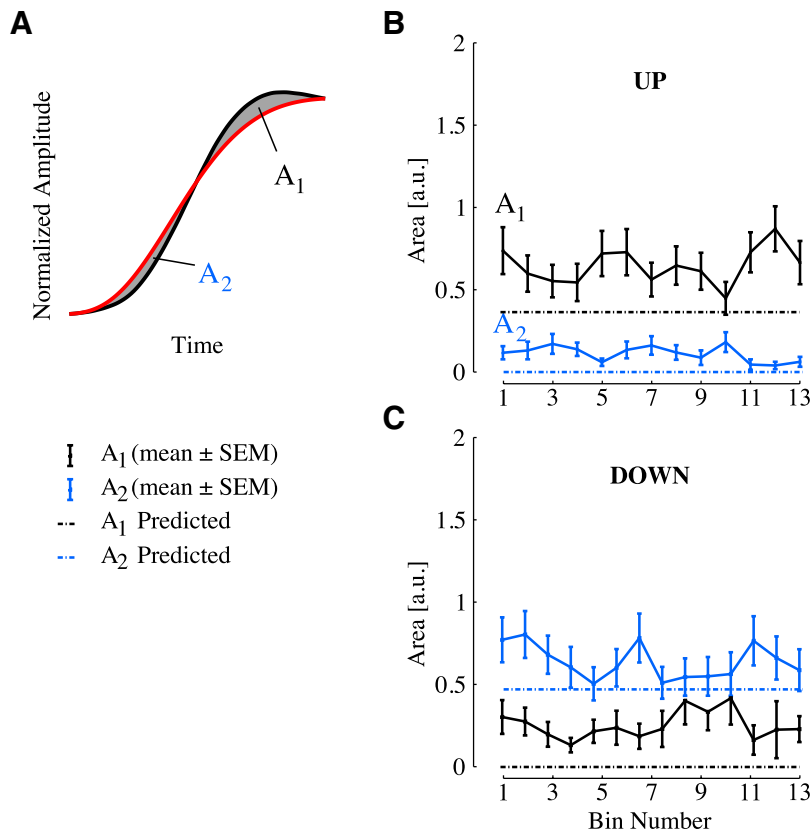


FIG. 8. The quantitative analysis of the effect of hypergravity. *A*: the illustration of the computation procedure; the amplitudes were normalized to the movement amplitude from movement onset to movement end. The time was unchanged. A_1 and A_2 are the areas between the hypergravity traces and the reference 1 *g* trace when the integrated differences were positive and negative, respectively. *B* (upward) and *C* (downward) show the areas A_1 and A_2 averaged across bins of 3 movements and across the subjects vs. the number of the bin.

To further argue for a reoptimization 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 (*Eq. 11*), but not reoptimized. The simulation of this alternative model predicted that the kinematics of movements in hypergravity is the same as that in normal gravity condition, yielding for A_1 and A_2 values very close to zero in Fig. 8. This demonstrates that the model based on the nonoptimizing strategy can be rejected.

DISCUSSION

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 using 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 reoptimization 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, on 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 reoptimization 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 to focus on the effect of a change in gravity and to avoid other factors coming 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 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 (*Eq. 3*) to formulate a control variable that is closer to the neural motor command, which is presumably accessible within the CNS 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 positions; moreover, the movements were performed in darkness without visual feedback. Our protocol was restricted to one movement amplitude from a single starting position, to collect a sufficient number of trials per subject and per flight. Then, our subjects were provided with continuous visual feedback to prevent 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 not only for the difference between vertical and horizontal movements in normal gravity, but also for 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 feedforward 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 CNS uses the internal representation of the gravitational torque to optimize the motor commands. Our sample does not permit the evaluation of whether the optimal feedback gains (L_k in Eq. 10) are also reoptimized 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 CNS 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 (2008) reported a similar result in the context of oscillatory movements performed under different gravity conditions. 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 (1999) 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 compared with 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 grav-

itational 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, although 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 one, suggest that reoptimization produces definitive changes in the movement kinematics (Izawa et al. 2008). It seems the question of which adaptation process (recalibration of the internal models or reoptimization) will be observed depending on the experimental conditions remains open to debate.

Second, under the hypothesis that the motor actions are reoptimized 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 reoptimization 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 with 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 both 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.

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