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Movement Stability Under Uncertain Internal Models of Dynamics

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¹Center for Systems Engineering and Applied Mechanics, Université catholique de Louvain, Louvain-la-Neuve; ²Institute of Neuroscience, Université catholique de Louvain, Brussels, Belgium; and ³Centre d'Etudes de la Sensorimotricité, Centre National de la Recherche Scientifique–Université Paris Descartes, Paris, France

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Crevecoeur F, McIntyre J, Thonnard J-L, Lefèvre P. Movement stability under uncertain internal models of dynamics. *J Neurophysiol* 104: 1301–1313, 2010. First published June 16, 2010; doi:10.1152/jn.00315.2010. Sensory noise and feedback delay are potential sources of instability and variability for the on-line control of movement. It is commonly assumed that predictions based on internal models allow the CNS to anticipate the consequences of motor actions and protect the movements from uncertainty and instability. However, during motor learning and exposure to unknown dynamics, these predictions can be inaccurate. Therefore a distinct strategy is necessary to preserve movement stability. This study tests the hypothesis that in such situations, subjects adapt the speed and accuracy constraints on the movement, yielding a control policy that is less prone to undesirable variability in the outcome. This hypothesis was tested by asking subjects to hold a manipulandum in precision grip and to perform single-joint, discrete arm rotations during short-term exposure to weightlessness (0 g), where the internal models of the limb dynamics must be updated. Measurements of grip force adjustments indicated that the internal predictions were altered during early exposure to the 0 g condition. Indeed, the grip force/load force coupling reflected that the grip force was less finely tuned to the load-force variations at the beginning of the exposure to the novel gravitational condition. During this learning period, movements were slower with asymmetric velocity profiles and target undershooting. This effect was compared with theoretical results obtained in the context of optimal feedback control, where changing the movement objective can be directly tested by adjusting the cost parameters. The effect on the simulated movements quantitatively supported the hypothesis of a change in cost function during early exposure to a novel environment. The modified optimization criterion reduces the trial-to-trial variability in spite of the fact that noise affects the internal prediction. These observations support the idea that the CNS adjusts the movement objective to stabilize the movement when internal models are uncertain.

INTRODUCTION

Stabilizing postural and movement control is a continuous challenge for the CNS, for which a reliable estimation of the state of the body is essential. For this purpose, the CNS has two sources of information: a prediction based on internal models, which allows for the computation of a prior estimate from the corollary discharges of the motor commands (Kawato 1999; Miall and Wolpert 1996; Wolpert and Flanagan 2001), and sensory feedback, which conveys information from the periphery (e.g., vision, proprioception, etc.). A promising hypothesis suggests that these sources are combined in a Bayesian integration process, in which each signal is given a relative importance proportional to its reliability (Kording and Wolpert

2004; Vaziri et al. 2006). The resulting estimate is optimal in the sense of minimal estimation variance.

In the context of movement control, a direct use of sensory feedback to monitor an on-line movement yields poor control performance and can lead to instability, given the presence of sensory noise and time delays (Mehta and Schaal 2002; Miall et al. 1993). Nevertheless, during motor adaptation, the internal prediction may be erroneous until the CNS acquires an internal model of the novel tool or limb dynamics (Wolpert et al. 2001). Under the hypothesis of Bayesian integration, this constrains the control strategy to rely more heavily on sensory feedback. Therefore during the transient effects of learning, there must be a mechanism that reduces the risk of variability and unstable oscillatory behavior despite uncertain internal representation of dynamics. Intuitively, when internal models are not available due to exposure to unknown dynamics, instability can be avoided by allowing a relative loss of accuracy and velocity, i.e., by changing the movement objective. By “movement objective” we refer to the criteria about performance in terms of velocity, accuracy, and motor costs, for example, that, in addition to the specification of the main goal of the movement (e.g., reach to the target), allows the CNS to select from an infinite number of possibilities the control parameters required to attain that goal. In the context of computational models, these criteria that make up part of the movement objective are expressed by the *cost function*. The present study tests the possibility that when the internal models suffer from uncertainty, the CNS adjusts the implicit movement objective to preserve movement stability.

To test this hypothesis we asked human subjects to hold a manipulandum in precision grip and to perform single joint point-to-point rotations in the vertical plane while transiently exposed to weightlessness. Gravity is known to play a central role in motor control (Bock 1998; McIntyre et al. 1998) and experimental evidence suggests that 0 g is a unique condition to which adaptations observed at other gravity levels do not generalize (Mierau et al. 2008; White et al. 2008). Thus transient exposure to weightlessness, where the internal model of arm dynamics must be updated, provides an effective means to investigate the mechanisms that compensate for uncertainty in the internal prediction. Indeed, we observed that subjects' ability to precisely adjust their grip force in anticipation of the load force was diminished in 0 g, reflecting a reduction in the accuracy of internal models (Flanagan and Wing 1993, 1997) and indicating that the internal prediction indeed suffered from uncertainty during exposure to the 0 g condition.

We went further to analyze changes in kinematics, coupled with the observations on the control of grip force, in the context of optimal feedback control. Indeed, this well-defined

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computational framework is known to be of high relevance for the modeling of motor control strategies (Braun et al. 2009; Izawa and Shadmehr 2008; Izawa et al. 2008; Liu and Todorov 2007; Todorov and Jordan 2002). This framework was naturally retained for this study because 1) it allows one to formulate the continuous sensorimotor mapping that may suffer from internal-model uncertainty on a single movement basis; 2) it relates the integration of prediction and sensory feedback for state estimation directly to Bayesian integration (Kalman filter); and 3) it allows one to directly test the hypothesis that a change in movement objective accounts for the effect of unknown dynamics on movement kinematics by adjusting the cost parameters that determine the control policy.

The simulations confirm the direct benefit of adjusting the cost function used to define the objective: the effect of internal model uncertainty on the movement endpoint variance was limited. In addition, the simulations were quantitatively in direct support to our hypothesis that, under noisy predictions, the movement cost function was adjusted during the transient exposure to the weightlessness condition. We suggest that such adjustment is applicable to any situation of exposure to unknown dynamics and can therefore be a general model for control strategies when internal models of dynamics are uncertain.

METHODS

Subjects

Ten right-handed volunteers (four males and six females; aged 25–52 yr) with no neurological disorders participated in the experiment. All subjects gave informed consent and complied with the medical requirements for parabolic flights. They were naïve relative to the purpose of the experiment and all experienced parabolic flight for the first time. The medical board committee of the European Space Agency (ESA) and the French Comité pour la Protection des Personnes, responsible for all life science experiments performed in France, approved the experimental protocol.

Parabolic flights

Parabolic flight experiments were launched on board the 47th and 48th ESA parabolic flight campaigns. Each flight was composed of 30 parabolas organized into six groups of 5 parabolas each, separated by short pauses of level flight. Two subjects were evaluated per flight in turn: the first subject during parabolas 1 to 15 and the second during parabolas 16 to 30. In practice, all the subjects performed the task during ≥ 14 consecutive parabolas. We found no difference between the first and second subjects with respect to the analyses reported in the following text.

Each parabola can be decomposed into three phases. First, the aircraft accelerates upward for nearly 20 s and the effective gravity inside the aircraft rises to 1.8-fold terrestrial gravity (1.8 g). Second, the engine thrust is reduced to compensate for only the air drag and the aircraft follows the parabolic trajectory of a free fall, during which time the effective gravity inside the aircraft is close to zero (0 g). This phase lasts about 22 s. At the end of the parabola, the power is turned up again and the acceleration redressing the trajectory generates another period of hypergravity (1.8 g).

Experimental procedures

Subjects were evaluated in a training session performed in normal Earth gravity several days before the flights. Subjects were seated in front of three visual targets aligned vertically and separated by 18 cm.

The center target was approximately in front of the subjects' shoulders, so that when they pointed toward this target their arm was in the horizontal position.

At the beginning of the 0 g phase of each parabola (or each block in normal gravity), the subjects grasped a manipulandum of 0.25 kg with a precision grip (i.e., between the thumb and the index finger) and aligned the manipulandum with the center target. The grip aperture was 4.5 cm. A sequence of targets was generated and the subjects were asked to align the handheld manipulandum to the current target by rotating the fully extended arm around the shoulder. Movements up (from center to top) and down (from center to bottom) were randomly interleaved to avoid anticipatory movements. Subjects aligned their arm in front of the center target after each trial. Subjects were provided with continuous visual feedback throughout the movements in both normal and zero gravity conditions. In flight, the subjects performed the same task during the 0 g phase and subsequent 1.8 g phase of each parabola. Data collected during the hypergravity phases were published in a previous study (Crevecoeur et al. 2009b).

Data collection

The positions of infrared markers placed on the manipulandum and the shoulder were sampled at 200 Hz (Codamotion; Charnwoods Dynamics, Leicestershire, UK). During flight, the gravity inside the aircraft was sampled at 800 Hz with a three-dimensional (3D) accelerometer (ADXL330; Analog Devices). Gravity measurements were used to remove trials performed at the beginning or end of the 0 g phases, where gravity was sometimes unstable. Trials performed in flight were included in the data set when the average absolute gravity across the movement was < 0.1 g.

After visual inspection of all trials and validation based on accelerometer signals about the effective g-level in the airplane and the performance of the subjects (removal of movements triggered in the wrong direction), the total number of valid trials was 1,172 in 0 g and 1,655 in 1 g, equally distributed between up and down directions (range: 88–138 trials per subject in 0 g and 134–192 in 1 g). The number of valid trials represented 89 and 94% of the total number of trials collected in 0 g and 1 g, respectively.

The manipulandum was equipped with two force and torque sensors, one under each finger, which allowed us to measure the normal and tangential forces at the interface between the manipulandum and the fingers (40 mm diameter, Mini 40 F/T transducers; ATI Industrial Automation, Apex, NC) with a resolution ≤ 0.02 N. Force signals were sampled at 800 Hz.

Data postprocessing

The position and force signals were digitally low-pass filtered with a zero phase-lag, fourth-order Butterworth filter. The cutoff frequencies for the position and force signals were set at 20 and 50 Hz, respectively. A straight line joining the shoulder position and the handheld load was used to compute the elevation angle of the arm with respect to the floor of the airplane as a function of time [$\theta(t)$, Fig. 1A]. Angular velocity and acceleration were computed from numerical differentiation of the position signals. Movement duration was estimated based on linear approximation of the speed profiles at a threshold equal to 10% of its peak value computed for each individual trial. The crossing of the linear regressions with the horizontal axis were used to estimate movement onset and end, as illustrated in Fig. 1 (t_0 and t_p).

For some movements, the subjects made corrective adjustments. These trials were identified by looking at the acceleration profile: corrections for target overshooting (Fig. 1, left) or undershooting (Fig. 1, right) were detected when the angular acceleration showed a local maximum after or before the end of the movement, respectively (Fig. 1C). The corrective displacement $\Delta\theta$ was defined as the displacement percentage from the time of the local maximum (t^*) to the movement

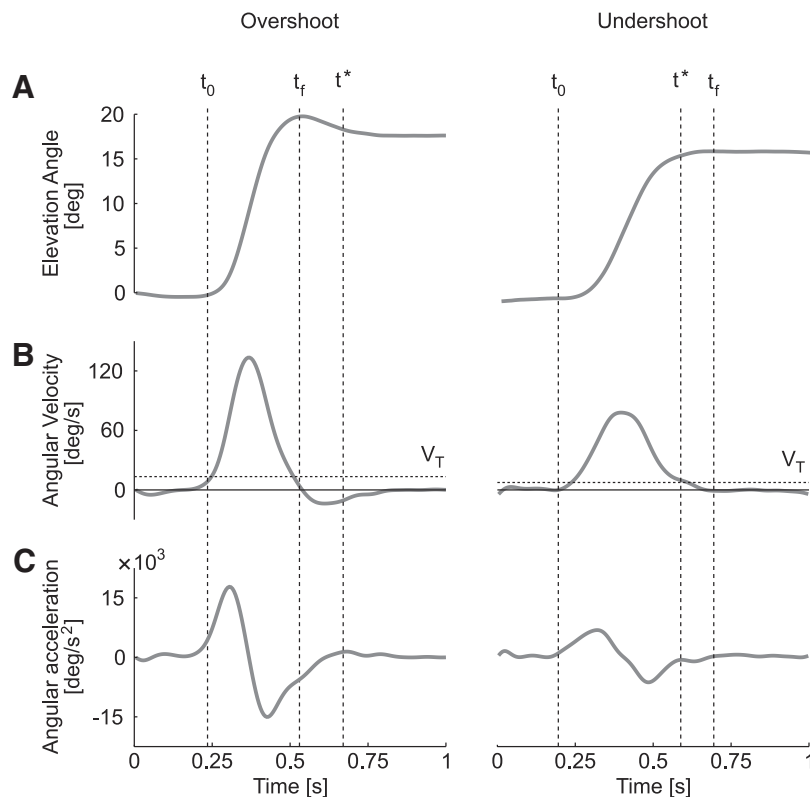


FIG. 1. Plots of the elevation angle (A), angular velocity (B), and angular acceleration (C) as a function of time for 2 selected trials. Typical overshoot (left) and undershoot (right) profiles are illustrated. V_T (horizontal dotted line) is the threshold equal to 10% of peak velocity, computed for each individual trial. The vertical dashed traces show the estimation of movement onset (t_0) and movement end (t_f) for these trials. The detection of overshoots and undershoots was based on the presence of local maxima in the acceleration profile (t^*).

end with respect to the total displacement from the movement onset to the movement end

$$\Delta\theta = \frac{\theta(t_f) - \theta(t^*)}{\theta(t_f) - \theta(t_0)} \times 100 \quad (1)$$

To avoid ambiguities in movement classification, we determined that a movement had an overshoot only if there was no preceding correction for undershoot, as defined earlier. We also identified overshoots only when the local maximum occurred before $t_f + 150$ ms, to avoid accounting for late corrections.

An important feature of pointing movements addressed in the present study is the skewness of the velocity profile. Based on the estimation of movement duration, the skewness was defined as the ratio between the duration of the acceleration phase and that of the total movement. This variable was equal to the time from movement onset until peak velocity when the movement duration was normalized to 1.

The grip force (GF) was defined as the mean of the absolute force components normal to the two sensor surfaces. Load force (LF) was defined as the vertical component of the tangential load relative to the manipulandum reference frame (Fig. 2A). In zero gravity, LF is proportional to the tangential acceleration and the ratio between LF and acceleration equals the mass of the manipulandum.

GF was then decomposed into two components. The static component (GF_S , Fig. 2B) was measured prior to the movement when the arm was stable. GF_S is the average GF in a time interval of 100 ms following the target onset. Then, the dynamic component (GF_I), corresponding to the grip force increment, was defined as the GF measured at the time of maximum LF (t_M in Fig. 2B), relative to the static component. The method for analyzing GF modulation is similar to that used previously (Crevecoeur et al. 2009a). However, in the present study we restricted the analysis to the positive LF peak, which allowed us to compare the performances of the subjects in the two gravitational conditions. Indeed, for a single point-to-point movement, the absence of weight in 0 g provokes a negative LF peak (Fig. 2B), corresponding to negative acceleration. In normal gravity, the down-

ward acceleration only decreases the LF and there is little to no GF modulation in phase with the downward acceleration (except for very fast movements, when the downward acceleration is greater than gravity). For this reason, a comparison of GF modulations in both gravitational contexts could be based only on the positive LF peaks.

Model

We considered single-joint rotation of a rigid body representing the combined mass and dimensions of the arm, forearm, and hand. The rotation axis was at the end of the rigid body, representing the shoulder rotation axis. We computed the mass and length of each segment as ratios to the mass and size of each subject. These ratios were obtained from classical anthropometric tables (Winter 1979). The manipulandum mass was added to the hand mass and the hand length was divided in half to mimic the grasp posture. These parameters permitted us to evaluate the inertia (I) of the whole system (arm-manipulandum) for each subject relative to the shoulder rotation axis.

In zero gravity, we assumed that two torques acted on the system: a shoulder muscular torque (T) and a viscous friction torque proportional to the angular velocity. The viscous friction constant G_v was equal to $0.63 + 0.095T_M$ (the linear model was taken from Nakano et al. 1999), where T_M is the average joint torque across the movement. For the simulations, T_M was estimated a priori as a function of the system inertia and movement amplitude and duration

$$T_M = 4I \frac{\theta(t_f)}{(t_f - t_0)^2} \quad (2)$$

This estimate of T_M corresponds to the average shoulder torque when the absolute angular acceleration is constant during the movement.

In addition to the mechanical equations, we introduced a simple physiological model to express T as a first-order low-pass response to the motor command (control input to the system, u). The time constant τ for the muscular response to the control input was set to 40 ms

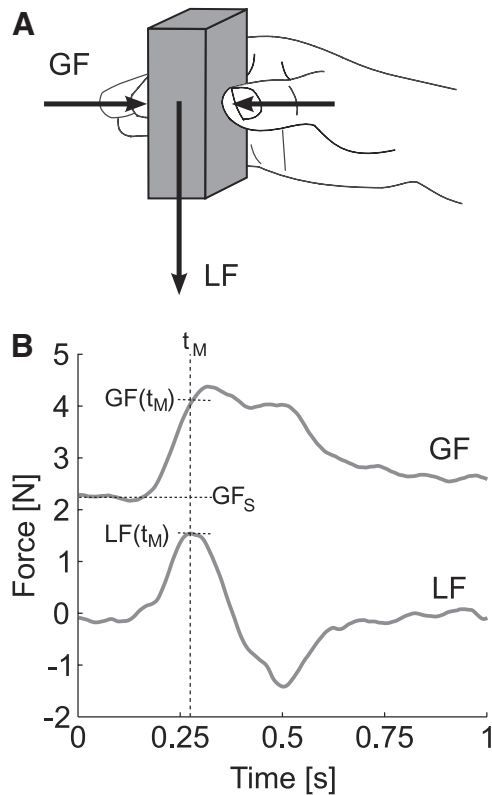


FIG. 2. Analysis of the precision grip forces. A: representation of the manipulandum held in precision grip between the thumb and the index finger. Black arrows are the grip force (GF, normal to the contact surfaces) and load force (LF, tangential to the contact surfaces). B: example of GF and LF as a function of time for one selected trial. The vertical dashed line is the time of maximum LF (t_M). The static grip force (GF_S) and the increments of grip force, measured as the difference between $GF(t_M)$ and GF_S , are illustrated.

(Winter 1979). Differential equations describing the dynamic system in continuous time are

$$I\ddot{\theta} = T - G_v\dot{\theta} \quad (3)$$

$$\dot{T} = \frac{1}{\tau}(u - T) \quad (4)$$

This system is linear, which allows us to design an optimal feedback controller in the presence of additive and signal-dependent noise sources.

Optimal feedback control

The CNS must be able to compensate for noise affecting the motor commands and sensory feedback. In addition to additive noise, multiplicative noise must be considered in a model of the signal-dependent motor noise properties. Importantly, the brain must also compensate for the presence of time delays in the sensory feedback loop. All of these features are expressed in the following state-space representation of the stochastic dynamics

$$\mathbf{x}_{k+1} = \mathbf{A}\mathbf{x}_k + \mathbf{B}(\mathbf{1} + \varepsilon_k)\mathbf{u}_k + \xi_k \quad (5)$$

$$\mathbf{y}_k = \mathbf{x}_{k-h} + \omega_k \quad (6)$$

In Eqs. 5 and 6, $\mathbf{x}_k$ represents the vector of the state variable at time k , including the elevation angle, angular velocity, and shoulder torque; and h is the feedback delay expressed in number of sample times. The matrices $\mathbf{A}$ and $\mathbf{B}$ were obtained from the Euler integration scheme and

from the system dynamics described in Eqs. 3 and 4 (details are provided in the Supplemental material).¹

The time step (δt) for the simulations of the discrete dynamics was equal to 10 ms and the feedback delay was set to 100 ms ($h = 10$). The prescribed final position, velocity, and shoulder torque were embedded in the state variable. Thus the state vector had six dimensions, the three first entries representing the state of the original system and the last three describing the final state. The noise terms ξ_k and ω_k are multivariate Gaussian variables with zero mean and covariance matrices $\Omega_\xi = \text{diag}(0 \ 0 \ \sigma^2 \ 0 \ 0 \ 0)$ and $\Omega_\omega = \sigma^2 \text{diag}(1 \ 1 \ 1 \ 1 \ 1 \ 1)$. With these definitions, ξ_k affects only the control signal, whereas ω_k affects the entire state feedback, including the perception of the target location embedded in the state. We set the amplitude of the additive noise to $\sigma = 0.001$. The multiplicative noise ε_k is a Gaussian random variable with zero mean, for which we set the variance equal to 0.04. The chosen parameters for the variance of the different noise sources are of the same order as that of the values used in previous studies (Liu and Todorov 2007; Todorov 2005). Variance of the additive noise was kept lower since we took into account the feedback delay, which increases the variability of the feedback signal and, in turn, the state estimation. It can be observed that increasing the delay increases the variability of the estimation of the trajectories (Todorov and Jordan 2002). The value of 100 ms for the feedback delay is compatible with the fact that voluntary responses to perturbations are typically observed after 120 ms (Kurtzer et al. 2008).

The optimal feedback control theory postulates that motor commands sent to the limb will seek a maximum reward (i.e., successful attainment of the task) at minimal motor costs. The cost of the movement was assumed to depend on both the state and control at each time step through the following equation

$$J_k = \mathbf{x}_k^T \mathbf{Q}_k \mathbf{x}_k + \mathbf{u}_k^T \mathbf{R} \mathbf{u}_k \quad (7)$$

The parameter $\mathbf{R}$ is the cost of motor commands and penalizes high control signals. The matrices $\mathbf{Q}_k$ allows us to express the constraints on the state variables related to the prescribed final state, representing the target. In practice, we defined a running period equal to $N_1 \delta t$, corresponding to the movement execution, during which values of $\mathbf{Q}_k$ ($k = 1, 2, \dots, N_1$) were set to 0 (i.e., the system was free to move unconstrained during the running period). We also defined a stabilization period, $(N_2 - N_1) \delta t$, following the running time, during which time the cost matrices were defined such that

$$\begin{aligned} \mathbf{x}_k^T \mathbf{Q}_k \mathbf{x}_k &= w_1 [\theta(k\delta t) - \theta_f]^2 + w_2 \dot{\theta}(k\delta t)^2 \\ k &= N_1 + 1, N_1 + 2, \dots, N_2 \end{aligned} \quad (8)$$

Equation 8 expresses that during the stabilization period the expected position must be close to the prescribed final position (θ_f) and the expected velocity must remain close to 0.

Under these assumptions, we can compute the optimal feedback gains (L_k) and Kalman gains for the state estimation (K_k) (see Todorov 2005 and the Supplemental material). The system described in Eqs. 5 and 6 was reduced to the nondelayed case by finite system augmentation. In short, the system was driven by

$$\mathbf{u}_k = -L_k \hat{\mathbf{x}}_k \quad (9)$$

where L_k was the optimal gain applied to the current estimate of the state of the system ($\hat{\mathbf{x}}_k$, augmented to take the feedback delay into account). This estimate was updated in two steps by computing the prior belief about the state

$$\mathbf{x}_{k+1}^p = \mathbf{A} \hat{\mathbf{x}}_k + \mathbf{B} \mathbf{u}_k + \eta_k \quad (10)$$

where η_k was a multivariate Gaussian random variable representing the internal uncertainty related to the prediction based on the internal model (the covariance matrix Ω_η will be defined in the following

¹ The online version of this article contains supplemental data.

text). Then, the prior estimate was updated by a correction based on the feedback measurement (Kalman filter)

$$\hat{\mathbf{x}}_{k+1} = \mathbf{x}_{k+1}^p + \mathbf{K}_{k+1}(\mathbf{y}_{k+1} - \mathbf{x}_{k+1}^p) \quad (11)$$

The particularity of this estimate is that the prediction noise (η_k) can be partially corrected by the sensory feedback. The corresponding control algorithm that takes multiplicative noise into account is provided in the Supplemental material. Thus the presence of uncertainty of the internal model forces the system to rely more heavily on sensory feedback.

Comparison between model and data

The system inertia for the simulations was set to the mean inertia averaged across all individual subjects ($0.568 \text{ kg} \cdot \text{m}^2$). The running period was set to the subjects' average movement duration measured in 1 g (480 ms) and the stabilization period was set to 500 ms (from 480 to 980 ms). Endpoint variance was computed from the angular position and velocity at the estimated final time. The final angular position was computed relative to the measured initial position for each individual trial. To estimate the variance of two-dimensional (2D) variables (position and velocity), we computed the area of the ellipsoid obtained by singular value decomposition of the covariance matrix. The same method was used to estimate the final time and endpoint variance on the simulations and experimental data (Fig. 1).

The optimal control policy (L_k in Eq. 9) and the Kalman gains (K_k , Eq. 11) depend on the ratio Q_k/R through the recursion formulas used to compute them (Todorov 2005; also see the Supplemental material). Therefore adjusting the cost parameters will have a direct impact on the optimal control strategy and state estimation. The change in cost function was obtained by decreasing w_1 and w_2 (the cost of error in position and velocity) and increasing R (the cost of effort). Decreasing Q_k only or increasing R only has a similar but weaker effect on the simulated trajectories. Therefore we consider the simultaneous adjustment of these cost matrices by dividing Q_k and multiplying R by the same factor α , resulting in an overall decrease in Q_k/R by a factor α^2 . We also considered cases where $\alpha < 1$ to test the effect of an increase in Q_k/R on the simulated trajectories, i.e., where we increased w_1 and w_2 and decreased R . The details about the setting of the cost parameters and the noise amplitude changed across the simulations are provided in *Simulation results* in the next section.

RESULTS

Effect of microgravity on the grip force modulation

The GF/LF ratio measured at the time of maximum load force (Fig. 2, t_M) was markedly increased in 0 g for all subjects and tended to decrease gradually across the parabolas. In normal gravity, this ratio was 1.53 ± 0.17 against 5.12 ± 1.34 during the first parabola (average across subjects $\pm$ SE). At the end of exposure to 0 g, the absolute ratio was 2.90 ± 0.44 . The evolution of the GF/LF ratio across parabolas could be attributed to the fact that subjects initially applied static grip forces (GF_S in Fig. 2B) that were comparable to the levels measured under the 1 g condition, despite the fact that the weight of the held object was zero. Static grip force across subjects ranged between 2.5 and 9.6 N in 1 g condition and between 1.7 and 13 N during the first four parabolas in the 0 g condition. This value decreased toward about 50% of this level at the end of the exposure to 0 g: the average GF_S across the last four parabolas ranged between 0.8 and 6 N. The decrease in GF_S was significant ($P < 0.01$, computed from linear regression of the subjects' individual means vs. the block number). Figure 3A shows the decrease in GF_S . Given the variability of GF_S across subjects, the average GF_S measured in each block (where one block corresponds to one parabola) were normalized for each subject to their individual means measured under normal gravity condition.

To address the quality of the internal models of dynamics, we computed the linear regressions between the increments of GF (GF_I) and LF at the times of load force peaks [$LF(t_M)$ in Fig. 2B]. The relationship

$$GF_I = a_0 + a_1 LF(t_M) \quad (12)$$

was significant for all subjects ($P < 0.05$, computed on the whole data set; data of up and down movements were pooled). We verified that there was no significant evolution of the load force peaks across the parabolas (one-way ANOVA, $P > 0.9$).

To address the evolution of the quality of the internal prediction, Eq. 12 was estimated for each subject on groups of five consecutive blocks to ensure a sufficient number of trials. The five-block window was slid starting from block 1 (including blocks 1 to 5) to block 10 (including blocks 10 to 14).

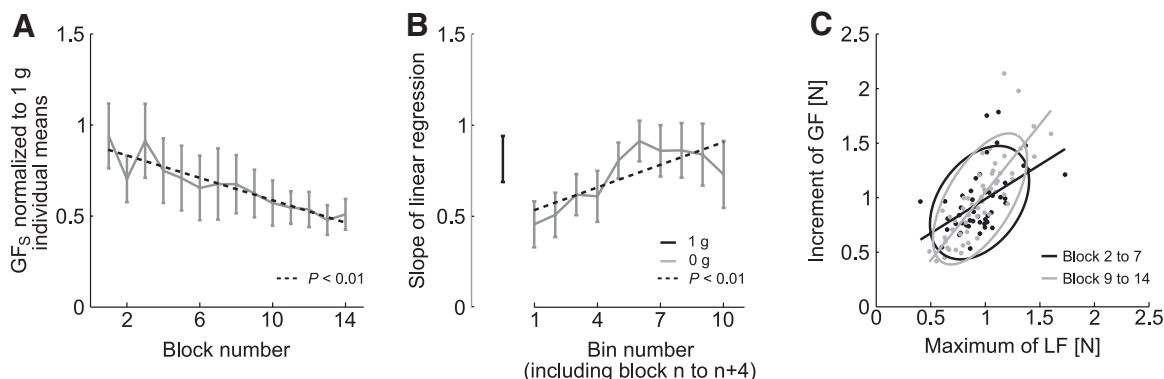


FIG. 3. A: evolution of GF_S averaged across subjects (means $\pm$ SE) vs. the block number corresponding to the parabolas. Means GF_S were normalized for each subject to their individual means. B: evolution of the slope of the linear regression of GF_I as a function of $LF(t_M)$. The linear regressions were computed on bins of 5 blocks. Bin number n contains the blocks number n to $n + 4$. The average slope across subjects and directions under normal gravity is shown in black. In A and B, the dashed line represents the least square linear regressions of subjects data vs. the block or bin number. C: raw data from one representative subject. Grip/load force coupling during the blocks 2 to 7 and 9 to 14 are shown in gray and black, respectively. The ellipses are the 95% confidence region computed from singular value decomposition of the estimated covariance matrix.

Nonsignificant regressions were observed in 20% of cases, of which half were observed in the first three bins (including parabolas 1 to 7). Figure 3*B* shows that the slope in Eq. 12 was initially lower than the slope measured under normal gravity condition and significantly increased as subjects adapted to the 0 g condition. There was no significant evolution of a_0 across the parabolas (one-way ANOVA, $P > 0.9$).

Based on this result, we defined the early exposure period as the first seven parabolas, during which the absolute grip force is characterized by an elevated offset (GF_S) and a lower-gain modulation (a_1). The change in strategy for grip force control is illustrated in Fig. 3*C* with raw data from one representative subject. Data are the increments of GF as a function of the corresponding maximum of LF extracted from blocks 2 to 7 (in black) and from blocks 9 to 14 (in gray). The slope of the relationship (a_1) was greater for the data extracted from blocks 9 to 14, supporting the idea that internal models gradually adapted to the 0 g condition. The 95% confidence ellipsoid also illustrates that the GF was more finely tuned to the LF variation. Indeed, the change in shape of the ellipsoid shows that the data extracted from blocks 9 to 14 are closer to the linear regression supporting a gradual refinement in the internal prediction of the LF peaks. This tendency was confirmed for seven subjects by an increase of the R^2 statistics between the regressions computed on block 2 to 7 and on blocks 9 to 14. These results are compatible with the presence of uncertainty affecting the internal prediction during the early exposure to weightlessness. Accordingly, the subsequent analysis of movement control mainly focuses on this period of learning (early exposure, first seven parabolas).

Effect of microgravity on the movement kinematics

During the early exposure period, the 2D endpoint variability (position and velocity) increased by a factor 1.9 relative to the normal gravity condition (data of up and down movements were pooled, averaged across subjects). There was a significant tendency for a decrease in endpoint variability during the whole exposure but without reaching the variability measured in 1 g ($P < 0.05$, linear regression of subjects' data vs. the block number).

Compared with normal gravity, the movements were slower in microgravity and presented reduced peak acceleration, peak velocity, and increased movement duration (Wilcoxon rank-sum test computed on raw data, $P < 0.01$). As in normal gravity condition, all trials performed in 0 g presented single peak velocity profiles. The effect of 0 g is shown in Fig. 4, *A* to *D* for one representative subject. In both directions, the velocity profiles diverged early from the average trajectory performed in normal gravity (Fig. 4, *B* and *D*). Figure 4, *B* and *D* also illustrates that the velocity profiles in 0 g presented a significant skewness in both directions (*t*-test, raw data compared with 0.5, $P < 0.01$).

The following tests used the Wilcoxon rank-sum test with Bonferroni correction to take multiple comparisons into account (the level of significance was set to 0.005 for a single test on data from individual subjects). The analysis of individual subjects revealed that, for upward movements, the decrease in peak angular acceleration in 0 g was significant for seven subjects ($P < 0.05$). The same tendency was observed for one of the three remaining subjects, but did not reach the level of statistical significance (individual $P = 0.09$). For upward movements, the increase in movement duration was significant

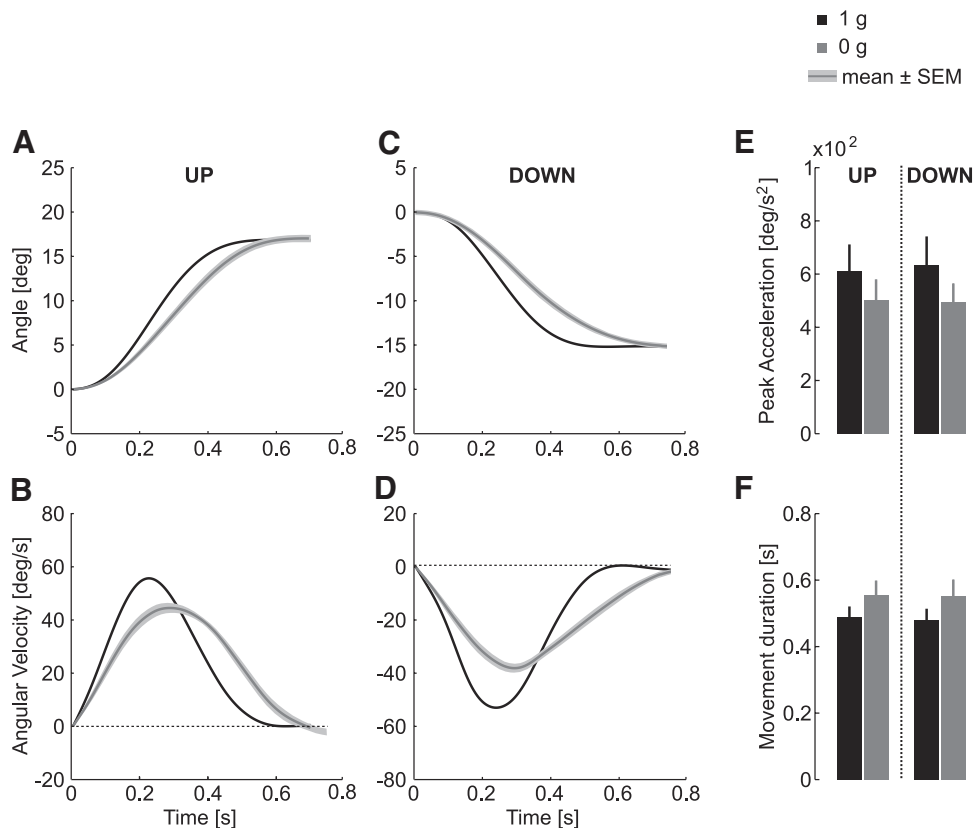


FIG. 4. Average trajectories in 1 g (black) and during the early exposure to 0 g (gray) from one representative subject. Shaded areas represent the SE, computed at each time step. *A* and *B* show the elevation angle and the angular velocity as a function of time for upward movements. *C* and *D* show the same plots for downward movements. Pooled subjects' data, showing the effect of 0 g on the peak angular acceleration and movement duration, are shown in *E* and *F*, respectively. In *E* and *F*, the vertical bar indicates the intersubject SE.

for eight subjects ($P < 0.05$). For the downward movements, the decrease in peak angular acceleration was significant for seven subjects ($P < 0.05$). In this direction, the increase in movement duration in 0 g was significant for six subjects ($P < 0.05$) and three of the remaining four showed a similar tendency without reaching the level of significance (individual P between 0.059 and 0.15). The analysis of the peak velocity for individual subjects revealed a weaker effect than the peak angular acceleration and the movement duration. Subjects' data are shown in Fig. 4, *E* and *F* for the peak acceleration and movement duration, for which the effect of 0 g was the strongest. There was no evidence for clear evolution of the kinematics parameters after the early exposure period, although the parameters of the grip force modulations seemed to stabilize.

Analyses of the overshoots and undershoots of the subjects revealed an increased tendency to undershoot the target in 0 g in both movement directions, logically accompanied by a decrease in the tendency to overshoot the target (which was the dominant strategy in 1 g). The proportion of trials presenting overshoots or undershoots is shown in Table 1. This proportion was evaluated on the data from all blocks to estimate percentages on a sufficient number of trials. There was no evidence that the trials presenting undershoot profiles were not uniformly distributed across the blocks. The change in gravity did not significantly affect the over/undershoot amplitudes. The average $\Delta\theta$ measured for up and down movements was equal to 12.3 and 3.1% in undershoot and overshoot trials, respectively.

It is well known that the endpoint variability depends on the duration of the movement, as a consequence of the speed-accuracy trade-off (Fitts' law). According to the optimal feedback control theory, movement variability also depends on the quality of the internal models. Therefore if the 0 g condition induces uncertainty in the internal models, as suggested by the grip/load forces coupling, we expect to observe higher trial-to-trial variability in 0 g for similar ranges of movement duration. To test this prediction more specifically than with the overall variability, as presented earlier, we divided separately up and down data for each subject into four subsets containing an equal number of trials. The division was based on the distribution of the measured movement time, using the percentiles 25, 50, and 75% of the distribution. The coefficient of variation of the movement amplitude (CV, defined as the SD normalized to the mean, expressed as a percentage) was evaluated on each subset of trials. Thus the relationship between CV and the movement duration was estimated in each gravitational condition by means of linear regressions computed on 80 points (10 subjects $\times$ 4 quartiles $\times$ 2 directions).

First, CV in 0 g was significantly greater than that in 1 g (Wilcoxon rank-sum, $P < 0.01$). In addition, Fig. 5 shows that

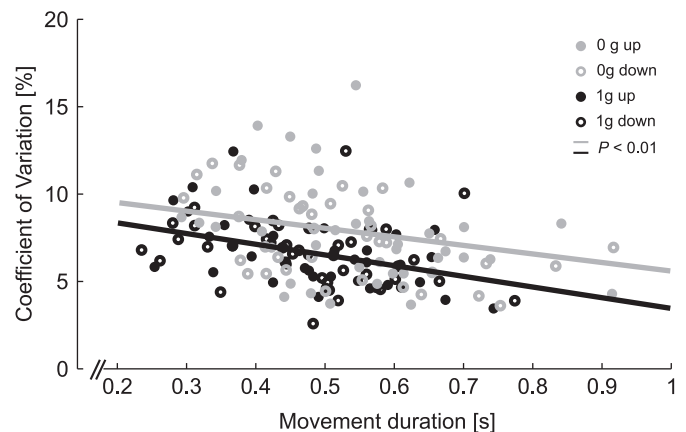


FIG. 5. Coefficient of variation as a function of movement duration computed for all subjects and movement direction. Lines are linear regressions. The sample of each subject was divided into 4 subsamples of equal size based on the distribution of the movement duration. Data from up and down movements are shown with filled and open circles, respectively. Normal gravity data are shown in black and zero gravity data are shown in gray.

the CV negatively correlated with the average movement duration of each subset in each gravitational condition (linear regressions, $P < 0.01$), which is a straightforward consequence of the speed-accuracy trade-off (Fitts' law). Under the 0 g condition, the speed-accuracy trade-off was shifted by a positive offset, suggesting that movements of similar duration were indeed more variable under the 0 g condition.

To summarize, the observed patterns of grip force/load force coupling indicate the presence of uncertainty in the internal prediction during early exposure, while subjects gradually adapted their internal representation of dynamics. The shift in speed-accuracy trade-off in 0 g suggests that such uncertainty has an impact on the movement variability across the measured range of movement duration, compatible with the assumption that internal models are used for on-line movement control. During early exposure, movements were longer with reduced peak angular acceleration and velocity, trajectories were skewed, and an increased tendency for target undershooting could be observed. We show hereafter that this change in movement kinematics is compatible with the hypothesis that the cost function was adjusted, reflecting a greater reliance on feedback in the formation of the optimal control strategy.

Simulation results

The results presented earlier suggest the presence of uncertainty, bias, or noise, affecting the internal prediction. One can logically exclude the hypothesis that systematic errors (bias) in the prediction could explain the experimental results. If subjects were using an internal model adapted to 1 g to control the movement in 0 g, the motor commands would aim at fighting against a force that is no longer acting on the limb. This would produce excessive shoulder torque and target overshooting for upward movements, which is in contradiction with our data. We therefore presume that the changes in performance in 0 g relate more to increased noise or uncertainty in the various control processes, even though on average the processes are approximately well tuned to the 0 g environment. We considered first the possibility that noise in the output stages of the control might explain our results. We note that movements

TABLE 1. Percentage of trials presenting an overshoot or undershoot in the two gravitational conditions for up and down movements

	Movements Up		Movements Down	
	1 g	0 g	1 g	0 g
Overshoot	63 $\pm$ 5.7%	41 $\pm$ 5.5%	64 $\pm$ 6.0%	49 $\pm$ 7.0%
Undershoot	24 $\pm$ 6.5%	39 $\pm$ 7.3%	16 $\pm$ 5.1%	33 $\pm$ 8.5%

Values are averaged across subjects $\pm$ SE.

TABLE 2. List of parameters across the simulations

	Baseline	Low Gain
Ω_η	0	0.2×10^{-4} diag (1 1 1 0 0 0)
R	10^{-5}	$\alpha 10^{-5}$
w_1	1	$1/\alpha$
w_2	0.1	$0.1/\alpha$

Simulations with adjusted cost function were obtained by varying α . Parameters that do not appear in Table 1 were kept constant in all simulations (see METHODS for numeric values).

were visually guided, providing the subjects with reliable feedback on the limb position and velocity. Thus it is unlikely that subjects had a reduced capacity to sense the position and velocity of the limb. In addition, increasing the covariance of the output feedback noise (ω_k , Eq. 6) by a factor 100 in simulations produced an increase in endpoint variability inferior to 5% relative to baseline (parameters of baseline simulation are listed in METHODS and in Table 2), which could not account for the increase that we measured experimentally from subjects' data. We therefore kept the variances of the additive and multiplicative motor noises (ξ_k and ε_k in METHODS, Eq. 5) and the variance of the output feedback noise constant across the simulations and concentrated instead on the effects of increased noise or uncertainty in the prediction of the state.

The effect of changing the cost matrices is illustrated in Fig. 6. The simulations shown in Fig. 6 were computed in the presence of prediction uncertainty ($\Omega_\eta \neq 0$; see Table 2). Augmenting the ratio Q_k/R to penalize position error during the stabilization period increases the norm of the feedback gains (L_k with $\alpha < 1$, Fig. 6A). Given the presence of feedback delays, the increase in L_k brings the system closer to instability, which should be avoided by the controller. An example of velocity profile obtained in this situation is shown in Fig. 6B: as a result of signal-dependent noise, prediction uncertainty, and feedback delays, although the expected trajectory minimizes the position errors, single trajectories exhibit oscillatory behavior and multiple velocity peaks (dashed gray), which is in contradiction with subjects' data. Decreasing the ratio Q_k/R has the opposite effect: the norm of the feedback gains is decreased (Fig. 6A, $\alpha > 1$), which reduces the risk of instability due to feedback delays and smooths out the velocity profile as illustrated in the example shown in Fig. 6B. Thus the following analyses focus on values of $\alpha > 1$ for testing the hypothesis that subjects adjusted the cost function in 0 g due to internal model uncertainty.

Figure 7 shows the effect of introducing the prediction noise and the effect of changes in the cost function obtained by varying α (see METHODS and Table 2 for details about the parameters changed across simulations). The baseline trajectories (black) were obtained without prediction noise ($\Omega_\eta = 0$), corresponding to a movement executed with a very good internal model. The red trajectories were obtained after introducing the prediction noise ($\Omega_\eta \neq 0$) while keeping constant the cost parameters (Q_k and R in Eq. 7). The issue of movement variability in this situation is obvious: the speed profiles represented in red clearly present deviations and trial-to-trial variations that are not compatible with empirical data from human subjects. In particular, single trajectories showed multiple velocity peaks (Fig. 7B) and the simulations' endpoint variability across trials increased by a factor 5 as a consequence of introducing the estimation noise (Fig. 7C).

We hypothesized that changing the relative weighting between Q and R would allow the CNS to derive control policies that are less sensitive to the variability in the estimate of the current state, based on the initial simulations reported earlier. More specifically, we reasoned that by applying a greater penalty to large motor commands (increasing R), fluctuations in the output due to fluctuations in the state estimate would be attenuated, at the expense of a greater tolerance for steady-state error on the final position (decreasing Q_k). The blue trajectories shown in Fig. 7, A and B, corresponding to our hypothesis, were obtained by decreasing the Q_k/R ratio by a factor α^2 (Q_k was divided by α and R was multiplied by α simultaneously; see METHODS). Changing α has a visible effect on the kinematics of the movements produced by the modified cost function. Figure 7, C–E shows the effect of α on the 2D endpoint variability, skewness, peak angular acceleration (PA), peak angular velocity (PV), movement duration (MD), and undershoot (US). PA, PV, and MD are plotted as a function of α in Fig. 7E relative to the baseline: we computed the value of each variable measured on the simulations as a percentage of the value obtained in the baseline simulation when $\Omega_\eta = 0$. This was done to address the variation observed in the experimental data measured for each subject relative to the values collected under Earth gravity condition. The undershoot was estimated on the simulations as the percentage of angular displacement achieved at the end of the running period. For each value of α , the parameters were averaged across 500 simulations.

Adjusting the cost function by changing the cost parameters achieves good quantitative predictions. Figure 8 shows the results after introducing the prediction noise with either normal

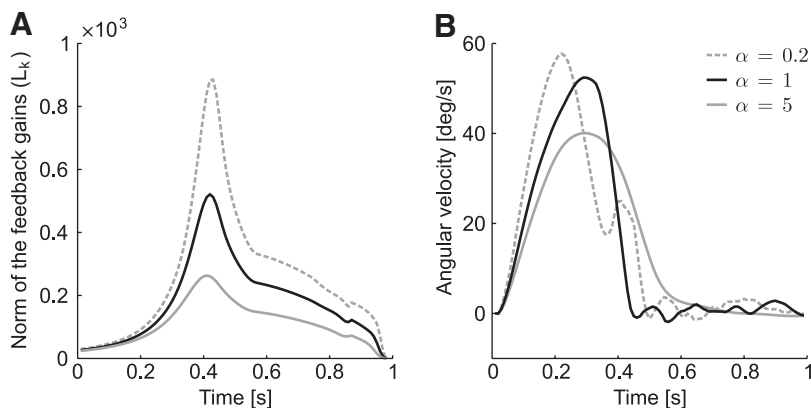


FIG. 6. A: examples of the norm of the optimal feedback gains (L_k) as a function of time in 3 distinct cases: the original cost function ($\alpha = 1$, black trace), the adjusted cost function with increased Q_k/R ratio ($\alpha < 1$, dashed gray trace), and the adjusted cost function with decreased Q_k/R ratio ($\alpha > 1$, gray trace). B: example of velocity profiles from single simulations computed with each series of feedback gains (same code as in A).

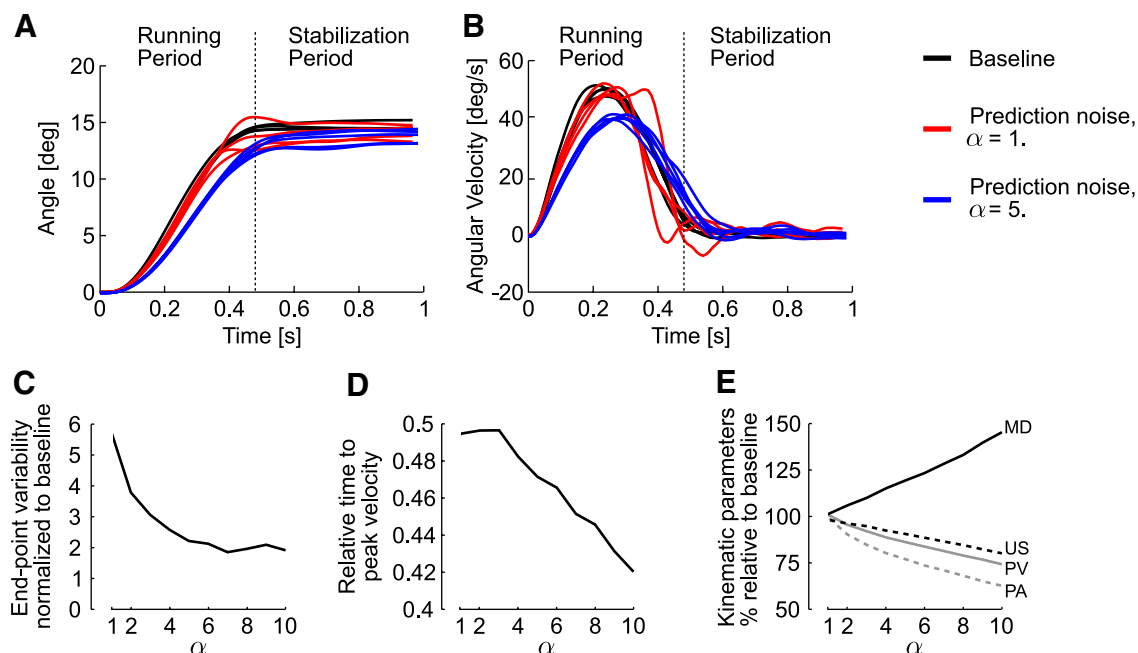


FIG. 7. A: angular displacement as a function of time for 3 simulation conditions: baseline (black); with prediction noise and normal control gain (red); with prediction noise and low control gain (blue). Four trajectories are represented for each simulation condition. B: corresponding angular velocity as a function of time. C: estimated 2-dimensional endpoint variability measured in the simulations as a function of α . Simulation variability was normalized to the endpoint variability of the baseline simulation. D: skewness in the velocity profiles of the simulated movements as a function of α . E: kinematics parameters of simulated movements expressed as percentage relative to baseline. The relative variation plotted against α is shown for the peak acceleration (PA), the peak velocity (PV), the movement duration (MD), and the undershoot (US). For each value of α , the kinematics parameters were estimated on 500 simulations.

cost parameters ($\alpha = 1$, red squares) or modified cost parameters ($\alpha = 5$, blue diamond). With $\alpha = 5$, the 2D endpoint variability was similar to the experimental results (Fig. 8A subjects' endpoint variability was normalized to their individual level of variability measured in the 1 g condition). Figure 8A shows that the variability of the red trajectories is clearly not compatible with our experimental results. Applying the same cost function to the system with increased estimation noise results in a predicted variability of the endpoint sixfold greater than the baseline (red), whereas the empirically measured variability increased by a factor of only 2 (black and gray). In addition, these trajectories do not account for the changes in kinematics parameters that were measured experimentally (Fig. 8, B and C). Using the same cost function should generate the same kinematics, on average, despite an increase in variability around the average. Thus the red dots in Fig. 8B are all located at the baseline (100%), whereas the data taken in 0 g (black and gray) deviate systematically from baseline. Furthermore, the original cost function predicts symmetrical ve-

locity profiles corresponding to the absolute optimal trajectory under 0 g, whereas subjects produced skewed velocity profiles in this condition (Fig. 8C). In contrast, the blue trajectories, based on the modified cost function, exhibited a level of variability that was similar to the variability measured under 0 g (Fig. 8A) and the modulation of the kinematics parameter was clearly consistent with the effect of 0 g on the movement profiles (Fig. 8, B and C). Thus adjusting the cost parameters in the presence of uncertainty of the internal models captures quantitatively all the presently tested features of the effect of 0 g on the movement kinematics that we measured here.

DISCUSSION

Summary

During the transient effects of motor adaptation, internal models are inaccurate and may suffer from uncertainty. The present study explores the adjustment of movement objective

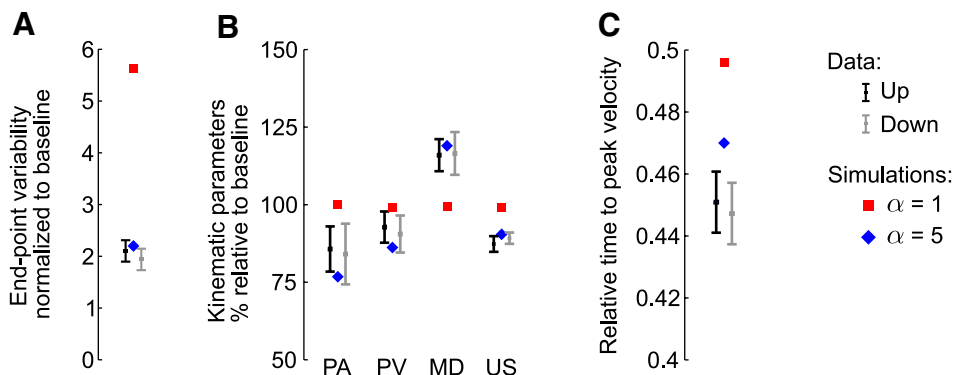


FIG. 8. Comparison between experimental data and model for $\alpha = 1$ (red square) and $\alpha = 5$ (blue diamond). A: endpoint variability. B: percentage of change for the peak acceleration (PA), peak velocity (PV), movement duration (MD), and target undershooting (US). Simulation results and experimental data were normalized to baseline and to 1 g, respectively. C: relative time to peak velocity. The vertical bars indicate the intersubject SE.

as a possible mechanism for preserving the movement stability under uncertain internal models. During the early exposure to novel gravitational context, grip force control was characterized by an elevated offset and low modulation. This effect is compatible with the presence of noise affecting the internal models. The shift in speed-accuracy trade-off supports that the uncertainty affects the control strategy and the trial-to-trial variability. The corresponding movements lasted longer, had lower peak velocities, and were performed with velocity profiles that were asymmetric. Subjects also increased their tendency to undershoot the target. In addition, overall endpoint variability increased in 0 g. Simulation results in good quantitative agreement with the data were obtained by injecting noise in the internal prediction and by adjusting the cost parameters in a particular fashion to vary the movement objective.

Grip-load coupling and prediction noise

The experimental GF modulation results motivated our theoretical approach. The time course of compensation of the load-force peaks enhanced the change in strategy for anticipatory grip-force scaling. In the context of Bayesian integration theory (Kording and Wolpert 2004), these results are consistent with the hypothesis that exposure to 0 g induces prediction noise: the CNS should therefore be less confident in the prediction and maintain a high constant level of grip force to compensate for the uncertainty. This is exactly what we implemented by introducing the prediction noise to simulate the internal prediction impairment.

In a previous experiment, Augurelle and colleagues (2003) reported that subjects without previous experience of micro-gravity dramatically increased their average grip force during the first parabolas when they performed oscillatory movements. The level of grip force then gradually decreased across parabolas to reach a steady level between the fifth and tenth parabolas. Hermsdörfer and colleagues (1999) observed a gradual decrease of the static grip force exerted against stationary objects across parabolas. These authors suggested that an observation period >5 parabolas would be necessary to observe stable grip force. In the present study, we found a gradual decrease and stabilization that was similar to that reported previously (Crevecoeur et al. 2009a), where the static grip force tended to stabilize after 10 parabolas. The differences in stabilization times (>5 to 10) are possibly due to the nature of the task (oscillatory movement vs. stationary holding and discrete movement), which could perhaps facilitate or impede grip-force scaling. However, all of these studies emphasized that initial grip force in 0 g is quite elevated and decreases gradually despite the fact there is no longer weight to be compensated. This is consistent with the hypothesis that uncertainty related to the 0 g environment encouraged subjects to maintain their grip force across parabolas.

Besides the general level of grip force, it was previously shown that grip-force modulation adjusts to the changes in load-force profiles induced by changes in gravity (Nowak et al. 2001) and the inertial load prediction stabilizes within four to five parabolas for naïve subjects, in both rhythmic and discrete movements (Augurelle et al. 2003; Crevecoeur et al. 2009a). However, in contrast to the changes in slope in the GF/LF relationship, there was no clear evolution of the load-force

peaks themselves across the parabolas, which suggests that the gradual evolution of the grip-force modulation is due to adaptation of internal models and not due to variations in arm movement kinematics and the associated load forces on the fingertips. Thus the internal prediction is processed in 0 g, but it may be less accurate, or considered as less reliable by the controller. Based on this hypothesis, we introduced the prediction noise to simulate the uncertainty affecting the internal models.

Alternative hypotheses in altered gravity

Although we observed an adaptation of GF/LF coupling over the course of 15 parabolas, we did not observe a consistent evolution of the kinematics of the movement over the same exposure time to weightlessness. Similar long-term modifications of movement kinematics were seen in an earlier study investigating similar movements over several days of continuous exposure to 0 g (Mechtcheriakov et al. 2002): peak acceleration and velocity were reduced and movement duration increased. In addition, these authors showed that the movements realized without visual feedback had greater errors. It was hypothesized that the slowdown of movements in weightlessness and the use of visual feedback permitted preservation of movement accuracy. However, they failed to justify that this hypothesis was realistic, given sensory noise and significant time delays. We solve this puzzle in the context of optimal feedback control and give an argument for the effect of 0 g on the control of movement that is grounded on computational results.

In the context of parabolic flights, Papaxanthis and colleagues (2005) reported a similar increase in movement duration at the beginning of exposure to 0 g for self-paced movements, although this difference vanished after practice. Their results therefore differ from our observations, in that we observed no tendency to recover the movement duration of the Earth gravity condition over the course of a similar number of parabolas. Differences in the protocols may account for the differing results concerning movement speeds; we restricted the movements to a single joint rotation, had no changes in pace, our target sequence was random, and our subjects performed the task in hypergravity after each exposure to 0 g, which could provoke washout between two consecutive parabolas.

A common result with the study from Papaxanthis et al. (2005), on the other hand, was the persistence of asymmetric velocity profiles in 0 g. It was proposed that it reflected a strategy based on the reproduction of the same limb kinematics in 0 g, at least initially, as one produces on the ground (skewed profiles are typical for vertical movements performed under normal gravity condition; Gentili et al. 2007). The idea is that the CNS would first adapt the motor command to reproduce stereotypical kinematics corresponding to the unperturbed condition (i.e., the Earth gravity in the present study) and only afterward would the movement kinematics be adapted to the dynamic context (Papaxanthis et al. 2005). Indeed, such an adaptive mechanism has been proposed in other experimental contexts (Lackner and DiZio 1994; Papaxanthis et al. 2005; Shadmehr and Mussa-Ivaldi 1994). The hypothesis that we propose in the present study provides an alternative explanation in the framework of optimal feedback control. Although

asymmetric trajectories are, in absolute, suboptimal in 0 g, we show that they are compatible with the effect of adjusting of movement objective on the movement kinematics to take into account the reduced confidence in the internal estimate of the state of the arm when first in 0 g.

Optimal control models based on the minimization of movement jerk (Flash and Hogan 1985) or joint torque (Nakano et al. 1999) predict that optimal trajectories in 0 g should present symmetrical profiles in 0 g. Similarly, the baseline trajectories obtained with the optimal feedback controller are symmetrical on average. Thus the presence of skewed velocity profiles in 0 g indicates that if reoptimization occurs (Izawa et al. 2008), it is surely not complete. It differs from the reoptimization that we observed within a similar exposure time to hypergravity (Crevecoeur et al. 2009b). However, in accord with the approach of the present study, this is compatible with the fact that the hypergravity has a limited effect on state estimation and internal prediction (Lackner and DiZio 2009; Nowak et al. 2001). Indeed, the correlation between the grip and load force increments were as good in hypergravity as in normal gravity, although the amplitude of the load variation was possibly overestimated (Crevecoeur et al. 2010). It suggests that hyper- and microgravity environments fundamentally differ by the difference of uncertainty related to the internal prediction to which subjects are exposed. Thus the question of adaptation after long-term exposure remains open. If confidence in the internal models and more demanding movement objective are restored after long-term practice, we expect to uncover evidence of optimality in the resulting movements. Alternatively, if a reoptimization is not observed, it would suggest that the interaction of muscular forces with external constraints that are absent in 0 g are necessary conditions for optimizing the motor commands.

Alternative proposals have been postulated, but not proven, to explain the slowing of point-to-point movements in weightlessness and the tendency toward less stable behavior at the end of the movement. Fisk et al. (1993) proposed a general reduction in motoneuron sensitivity stemming from the absence of descending influences from the vestibular apparatus to the spinal cord and from a deterioration of proprioceptive feedback. These effects would attenuate both the driving forces programmed to accelerate and decelerate the limb and the strength of reflex connections that would lead to a reduction of stiffness and damping. An underestimation of the mass in 0 g (Ross et al. 1984) would also result in a motor command that is smaller than necessary to achieve the desired movement and a level of cocontraction less than what would normally be required to stabilize the true mass at the end of the movement. Here we present a third hypothesis, couched in the theory of optimal feedback control. We argue here that the modifications to movement kinematics stem from a reoptimization of the control scheme, taking into account the greater uncertainty about the estimated state of the limb and a need to limit trial-to-trial variations. Thus instead of attributing observed changes in motor behavior in 0 g to the attenuation of graviceptor information (absence of descending vestibular influences), to perturbed sensory feedback, or to errors in mass estimation and motor programming (erroneous inverse models), we instead propose that humans modify movement parameters as a part of an optimization process that strives to balance needs in terms of performance parameters (error,

variability) with the metabolic costs of elevated feedback gains, taking into account the greater incertitude that the CNS might have when faced with the highly unusual weightless environment.

Stabilizing mechanisms

Artificial feedback delays alter the performances of subjects in a tracking task (Foulkes and Miall 2000; Miall and Jackson 2006): tracking error increases and corrective movements present a reduced frequency content of the motor responses to target jumps. Such a strategy could be explained by a reduction in control gain (Miall et al. 1993), producing stable corrective movements, although the resulting tracking is slow and sluggish. This effect is qualitatively similar to the effect of 0 g observed in the present study. Our approach interprets this behavior in the context of flexible optimal feedback control with adaptive cost function. This strategy may generalize to any situation of motor task in which movements are exposed to a higher risk of instability.

Stabilizing control is also closely related to the adjustment of limb impedance. The adjustment of stiffness and damping parameters has been proposed as a mechanism for stabilizing the movements and during motor adaptation and acquisition of internal models (Burdet et al. 2001; Franklin et al. 2003, 2008). The control strategy proposed in the present study could be combined with the learning mechanism proposed by Franklin et al. (2008): our approach considers the net motor command, which is independent from possible changes in the level of cocontraction at the shoulder joint. Thus we cannot assess whether there was a concomitant adjustment of limb impedance during the adaptation phase of our experiments. The adjustment of movement cost function and the optimal setting of limb impedance may be two cooperative mechanisms for maintaining the stability in both postural and movement control.

Benefits of optimal feedback control

A model based on optimal feedback control (OFC) was a natural choice, given the behavioral and neurophysiological evidences for similarities with movement control (Scott 2004; Shadmehr and Krakauer 2008). We postulated that, in this computational framework, early exposure to 0 g would introduce uncertainty and variability to the state estimation process, due to the novelty of the 0 g environment. However, when we computed the optimized control policies after introducing internal models uncertainty, we found that OFC predicts limb movements that differ significantly from what was observed in terms of movement speed and variability of trajectories across trials. If the CNS operates based on OFC principles, one concludes that the cost function must change in face of the greater estimation noise, presumably to reduce uncertainty and variability in the outcome. Intuitively, one might guess that the cost terms penalizing position and velocity errors at the final position should be increased to minimize quadratic error of these parameters in the optimization process. However, we showed that such an approach increases the risk of instability and amplifies the variability of single simulations. Our simulation results illustrate that the opposite approach should be taken when dealing with uncertainty and noise in the internal

state estimator. By penalizing high motor commands (increasing R), reactions to errors in the state estimation will be attenuated, leading to a reduction in trial-to-trial variability, but at the expense of a greater tolerance for steady-state error (undershoot) and slower movements (decreasing Q_k). Modifying the cost function in this way resulted in good quantitative agreement between the OFC model and the human behavior in 0 g on a single movement basis. In addition, changing these parameters to preserve movement stability has a direct consequence on the increase in endpoint variance that follows the introduction of uncertainty in the internal models. It makes a direct link between the stabilization of a single movement and the overall minimization of endpoint variance, which is known to be a determining factor in motor control (Harris and Wolpert 1998).

In the presence of sensory noise and feedback delays, complex movements with a highly demanding objective as a golf drive (Q_k elevated for movement precision and R low for execution speed) can be achieved only after long-term training and acquisition of a very good internal representation, mostly based on prediction. Thus our approach provides significant insight about why good predictions are observed before restoring the control performances during manipulation of an object with unknown dynamics (Flanagan et al. 2003). Flanagan and colleagues proposed that the forward model, which was found to adapt far more rapidly than the controller, was used to train the controller. We propose an interpretation of this phenomenon in the context of optimal feedback control as prediction and control are integrated in a single sensorimotor process. Control performances depend directly on the quality of the state estimate, which depends itself on the quality of the internal models. Thus learning to predict first is a necessary condition for maintaining the movement stability prior to restoring high control performances.

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DISCLOSURES

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

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