INTRODUCTION

Purposeful motor acts consist of two apparently contradictory tasks. One is to move one or several body segments toward a goal, and the other is to change the position of other segments to maintain equilibrium. One of the major functions of the CNS is to coordinate equilibrium and movement. In humans, static equilibrium during stance is maintained when the center of mass (CM) projection is located inside the supporting area delimited by the feet. During forward or backward upper trunk movements, a kinematic synergy has been described by Babinski (1899), which consists in a simultaneous displacement of the hip and knee in a direction opposite to the upper trunk movement and which is responsible for the stabilization of the CM projection within the base of support. This CM stabilization is here considered as the result of the kinematic synergy that is defined as the ratio between the hip, knee, and ankle angle changes occurring during the movement.

The control of the kinematic synergy and the minimization of the CM shift during trunk bending have been demonstrated by two sets of studies. The first set is based on experimentation in normogravity. The kinematic synergy may result from two mechanisms: a passive interaction between body segments and an active control. The dynamic interactions between segments have been modeled by Ramos and Stark (1990), who have shown that acceleration of the trunk causes contiguous segments to accelerate in the opposite direction according to the action-reaction law. With feet fixed to the floor, the net result of the interaction is a backward CM shift that would cause falling. Therefore the kinematic synergy may not be due only to the dynamic interactions between body segments but also to a central control that may coordinate the motion of the various joints participating in the kinematic synergy (Alexandrov et al. 1994, 1998; Crenna et al. 1987; Oddsson and Thorstenson 1987; Pedotti et al. 1989). Indeed, this argument is mainly based on three pieces of evidence. First, Crenna et al. (1987) showed that the peak velocity of both the upper and lower body segments was reached synchronously in all the subjects studied. There may exist a central control that synchronizes the timing of the upper and lower body segmental movements. Second, the kinematic synergy is initiated by a stable muscle synergy simultaneously involving trunk, thigh, and leg muscles (Crenna et al. 1987; Oddsson and Thorstenson 1987; Pedotti et al. 1989). This finding also indicates that a single central command may coordinate the motion of the various joints participating in the kinematic synergy. Third, a principal component analysis on the ankle, knee, and hip angle changes occurring during forward and backward trunk movements showed that only one principal component (PC1: one degree of freedom multijoint movement) accounted for >99% of the whole movement, which was characterized by fixed ratios between the changes in ankle, knee, and hip joint angles (Alexandrov et al. 1994, 1998). The same proportion of the movement was represented by PC1 at both fast and slow velocities. These observations suggest that the high level of coupling between the angles does not entirely result from dynamic interactions between segments, which depend on
movement velocity, but that this coupling is centrally controlled.

The second set of studies concerns experimentation in microgravity. Unfortunately, these studies can be usually performed only on a small number of subjects. The specific aim of these investigations has been to see whether the kinematic synergy during trunk bending, minimizing the CM shift during movement under equilibrium constraints, is abolished when the equilibrium constraints disappear. During long-term space flights, the CM shift during movement was minimized by a kinematic synergy that remained invariant in spite of the absence of equilibrium constraints (Massion et al. 1992, 1993, 1997). The same results have been observed during trunk bending performed under water (Massion et al. 1995). These observations suggest that the kinematic synergy results from a stereotyped control that is centrally programmed independently from gravity constraints. However, this invariant kinematic synergy is implemented by a muscular synergy that is strongly modified in microgravity. For example, backward trunk bending in normogravity is initiated by a set of muscles behind the body (erector spinae, semimembranosus, and soleus) (Crenna et al. 1987; Oddsson and Thorstenson 1987; Pedotti et al. 1989). During a long-term space flight, the early soleus activation is replaced by an early tibialis anterior activation (Massion et al. 1992). The preservation of the kinematic synergy in contrast to the adaptation of the muscle synergy in microgravity is rather surprising. It suggests that, although the afferent inputs from sensors monitoring the gravity axis (otoliths, body graviceptors) (see Dietz et al. 1992; Mittelsstaedt 1998) and the body configuration (proprioceptive inputs) are biased, an internal representation of the body segment geometry, mass, and inertia is preserved and is used during trunk bending to minimize the anteroposterior CM shift. The sensory inputs from the feet in contact with the shoes and the space cabin floor to which they are fixed should play an important role in this representation. The possible perception of body segments inertia that should remain in microgravity might be another source for updating the representation (Pagano et al. 1996).

Previous investigations in microgravity had, however, a series of limitations. First, they had been performed on a restricted number of subjects (only 1 or 2 per flight). Second, they concerned in-flight recording 1 or 2 wk after space flight onset, where long-term adaptation to microgravity already took place. They did not inform about the very short-term adaptation that characterizes the microgravity episodes of parabolic flights. Third, no accurate quantification of the kinematic synergy was performed on the basis of the principal components analysis as well as no extensive analysis of the electromyographic (EMG) pattern including distal, proximal, and axial muscles (the EMG analysis was restricted to the distal muscles). The present study was performed during parabolic flights, with kinematic and EMG data acquisition comparable to ground-based experiments. The three following questions were addressed. 1) Is the anteroposterior position of the CM during trunk movement still minimized in microgravity in absence of equilibrium constraints and how is the time course of the CM shift during movement both in normo- and microgravity? 2) Is the coupling between hip, knee, and ankle angle changes during movement maintained during short-term microgravity episodes? 3) How does the EMG pattern inform on how this coupling is implemented in microgravity?

**METHODS**

**Experimental protocol**

Experiments were performed in a Caravelle aircraft on five adult subjects. None of the subjects had previously been exposed to parabolic flight conditions. The subjects wore special shoes that were attached to a platform through a ski binding (Fig. 1). First, they were asked to adopt an erect posture, to look straight ahead, and to keep their hands clasped behind their back. Then, in response to a tone, they were instructed to bend the trunk (the head and the trunk together) forward by $\sim 35^\circ$, as fast as possible, to hold the final position for 3 s and then recover the initial erect posture.

Two experimental series were performed by each subject: one under standard conditions of a steady-level flight and the other during microgravity episodes of the parabolic flight. During the flight, 30 parabolas were executed, each of them providing 20 s at a level of $\sim 0.02 \pm 0.018$ (SD) g. All recorded parabolas had the same pattern: the pull-up and pull-out phases were both usually stabilized around a 20-s period of 1.8 g. The zero-g phase occurred between the two phases. Two consecutive parabolas were separated by a steady-level flight phase lasting from 2 to 5 min. The subject first performed a set of seven trials in microgravity. Given the short duration of the

![Fig. 1. Top: plane trajectory. All parabolas had the same pattern: the pull-up phase was usually stabilized around 1.8 g during 20 s, followed by the 0-g phase (microgravity), which lasted $\sim 20$ s. The pull-out phase was also a 20-s period of 1.8 g, with return to 1 g (normogravity). Two consecutive parabolas were separated by a steady-level flight phase lasting for at least 2 min. Bottom, left: experimental setup inside the cabin and starting position of the subject. Right: stick-diagram of a trunk movement in microgravity. It can be noticed that the forward movement of the trunk is accompanied by a hip and knee movement in the opposite direction. This kinematic synergy is preserved in microgravity in spite of the equilibrium constraints disappearing.](http://jn.physiology.org/DownloadedFrom)
microgravity episodes, no more than two trials could be performed during each parabolic phase. A second set of seven trials was performed in normogravity during a steady-level flight phase of 5 min.

Recording system and data processing

Kinematic analysis was performed by means of the E.L.I.T.E. system: an automatic TV-image processor (Ferrigno and Pedotti 1985). Two cameras placed 3.5 m in front of the subject, recorded the three-dimensional (3D) movements of seven passive retroreflective markers placed on the right side of the subject on the head (2: external meatus, external angle of orbit), acromion (1), iliac crest (1), trochanter (1), knee joint (at the level of the tibial plateau) (1), and ankle (over the lateral malleolus) (1). Under the present experimentation, the field of view explored by the system was 2 * 2 * 1 m, and the accuracy was 0.67 mm. Because the movements were performed in the sagittal plane (perpendicular to the long axis of the aircraft), only this plane was included in the analysis. The sampling frequency was 100 Hz.

EMG activity was recorded (using surface bipolar configuration with an interelectrode distance of 2 cm) on the right side of the subject, from the rectus abdominis (RA), erector spinae at the level of L4 (ES), vastus lateralis (VL), semimembranosus (SM), tibialis anterior (TA), and gastrocnemius lateralis (GL). The signal was amplified (gain 1,000) and filtered through a 10- to 200-Hz band-pass. The sampling frequency was 2,400 Hz.

Parameters recorded

To describe the trunk movement characteristics, the following parameters were measured on the basis of the kinematic recordings: 1) trunk movement duration, 2) trunk movement amplitude (difference between the final stabilized position of the trunk segment 400 ms after the end of the movement and the initial position of this segment), and 3) mean angular velocity of the trunk (V_{mean}), corresponding to the ratio between the amplitude of the trunk segment and the movement duration.

Biomechanical modeling

A biomechanical model of the CM was developed from the kinematic data, based on the anthropometrical model of Zatsiorsky and Seluyanov (1983).

For each body segment (i), the anthropometric data of interest were as follows: 1) the mass of the segment (mi) and 2) the distance between the CM position and the axis of rotation of the segmental distal joint (ICMi). The kinematic data of interest were as follows: 1) the position of the axis of rotation of the distal joint (xOi) given by the position of the markers placed on the body and 2) the angle defined by each segment (delimited by 2 markers) with respect to the horizontal axis (θ).

The general equation obtained was as follows

\[ x_{CM} = \frac{\sum (m_i \times x_{CM_i})}{\sum m_i} \quad \text{and} \quad y_{CM} = \frac{\sum (m_i \times y_{CM_i})}{\sum m_i} \]

with

\[ x_{CM_i} = x_{Oi} + l_{CM_i} \times \cos (\theta_i) \]

and

\[ y_{CM_i} = y_{Oi} + l_{CM_i} \times \sin (\theta_i) \]

From this modeling we measured the following: 1) the initial CM position corresponding to the CM position 200 ms before the onset of the movement, 2) the final stabilized CM position corresponding to the CM position 400 ms after the offset of the movement, 3) the CM shift in the anteroposterior direction, and 4) a theoretical CM shift due only to the trunk movement was obtained by simulating the movement performed on the basis of data collected on the trunk movement, after “freezing” the anteroposterior position of all body segments (pelvis, thigh, and leg) but moving the trunk in the position adopted at the start of the data acquisition. With this procedure it was possible to evaluate the theoretical CM shift due to the trunk bending alone.

Each measure of the theoretical and actual CM shift was the difference between the value at the time of measurement and t0 (200 ms before the movement onset). Then we calculated a CM shift compensation index (CI in %) corresponding to the difference between the theoretical and the actual CM shift normalized with respect to the theoretical CM shift (see Fig. 2). This index is global and does not reflect specific contribution of mechanisms determining the CM horizontal position, such as dynamic interactions between segments, the effect of gravity forces and the active control by the CNS. CI was calculated during two time periods: an early CM compensation from 100 ms after the movement onset to 400 ms after the movement onset, and a late CM compensation from 200 ms before the movement offset to 400 ms after the movement offset. The index values represented in Figs. 6 and 7 correspond to the averaged values calculated for individual trials for each subject.

The trunk movement onset and offset times were defined as points on the theoretical CM velocity curve (calculated from theoretical isolated trunk displacement), where it crossed a threshold corresponding to 5% of the peak velocity.

CI quantifies the compensation for the theoretical CM shift that occurs during trunk bending. The following three situations can occur. 1) The actual CM shift was equal to or bigger than the theoretical CM shift. In this case, CI yields a value ≤ 0%, which means that there was no compensation for the CM shift. 2) The actual CM shift was smaller than the theoretical CM shift. The value of the index ranges between 0 and 100%, expressing the degree of a partial CM compensation. 3) The actual CM shift was zero or occurred in the opposite direction to the theoretical CM shift. Here the value of the index is ≥ 100%, which means that either a complete compensation or overcompensation for the CM shift occurred.

Principal components analysis

Kinematic synergies involved in the CM control during the movement were quantified by performing a principal components analysis on the angular changes occurring at the hip, knee, and ankle joints using the procedure described by Mah et al. (1994) and Alexandrov et al. (1998). This analysis quantifies linear covariations occurring over time between these three joint angles.

The general principle is that all the angles studied (φ1, φ2, and φ3: hip, knee, and ankle, respectively) during the trunk movement in the sagittal plane can be expressed by a transformation matrix as a linear combination of three components PC1, PC2, and PC3 (see Fig. 3).

The linear combination is expressed in the form

\[ \phi_i(t) = r_{i1} \cdot PC_1(t) + r_{i2} \cdot PC_2(t) + r_{i3} \cdot PC_3(t) \]

with \( \phi_i(t) \), \( \phi_2(t) \), and \( \phi_3(t) \) corresponding to the three angle values during time adjusted to the same baseline, and with the transformation matrix

\[ M = \begin{bmatrix} r_{11} & r_{12} & r_{13} \\ r_{21} & r_{22} & r_{23} \\ r_{31} & r_{32} & r_{33} \end{bmatrix} \]

where \( r_{ij} \) is the respective contribution of a component PCi to each angle \( j \) (i and j = 1, 2, 3).

The principal component analysis method yields a transformation matrix M in such a way that the components are linearly independent.
FIG. 2.  

A: diagrams showing the theoretical center of mass (CM) shift (obtained after freezing all segments but the trunk) and the actual CM shift during a single forward trunk movement. The zero value corresponds to the ankle joint axis, a positive deviation corresponds to a CM shift forward and a negative deviation to a backward CM shift.  

B: theoretical and actual CM shift between the onset of the trunk movement and 400 ms after the offset of the movement during the same trial. Note the small actual CM shift with respect to the large theoretical CG shift. This shows that a marked CM compensation has occurred which has been quantified in C.  

C: compensation index (CI) corresponding to the difference between the theoretical and actual CM shift with respect to the theoretical CM shift. One hundred percent indicates a full compensation and no actual CM shift, whereas 0% indicates a lack of compensation and an actual CM shift equal to the theoretical CM shift.

FIG. 3. Single trial diagram of the hip ($\varphi_1$), knee ($\varphi_2$), and ankle ($\varphi_3$) angle time course on the left and that of the 3 components PC1, PC2, and PC3 on the right during forward trunk bending. The movement comprised hip flexion and short-lasting knee flexion followed by a slight extension and ankle extension. The kinematic synergy corresponding to the ratio between the hip, knee, and ankle angle changes occurring during the movement was strongly accounted for a single component PC1. The PC2 component, which was present only during fast movements, corresponds to the initial knee flexion (Alexandrov et al. 1998). The PC3 component is at the noise level.
and ranked in order of decreasing variance. PC1; the first component is therefore the component with the highest variance. The percentage participation of a component PC variance in the total variance, that is to say the contribution of a component to the movement is defined by

\[ \lambda_i = \frac{\text{Var}(\text{PC}_i)}{\text{Var}(\text{PC}_1) + \text{Var}(\text{PC}_2) + \text{Var}(\text{PC}_3)} \times 100 \]

If the total variance of the three angles is represented by a single component (PC1), it means that the three angles are coupled during the movement (one degree of freedom movement).

To estimate the intertrial variability of the component PC contribution to all three angles, an index \( V_i \) was calculated

\[ V_i = \left( \frac{SD_1^2 + SD_2^2 + SD_3^2}{\sqrt{r_1^2 + r_2^2 + r_3^2}} \right) \times 100 \]

where \( r_i \) and \( SD_i \) \((i = 1, 2, 3)\) are the contribution of a component PC to each of the three angles averaged across the trial series and their standard deviation, respectively (Alexandrov et al. 1998).

From the principal component analysis, the following variables were analyzed: 1) the contribution of the PC component to the movement, \( \lambda_i \), 2) the contribution of a component PC to each angle \( \varphi_i(t) \) represented by \( r_{ip} \), and 3) the index of intertrial variability of the component PC contribution to all three angles (\( V_i \) index).

**EMG analysis**

The EMG analysis was based on the muscle pattern’s observation and the qualitative comparison of the superposition of trials under both normo- and microgravity, the results obtained with this method being enough glaring.

**Statistical analysis**

Not all data could be analyzed. Varying between subjects, the number of trials used for analysis ranged from three to seven. The mistrials were due to extreme experimental conditions. Including the total number of trials in normo- and microgravity, trials that were lost among all 5 subjects were 18 of 70. A nonparametric test (Mann-Whitney test) was used for assessing the effect of gravity on the following variables: the amplitude, duration, mean angular velocity of the trunk, initial and final CM position, contribution of the PC component to the movement (\( \lambda_i \)), and contribution of PC to each angle (\( r_{ip} \)). The significance level was set at \( P < 0.05 \).

The CM compensation index was first subjected to the Wilcoxon test to determine whether there existed a significant difference between the calculated index and the 0 value corresponding to a lack of compensation. Then the time courses of both the early and late CI were studied first by performing an ANOVA and then a linear regression analysis, to determine the sign of these changes (increase or decrease during time).

**RESULTS**

Figure 4 shows a trunk flexion in one subject. Six trials in normogravity (1 trial has been eliminated) and seven trials in microgravity are presented. Both in normo- and microgravity, the shoulder marker moved forward, whereas the hip and knee markers moved in the opposite direction. The only difference was that in microgravity, the initial positions of the shoulder, hip, knee, and CM were more variable. This axial synergy remained unchanged, maintaining in both cases the CM projection within the limits of the support base.

**Kinematic parameters of the trunk movement**

The trunk movement amplitude, duration, and the mean angular velocity (\( V_{\text{mean}} \)) of the trunk segment were calculated for the five subjects during the forward trunk movement under both normo- and microgravity. The range of individual mean value of the movement amplitude varied from 35 ± 3° to 62 ± 3° in normogravity and from 32 ± 3° to 41.5 ± 8° in microgravity. There was a significant decrease in three of the five
subjects (S2: Z = 0.036, P < 0.05; S3: Z = 0.005, P < 0.01; S5: Z = 0.003, P < 0.01), whereas the decrease for the last two did not reach the level of significance. The movement duration remained unchanged (varying between subjects the variation was from 636 ± 137 ms to 1,052 ± 93 ms in normogravity and from 650 ± 83 ms to 1,010 ± 130 ms in microgravity). This resulted in a lower mean velocity varying between subjects from 34 ± 3°/s to 67 ± 5°/s in normogravity and from 33 ± 7°/s to 56 ± 10°/s in microgravity.

**Analysis of the center of mass position and compensation index**

The CM time course in normo- and microgravity as illustrated in Fig. 4 was further analyzed in two ways. First the initial and final positions were measured in each trial and subject. Second, the CM shift was evaluated by the CI.

**Initial and final CM position**

The initial and final CM positions obtained through biomechanical modeling were validated in similar experiments performed on the ground, on a force platform. The validation was performed in two subjects (S1 and S4). The results showed that the mean difference between the calculated CM positions and the CM positions measured on the platform were 7.5 ± 2.7 mm and 5.9 ± 3.7 mm, respectively.

Figure 5A shows for each subject and each trial the initial anteroposterior CM position in normo- and microgravity, 200 ms before the movement onset. For each subject, the 0 value corresponds to the ankle joint axis. Varying between subjects, the mean initial CM position was situated from 2 to 11 cm in front of the ankle joint axis. An ANOVA showed that the initial CM position did not change significantly in both normo- and microgravity in four of the five subjects (S1, S2, S3, and S4). In subject S5, the mean initial CM position in microgravity was situated 2.8 cm in front of that in normogravity (S5, Z = -2.68, P < 0.01). This shift was nevertheless far from exceeding the stability limits.

Figure 5B shows for each subject and each trial the initial (200 ms before the movement onset) and the final (400 ms after the movement offset) CM position in microgravity. An ANOVA showed that the final CM position did not change with respect to the initial position in any subject except for subject S3, where the mean final CM position was situated 3.1 cm posterior to its initial position (S3, Z = 2.1, P < 0.05).

**CM compensation index during movement**

**Early CI.** Figure 6 shows for each subject, the mean value of the early CI under both normo- and microgravity. Only indexes statistically different from 0 are linked together in the figure. This figure shows that the index differed significantly from 0 as early as 100 ms after the movement onset in four subjects of five, both in normo- and microgravity.

It can be noticed that CI slightly increased with time in three of the five subjects (S1, S2, and S4) in normogravity, and in two of the five subjects (S1 and S2) in microgravity. This increase was statistically significant, as shown by the linear regression analysis.

The mean value of the CI calculated from 100 to 400 ms after the movement onset varied from 54 to 110.6% in normogravity and from 64.3 to 144.8% in microgravity. The population average was 88.9 and 106.7%, respectively, indicating an increasing trend in microgravity.

**Late CI.** Figure 7 shows the late CI in each subject under both normo- and microgravity. This figure shows that in all subjects the index was always significantly different from 0 under both normo- and microgravity. A high level of compensation for the CM shift can be noticed during the final part of the movement and during the final stabilization of the trunk.

This figure shows that the index decreased slightly with time in three of the five subjects (S1, S4, and S5) under both normo-
and microgravity. The decrease was statistically significant, as shown by the linear regression analysis.

The mean value of the CM compensation index (from 200 before to 400 ms after the movement offset) ranged between 65.5 and 107.6% under normogravity, and between 71.5 and 151.9% under microgravity. The population average was 91.9 and 99%, respectively, indicating no marked differences between the two conditions.

To conclude, the analysis of the CI time course during forward trunk bending shows that CM shift is minimized from the movement onset to the final trunk stabilization, in spite of the absence of equilibrium constraints in microgravity. A trend toward an increase of the index was noticed around movement onset in microgravity, as compared with normogravity. No clear-cut difference between the two conditions was noticed during the final part of the movement and the final stabilization of the trunk.

Quantitative analysis of the axial synergies by principal components analysis

The contributions of PC1 and PC2 to the trunk movement for each subject under normo- and microgravity are shown in Fig. 8. The figure shows that PC1 accounted for >99% of the movement ($\lambda_1 > 99\%$), whereas the contribution $\lambda_2$ of PC2 was lower than 1%; the contribution $\lambda_3$ PC3 (not shown) was negligible (<0.2%) under both normo- and microgravity. These results indicate that a single component accounts for the forward trunk movement under both normo- and microgravity. This suggests a strong coupling between joint angles, expressed by a fixed ratio between the angles through time (see METHODS).

The intertrial variability of the PC1 contribution to the three angles ($\varphi_1$, $\varphi_2$, and $\varphi_3$) was estimated in terms of the index $V_1$ (%) under both normo- and microgravity. The index fell between 1.9 and 5.4% under normogravity and between 4.3 and 9.4% under microgravity. The population average was 3.1 and 6.5%, respectively. This indicates that the variability of PC1 contribution to all three angles ($\varphi_1$, $\varphi_2$, and $\varphi_3$) was twice as high in microgravity as in normogravity. Nevertheless, the intertrial variation remained lower than 10%.

The contributions of PC1 to angles $\varphi_1$, $\varphi_2$, and $\varphi_3$, denoted by $r_{11}$, $r_{12}$, and $r_{13}$, respectively, for each subject under both normo- and microgravity are given in Fig. 9.

As can be seen from Fig. 9, the contributions of PC1 to $\varphi_1$ and $\varphi_2$ ($r_{11}$ and $r_{12}$) were negative, whereas that to $\varphi_3$ ($r_{13}$) was positive. Based on increasing changes in PC1 observed with time, the negative sign in $r_{11}$ and $r_{12}$ indicates that $\varphi_1$ and $\varphi_2$ decreased with time corresponding to a trunk flexion and a knee extension. In the same way, the positive sign in $r_{13}$ indicates that $\varphi_3$ increased with time, which corresponds to an
activity was increased, both during erect posture and movement (subject 1: RA and SM; subject 3: VL and TA). Similar observations were made in the other subjects (not shown, subject 2: VL, TA, and GL; subject 4: RA and VL; subject 5: VL, SM, and TA). Co-contraction was often seen. Joint stiffness should reduce the intersegmental disturbance when marked changes in the constraint related to the microgravity makes the control of the movement less accurate and biases the sensory information (graviceptors, proprioceptors) on which the control relies. Second, the initial agonist bursts were reduced or masked by the increased tonic activity (subject 1 in the figure, subject 4 not shown). Third, the antagonist bursts involved in the movement during the braking phase disappeared or were strongly reduced (subjects 1 and 3 in the figure, subjects 2, 4, and 5 not shown). These results demonstrate a marked reorganization of the EMG activity in microgravity in the whole population of subjects.

**DISCUSSION**

The aim of this study on the trunk bending was to answer three main questions. The first question was whether the anteroposterior CM position during trunk bending was still regulated during short-term microgravity in absence of equilibrium constraints and how was the time course of the control of the CM position organized under both normo- and microgravity. Three main results were obtained: first, the initial CM position under microgravity was close to that under normogravity. Second, the final CM position in microgravity was close to its initial position in the same condition, and third, the actual CM shift during the movement was always smaller than a theoretical CM shift, which would have been induced by trunk movement alone. These results indicate that the CM shift remains minimized in short-term microgravity episodes, in spite of no equilibrium constraints and that this minimization persists throughout the whole movement, as well as during the final period of trunk stabilization. In addition, the time course of this minimization remains qualitatively the same under both normo- and microgravity. The minimization of the anteroposterior CM shift during trunk bending has been also observed during a long-term (2–3 wk) space flight (Massion et al. 1993, 1997) and under water, which simulates microgravity environment (Massion et al. 1998). A minimization of CM shift was also seen during microgravity episodes of parabolic flights when subjects performed a leg-raising movement, where a trunk inclination in the opposite direction to the raised leg compensated precisely for the CM shift expected to occur (Mouchinino et al. 1996). In this paradigm, it was, however, noticed that the CM shift toward the supporting leg, which preceded leg raising in normogravity was not present in microgravity and was thus gravity dependent. These observations suggest that there exists an internal model of the body segment mass and inertia, which is preserved in microgravity and is used to minimize anteroposterior or lateral CM shifts that the movement may provoke.

The fact that the initial CM position was also maintained during erect posture in microgravity episodes of the parabolic flight might indicate that the internal model of the body geometry and mass as well as of the segments’ orientation with respect to the external world is preserved despite missing information from ooliths and body graviceptors (Dietz 1994; Mittelstaedt 1998; Roll et al. 1993) and biased input from muscle proprioceptors. However, this internal model is no more adequate when microgravity is long-lasting. A forward inclined posture was described...
by Clement et al. (1984) during the first days in flight; a forward body inclination was also observed under water (Massion et al. 1995). This initial inclined posture was compensated after 1 wk in-flight. Thereafter, the anteroposterior positioning of the CM with respect to the feet and the body segment orientation with respect to the space seem to be regulated independently, indicating different control mechanisms. Concerning first the anteroposterior CM position, a backward CM positioning has been described by Pozzo et al. (1995) before the performance of a whole body lifting task after 2 wk in-flight, and was interpreted as being task dependent. However, during long-term microgravity episodes (150 days), the backward shift of the CM initial position, which can be seen after 3 wk in-flight, is progressively reduced and is replaced by a ground-based positioning inside the support area at the end of the flight (Baroni et al. 1999). Concerning the segment orientation with respect to the space, it is rather preserved in microgravity. The head axis remains vertical during long-term microgravity (Amblard et al. 2000), even when oscillatory movements are performed as it is during parabolic flight (Amblard et al. 1995, 1997). The trunk axis is inclined forward (Massion et al. 1997) or is close to the vertical (Pedrocchi et al. 2000). In fact, data from the literature suggest that body orientation is mainly based on a top-down model starting from the head position with respect to the space (Mergner et al. 1997). In contrast, the CM position with respect to the floor is probably based on a bottom-up organization from the feet to the head (Assaiante and Amblard 1995) and depends on sensors input from the feet. In the present experimental condition, the cutaneous information from the feet was present, due to the attachment of the feet to the floor. In absence of otolithic and accurate proprioceptive information about the gravity vector, this information, probably together with a short-term memorized sensorimotor representation, may have been used for an accurate positioning of the CM during erect posture.

The second question raised in this study concerns the maintained kinematic synergy and the associated coupling between hip, knee, and ankle angle changes in microgravity. Two main results emerge from the principal components analysis of the hip, knee, and ankle angle changes occurring during the movement. The first one is that under both normo- and microgravity, the contribution of only one component (PC1) accounts for >99% of the movement ($\lambda_1 > 99\%$). This result indicates that
the kinematic synergy is characterized by a strong coupling between angles. The coupling remained fixed through the course of the movement even if its variability ($V_1$) was increased in microgravity. The maintenance of the strong coupling between angles in absence of equilibrium constraints suggests that the kinematic synergy is an invariant parameter controlled by the CNS (Alexandrov et al. 1998), which is independent from the gravity constraint according to the present experimentation. The second result concerns the relative contribution of PC1 to the hip, knee, and ankle angles, which is changed very little in microgravity. When a change was present, it was preponderant at the knee level: it consisted of a decrease in knee extension (from 2.6 to 5.5° varying between subjects) or in a change from a knee extension in normogravity (mean value of 3.9°) to a knee flexion in microgravity (mean value of 7.1°). It is interesting to note that on the basis of the anthropometric model of Winter (1990), Alexandrov et al. (1998) previously calculated, the relative effect of hip, knee, and ankle angle changes on the CM shift for a standard subject weighing 70 kg and measuring 170 cm. These authors demonstrated that a 1° change in the ankle angle generates a CM shift of 1.43 cm, which is twice as large as that generated by a 1° change in the knee angle (CM shift of 0.75 cm) and eight times larger than that generated by a 1° change in the hip angle (CM shift of 0.17 cm). These results indicate that the trend to knee flexion observed in microgravity should shift the final CM position backward. This was actually observed in subject S3. In subjects S1 and S5 where the increase in knee flexion was significant, the backward CM shift was prevented by a simultaneously decreased ankle dorsiflexion (see Figs. 5 and 9). A motor equivalent appears that is probably able to maintain an efficient CM minimization during the movement in microgravity.

How the CNS is able to perform the same kinematic performance in microgravity in spite of the equilibrium constraints disappearing was the third question raised in this study. In this context, the hierarchical model of the central organization of postural control including two stages as proposed by Clement et al. (1984) and Gurﬁnkel et al. (1981) (see Massion 1997) is strongly supported by experiments in microgravity (Clement et al. 1984; Clement and Lestienne 1988). The first stage of the model comprises an internal representation of the body. This includes a representation of body kinematics based on proprioceptive input from muscles from the eyes to the feet (Gurﬁnkel et al. 1988; Roll and Roll 1988), a representation of contact forces (Cordo and Nashner 1982; Marsden et al. 1981), of the body mass and inertia (Dietz et al. 1989, 1992), as well as the orientation of the body with respect to the external world (Hlavacka et al. 1995; Mergner et al. 1993). According to Gurﬁnkel et al. (1993a,b), this body schema remains rather stable in microgravity, although there are important changes in the sensory input. Perception of complex tactile stimuli or orientation of drawn ellipses, for example, are unchanged under microgravity, indicating that an egocentric reference
frame is still used in the absence of gravity to perform perceptual or spatial orientation tasks efficiently. The second stage of the model concerns the implementation of postural control by muscle forces assisted by local feedback. The invariant kinematic synergy that minimizes the CM shift during trunk bending both in normo- and microgravity as observed in the present study seems to depend on the level of the internal body representation. This allows us to predict the consequence of the trunk movement on equilibrium and to select the appropriate coupling between joints to minimize the CM shift. The kinematic synergy reflects an organization in term of postural space. According Feldman and Levin (1995), a referent body configuration in terms of joints position in space can be defined by setting the threshold of the stretch reflex of the various muscles at an appropriate level. The actual body posture differs from the referent posture due to the influence of the external forces such as gravity. Examples of movements organized in terms of postural space were given by Desmurget et al. (1996) for reaching movements and by Feldman and Levin (1995) for pointing movements. The implementation of the kinematic synergy by the muscle forces has to adapt to the changes in constraints due to the microgravity. It might be performed in line with the equilibrium point theory (Bizzi et al. 1982, 1992; Feldman 1980; Feldman and Levin 1995) indicating that a new referent joint position is planned. Alternatively, it could be implemented by an inverse dynamic model build up through learning (Gomi and Kawato 1996). In both alternatives, the muscle forces in microgravity should be modified as a function of the new constraints. It has been previously observed during a long-term space flight that an early soleus activation observed during backward trunk bending is replaced by an early tibialis anterior activation (Massion et al. 1992, 1993). In the present study, during a parabolic flight, the EMG activity showed an important reorganization to preserve the invariant synergy at the kinematic level. These results are in agreement with the observation of Lackner and Dizio (1992, 1996) on single movement performance in microgravity and with Macpherson’s hypothesis (Macpherson 1988) proposing that the muscle synergy in the postural domain is flexible and determined by biomechanical constraints.

In conclusion, the results of the present study show that the anteroposterior CM shift remains minimized in short-term microgravity, both during erect posture and during trunk bending. This minimization occurs through a kinematic synergy, which is an invariant parameter controlled by the CNS, which fixes the ratio between the hip, knee, and ankle angle changes during the movement. This control depends on both an internal representation of the body segment geometry and mass, which remains stable in microgravity thanks to an adaptable muscle synergy.

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