Static and dynamic postural control in long-term microgravity: evidence of a dual adaptation

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Baroni, Guido, Alessandra Pedrocchi, Giancarlo Ferrigno, Jean Massion, and Antonio Pedotti. Static and dynamic postural control in long-term microgravity: evidence of a dual adaptation. J Appl Physiol 90: 205–215, 2001.—The adaptation of dynamic movement-posture coordination during forward trunk bending was investigated in long-term weightlessness. Three-dimensional movement analysis was carried out in two astronauts during a 4-mo microgravity exposure. The principal component analysis was applied to joint-angle kinematics for the assessment of angular synergies. The anteroposterior center of mass (CM) displacement accompanying trunk flexion was also quantified. The results reveal that subjects kept typically terrestrial strategies of movement-posture coordination. The temporary disruption of joint-angular synergies observed at subjects’ first in-flight session was promptly recovered when repetitive sessions in flight were analyzed. The CM anteroposterior shift was consistently <3–4 cm, suggesting that subjects could dynamically control the CM position throughout the whole flight. This is in contrast to the observed profound microgravity-induced disruption of the quasi-static body orientation and initial CM positioning. Although this study was based on only two subjects, evidence is provided that static and dynamic postural control might be under two separate mechanisms, adapting with their specific time course to the constraints of microgravity.

motor control; posture; sensorimotor adaptation; motion analysis

It is well known that exposure to weightlessness causes major changes in the sensory-perceived environment and in external constraints, such as those related to static and dynamic equilibrium control. As a consequence, the quantitative description of the adaptation of the human motor system to the sustained gravitational-altered condition represents a unique opportunity for better identification of the variables primarily controlled in postural control and detailed description of the complex role of gravity in movement-posture coordination (15).

When the experimental observation extends for a long period of time, such as for several months of weightlessness exposure, the complete process of sensorimotor adaptation to the unusual environment can be described (19). Long-term analysis of human motor behavior in weightlessness may provide particularly enlightening information for motor rehabilitation, where functional recovery depends on the patients’ ability to learn new motor strategies that are compatible with their permanent lesions. It is also crucial for future space missions when astronauts will be required to work in weightless conditions and perform demanding skillful tasks over long periods of time.

In a recent study, the static control of posture was quantitatively investigated in two subjects during 4 mo of microgravity exposure for the first time (3). Results confirmed the strong effect of weightlessness on the control of whole body static orientation already obtained in the frame of short-term space missions (4, 22, 23) and parabolic flights (17, 30). However, the long-term observation revealed that the anteroposterior (AP) position of the body center of mass (CM), which is a fundamental reference for postural control in normogravity (21), was involved in a long-term process of adaptation throughout the entire flight toward the reemergence of typical ground-based CM positioning compatible with equilibrium. Although this result was obtained on a limited data set in flight, it suggested that a long-term process of adaptation to the weightless environment might lead to the reemergence of normogravity strategies of quasi-static postural control based on CM AP regulation.

In light of this result, the present study addresses the question of the long-term adaptation of the dynamic control of posture in weightlessness. The aim was to check whether gradual adaptation processes to microgravity, which are comparable to those observed for static posture, were present, suggesting that static and dynamic postural control might be ruled out by the same mechanism. In contrast, different modes of long-term adaptation would indicate that static and dynamic postural regulations are governed separately,
reacting specifically to the prolonged microgravity exposure.

Related investigations of the dynamic movement-posture coordination during short-term space missions and parabolic flights pointed out a possible different adaptation of static and dynamic postural regulation to weightlessness. Clement et al. (4) reported that the unaltered postural adjustments accompanying arm raising and standing on tiptoe performed by two subjects during the few days of their permanence in orbit were observed, despite a marked disruption of the initial static whole body position. In a later study, during a 7-day spaceflight, Clement et al. (5) reported forward-biased, quasi-static postural regulation, together with preserved anticipatory and compensatory postural adjustments. Further experimental evidence was provided by Massion et al. (22, 23) and Vernazza-Martin et al. (35), who observed unaltered movement coordination and dynamic CM position control, despite a persistent, biased trunk orientation and variable initial CM positioning during short-term space missions and microgravity exposure on parabolic flights.

Although only two subjects took part in the reported analysis of long-term microgravity, our results provide further evidence that terrestrial movement-posture coordination strategies based on CM position control are typically unchanged during the whole duration of spaceflight. This occurs despite the observed bias affecting the quasi-static regulation of whole body orientation (3) and the temporary impairment of the kinematic synergies observed for both subjects at their first inflight session.

METHODS

Experimental design. Two subjects, one aged 40 yr (subject A) and the other 38 yr (subject B), took part in the study. Subject A was on his second spaceflight, whereas subject B was on his first mission in orbit. The experiments were performed on board the core module of the Russian space station Mir, during the 179-day European Space Agency mission Euromir95.

The test subject was firmly fixed to the floor of the space module with Velcro shoes and straps and was asked to stand in the upright position with his hands clasped behind his back. On the command “go,” he was instructed to bend his trunk forward by 30° along the anatomic AP direction and then return to the initial position. The movement had to be performed as fast as possible. The forward trunk bending was followed by a symmetrical backward trunk inclination, which this paper does not deal with. The movement was performed both with eyes open (EO) and closed (EC). Ten trials were acquired for each experimental condition. For subject A, inflight data were collected on flight day 11 (FD11), FD19, FD69, and FD113; for subject B, experimental sessions were performed only late in flight on FD150. An on-ground baseline data set was acquired for both subjects 17 days before flight (F17). Postflight sessions were performed 1 day after reentry (R1) for both subjects, on R+3 for subject B and on R+5 for subject A. Only data acquired in these latter postflight sessions were used as the postflight data sets in this study.

Data collection and kinematic analysis were carried out by using a space-qualified version of the ELITE automatic optoelectronic motion analyzer (13), working with passive markers at a 50-Hz sample rate (12). Seven retroreflective markers were applied to the subjects’ skin using biocompatible adhesives. Markers were positioned on easily identifiable anatomic landmarks and/or bony processes, as shown in Fig. 1. The marker repositioning error between different experimental sessions was estimated to be <1.5 cm (3).

The two-dimensional marker coordinates that were measured on the ground and during flight underwent on-ground postprocessing consisting of tracking, three-dimensional (3D) reconstruction (13), and filtering (7). System accuracy was assessed as equal to 1/1,700 of the working volume diagonal.
(3,285 mm), meaning a error in locating the 3D positions of the markers of <2 mm (12).

Angle analysis. Angle analysis was carried out on the ankle, knee, and hip joints. For each trial, the movement start was defined as follows

\[
X_{n+1} - \frac{1}{N} \sum_{i=1}^{n} X_i \geq 2 \ast \frac{\sum_{i=1}^{n} (X_i - \bar{X})^2}{n-1}
\]

where \(X_i\) is the position of the marker on the acromion (see Fig. 1). Movement onset was, therefore, indicated when the difference between the current \((n+1)\) position of the marker and the mean value of the previous \(n\) positions became equal or greater than twice the standard deviation (95% of the population) on the previous \(n\) frames. The end of the movement was found in a similar manner, taking into account the phase in which the subject recovered the erect posture before the execution of the backward-leaning movement.

Joint angles were analyzed on the anatomic sagittal plane, which was reconstructed from the 3D movement description (3). The anatomic AP axis \(\left(V_{AP}\right)\) was analytically defined as follows

\[
\tilde{V}_{AP} = \tilde{V}_p \times \tilde{V}_{R}
\]

where the symbol \(\times\) denotes cross product, \(\tilde{V}_p\) is the vertical direction, and \(\tilde{V}_R\) is the normal of the regression plane among the positions of the markers placed on the acromion and great trochanter (see Fig. 1) during forward bending.

As indicated in Fig. 1, the ankle angle \((\alpha)\) was taken as the angle between the line connecting the knee to the lateral malleolus and the AP axis; the knee angle \((\beta)\) was taken as the angle between the line connecting the femoral condyle to the greater trochanter and the line connecting the femoral condyle to the lateral malleolus; and, according to Massion et al. (22, 23), the hip angle \((\gamma)\) was taken as the angle between the line connecting the acromion to the iliac spine (trunk axis) and the line connecting the greater trochanter to the femoral condyle. Trunk inclination \((\delta)\) was also measured and was taken as the angle between the trunk axis and the vertical axis. The range of angular motion (ROM) was measured as the difference between the joint angles at the initial position and at the maximum forward trunk bending.

Principal component analysis. Principal component (PC) analysis was applied on ankle \((\alpha)\), knee \((\beta)\), and hip \((\gamma)\) joint angles (see Fig. 1) to assess their linear correlation over time (1, 14, 20). PC analysis transforms the vector that represents the time variation of the three joint angles \(\alpha(t), \beta(t), \gamma(t)\) around their average values \((\mu_\alpha, \mu_\beta, \mu_\gamma)\) into a sum of orthogonal time-dependent components \(PCit(t)\), where \(i = 1, 2, 3\) weighted with three constant orthonormal vectors with components \(w_{i,j}\) (where \(i, j = 1, 2, 3\) ). Analytically, this transformation is given by

\[
\begin{bmatrix}
\alpha(t) - \mu_\alpha \\
\beta(t) - \mu_\beta \\
\gamma(t) - \mu_\gamma
\end{bmatrix} = \begin{bmatrix}
w_{11} & w_{12} & w_{13} \\
w_{21} & w_{22} & w_{23} \\
w_{31} & w_{32} & w_{33}
\end{bmatrix} PC1(t)^T + \begin{bmatrix}
w_{11} & w_{12} & w_{13} \\
w_{21} & w_{22} & w_{23} \\
w_{31} & w_{32} & w_{33}
\end{bmatrix} PC2(t)^T + \begin{bmatrix}
w_{11} & w_{12} & w_{13} \\
w_{21} & w_{22} & w_{23} \\
w_{31} & w_{32} & w_{33}
\end{bmatrix} PC3(t)^T
\]

where \(T\) denotes the transpose operation, and the vectors \(\mathbf{w}_j = (w_{1,j} w_{2,j} w_{3,j})^T\) are the PC loadings that correspond to the eigenvectors of the \(j\) th eigenvalue of the correlation matrix of the data.

PC(i \(i = 1, 2, 3\)) gives the minimum number of statistically independent linear components that describe the time-dependent processes. Therefore, if trunk bending is performed according to certain intrinsic kinematic constraints on the joint angles, then the number of PCs sufficient to describe the movement with good approximation will be less (possibly even only 1) than the number of kinematic degrees of freedom (3 in this case). In our analysis, we used the percentage of total angular variance (TAV) described by the first PC as a way of measuring how accurately the movement could be described using only one linearly independent variable, namely the first PC (PC1). We called this index the PC1 factor and obtained it analytically using the following formula

\[
PC1 = \frac{\sum \text{var} (w_{11} \ast PC1) + \sum \text{var} (w_{21} \ast PC1) + \sum \text{var} (w_{31} \ast PC1) \ast \text{TAV} \ast 100}{\text{TAV} \ast 100}
\]

where \text{var} is variance, and TAV is defined as the sum of the angle variances over time. In addition, we used the PC loadings \(\mathbf{w}_j\) as a way to quantify the level of encoding of each angular time process in the specific PC. Indeed, according to Eq. 1, vector \(\mathbf{w}_j = (w_{1,j} w_{2,j} w_{3,j})^T\) accounts for the contribution of the \(j\) th PC to the specific joint-angular variation \((i = 1, 2, 3)\).

It is important to stress here that, unlike Mah et al. (20), who explicitly assumed to include the effects of signal standard deviations in their PC analysis, we carried out a preliminary normalization by dividing the time course of each angle by its standard deviation. This was done to mask out the effect of different signal amplitudes. The relevance of this effect is clear if we consider that the total angular variation described by PC1 (PC1 factor) on three random processes with standard deviations comparable to trunk-bending joint angles was found to be 88%. After normalization, this value was reduced to the expected 33%.

CM kinematics. The displacement of the CM with respect to the ankle-joint axis was estimated using a seven-segment biomechanical model. The position of the CM and the mass of the various body segments were taken from anthropometric tables (8, 36). The model was validated according to the protocol proposed by Rabuffetti and Baroni (31) during various standing activities performed by a pool of control subjects (axial movements, leg raising, squatting, and jumping on the spot). The model was also tested in quasi-static conditions by comparing the model-estimated CM projection with the position of the center of pressure (CP), which was measured by using a piezoelectric force platform. The results showed high correspondence along the AP axis \((\text{CP}_{AP} - \text{CM}_{AP}) = 0.20 \pm 1.64 \text{ mm})\). In addition, the theoretical CM shift, which would have been caused only by the forward trunk bending in absence of any postural adjustment at the lower limb level, was estimated according to Vernazza-Martín et al. (35) and was used to evaluate the effects of the kinematic synergies on the actual CM AP shift. For this aim, the following CM compensation index was calculated as (35)

\[
\text{CM compensation index} = \frac{\text{CM}_{\text{theoretical}} - \text{CM}_{\text{actual}}}{\text{CM}_{\text{theoretical}}} \times 100
\]

where \(\text{CM}_{\text{theoretical}}\) is the model-predicted CM shift that would have occurred if no postural corrections had been produced, and \(\text{CM}_{\text{actual}}\) is the model-predicted CM shift accounting for the measured postural adjustments.

Statistical analysis. A one-way between-group variance analysis (ANOVA) was carried out with the aid of the soft-
ware package Statistica (StatSoft, Tulsa, OK). The hypotheses of the ANOVA model were checked by assessing the data fit to the normal distribution (Kolmogorov-Smirnov and $\chi^2$ tests) and the homogeneity of the variances (Levene's test). The level of significance was confirmed each time by using the nonparametric between-group ANOVA-equivalent Kruskal-Wallis ANOVA by ranks. Specific effects were evaluated by using Scheffe's post hoc comparisons of means. The null hypothesis was rejected when probability fell below 0.05.

RESULTS

Movement kinematics. Figures 2 and 3 report, for subjects A and B, respectively, movement kinematics (exemplifying stick diagrams and joint-angle time courses), the theoretical AP CM displacements (the one that would have been caused by trunk bending only, see METHODS), and the actual CM AP shift with respect to the initial position. The corresponding joint ROM at the peak forward-bending position (average ± SD) is shown in Table 1.

The stick diagram representation highlights the marked backward bias of the initial posture for subject A on FD11 and subject B on FD150. According to Baroni et al. (3), the progressive recovery of the initial erect posture disruption is evident for subject A, giving rise by FD113 to an in-flight initial posture compatible with equilibrium requirements. This observation is not confirmed for subject B, who still exhibited, late in flight, a backward-biased initial posture accompanied by a forward inclination of the trunk. Despite the evident bias in static postural regulation with marked...
differences between the two subjects, it is evident that, during the dynamic phase of the movement, both sub-
jects displaced the lower body segments (thighs and pelvis) in the opposite direction with respect to the forward trunk bending at all sessions in flight. Thus the typically terrestrial synergistic production of the prime movement and postural adjustments turned out to be consistently used throughout the whole mission. These unaltered “axial synergies” efficiently compen-
sated the dynamic CM displacement caused by the trunk bending, as qualitatively represented by the theoretical CM displacement. A procedure of intra-
session time normalization of the re-
ported trials (see Fig. 2) was performed.

Table 1. Joint-angle variation with respect to the initial posture at the peak forward-bending position

<table>
<thead>
<tr>
<th></th>
<th>Ankle [°]</th>
<th>Knee [°]</th>
<th>Trunk [°]</th>
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<tbody>
<tr>
<td><strong>Subject A</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F-17</td>
<td>10.1±1.3</td>
<td>6.2±0.9</td>
<td>42.7±4.2</td>
</tr>
<tr>
<td>FD11</td>
<td>7.3±2.6</td>
<td>1.7±1.0</td>
<td>24.6±2.4</td>
</tr>
<tr>
<td>FD19</td>
<td>9.0±2.1</td>
<td>4.6±3.1</td>
<td></td>
</tr>
<tr>
<td>FD69</td>
<td>8.0±4.6</td>
<td>30.9±4.0</td>
<td></td>
</tr>
<tr>
<td>FD113</td>
<td>5.6±1.8</td>
<td>50.8±6.2</td>
<td></td>
</tr>
<tr>
<td>R+5</td>
<td>3.8±1.2</td>
<td>36.1±1.9</td>
<td></td>
</tr>
<tr>
<td><strong>Subject B</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F-17</td>
<td>11.5±1.7</td>
<td>3.9±2.6</td>
<td>41.4±6.9</td>
</tr>
<tr>
<td>FD150</td>
<td>7.6±2.8</td>
<td>-6.4±7.8</td>
<td>37.1±5.4</td>
</tr>
<tr>
<td>R+3</td>
<td>9.4±4.9</td>
<td>50.3±4.4</td>
<td></td>
</tr>
</tbody>
</table>

Values are means ± SD and are reported for angles at ankle (α), knee joint (β), and trunk inclination (δ) under normal vision (eyes open). For angle definition and convention, see Fig. 1: F-17, 17 days before flight; FD11, FD19, FD69, FD113: flight days 11, 19, 69, 113; R+5, R+3, 5 and 3 days after reentry.
different experimental sessions (ANOVA with post hoc comparison) revealed a gradually decreasing significance in the differences between preflight and in-flight sessions. On FD113, the ROM of angle $\delta$ was found not to differ significantly ($P = 0.82$) with respect to the reference on-ground data. The trunk ROM was found to be highly sensitive to the presence of visual cues in microgravity. Both subjects showed significantly larger trunk-bending amplitudes with their eyes shut during all in-flight sessions [ANOVA with visual condition as independent variable, lowest significance $F(1,17) = 5.52, P = 0.031$ for subject A on FD19], except on FD113, when a significantly larger range of trunk motion was exhibited by subject A ($P = 0.03$) in the EO condition.

Kinematic synergies. The evaluation of the postural adjustments accompanying trunk bending revealed that the plantarflexion of the ankle-joint angle ($\alpha$) remained close to preflight values and was quite independent of the initial body configuration, which varied during the flight (see Fig. 2 and cf. Fig. 3). Statistical analysis on angle $\alpha$ ROM confirmed the lack of significant differences between the normogravity and microgravity ankle motion for both subjects [subject A: $F(1,34) = 1.12, P = 0.29$; subject B: $F(1,14) = 2.67, P = 0.12$].

Noteworthy is the different knee-joint kinematics between the two subjects in flight. Whereas subject A still extended his knee when bending forward, subject B flexed his knee on reaching the peak forward position. Indeed, the specificity of the knee-joint kinematics was found to be the major factor influencing the level of movement coordination, which was significantly decreased at the subjects’ first in-flight session, as reported in Fig. 4.

Before flight, the strong coupling in the time of joint-angular variation shown by subject A (mean PC1 factor is $98.9 \pm 0.8\%$) is opposed to a slight, lower coordination with higher variability exhibited by subject B (PC1 factor $= 93.9 \pm 5.2\%$). When trunk bending was performed in microgravity, both subjects showed a significantly reduced level of coordination among joint angles with respect to the on-ground reference data, as indicated by the considerable decrease in the PC1 factor at their first inflight session (PC1 factor $= 83.4 \pm 8.6\%$ for subject A on FD111 and $69.1 \pm 10.7\%$ for subject B on FD150). Starting from his second experimental session on FD19, subject A exhibited a prompt recovery of the joint-angular synergies, which were maintained for the rest of the flight. Statistical analysis of the PC1 factor for subject A (post hoc comparison with test session as independent variable) revealed that the overall statistical significance [$F(4,23) = 13.7, P = 0.000007$] was mainly attributable to significant differences between preflight and early in-flight (FD111) sessions ($P = 0.00023$).

A decreased movement coordination was also confirmed by statistics for subject B, when the PC1 factor was compared between preflight and in-flight trials [$F(1,10) = 13.1, P = 0.004$]. At the postflight sessions, both subjects highly coordinated the postural adjustments with the prime movement, showing PC1 factor values close to 100%, with no significant differences with respect to preflight trials [subject A: $F(1,7) = 0.7, P = 0.4$; subject B: $F(1,4) = 1.07, P = 0.4$].

The comparative representation of exemplifying joint angles and PC1, PC2, and PC3 time courses (Fig. 5) suggests that, in the presence of high coordination (on F–17 and on FD113 for subject A; preflight for subject B) (Fig. 5, left; see Fig. 4), the kinematic synergy among hip, knee, and ankle joints is accounted for by the single component PC1, with PC2 only related to the initial slight knee flexion (on F–17 for subject B) (35) and with PC3 at noise level. By contrast, when movement-posture coordination was low (on FD11 for subject A; on FD150 for subject B) (Fig. 5, right; see Fig. 4), its decrease is mainly attributable to the knee-joint kinematics, as indicated by the similar time courses of knee-angular variation and PC2. In this case, movement execution is governed by two degrees of freedom: PC1, accounting for hip and ankle-joint covariation, and PC2, related to the additional independent factor represented by the knee-angular variation.

This result is generalized in Fig. 6, in which PC1 loadings for hip and knee angles are reported. As introduced in METHODS, PC1 loadings quantify the contribution of PC1 to the specific joint-angular variation, thus representing the level of encoding of each joint kinematics accounted by PC1. For both subjects, the PC1 loading associated with the hip angle ($\gamma$PC1 loading) is always negative and close to unity, thus accounting for the main part of hip angular variation at all sessions. The negative sign is due to the increasing time of the PC1 time course, as opposed to a time decrease of angle $\gamma$ (see Fig. 5).

Fig. 4. Principal component (PC) analysis results. PC1 factor, i.e., the percentage of total angle variance expressed by the first principal component, is reported for both subjects. *Statistical significance ($P < 0.05$) compared with normogravity values (F–17). Subject A regained terrestrial preflight values by FD19 and maintained them throughout the whole 4-mo flight and on return to Earth. Subject B still performed movements in a poorly coordinated way late in flight on FD150 during his first in-flight session.
Important changes involved the PC1 loading associated with the knee angle (βPC1 loading) for both subjects at their first in-flight session. Subject A showed significant reduction of βPC1 loading on FD11, denoting decreased coordination of the knee joint with the prime movement. The same result was found for subject B on FD150, when the change in sign accounted for an in-flight switch from the on-ground knee extension (pre- and postflight) to the knee flexion accompanying the forward bending (see Figs. 3 and 5). Noteworthy is the increase in βPC1 loading shown by subject A on FD19 and FD69. The reason is that the more flexed initial posture at knee level characterizing these two in-flight sessions (see Fig. 2 and cf. Fig. 3) implies the performance of a more pronounced and highly coordinated knee extension with respect to the trials on ground and on FD113, which are characterized by a more extended initial postural attitude (see Fig. 2 and cf. Fig. 3).

**Fig. 5.** Comparison of hip, knee, and ankle time courses and PC time courses for exemplifying trials at all sessions. For the trials with high-movement coordination (see PC1 factor preflight for both subjects and on FD113 for subject A), the overall joint-angular variation is well interpreted by the first principal component (PC1), being PC2 and PC3 at noise level. The decrease in movement coordination (see PC1 factor on FD11 and FD150) is explained by the independent knee-joint kinematics, which is well described by the second principal component (PC2). The motor task is here characterized by 2 kinematic degrees of freedom.

**Fig. 6.** PC1 loadings for hip (γPC1 loading) and knee (βPC1 loading). The emergence of a second degree of freedom for the total angular variation description is associated with a decrease (on FD11 for subject A) or a change in sign (on FD150 for subject B) of the PC1 loading related to the knee joint (βPC1 loading). Increased βPC1 loadings on FD19 and FD69 denote a stronger and highly coordinated contribution of the knee-joint kinematics to the overall movement execution.
CM kinematics. The CM kinematics associated with trunk bending are summarized in Fig. 7.

Interestingly, despite the large backward bias in absolute CM positioning during the flight (see Fig. 7, top, and cf. Fig. 3), the final CM position at the peak forward leaning was found to be displaced very little with respect to its initial position (see Fig. 7, bottom). The amount of compensation and/or overcompensation of the CM theoretical shift, which would have been caused by the trunk forward bending in the absence of postural corrections (see Figs. 2 and 3), is related to the ratio of the range of trunk flexion to the size of the postural adjustments. The corresponding values of the CM compensation index are reported in Table 2.

The in-flight mean CM compensation index accounts for a marked overcompensation of the CM shift. Indeed, both subjects showed a dynamic backward displacement of the CM, which is opposite in direction with respect to the theoretical forward CM shift. This caused a markedly higher CM compensation index (>100%) than the one measured before flight and in postflight sessions (always <100%) (see Figs. 2 and 3). It is worth noting that the CM overcompensation observed in flight does not imply higher postural destabilization. Indeed, values of the CM compensation index between 100 and 200% account for a lower CM displacement (in the opposite direction) with respect to the CM theoretical shift.

Despite the change in direction with respect to on-ground trials, the CM relative shift in microgravity exhibited a stable pattern, with absolute values ranging between 3 and 4 cm with respect to the initial position. This is a striking result if one considers the significant changes between on-ground and in-flight sessions affecting the initial joint-angle configuration (see Figs. 2 and 3), the level of movement coordination (see Fig. 4), and the relative contribution of each joint angle to the whole movement production (see Figs. 5 and 6). When statistics were performed on the absolute values of the CM shift in normogravity and microgravity, no significant differences were found for subject A \([F(5,25) = 5.203, P = 0.1]\). The same result was found when the outcomes were compared between the two subjects \([F(4,29) = 2.342, P = 0.08]\). It is as if the overall movement organization, whose features appear to be subject specific and depend on the time course of sensorimotor adaptation during flight, would guarantee, in any case, to keep the CM shift associated with the trunk bending within the narrow limits of dynamic whole body balance.

In addition, when the AP relative CM displacement was statistically analyzed in EO and EC conditions, no significant differences were found. This result suggests a rather independent CM control from the presence of visual cues, which is in contrast to the observed sensitivity to vision found for the prime movement kinematics.

DISCUSSION

The first consideration is that the reported analysis is based on a data set from only two subjects. This is a common problem when experiments involving human subjects are performed in space. This limitation hinders us from generalizing our results and drawing definitive conclusions on the adaptation of human pos-

Table 2. Index of CM compensation

<table>
<thead>
<tr>
<th>Subject</th>
<th>CM compensation index</th>
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<tr>
<td><strong>Subject A</strong></td>
<td></td>
</tr>
<tr>
<td>F−17</td>
<td>88.9 ± 33.7</td>
</tr>
<tr>
<td>FD11</td>
<td>162.3 ± 37.3</td>
</tr>
<tr>
<td>FD19</td>
<td>193.3 ± 37.5</td>
</tr>
<tr>
<td>FD69</td>
<td>189.2 ± 22.3</td>
</tr>
<tr>
<td>FD113</td>
<td>152.6 ± 15.4</td>
</tr>
<tr>
<td>R+5</td>
<td>102.2 ± 19.7</td>
</tr>
<tr>
<td><strong>Subject B</strong></td>
<td></td>
</tr>
<tr>
<td>F−17</td>
<td>101.4 ± 16.6</td>
</tr>
<tr>
<td>FD150</td>
<td>130.1 ± 15.5</td>
</tr>
<tr>
<td>R+3</td>
<td>83.8 ± 7.4</td>
</tr>
</tbody>
</table>

Values are means ± SD. Center of mass (cm) is the percent ratio calculated by subtracting the actual CM shift from the theoretical CM shift (the one that would have been caused by the trunk flexion only) and normalizing the obtained difference by the CM theoretical shift (see METHOD).
tural control to microgravity. On the other hand, this investigation provides a unique experimental contribution toward the deeper understanding of human motor behavior in prolonged weightlessness and, possibly, represents a driving factor for future related experimental activities in the frame of the forthcoming International Space Station exploitation phase.

From this perspective, it is worth noting that consistent results between the two investigated subjects were obtained when the performances of their respective first experimental sessions in-flight were compared (FD11 for subject A; FD150 for subject B). Both subjects were found to keep the CM AP position close to that of the initial erect posture (see Figs. 2, 3, and 7), suggesting that they were able to maintain efficient control of the CM AP positioning during the whole flight duration. In addition, both subjects consistently exhibited typically terrestrial postural adjustments, despite relevant changes affecting the kinematics of the prime movement (trunk ROM and velocity; see Figs. 2 and 3). At their first experimental sessions in flight, both subjects showed markedly modified joint-angular synergies (PC1 factor; see Fig. 4) and the emergence of a second degree of freedom, mainly related to the knee-joint kinematics (see Figs. 5 and 6). For subject A, who performed repetitive sessions in flight, the coupling among joint activation was found to be recovered, starting from his second in-flight session on FD19, suggesting that kinematic synergies might be rapidly regained as an efficient strategy for multijoint movement execution in microgravity.

The performance of forward trunk bending appeared to be markedly slower. Early in flight (subject A on FD11), this was due to the decreased movement amplitude associated with a rough preservation of the movement duration. A reduced ROM is a common observation in microgravity (18) and is interpreted as related to a reduced sensitivity of the spindle afferents and a reduced gain of the myotatic loop, resulting in lower agonist muscle activation. Late in the mission (subject A on FD113; subject B on FD150), the long-term sensorimotor adaptation allowed subjects to recover the required trunk range of motion; however, this was accompanied by a longer time required for the movement execution (see Table 1, Figs. 2 and 3). The slowing down of the movement in weightlessness might depend on the need to shift from a predominantly feed-forward mode of control to a predominantly feedback mode, mainly useful for the fine tuning of the CM trajectory during the trunk movement.

Regardless of the modifications of trunk flexion kinematics along the flight, both subjects consistently exhibited typically terrestrial postural adjustments involving ankles, knees, and pelvis at all sessions (see Figs. 2 and 3). This resulted in the efficient compensation of the CM displacement, which remained confined within a few centimeters from the beginning to the end of the flight (see Fig. 7) and was irrespective of the CM positioning at the initial erect posture, which deeply changed throughout the flight (see Fig. 7 and cf. Fig. 2). This result is in agreement with the outcomes of previous investigations during parabolic flights and short-term space missions, in which microgravity was reported to deeply affect the static body orientation and initial CM positioning (inducing subject-specific forward or backward biases) (3) but to have little influence on dynamic movement-posture coordination and CM position control (4, 5, 22, 23, 35).

The different sensitivity of static and dynamic control of posture and CM positioning might originate from the involvement of different sensory cues for quasi-static whole body orientation and for the dynamic movement-posture coordination. On one hand, the somesthetic perception, with respect to the external environment, mainly relies on integrating the information received from vision and various types of gravity-related sensory cues [otoliths and truncal graviceptors (24); muscle force proprioceptors (9); cutaneous sole plantar inputs (16)] and on microgravity-biased muscle spindle length and velocity-sensing spindle afferents (18). On the other hand, dynamic sensory cues, such as those sensing the mass distribution and inertial properties of body segments (34), the labyrinthine information (2), and the dynamic cutaneous (16) and proprioceptive (33) inputs, are unaffected by exposure to microgravity and are used to achieve proper kinesthetic perception in a weightless environment. When this unbiased sensory support is counted on, centrally encoded, stereotyped strategies of CM displacement control would be consistently used in flight for dynamic movement-posture coordination during trunk movement. The dynamic CM control would be organized, at least partly, in a closed-loop mode with respect to the initial CM AP position, which would continue to serve as an egocentric frame of reference for motor control (11), despite its static bias with respect to the external environment (see Figs. 2, 3, and 7).

This view was questioned by Pozzo et al. (30), who doubted the role of CM positioning for postural control on the basis of findings in short-term microgravity. They reported that subjects asked to perform whole body lifting tasks exhibited an initial backward-biased CM positioning followed by a markedly increased dynamic CM shift with respect to normogravity. One interpretation of these contrasting results is that the sensorimotor adaptation to weightlessness might be task dependent. The goal-directed task represented by whole body lifting could be performed on the basis of different reference values with respect to the trunk-bending task. An alternative and not exclusive interpretation is that the complexity of the whole body lifting task would require a longer time for adaptation, comparable with the long-term adaptation described for static CM positioning, which only recovered the ground-based value at the end of the flight (3).

According to our results on upper trunk bending, the only noticeable difference between normo- and microgravity CM dynamic control is the direction of the residual CM shift: for both subjects, the CM moved...
forward in normogravity and backward in microgravity. We do not feel confident to speculate on this result, apart from noting that the CM relative displacement in microgravity was consistently confined within narrow limits. The observed change in direction could be interpreted as an overcompensation of the CM shift due to the reduced amplitude of the trunk movement and the preservation of the postural adjustments (see Table 2) (35). This could also depend on the backward-leaning initial posture (see Figs. 2 and 3), as well as the observed increased role of the knee joint in task execution. However, backward shift is not specific to microgravity. In normogravity, it was shown that the direction of the CM shift was subject dependent, observing both forward and backward CM shifts (1). In conclusion, when similar experiments were performed on parabolic flights, only two of the five recorded subjects showed a backward CM shift when trunk forward bending was performed during the 0-g phase of the parabola (35).

Interestingly, subject A accomplished CM displacement control in weightlessness by regaining and progressively refining typically terrestrial motor strategies based on synergistic joint-angle activation. Indeed, strong kinematic synergies were described as underlying the minimization of the CM shift during trunk bending in normogravity (6, 21, 26–28), as well as during short-term microgravity exposure (parabolic flights (35), short-term space missions (22, 23)). The characteristic coupling among hip-, knee-, and ankle-joint movements, illustrated by the PC analysis in normogravity (1) and on parabolic flights (35), was, in this case, deeply modified during the first in-flight recording session for both subjects, regardless of the time elapsed since their exposure to weightlessness (see Fig. 4). The decrease in movement coordination was characterized by a strong representation of a second component (PC2) mainly related to the knee movement (see Fig. 5). This result could be interpreted as indicating that, in the presence of a biased internal representation of the body configuration, due to the impaired sensory cues in a microgravity environment and the low familiarity with the motor task, the subjects adjust the CM position continuously by using movements of the knee joint, which present the lowest inertial characteristic compared with the ankle and hip joints (25), comparable to a skier during a fast descent. The impaired kinematic synergy underwent short-term adaptation, which was most probably favored by the increasing familiarity with the specific protocol. As early as at the second in-flight recording (for subject A), the strong coupling between the angle changes (PC factor >95%; see Fig. 4) was recovered and served to refine the overall movement organization toward a more efficient task production, which is in agreement with the provided instruction.

The last consideration concerns the possible origin and purpose of the observed postural adjustments in weightless conditions, where there is no need for equilibrium control. Let us first consider the theory that the unaltered opposite displacements of lower body segments that accompany voluntary trunk movements and the resulting compensation of CM shift are simply an effect induced by passive dynamic interactions between segments when trunk bending is performed. As shown by the modeling study of Ramos and Stark (32), these interactions in normogravity would have provoked backward falling in the absence of the anticipatory tibialis anterior activation seen at the onset of the trunk bending (6). On the basis of experimental observation in normogravity and modeling studies, it was concluded that the postural adjustments cannot have a purely passive origin but must be produced by centrally controlled commands that are mainly focused on ankle flexor muscles. Comparable conclusions were drawn by Eng et al. (10) when they modeled the dynamic interactions between segments during arm raising. Although no comparable modeling studies on the interactions between segments during trunk bending were performed in microgravity, it would be surprising that, in the very different gravitational context and in the presence of the observed modification of prime movement kinematics, the kinematic synergies would result solely from the passive effect of the dynamic interactions between segments (1).

In conclusion, the reported analysis in long-term microgravity, although based on the analysis of only two subjects, provides evidence that the static control of the CM AP position during erect posture and the dynamic control of the CM position during trunk bending might depend on two different control mechanisms. The quasi-static CM positioning appears to be deeply disrupted by microgravity exposure and eventually exhibits a long-term adaptation toward the restoring of the ground-based AP CM position compatible with equilibrium (3). By contrast, the dynamic CM control during trunk bending is maintained during the whole spaceflight. As on Earth, the dynamic movement posture coordination produces an evident minimization of the CM shift, regardless of subject-specific biases affecting the initial whole body configuration. The idea that the observed dynamic CM stabilization mainly serves as a way of counteracting the inertial perturbing effects of prime movement performance is a fascinating topic for further investigations. The role of postural adjustments in dynamically regulating body stability may indeed be maximized in microgravity, where the need to maintain equilibrium is no longer a constraint. This idea is in accordance with evidence that motor coordination aims at minimizing the displacement of the CM projection (and, with good approximation, also the CP). Indeed, this would reduce the variation of the “arm” of the total moment, both of reactive and inertial forces around the ankle joint. From this point of view, the main function of postural strategies in space could be interpreted as serving to reduce movement-induced perturbations at the interface between the human body and the external environment, with implications regarding the energy required to produce the movements themselves (29).
REFERENCES


