

Sensorimotor adaptation of point-to-point arm movements after spaceflight: the role of internal representation of gravity force in trajectory planning

Jérémie Gaveau,^{1,2} Christos Paizis,^{1,3} Bastien Berret,⁴ Thierry Pozzo,^{1,2,4,5}
and Charalambos Papaxanthis^{1,2}

¹UFR STAPS, Université de Bourgogne, Dijon; ²INSERM, U887, Motricité-Plasticité, Dijon, France; ³Centre d'Expertise de la Performance, Dijon, France; ⁴Department of Robotics, Brain and Cognitive Sciences, Istituto Italiano di Tecnologia, via Morego, Genova, Italy; and ⁵Institut Universitaire de France, Université de Bourgogne, Campus Universitaire, UFR STAPS, Dijon, France

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Gaveau J, Paizis C, Berret B, Pozzo T, Papaxanthis C. Sensorimotor adaptation of point-to-point arm movements after spaceflight: the role of internal representation of gravity force in trajectory planning. *J Neurophysiol* 106: 620–629, 2011. First published May 11, 2011; doi:10.1152/jn.00081.2011.—After an exposure to weightlessness, the central nervous system operates under new dynamic and sensory contexts. To find optimal solutions for rapid adaptation, cosmonauts have to decide whether parameters from the world or their body have changed and to estimate their properties. Here, we investigated sensorimotor adaptation after a spaceflight of 10 days. Five cosmonauts performed forward point-to-point arm movements in the sagittal plane 40 days before and 24 and 72 h after the spaceflight. We found that, whereas the shape of hand velocity profiles remained unaffected after the spaceflight, hand path curvature significantly increased 1 day after landing and returned to the preflight level on the third day. Control experiments, carried out by 10 subjects under normal gravity conditions, showed that loading the arm with varying loads (from 0.3 to 1.350 kg) did not affect path curvature. Therefore, changes in path curvature after spaceflight cannot be the outcome of a control process based on the subjective feeling that arm inertia was increased. By performing optimal control simulations, we found that arm kinematics after exposure to microgravity corresponded to a planning process that overestimated the gravity level and optimized movements in a hypergravity environment (~ 1.4 g). With time and practice, the sensorimotor system was recalibrated to Earth's gravity conditions, and cosmonauts progressively generated accurate estimations of the body state, gravity level, and sensory consequences of the motor commands (72 h). These observations provide novel insights into how the central nervous system evaluates body (inertia) and environmental (gravity) states during sensorimotor adaptation of point-to-point arm movements after an exposure to weightlessness.

motor control; hand kinematics; inertia; humans

PREVIOUS INVESTIGATIONS have suggested that the central nervous system (CNS) uses an internal model of gravity to estimate the time to contact with an approaching object (McIntyre et al. 2001) and to control arm movements in an optimal way (Berret et al. 2008a; Crevecoeur et al. 2009b; Gentili et al. 2007; Papaxanthis et al. 2003). Several experiments in microgravity have corroborated the robust assimilation of our sensorimotor system to Earth's gravitoinertial environment. Weightlessness alters proprioception (Bock et al. 1992; Roll et al. 1998), causes orientation illusions (Lackner and DiZio 2000), and

influences motor performance (Fisk et al. 1993; Kingma et al. 1999; Papaxanthis et al. 1998, 2005; Pozzo et al. 1998; White et al. 2005, 2008). After a sufficient exposure to weightlessness, subjects are able to develop new motor strategies to appropriately control their movements (Crevecoeur et al. 2010a; Papaxanthis et al. 1998, 2005); in consequence, a readaptation to normal gravity conditions is necessary. For instance, after spaceflight, movement kinematics are modified (Bloomberg et al. 1997; Layne et al. 1997; Papaxanthis et al. 1998), and actions require much greater than normal effort (Harm and Parker 1993; Lackner and DiZio 2000). Motor performance decrements persist for several days, and their severity depends on the duration of spatial missions.

Biological movements are the most efficient in the sense that they optimize some performance criteria, which may include the goal of the movement, the current state of the musculoskeletal system, and the environment (Todorov 2004). After an exposure to weightlessness, the CNS operates under new dynamic and sensory contexts. How cosmonauts challenge sensorimotor changes after spaceflights and what optimal solutions they find to control their movements are still under discussion. Up to now, most of the experiments have investigated the physiological modifications caused by an exposure to microgravity and their time course of recovery. However, adaptation to novel perceptual and/or dynamic contexts require an accurate estimation of the sources that cause sensorimotor perturbations and errors. To find optimal solutions for rapid adaptation after spaceflight, cosmonauts have to decide whether parameters from the world or their body have changed and to estimate their properties. Bayesian estimation for inferring the source of motor errors was recently proved relevant to explain motor adaptation to velocity-dependent force fields, rotating rooms, and inertial perturbations (Berniker and Kording 2008). Interestingly, Crevecoeur and collaborators (2010b) reported that subjects make errors when estimating the origin of perturbations in a new dynamic environment. Precisely, they suggested that errors in grip force/load force coupling during vertical arm movements in hypergravity (parabolic flights) were due to a misestimating of the mass of the held object, which remained unchanged in hypergravity, and not to the actual change of the gravity level.

In the present study, we investigated sensorimotor adaptation after a medium-term (10 days) exposure to microgravity. Five cosmonauts performed forward point-to-point arm movements in the sagittal plane 40 days before and 24 and 72 h after

Address for reprint requests and other correspondence: C. Papaxanthis, Unité 887, Institut National de la Santé et de la Recherche Médicale, Dijon 21000, France (e-mail: charalambos.papaxanthis@u-bourgogne.fr).

a spaceflight mission of 10 days. We examined the adaptation time course of arm kinematics, performed optimal simulations based on the minimisation of the absolute work (Berret et al. 2008a), and carried out a control experiment in which we tested the effects of various inertial loads on arm movement kinematics. More specifically, we examined whether the CNS attributed performance decrements after spaceflight to variations in the external environment (gravity force level) or to variations in the inertial properties of the body. We expected that, because cosmonauts had already experienced environmental changes (from 1 to 0 g) and had enough time to adapt their movements (10 days in weightlessness), they would attribute sensorimotor errors after the spaceflight to changes at the environment (i.e., gravity level) rather than to modifications in their body state (i.e., mass). The present study could provide interesting advice as to whether a statistical prior (Kording and Wolpert 2004) can guide sensorimotor adaptation when an omnipresent and constant feature of our daily environment, such as the gravity force level, is changed.

MATERIALS AND METHODS

Experiments Before and After Spaceflight Missions

The experiments described in this study were carried out before and after three spaceflight missions of 10 days at the International Space Station. Five male cosmonauts, with an age range between 30 and 45 yr (mean age: 39 yr), took part in the experiments. All were right-handed, and four of them had already participated in spaceflights. Cosmonauts were tested three times: 40 days before the spaceflight (BF) and 24 ± 1 h (R1) and 72 ± 3 h (R3) after their return to Earth. This schedule was decided by the spaceflight authorities, and only the acquisition of kinematic data was allowed. Spaceflights were separated by a time interval of 6 mo. Two cosmonauts were tested during the first spaceflight, two others during the second, and the fifth cosmonaut during the third spaceflight. Experiments were carried out in agreement with legal requirements and international norms (Declaration of Helsinki, 1964).

Experimental protocol. Cosmonauts were comfortably sat on a chair with their trunk aligned in the vertical position supported by the back of the chair. Their feet were placed flat (10 cm apart at the heels), and their shanks were aligned with the vertical axis. The task consisted of pointing forward with the dominant (right) arm toward a target (a reflective marker of 1-cm diameter) attached to a wooden dowel (Fig. 1A). The distance between the index finger and the target

was 35 cm. At the starting position, the right shoulder, right index finger, and target were aligned in the horizontal plane. Furthermore, the shoulder elevation, shoulder azimuth, shoulder torsion, and elbow anatomic angles were $\sim 15^\circ$, 0, 0, and 120° , respectively. This initial position of the right arm was stable during all trials performed before and after the spaceflight. The accomplishment of arm movements required a shoulder flexion of $\sim 60^\circ$ and an elbow extension of $\sim 95^\circ$. Arm movements were performed under normal visual acuity conditions (i.e., cosmonauts were able to see their arm and the target) at two different speeds: natural (cosmonauts were instructed to move at a natural self-selected speed) and fast (cosmonauts were instructed to move very fast). No further instructions were given about hand path or arm postures. In each experimental session (BF, R1, and R3), cosmonauts performed a total of 24 trials (12 trials for each speed condition), which were randomly given to them. Trials were separated by a time interval of 30 s to avoid muscular fatigue, in particular during R1.

Data recording and analysis. An optoelectronic motion analysis system (ELITE system, BTS), with three television cameras (sampling frequency: 100 Hz), was used for data acquisition. The motion of the arm was recorded by placing reflective markers (plastic spheres of 1 cm in diameter) on well-defined anatomic locations on the right arm: the shoulder (acromion), elbow (epicondyle), wrist (radius styloid process), hand (second metacarpophalangeal joint), and nail of the index finger. After three-dimensional calibration, the spatial resolution for movement measurements in the present experiment was <1 mm. Data processing was performed using custom software written in Matlab (Mathworks, Natick, MA). Recorded kinematic signals in the three axes of the space (X, Y, Z) were low-pass filtered using a digital fifth-order Butterworth filter at a cutoff frequency of 10 Hz. The start and end of each trial was defined as the time that finger tangential velocity went above or fell below 5% of maximum velocity. After this analysis, we calculated the following kinematic parameters of the marker placed on the right index fingertip (see Fig. 1, B and C): 1) movement duration (MD); 2) peak velocity (V_{peak}); 3) symmetry of velocity profile, defined as the ratio of acceleration duration to total MD (AD/MD; a ratio equal to 0.5 indicates symmetrical velocity profiles); and 4) hand path linearity, defined as the ratio of maximum perpendicular path deviation from a straight line connecting the initial and final points of the trajectory (Dev/L; a ratio equal to 0.5 indicates semicircular hand paths). To better illustrate variations in hand trajectories before and after spaceflight, we normalized finger paths and finger tangential velocity profiles for each trial and each cosmonaut. The normalization assured that paths and velocity profiles were independent of the distance travelled and MD. Paths were first scaled and rotated so as to align the start and end points of the movements. Velocity profiles were normalized in time and in amplitude. To

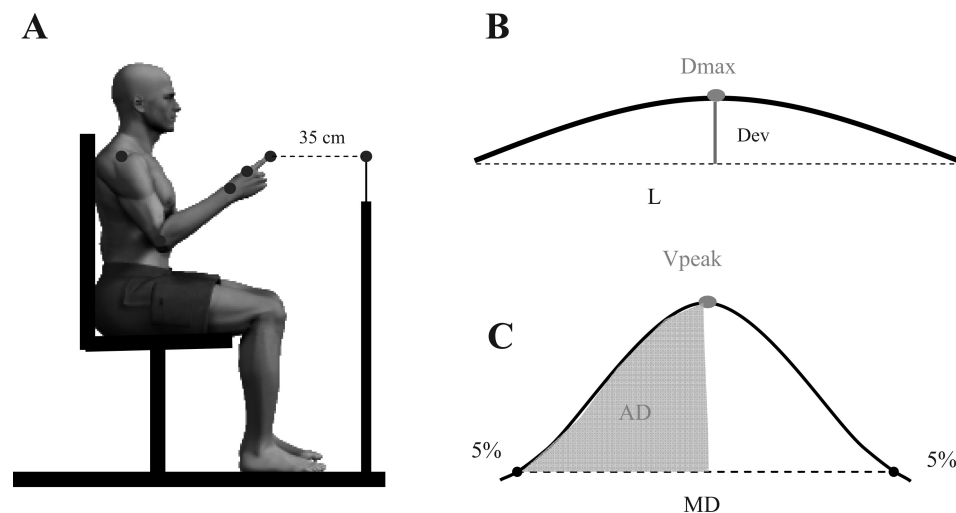


Fig. 1. A: initial position of the participants (right side view), anatomic locations on the right arm in which reflective markers were placed, and motor task. Participants performed forward-pointing arm movements in the sagittal plane. B and C: illustrations of the kinematic data analysis. B: hand paths. Shown is the maximum perpendicular path deviation (D_{max}) from a straight line (L) connecting the initial and final points of the trajectory. Dev, deviation. C: hand velocity profiles. V_{peak} , peak velocity; MD, movement duration; AD, acceleration duration.

quantify changes in the shape of hand path curvatures and velocity profiles after spaceflight, we used two complementary methods. First, we compared Dev/L and AD/MD between the three experimental sessions (BF, R1, and R3). This comparison indicated whether geometric (Dev/L) and temporal (AD/MD) parameters of arm movements change and adapt after an exposure to microgravity. Additionally, changes in hand path curvatures and velocity profiles, before and after spaceflight, were evaluated using a reference hand trajectory: that predicted by the minimum jerk model (Flash and Hogan 1985). This model predicts straight hand paths and symmetrical velocity profiles independently of kinematic and dynamic constraints. We calculated the differences (i.e., whole deviation) between hand trajectories (paths and velocity profiles) recorded experimentally and those predicted by the minimum jerk model for our point-to-point arm movements. Our reasoning was as follows: if these differences remained stable before and after spaceflight, we could consider that microgravity did not affect hand trajectories. On the contrary, if differences increased or decreased, we could conclude that an exposure to microgravity influences hand kinematics.

The whole deviations were quantified by the mean squared error (MSE) for hand paths and hand tangential velocity profiles.

Hand paths were computed as follows:

$$\frac{1}{N} \sum_{n=1}^N [(x_n^{\text{exp}} - x_n^{\text{MJ}})^2 + (y_n^{\text{exp}} - y_n^{\text{MJ}})^2 + (z_n^{\text{exp}} - z_n^{\text{MJ}})^2]$$

where n is the index of 10-ms sampling points; $(x_n^{\text{exp}}, y_n^{\text{exp}}, z_n^{\text{exp}})$, and $(x_n^{\text{MJ}}, y_n^{\text{MJ}}, z_n^{\text{MJ}})$ are the coordinates of the actual data (exp) and those predicted by the minimum jerk model (MJ); and N is the total number of sampling points related to the actual movement duration. MSE was calculated for each experimental session (BF, R1, and R3).

Hand tangential velocity profiles were computed as follows:

$$\frac{1}{N} \sum_{n=1}^N [(v_n^{\text{exp}} - v_n^{\text{MJ}})^2]$$

where $(v_n^{\text{exp}}, v_n^{\text{MJ}})$ are the velocity coordinates of actual data (exp) and those of predicted data (MJ), respectively. MSE was calculated for each experimental session (BF, R1, and R3).

We also calculated gravitational and net (inertial, interaction, Coriolis, and centripetal components) torques exerted at the shoulder and elbow joints using the equations described by Berret et al. (2008a). To test the influence of spaceflight on both gravitational and net torques, we calculated the MSE between R1 and BF, as well as between R3 and BF for the shoulder and elbow joints, separately.

Net torques (τ_n) were computed as follows:

$$\frac{1}{N} \sum_{n=1}^N [(\tau_n^{\text{BF}} - \tau_n^{\text{R1}})^2]$$

$$\frac{1}{N} \sum_{n=1}^N [(\tau_n^{\text{BF}} - \tau_n^{\text{R3}})^2]$$

Gravitational torques (τ_g) were computed as follows:

$$\frac{1}{N} \sum_{n=1}^N [(\tau_g^{\text{BF}} - \tau_g^{\text{R1}})^2]$$

$$\frac{1}{N} \sum_{n=1}^N [(\tau_g^{\text{BF}} - \tau_g^{\text{R3}})^2]$$

Statistical analysis. For each cosmonaut, we calculated the average values for all the parameters detailed above. Due to the small number of subjects ($n = 5$) and to the fact that not all variables showed normal distributions (Shapiro-Wilk tests), we performed nonparametric tests (Wilcoxon tests). Results were considered to be significant at $P < 0.05$.

Optimal simulations for different gravity levels. We modeled the human arm as a standard rigid body with two degrees of freedom

moving in the sagittal plane. We considered that torques are smoothly produced by muscle activation and that the CNS controls the second derivative of these torques:

$$\tau = M(\theta)\ddot{\theta} + C(\theta, \dot{\theta}) + G(\theta)$$

$$\dot{\tau} = u$$

where M is the inertia matrix, C is the Coriolis/centripetal torque, and G is the gravitational torque (see Berret et al. 2008a for their values); u is the control vector (it can be considered as the input to the motor neurons), θ is the joint angle, and dots indicate the time derivatives. $G(\theta) = g\tilde{G}(\theta)$ with $\tilde{G}(\theta)$ independent of gravity acceleration (g is the acceleration of the ambient gravitational field, 9.81 m/s^2).

We tested two alternative adaptation processes. First, we hypothesized that cosmonauts would optimize their movements for a greater gravitational force field after a spaceflight. We based this assumption on the fact that cosmonauts felt that their body was heavier than usual when coming back to Earth [sensation of a hypergravity environment (see Lackner and DiZio 2000)]. Alternatively, we tested optimal movements for a 0-g environment. This hypothesis implies that cosmonauts had completely adapted their movements to microgravity and continued to apply this optimal control strategy after landing.

An optimal control strategy for a 0- or 2-g environment, while actually being in 1 g, could be compensated during movement execution using a corrected motor command, as follows:

$$u = u^{0g} + u^{\text{grav } 1g}$$

$$u = u^{2g} - u^{\text{grav } 1g}$$

where u^{0g} and u^{2g} denote feedforward control and $u^{\text{grav } 1g}$ is the compensating signal taking into account the actual gravity field.

Such a corrective motor strategy is related to the separation principle between static and dynamic forces during movement execution (Crevecoeur et al. 2009a; Flanders and Herrmann 1992; Flanders et al. 1994). To solve the degree of freedom problem and derive a unique feedforward motor command (u), we assumed optimal control. The first possibility was to consider kinematic costs, such as minimum hand or angle jerk models. A second possibility was to consider a dynamic cost function, such as energy cost. Following previous findings (Berret et al. 2008a), we proposed a hybrid model minimizing a compromise between kinematic and dynamic costs.

The cost function (J) was thus defined as follows:

$$J = \int_0^T j_{\text{dyn}} + j_{\text{kin}} dt$$

$$j_{\text{dyn}} = \left| \dot{\theta}_1 \tau_1 \right| + \left| \dot{\theta}_2 \tau_2 \right| \text{ and } j_{\text{kin}} = \alpha (\ddot{\theta}_1^2 + \ddot{\theta}_2^2)$$

where j_{dyn} is dynamic cost, j_{kin} is kinematic cost, θ_1 and θ_2 are shoulder and elbow joints angles, τ_1 and τ_2 are shoulder and elbow joints torques, α is a parameter used to take into account the different units of each cost component, and T is MD (measured experimentally).

The dynamic cost is a measure for mechanical energy expenditure, whereas kinematic cost is a measure of movement smoothness in joint space. In this study, we scaled the costs so that their relative contribution was approximately the same during fast and normal speed conditions. This corresponded to $\alpha = 0.05$ and 0.2 for fast and normal conditions, respectively. This setting was kept fixed for all cosmonauts and all gravitational environments. Anthropometric parameters were adjusted for each cosmonaut based on their mass, height, and forearm/upper arm lengths (Winter 1990).

The optimal control problem defined by the dynamics and cost function was eventually solved using an efficient numerical method. Here, we used the open-source Matlab software GPOPS, which implements a pseudospectral method to find near optimal solutions (Benson et al. 2006; Garg et al. 2009; Rao et al. 2010). We checked a posteriori that Pontryagin's necessary conditions for optimality

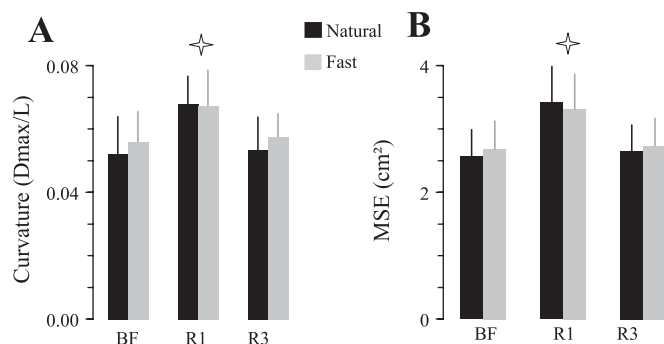


Fig. 2. Spatial features. *A*: average values (\pm SD) of hand path curvature for the two speed conditions [natural (N) and fast (F) arm movements] and three experimental sessions [before the spaceflight (BF) and 24 ± 1 h (R1) and 72 ± 3 h (R3) after the return to Earth]. *B*: average values (\pm SD) of mean squared errors (MSE) between hand paths recorded experimentally and those predicted by the minimum jerk model. Stars show significant differences between BF-R1 and R1-R3.

were satisfied. We compared the simulated hand path curvatures (Dev/L) and symmetry of velocity profiles (AD/MD) with those recorded experimentally (group of cosmonauts) using nonparametric tests (Wilcoxon tests). Results were considered to be significant at $P < 0.05$.

Control Experiment

Ten righthanded adults (7 men and 3 women, mean age: 37 ± 6.2 yr) participated in the control experiments, which were carried out in agreement with legal requirements and international norms (Declaration of Helsinki, 1964). Apparatus, motor task, arm initial position, and instructions were exactly the same with those of spaceflight experiments. The purpose of the control experiment was to examine whether variations in arm inertia could influence hand kinematics and to compare these changes, if any, with those after spaceflight. Participants were required to perform natural and fast arm pointing movements under five load conditions: without additional load (NL) and with additional loads of 0.25–0.35 kg (L1), 0.5–0.6 kg (L2), 0.85–0.95 kg (L3), and 1.25–1.35 kg (L4). Control experiments were carried out in two distinct sessions with a time interval of 5 mo. *Session I* comprised the NL, L1, and L3 conditions, whereas *session II* comprised the L2 and L4 conditions. All participants performed 20 trials in each load condition (a total of 200 trials); within each session, the order of loads and speeds was randomized. Additional loads were fixed on the center of rotations of the upper arm (half of the load) and the forearm (half of the load) and were calculated separately for each participant to produce an increase of arm inertia of 10% (L1), 25% (L2), 40% (L3), and 55% (L4). Data acquisition and analysis were similar with the spaceflight experiment. All variables showed normal distributions (Shapiro-Wilk tests). We used repeated ANOVA to test the effects of load and speed on hand path curvature and the symmetry ratio of velocity profiles. Post hoc analysis was performed by means of Scheffé tests. Comparisons between the group of cosmonauts and the control group were performed using nonparametric tests (Mann-Whitney tests). Results were considered to be significant at $P < 0.05$.

Optimal simulations for different inertial loads. We performed optimal simulations (see above) in a normal gravity environment by progressively increasing the mass of the arm (from NL to L4). Anthropometric parameters, movement duration, and arm mass were adjusted individually so as to reproduce the NL, L1, L2, L3, and L4 experimental conditions. Our model optimized net torques at the shoulder and elbow joints for the different load conditions while compensating for the increase in gravity torque (due to the added loads) during movement execution (see *Optimal simulations for different gravity levels*).

RESULTS

Spaceflight Experiment

Hand path curvatures. All cosmonauts performed planar arm movements in the sagittal plane before (BF) and after (R1 and R3) the spaceflight; shoulder azimuth and torsion angles showed very small displacements ($<0.9^\circ$). Cosmonauts consistently produced slightly curved hand paths (see Figs. 2 and 3). All curvatures had positive values as their maximum deviation from straightness was oriented upward. It was noticeable that spaceflight significantly influenced hand path curvatures, which were significantly greater during the R1 session than during the BF and R3 sessions (for both speed and session comparisons, $Z > 2$ and $P < 0.05$). In the R3 session, hand path curvature decreased and returned to BF values (for both speed comparisons, $Z < 1.5$ and $P > 0.1$). We obtained similar results for the whole deviation from straightness (Fig. 2*B*). The difference between the experimental and simulated (minimum jerk) paths increased in the R1 session (for both speed and session comparisons, $Z > 2$ and $P < 0.05$), indicating that the exposure to microgravity significantly affected the shape of hand paths, but returned to BF values in the R3 session (for both speed comparisons, $Z < 1.5$ and $P > 0.1$). Typical hand paths from one cosmonaut and average-normalized hand paths from each cosmonaut are shown in Fig. 3, *A* and *B*, respectively. All cosmonauts showed similar behavior, i.e., greater path curvatures in R1 and similar path curvatures in BF and R3. Figure

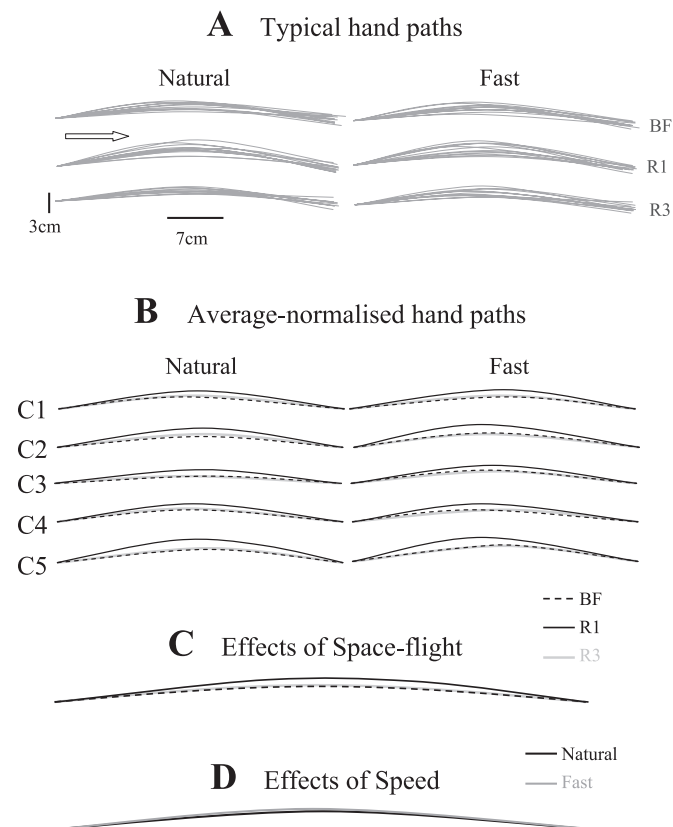


Fig. 3. Hand path curvatures. *A*: typical hand paths ($n = 12$) from one cosmonaut. The arrow indicates the movement direction. *B*: average-normalized hand paths from each cosmonaut (cosmonauts C1–C5). *C*: comparison of averaged-normalized hand paths between the three sessions (BF, R1, and R3). *D*: comparison of averaged-normalized hand paths between natural and fast speeds.

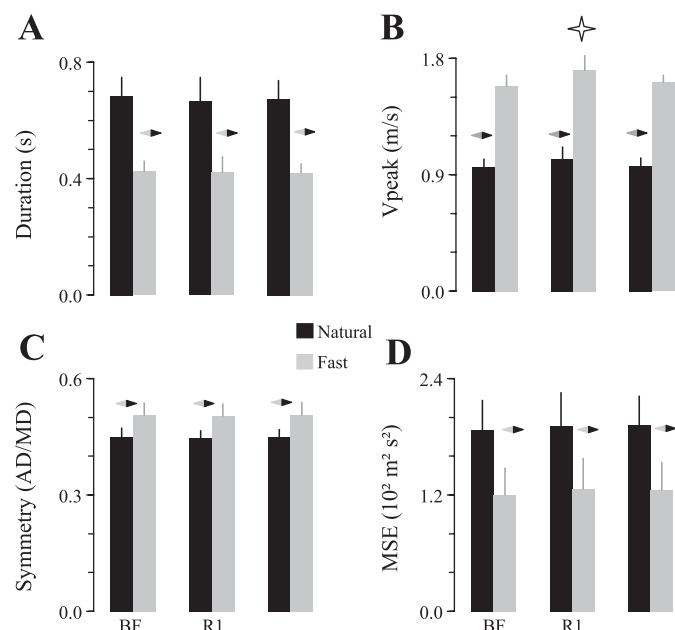


Fig. 4. Temporal features. A–D: average values (\pm SD) of MD (A), V_{peak} (B), symmetry (AD/MD) of velocity profiles (C), and MSE between hand velocity profiles recorded experimentally and those predicted by the minimum jerk model (D). Stars show significant differences between BF–R1 and R1–R3; diamonds indicate differences between natural and fast speeds.

3C shows average-normalized hand paths from all cosmonauts before and after the spaceflight.

Path curvature was almost similar, or slightly greater, for fast compared with natural arm movements (see Fig. 2A). The statistical analysis for path linearity (Dev/L) showed that speed did not significantly affect path curvature in either the preflight (BF) or postflight (R1 and R3) sessions (for all comparisons, $Z < 1.5$ and $P > 0.1$). This finding is qualitatively shown in Fig. 3D, in which average and normalized hand paths from all cosmonauts are plotted to show the comparison between natural and fast speeds.

Note that a trial-by-trial analysis did not show any adaptation process in R1. The first ($\text{Dev/L} = 0.070 \pm 0.008$, average value

of 5 cosmonauts and 2 speeds) and last ($\text{Dev/L} = 0.069 \pm 0.009$) trials were not statistically different ($Z < 0.7$ and $P > 0.5$).

Hand velocity profiles. Average (\pm SD) values of temporal parameters are shown in Fig. 4. Spaceflight did not affect MD (Fig. 4A) for either natural (for all session comparisons, $Z < 0.4$ and $P > 0.6$) or fast (for all session comparisons, $Z < 0.7$ and $P > 0.2$) arm movements. However, peak velocities (Fig. 4B) slightly increased in R1 (for both speeds, $Z > 2$ and $P < 0.05$) and returned to preflight values in R3 (for both speeds, $Z < 0.9$ and $P > 0.3$). As could be expected from our requirements, durations and peak velocities were, respectively, shorter and greater for fast compared with natural arm movements (for all comparisons, $Z > 2$ and $P < 0.05$). A trial-by-trial analysis for movement duration and peak velocity did not reveal any adaptation process in R1. The first ($\text{MD} = 0.55 \pm 0.05$ s, $V_{peak} = 1.37 \pm 0.08$ m/s, average values of 5 cosmonauts and 2 speeds) and last ($\text{MD} = 0.54 \pm 0.05$ s, $V_{peak} = 1.36 \pm 0.07$ m/s) trials were not statistically different (in both cases, $Z < 1.2$ and $P > 0.2$).

All cosmonauts performed arm movements with single-peaked velocity profiles. Typical hand velocity profiles from one cosmonaut and average-normalized hand velocity profiles from each cosmonaut are shown in Fig. 5, A and B, respectively. Velocity profiles were almost similar before and after the spaceflight. Statistical analysis showed that the symmetry (AD/MD) of hand velocity profiles (Fig. 4C) was similar between the BF, R1, and R3 session (for all comparisons, $Z < 0.5$ and $P > 0.1$). We obtained similar results when comparing the velocity profiles recorded experimentally with the velocity profiles predicted by the minimum jerk model (Fig. 4D). Their differences (MSE) remained stable throughout the sessions (for all comparisons, $Z < 0.5$ and $P > 0.1$), indicating that the shape of the velocity profiles did not vary after the spaceflight. This finding is qualitatively shown in Fig. 5C, where we plotted for comparison average-normalized hand velocity profiles from all cosmonauts before and after the spaceflight.

Interestingly, velocity profiles were more symmetrical for fast than for natural arm movements. Statistical analysis showed that movement speed significantly affected the sym-

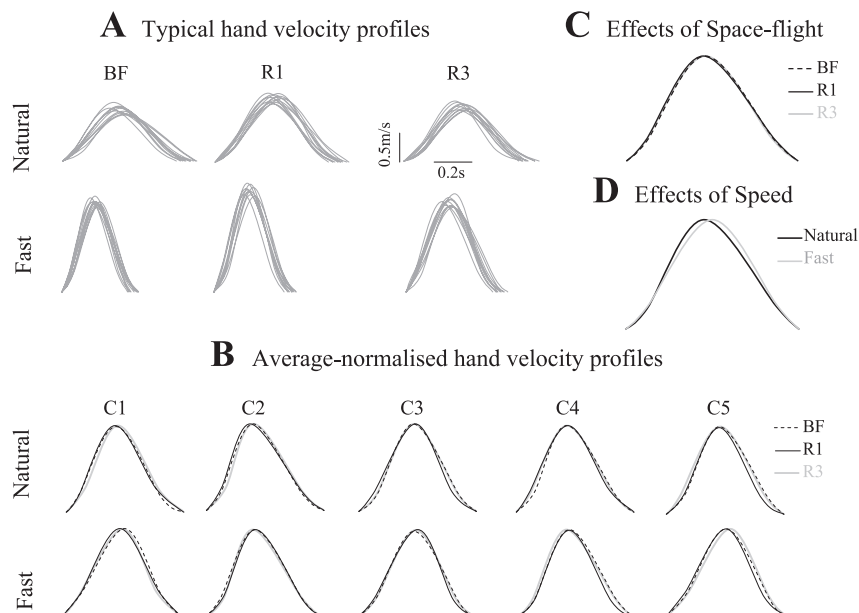


Fig. 5. Hand velocity profiles. A: typical hand velocity profiles (12 trials) from one cosmonaut. B: average-normalized hand velocity profiles from each cosmonaut. C: comparison of average-normalized hand velocity profiles between the three sessions (BF, R1, and R3). D: comparison of average-normalized hand velocity profiles between natural and fast speeds.

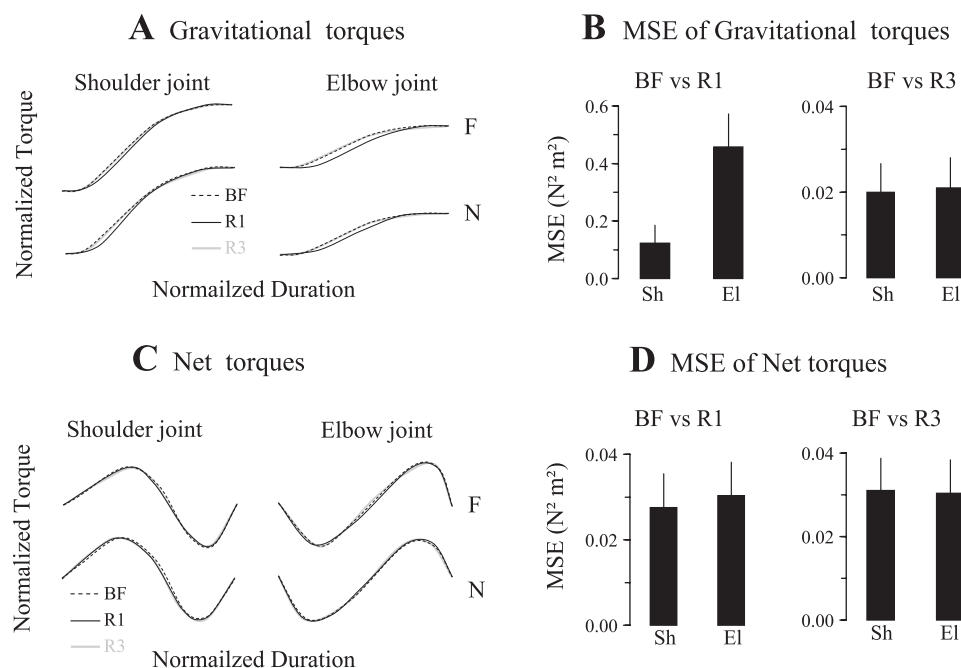


Fig. 6. Gravitational and net torques. A: average-normalized (five cosmonauts) gravitational torques for the shoulder (Sh) and elbow (El) joints. B: average (\pm SD) values of MSE of gravitational torque. C: averaged-normalized (five cosmonauts) net torque for the two joints, the two speeds, and the three sessions. D: average (\pm SD) values of MSE of net torque (BF).

metry of hand velocity profiles in all sessions ($Z > 2$ and $P < 0.05$). This finding is qualitatively shown in Fig. 5D, in which we plotted for comparison the average and normalized hand velocity profiles from all cosmonauts according to movement speed. A trial-by-trial analysis for the symmetry of velocity profiles did not reveal any adaptation process in R1. The first (AD/MD = 0.48 ± 0.03 , average value of 5 cosmonauts and 2 speeds) and last (AD/MD = 0.47 ± 0.03) trials were not statistically different ($Z < 0.5$ and $P > 0.6$).

Gravitational and net torques. Before movement onset, the average (\pm SD) gravitational torque was 5.31 ± 1.42 N·m for the shoulder joint and 3.29 ± 0.94 N·m for the elbow joint, whereas at the end of the movement it was 12.10 ± 1.83 and 4.59 ± 1.18 N·m, respectively. As the initial and final orientation of the arm was stable across sessions and trials, gravitational torques were constant for these two positions. However, because hand path curvature changed in R1, the time course of gravitational torques also changed. This is shown in Fig. 6A, in which normalized gravitational torques (average of 5 cosmonauts) are shown for the shoulder and elbow joints, separately. It was noticeable that in R1 shoulder and elbow gravitational torques decreased during the motion of the arm. Mechanically, this is explained by the fact that greater hand paths in R1 required smaller elbow extension and, therefore, smaller shoulder and elbow gravitational torques. Figure 6B shows MSE values for the shoulder and elbow gravitational torques (natural and fast movements were averaged together). Discrepancies in gravitational torques were large between BF and R1 and very small between BF and R3.

Table 1 shows the peak net torque (average values of 5 cosmonauts) for natural and fast arm movements before and after the spaceflight. In R1, peak net torques slightly, but significantly, increased (for all comparisons, $Z > 2$ and $P < 0.05$) and returned to BF values in R3 (for all comparisons, $Z < 0.5$ and $P > 0.1$). This adaptation paralleled that of peak velocity. In Fig. 6C, normalized net torques (average of 5 cosmonauts) are shown for the shoulder and elbow joints, separately. It appears that cosmonauts used an appropriate scaling strategy because the shape of the torque profiles after normalization was similar between the BF, R1, and R3 sessions. This is consistent with the finding that hand velocity profiles remained unchanged after the spaceflight. Figure 6D shows MSE values for the shoulder and elbow net torques (natural and fast movements were averaged together). Discrepancies in net joint torques were very small between BF and R1 as well as between BF and R3.

Optimal simulations for different gravity levels. We hypothesized that, after returning from a spaceflight, cosmonauts misperceived the level of gravity force, i.e., they sensed themselves being in a higher than normal gravito-inertial context. Therefore, we simulated arm pointing movements in a normal gravity environment (similar to our BF measurements) and arm pointing movements in a hypergravity environment (progressively, from 1 to 2 g). We assumed that an optimal strategy in a hypergravity context could correspond to our R1 measurements. We also simulated arm movements in a microgravity environment to test the possibility that cosmonauts still used an optimal strategy developed during spaceflight in R1.

Table 1. Average peak net torques for the two speeds, two joints, and three sessions

	Natural Arm Movements			Fast Arm Movements		
	BF	R1	R3	BF	R1	R3
Shoulder joint	1.33 ± 0.09	1.41 ± 0.11	1.35 ± 0.08	5.47 ± 0.35	5.96 ± 0.52	5.55 ± 0.42
Elbow joint	-3.88 ± 0.21	-4.17 ± 0.32	-3.62 ± 0.18	-14.83 ± 0.95	-16.09 ± 0.95	-14.66 ± 0.90

Values are means \pm SD (in N·m). BF, before the spaceflight; R1, 24 \pm 1 h after the spaceflight; R3, 72 \pm 3 h after the spaceflight.

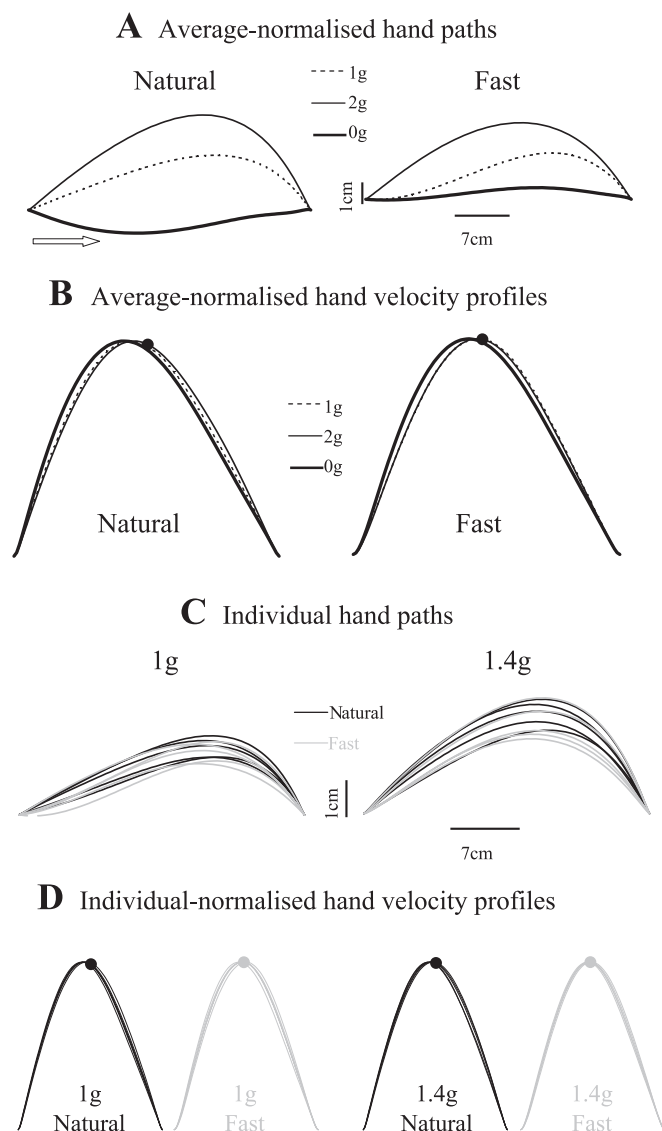


Fig. 7. Optimal simulations. *A*: average-normalized (five cosmonauts) simulated hand paths. *B*: average-normalized (five cosmonauts) simulated hand velocity profiles. *C*: individual simulated hand paths for 1- and 1.4-g levels. *D*: individual simulated hand velocity profiles for 1- and 1.4-g levels. 1 g, normal gravity; 2 g, hypergravity; 0 g, microgravity. Solid circles (black or grey) on velocity profiles indicate temporal symmetry (AD = deceleration duration). The arrow indicates the movement direction.

Figure 7, *A* and *B*, shows mean simulated trajectories (average of 5 cosmonauts). Hand paths and velocity profiles of the 1-g level (thin dotted lines) qualitatively and quantitatively corresponded to our experimental findings in the BF session (for both Dev/L and AD/MD, $Z < 0.5$ and $P > 0.6$). Furthermore, hand kinematics of the 2-g level (thin solid lines) qualitatively matched our experimental findings in R1. Notably, hand path curvature significantly increased in the 2-g level compared with the 1-g level and was almost identical between normal and fast arm movements. Furthermore, hand velocity profiles were similar between 1- and 2-g conditions but changed according to movement speed (more symmetrical for fast movements). Decreasing the level of gravity progressively in our simulations, we observed that optimal control at a gravity level of 1.4 g (i.e., 13.7 m/s^2) predicted hand kinematics similar to those recorded in R1. This qualitative observation

was confirmed by the statistical analysis. We compared the curvature values recorded experimentally with those predicted by the optimal model (1.6, 1.5, 1.4, 1.3, and 1.2 g) and found significant differences for all g levels ($Z > 2.02$ and $P < 0.05$) except for the 1.4-g level ($Z < 0.6$ and $P < 0.5$). Individual hand path and velocity profiles simulated for each cosmonaut under both speed conditions are shown in Fig. 7, *C* and *D*, and support the consistency of our simulation findings. Conversely, it is evident that in R1 cosmonauts did not reproduce an optimal strategy developed during the exposure to microgravity, because the 0-g level simulation (thick solid lines) did not predict the data recorded in R1.

Control Experiment

All participants performed planar arm movements in the sagittal plane (shoulder azimuth and torsion angles were inferior to 1°).

Hand velocity profiles. The symmetry of velocity profiles (Fig. 8*A*) was significantly influenced by speed ($F = 6.68$ and $P = 0.03$). AD/MD was smaller for natural compared with fast arm movements. In addition, load also influenced the symmetry of velocity profiles ($F = 8.02$ and $P < 0.001$). AD/MD progressively decreased when load increased (NL was different

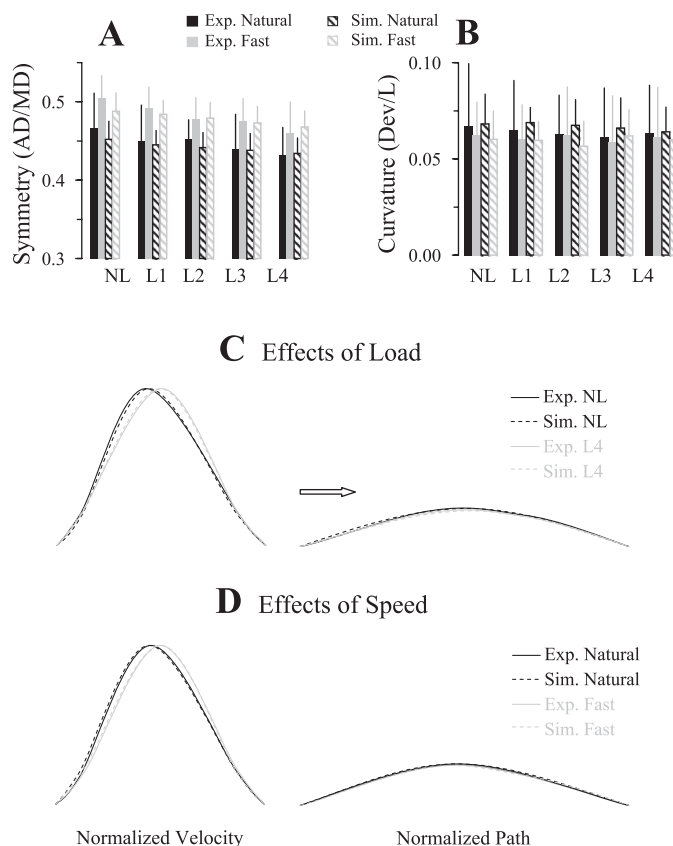


Fig. 8. Control experiments. *A*: average values (\pm SD) of the symmetry of the velocity profiles. *B*: average values (\pm SD) of the path curvature. *C*: average-normalized hand velocity profiles (left) and hand paths (right) showing the effects of load. *D*: average-normalized hand velocity profiles (left) and hand paths (right) showing the effects of speed. NL, without additional load; L1, additional load of 0.25–0.35 kg; L2, additional load of 0.5–0.6 kg; L3, additional load of 0.85–0.95 kg; L4, additional load of 1.25–1.35 kg. The arrow indicates the movement direction; Exp., experimental data; Sim., simulation data.

from L2, L3, and L4; L2 was different from L4; in all cases, $P < 0.05$). No interaction effect was found between the two factors ($F = 0.15$ and $P = 0.96$). Participants qualitatively showed the same results in the NL condition as the five cosmonauts in the BF session. For the control group, average movement durations were 0.66 ± 0.02 s (natural) and 0.35 ± 0.02 s (fast). No significant differences were found between cosmonauts and the control group for MD, V_{peak} , and symmetry of velocity profiles (for all comparisons, $Z < 1.5$ and $P > 0.1$).

Hand path curvatures. Participants consistently produced curved hand paths with positive curvatures (Fig. 8B). Path curvature did not vary with either speed ($F = 0.15$ and $P = 0.71$) or load ($F = 1.03$ and $P = 0.41$), and no interaction effect was found between load and speed ($F = 0.17$ and $P = 0.95$). Participants in the NL condition qualitatively showed the same results as the five cosmonauts in the BF session. No significant differences ($Z < 0.7$ and $P > 0.5$) were found between cosmonauts and the other participants for path linearity (Dev/L).

Optimal simulations for different inertial loads. Hand trajectories predicted from optimal simulations qualitatively and quantitatively matched those of the control experiment (see Fig. 8, A and B). Notably, for both natural and fast speeds, the symmetry of velocity profiles decreased when mass increased ($F = 13$ and $P < 0.001$), whereas load had no effect on hand path curvature ($F = 1.44$ and $P > 0.24$). Two-tailed t -tests between simulated and experimental data did not reveal significant differences for either path curvature (in all cases, $t < 0.7$ and $P > 0.5$) or the symmetry of velocity profiles (in all cases, $t < 0.9$ and $P > 0.8$).

Figure 8, C and D, qualitatively shows the experimental and simulated hand paths and velocity profiles. For clarity reasons, we show data from the L2 and L4 conditions.

DISCUSSION

In the present study, we investigated sensorimotor adaptation of arm movements after a spaceflight mission of 10 days. We mainly found that while hand path curvature increased 1 day after landing (R1) and returned to the preflight level on the third day (R3), hand velocity profiles remained unaffected. Control experiment showed that loading the arm with different masses did not affect path curvature, suggesting that changes in path curvature recorded in R1 were not the outcome of a control process based on the subjective feeling that the mass of the arm was increased. By performing optimal simulations, we found that arm kinematic features after a spaceflight corresponded to a control process that overestimated the gravity level and optimized movements in a hypergravity environment.

Hand Kinematics Before Spaceflight

Cosmonauts and participants from the control group performed arm movements with similar kinematic features. Paths were slightly curved and did not differ according to movement speed. Similar curvatures have been previously observed under a variety of experimental conditions (Atkeson and Hollerbach 1985; Gottlieb et al. 1997; Papaxanthis et al. 1998, 2003; Uno et al. 1989). However, it was of interest in our study that hand velocity profiles varied with movement speed. Velocity profiles of natural arm movements were asymmetric (acceleration duration was shorter than deceleration duration), whereas those

of fast arm movements were symmetrical. Arm kinematics observed in our experiments could be the outcome of a control strategy that optimizes gravity force. Our minimum absolute work model (Berret et al. 2008a) predicted similar hand paths and velocity profiles with those recorded experimentally. These results are in accordance with the general consensus that the brain optimally integrates external force into the motor planning process (Berret et al. 2008a; Crevecoeur et al. 2009b; Izawa et al. 2008).

Hand Kinematics After Exposure to Microgravity

One day after the spaceflight (R1), hand path curvatures were significantly greater from those recorded before flight (BF) and returned to BF values 3 days after landing (R3). Although we cannot report the exact time of adaptation of hand path curvatures, which could be any time between 24 h (R1) and 72 h (R3), it is remarkable that the five cosmonauts showed consistent motor behavior. Previous studies have also reported changes in the spatial features of movement after spaceflight. Papaxanthis et al. (1998) found that cosmonauts increased their hand path curvatures during upward arm movements after 6 mo in microgravity. Similarly, Courtine et al. (2002) observed greater curvatures for the foot displacements during natural walking after a long spaceflight experience. All together, these results indicate that geometric features of movements dramatically change after an exposure to microgravity and undergo a long adaptation process.

The shape of velocity profiles in R1 was similar to that recorded in BF, despite the fact that hand curvature and movement speed changed in R1. This indicates that cosmonauts used an appropriate scaling strategy at the level of net joint torques to produce similar velocity profiles. As several studies have reported, the shape of velocity profile changes with extensive practice in microgravity (Crevecoeur et al. 2010a; Papaxanthis et al. 1998, 2005); we cannot exclude the possibility that a rapid adaptation of velocity profile occurred during the first day after landing (i.e., before R1 measurements). However, in our study, the appealing finding was that spatial and temporal features of arm movements exhibited different time scales to return to baseline values after a spaceflight. This broadens previous studies that proposed that the CNS may decouple spatial and temporal aspects of arm movements (Biess et al. 2007; Crevecoeur et al. 2009a; Torres and Andersen 2006).

Sensorimotor Adaptations After Spaceflight

After a long exposure to microgravity, sensorimotor function is dramatically affected. Physiological modifications occurring both at the peripheral and central levels could account for the cosmonauts' motor behavior after spaceflight. Vestibulospinal interactions, which considerably vary after spatial missions (for a review, see Lackner and DiZio 2000; Miyoshi et al. 2003; Reschke et al. 1986), could directly affect arm movement kinematics. Descending influences from the otoliths on α - and γ -motoneurons may amplify muscle tone and the gain of spinal reflex pathways and, accordingly, could affect stiffness and viscosity. Such a transient influence of peripheral factors on arm movement control has been revealed during parabolic flight experiments (Fisk et al. 1993). In addition, perturbation of the vestibular system, by means of galvanic stimulation in normal gravity conditions, modifies the kinematics of arm movements (Bockisch and Haslwanter 2007;

Bresciani et al. 2002, 2005). The greater path curvatures observed in R1 could be partially explained by these impedance-based hypotheses. However, our findings that fast and natural arm movements were similarly affected after an exposure to microgravity is inconsistent with purely peripheral influences on arm kinematics. Under such a hypothesis, slow and fast arm movements should be differently affected after landing (Fisk et al. 1993), and feedback corrections should produce velocity profiles with multiple local maxima.

While we cannot underestimate the role of peripheral factors on arm motor performance, we consider that adaptations occurring at the central level have a major influence on arm motor performance after a spaceflight. These adaptations are reliant on the way that the brain estimates the origin of motor errors (Berniker and Kording 2008). What has changed: the properties of the body, the environment, or both? Here, we propose that cosmonauts overestimated Earth's gravity level and optimally controlled their arm movements as they would do in a hypergravity environment. Two findings guided us to this conclusion. First, optimal trajectories (hand paths and velocity profiles) in a hypergravity context (1.4 g) were qualitatively and quantitatively similar to those recorded in R1. Second, the greater path curvatures recorded in R1 were linked to smaller gravity torques on the shoulder and elbow joints. This suggests that cosmonauts tried to decrease the mechanical effects of gravity on the moving limbs. The assumption that cosmonauts overestimated the background gravity force level is consistent with their sensation that they are heavier (this feeling was orally confirmed by all cosmonauts who participated in our study). Such observations are in agreement with many data from the literature. For example, after reentry on Earth, cosmonauts consider that their movements require much greater than normal effort (Harm and Parker 1993; Reschke et al. 1994; Ross et al. 1987). In addition, they feel that they move downward too rapidly when lowering their body in a deep knee bend (Lackner and DiZio 2000). Interestingly, these sensations are identical to those that subjects experience in hypergravity periods during parabolic flight (Lackner and Graybiel 1981). Thus, a return from microgravity (from 0 to 1 g) could be equated with an exposure to hypergravity (from 1 to 2 g).

An alternative hypothesis could be that, after a spaceflight, the brain attributes abnormal sensations and sensorimotor errors to changes in the mass of the body. Although it is difficult to infer how cosmonauts perceive their body mass and gravity level after a spaceflight, the findings of the control experiments seem to suggest that changes in path curvature (R1 measurements) cannot be ascribed to a control process based on the subjective feeling that their arm inertia has increased. Indeed, we found that loading the arm with different masses did not affect path curvature, whereas it did affect the shape of hand velocity profiles. These results were also confirmed by optimal simulations in which we tested the effects of different masses on hand trajectory.

Why, after a spaceflight, did cosmonauts mainly misestimate environmental states (gravity force) but not body states (inertia), despite the fact that the body is more variable than the world? This finding is original and somehow unexpected, since Crevecoeur et al. (2010b) showed that during a short exposure to hypergravity subjects modified their grip force control because they overestimated the mass of the object (which did not change) and not the level of gravity (which really changed). Here, we propose that the cosmonauts' estimation that the

gravity force level has changed after the spaceflight was based on their prior experience in microgravity. Exposed for 10 days in weightlessness, cosmonauts had experienced changes in the world (from 1 to 0 g) and, consequently, considered that the gravity force level had changed once more when they reentered normal gravity. In other words, their motor adaptation was guided by a Bayesian prior assumption (Kording and Wolpert 2004) that the world, and not their mass, had changed. Note that we cannot exclude the premise that the cosmonauts did not perceive changes in their body mass when they were initially exposed to microgravity (see Crevecoeur et al. 2010b). However, because this estimation would be erroneous (in fact, from 1- to 0-g gravity level changes and not body mass), cosmonauts would have to reconsider their estimations to correctly adapt their movements. White et al. (2005) showed a complete adaptation of grip force/load force coupling with extensive practice in microgravity. This suggests that, after a sufficient exposure to microgravity, subjects are able to distinguish that the world, and not their body, has changed. Therefore, after reentry on Earth, based on their previous experience, cosmonauts attributed errors to changes in the world. It is of interest, however, that while the qualitative estimation of what has changed was correct, the quantitative estimation was not accurate (overestimated). Our simulations suggest that, at least 1 day after landing, optimal trajectories corresponded to a gravity level of 1.4 g. This could be due to abnormal vestibular and proprioceptive information (for a review, see Lackner and DiZio 2000), which makes the cosmonauts feel as though they are in a hypergravity environment. Note that the hypothesis according to which the CNS used an optimal strategy developed in microgravity in R1 was not acceptable (see Fig. 7A, thick solid lines).

Our experimental and simulated results are in agreement with previous findings (Crevecoeur et al. 2010b; Izawa et al. 2008), which reported that during motor adaptation the CNS constructs an internal model of the environment and produces a new motor plan that minimizes an implicit cost. In general, these findings reinforce the idea that the brain uses statistical priors (Kording and Wolpert 2004) in sensorimotor control. Such a powerful theoretical strategy is used by cosmonauts to infer changes in the most consistent feature of our terrestrial environment: that is, gravity force. In summary, our findings suggest that the adaptation of motor control after an exposure to microgravity proceeds with two steps. The first is by a transient adaptation: our brain, operating under new dynamic conditions, searches for an optimal movement plan in a new dynamic and sensory context. Since sensory cues provide biased information about body perception and the gravity force level, the transient optimal solution is to minimize movement cost in a hypergravity environment (R1 measurements). The second step corresponds to a complete adaptation: through time and practice, the sensorimotor system is recalibrated to normal gravity conditions and progressively produces accurate estimations of the initial state of the body, the gravity level, and the sensory consequences of the motor commands (i.e., learn an accurate forward model). As a consequence, the brain reproduces optimal solutions corresponding to a normal gravity environment (R3 measurements).

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DISCLOSURES

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

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