

## RESEARCH ARTICLE

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## Proprioceptive information processing in weightlessness

Received: 25 March 1997 / Accepted: 26 May 1998

**Abstract** The “illusions” experiment carried out on five astronauts during the last two French-Russian flights (Antarès in 1992 and Altair in 1993) and in the Russian Post-Antarès mission (1993) was designed to investigate the adaptive changes in human proprioceptive functions occurring in weightlessness at both the sensorimotor and cognitive levels, focusing on two kinds of responses: (1) whole-body postural reflexes, and (2) whole-body movement perception. These kinesthetic and motor responses were induced using the tendon-vibration method, which is known to selectively activate the proprioceptive muscular sensory channel and to elicit either motor reactions or illusory movement sensations. Vibration (70 Hz) was therefore applied to ankle (soleus or tibialis) and neck (splenii) muscles. The subject’s whole-body motor responses were analyzed from EMG and goniometric recordings. The perceived vibration-induced kinesthetic sensations were mimicked by the subjects with a joystick. The main results show that a parallel in-flight attenuation of the vibration-induced postural responses and kinesthetic illusions occurred, which seems to indicate that the proprioceptive system adapts to the microgravity context, where standing posture and conscious coding of anteroposterior body movements are no longer relevant. The same sensory messages are used at the same time in different sensory motor loops and in the coding of newly developed behavioral movements under microgravity. These results suggest that the human proprioceptive system has a high degree of adaptive functional plasticity, at least as far as the perceptual and motor aspects are concerned.

**Key words** Microgravity · Muscle proprioception · Posture · Kinesthesia · Man

### Introduction

By integrating all the various sensory data arising either from the body itself or from its surroundings, the central nervous system (CNS) is able to build up an overall picture, which is basic to the organization of goal-directed postural and kinetic motor activities. In fact, this constantly updated central representation corresponds to what has been successively named *postural scheme*, *body scheme* or *body image* (Head and Holmes 1912; Schilder 1950), depending on whether the term has been taken to have either more biological or more psychological connotations.

Among the many sensory signals incessantly converging to the brain, in particular the labyrinthine, cutaneous, and muscle proprioceptive ones are known to contribute directly to setting up and maintaining this postural frame of reference, one of the main characteristics of which is that it is oriented in relation to gravity (Young et al. 1984; Gurfinkel et al. 1988).

In weightlessness, all these sensory inputs undergo considerable alterations. The otoliths detect linear acceleration rather than the orientation of the head with respect to the gravity vector; the somatosensory inputs (touch and pressure cues) no longer provide the necessary information, unless an astronaut is using a body part as a means of fixation; and the muscle proprioceptive input probably remains functional, although both the content and the central processing of proprioceptive signals are greatly changed (Money and Cheung 1991).

Muscle proprioceptive messages provide the main information necessary for coding postural configurations and body movements as well as for exerting both reflex and automatic controls on these configurations and movements. In fact, these messages undergo a two-fold processing at different levels in the CNS: *cognitive processing*, which is responsible for the body’s awareness of

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its position and movements and contributes to spatial orientation ability as well as the ability to locate and reach objects in extra-personal space (Roll et al. 1991), and *sensorimotor processing*, which operates via reflex and automatic loops and has decisive effects on the regulation of posture and movement as well as participating in their central programming.

Many studies have dealt with the effects of microgravity on these basic mechanisms involving proprioceptive information processing. However, most of them have specifically focused on one of these mechanisms, using either a reflexological approach to analyze spinal excitability (Baker et al. 1977; Kovlovskaya et al. 1982; Vorobyov et al. 1982; Berger et al. 1992) or vestibulo-spinal reactivity (Reschke et al. 1984, 1986; Young et al. 1986), or psychophysical methods to study higher cognitive functions, such as body or limb-movement perception (Lestienne et al. 1977; Lackner and Graybiel 1979, 1981; Watt et al. 1985) or body representation in terms of systems of coordinates (Lestienne 1988; Gurfinkel et al. 1993).

With the method used here, it was possible to approach muscle proprioceptive functions at both their perceptual and sensorimotor levels, since it has by now become clearly established that the observed body-related perceptual and motor reactions induced by mechanical tendon vibration result from a selective activation of Ia muscle sensory afferents (Burke et al. 1976a, b; Roll and Vedel 1982; Roll et al. 1989b). In fact, the sensory messages evoked by vibratory stimulation always carry kinesthetic information, but, depending on the postural context, they give rise either to an actual body movement or to an illusory feeling of movement, which is perceived by the subject as it were a real movement. In human subjects maintaining erect posture, vibration applied to muscle tendons is known to induce involuntary whole-body sways in the forward or backward direction, depending on which muscles are vibrated (Eklund 1972; Roll and Roll 1988; Smetanin et al. 1993). This vibration-induced falling (VIF) strongly suggests that central neural structures involved in the processing of the proprioceptive messages contribute to the dynamic control of human vertical posture, on which any spatially oriented motor behavior is based. However, when the body motion due to vibratory stimulation is mechanically restricted, proprioceptive stimulation is able to induce whole-body postural illusions. In normal gravity, vibration applied to lower-leg muscles gives rise to an illusory body tilt in the anterior-posterior plane (Eklund 1972; Roll et al. 1989a, 1993).

In this study, the VIF was used as a test to evaluate the contribution of the muscle proprioceptors to basic postural control under weightless conditions, and whole-body illusions was used as a test to evaluate the contribution of the proprioceptive input to the conscious coding of body posture and movement under the same weightless conditions.

An approach of this kind was previously used in a preliminary study on the proprioceptive system in weight-

lessness (Roll et al. 1993). Data from the second French-Soviet mission (Aragatz in 1988) have in fact shown that an early sensorimotor and perceptual rearrangement occurred during the first few days of flight. In that study, however, only the perceptual and motor effects induced by stimulating ankle muscles (tibialis and soleus), which are directly involved in the postural regulation, were studied, and data were obtained on only two subjects.

It was therefore decided to further investigate how the proprioceptive information was processed in weightlessness, and whether this processing adapted in any way to the new environmental conditions. In particular, we started with the assumption that, in most oriented activities, proprioceptive signals from various muscles, from the eyes to the feet, are combined together to build up a central representation of the body posture. This was demonstrated by the fact that, for instance, the same forward body-tilt illusion could be induced by applying 70-Hz frequency vibration to the eye superior recti, dorsal neck, or soleus muscles of a fixed subject maintaining erect posture with his eyes closed (Roll and Roll 1988). Is this "proprioceptive chain" still functional in microgravity, or does the biomechanical disorganization resulting from a weightless environment lead the CNS to reprocess the sensory messages by selecting or ruling out some of them?

To answer this question, we extended our study to include neck-muscle in addition to ankle-muscle stimulation, and experiments were performed on five astronauts during three orbital flights aboard the Mir station so as to enlarge our body of data. Moreover, as it is well known that, in microgravity, a redistribution of tonic activity occurs in the muscles mainly involved in postural stance (Clément et al. 1984; Lestienne and Gurfinkel 1988), we studied the changes in activity of these muscles under both static postural control and dynamic conditions while responding to proprioceptive stimulation as a function of the phases of the mission (pre-, in-, post-flight). More specifically, we analyzed the EMG activity of the soleus, tibialis, biceps femoris (f.), and quadriceps f. muscles in three stabilized body positions (upright, inclined forwards, and backwards) before vibratory stimulation and in the upright position during vibratory stimulation.

## Materials and methods

### Subjects and test schedule

Three Russian and two French male astronauts (mean age 38 years) participated in the experiment aboard the MIR space station during the last two French-Russian missions, Antares in 1992 (two subjects) and Altair in 1993 (two subjects) and, in between, the Russian Post-Antarès mission in 1993 (one subject). Depending on the mission, the astronauts spent between 14 and 169 days in weightlessness; however, only the in-flight data recorded between day 4 and day 20 after launching are included in the present results.

In all the missions, both the timing of tests and their number were almost identical with all the astronauts. All the subjects (S1-S5) were tested on days 60 and 30 before launching in the

Moscow Mir-station model; an additional pre-flight test was carried out on day 8 on three subjects (S1–S3) at the launching center. The in-flight experiments took place during a 16-day period (from day 4 to day 20 after launching), during which the astronauts were tested three (S1–S3) or four (S4, S5) times according to the following schedule: S1 (days 4, 7, 13), S2 (days 5, 9, 12), S3 (days 6, 9, 12), S4 (days 5, 10, 13, 20), S5 (days 6, 9, 12, 19). Regarding the post-flight tests, subjects S1 and S4, who underwent a short-term-flight (2 or 3 weeks in weightlessness), both performed experiments on days 1 and 5 after landing. Two (S2 and S5) of the remaining subjects, who had spent almost six months in weightlessness, were tested on days 3 and 5, and the last one (S3) was tested on day 4 and 7. An additional opportunity of testing a long-duration flyer on day 7 was available, but with only one subject (S2).

#### Experimental set-up

Under all the conditions, the subjects were equipped with an adjustable jacket, which was especially designed for the experiment and fitted out with a large number of pockets and strap loops serving to guide the cables and to fit various sensors. The main electronic case (superpocket, 35×16×6 cm) was fixed to the jacket at waist level. It included a microprocessor, which monitored the experiment via flexible cables located on its right and left sides, which were in turn connected to the stimulation and recording devices.

All the tests were performed on standing, blindfolded subjects. Depending on whether the subject's expected responses were motor or perceptual, however, two kinds of body restraint systems were used. In the case of motor reactions, the subject was restrained by means of a foot rest, which was firmly attached to the ground and allowed forward and backward body tilt to occur around the ankle. In the perceptual tests, the subjects kept the detachable foot-rest soles, which could be strapped to the ground with velcro bands, and they were firmly immobilized against the Mir-station wall by means of a rolling belt buckled to the chest level. Pre- and post-flight tests were performed in the Moscow Mir-station model, except for two sessions in which an experimental set-up was used mimicking that of the station.

#### Stimulation device

Proprioceptive stimulation was delivered by means of five anatomically shaped mechanical vibrators. In order to minimize any vibration spread, they were fixed with punched elastic bands to the anterior and posterior part of the ankle, on the soleus and tibialis muscle tendons of both legs, and to the posterior part of the neck on the splenius muscles. Two catches fixed to one side of the vibrator could be used to tighten the vibrator using the holes of the elastic bands fixed to the other side of the vibrator, which were placed around the ankle and the neck. The neck vibrator could be correctly tightened by placing the elastic band on the chin. In addition, during the first in-flight test, the astronauts were asked to check the coupling of the vibrators to the tendons and to readjust it if necessary. The vibrators consisted of bi-axial DC motors equipped with small eccentric masses. The vibration time was either 10 s (perceptual test) or 5 s (motor test); a set vibration frequency (70 Hz) was applied with an amplitude of between 0.2 and 0.5 mm peak to peak.

#### Recording device

The subject's perceptual and motor responses were recorded by means of mechanical and physiological sensors. Two mechanical sensors were used in the experiment:

1. A high precision goniometer fixed to the foot support and fastened to the subject's leg by an adhesive band. By detecting the ankle angle, this sensor made it possible to accurately record the amplitude of the subject's vibration-induced body tilt as well as his resting position.

2. A joystick, including two high-precision goniometers, was located on the right side of the superpocket. By moving the joystick along the three axes, the subject could mimic both the direction and the amplitude of the perceived body displacements (backwards, forwards, left-right, up-down).

Physiological sensors consisting of four pairs of EMG electrodes were placed on the soleus, tibialis, quadriceps f., and biceps f. muscles of the right leg. A reference electrode was fixed to the subject's right knee.

EMG signals originating from the four leg muscles were recorded at the same time during a entire trial, that is, prior to, during, and after the ankle- and neck-muscle vibration. A small microphone strapped to the jacket, under the subject's chin, was used to record his comments during the experiment. All these mechanical, physiological, and audio signals were stored in a small portable seven-channel tape recorder (TEAC, HR30) placed in a jacket pocket. The data stored on magnetic tapes were returned to the earth and fed into a computer for off-line analysis.

#### Procedure

Subjects underwent extensive training during a period of several months before the first pre-flight test. In both training and test sessions, the astronauts worked in pairs: one of them was the experimenter and helped with the subject's equipment and the monitoring of the experiment from a remote control box. At each session, each subject underwent four experimental sequences during which vibration was successively applied to the soleus, tibialis, and neck-muscle groups.

The *motor reactions* were tested in the two first sequences in standing subjects with their feet restrained. Under these conditions, the subject was required to stand upright 2 s prior to the vibration, and a 5-s stimulation was then applied. A tone indicated the beginning and the end of each trial, during which the postural activity was continuously recorded. Two trials were carried out per muscle group; in the first sequence, however, two additional trials were performed, in which the subjects were asked to tilt their body 10° forwards or backwards before applying soleus- and tibialis-muscle vibration. In the second sequence, axial loads were applied by means of elastic stretchers running vertically between the subject's jacket and the foot rest. One of the stretcher ends was permanently fixed to the middle of each lateral side of the foot rest and the other end was hooked to rings fitted on the jacket under the subject's armpits. The resulting mechanical effect was that of gravity-like downward forces (50 kg) exerted parallel to the long body axis. To maintain an erect posture under these conditions, the subjects had to resist these forces by locking their knees and increasing their muscle activity.

The *perceptual reactions* were tested in the third sequence in standing subjects with their body restrained at the waist level under 10-s vibration conditions. As no motor reaction could occur, they were instructed to copy the virtual whole-body movements they perceived by moving the joystick along the three axes.

Both *perceptual and motor reactions* were tested in an additional sequence carried out under free-floating conditions. Under these conditions, the subjects were asked to first adopt an erect-like posture by grasping a handrail on the station ceiling, and they then released the handrail for some minutes and the stimulation was turned on.

#### Data processing and analysis

As both the timing of the tests and their number were almost identical with all astronauts, the data obtained on five astronauts were pooled in three groups corresponding to the pre-, in-, and post-flight phases of the missions. Additional data on two astronauts after 3, 4 and 5 months in weightlessness have been analyzed and discussed elsewhere.

The digitized EMG data of each muscle were analyzed using the RMS method during two recording periods (500 ms duration;

1250 Hz sampling frequency). The values obtained give, first, the mean level of muscle activity occurring during static postural stance prior to the vibratory stimulation (T0) and, then, the changes in this activity which occurred during the dynamic phase of the response after 5 s of vibration (T5). The effects of mission phase and subject position at T0 and those of the mission phase and vibrated muscle at T5 on the mean activity of each muscle were tested by means of separate three-way ANOVAs. Moreover, the effect of in-flight body-load variations on the mean activity of each muscle was analyzed using a two-way ANOVA.

On the other hand, the latency, amplitude, and mean velocity of either actual or illusory body tilt were determined from the ankle and joystick mechanograms. The effects of the mission phase (pre-, in-, and post-flight) and the vibrated muscle group (soleus, tibialis, and dorsal neck) on these variables were analyzed by means of separate two-way ANOVAs. Lastly, a two-way ANOVA was run in order to evaluate the influence of in-flight application of elastic loads on the vibration-induced body tilt amplitude.

## Results

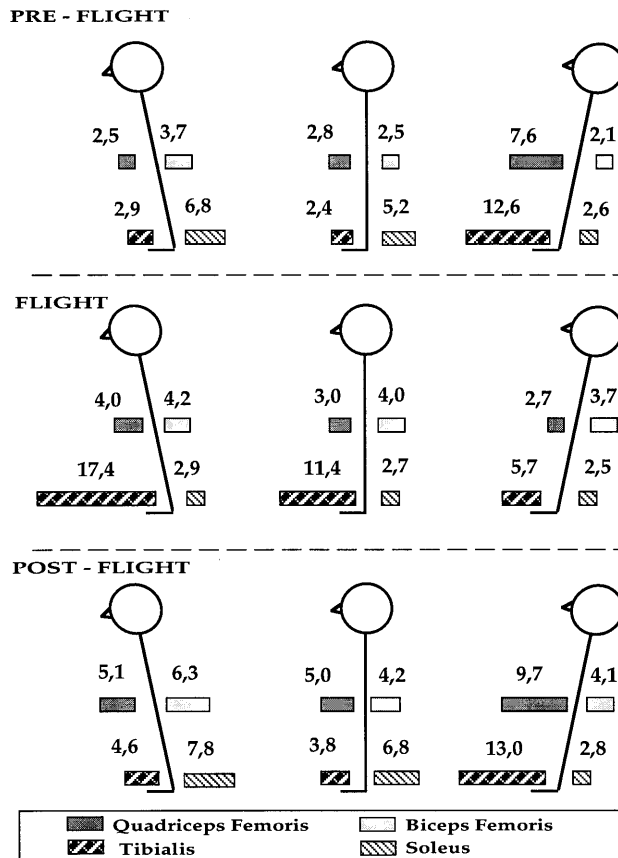
### Sensorimotor Reorganization of proprioceptive origin

#### Static postural EMG patterns (Fig. 1)

Looking at the EMG data obtained in the stabilized position before any muscle stimulation as a whole, the most striking fact which emerges is that the mean activity recorded in each of the four muscles investigated depended greatly on the subject's position [soleus:  $F(2, 8)=11.68$ ,  $P<0.005$ ; biceps f.:  $F(2, 8)=4.6$ ,  $P<0.05$ ; quadriceps f.:  $F(2, 8)=9.5$ ,  $P<0.01$ ; tibialis:  $F(2, 8)=3.35$ ,  $P<0.10$ ]. The general effect of the mission phase was clearly visible in the quadriceps-f. activity [ $F(2, 8)=11.49$ ,  $P<0.005$ ] and to a lesser extent in that of the tibialis and soleus ( $P<0.10$ ), with a highly significant interaction ( $P<0.005$ ) between these two factors in all the muscle groups except for the biceps f.

As shown in Fig. 1, in upright posture and under 1-G conditions, the most predominant activity occurred in the soleus muscle. When the body was voluntarily tilted 10° forward, the soleus activity increased significantly [ $F(1, 4)=7.78$ ,  $P<0.05$ ], as did that of the biceps f. [ $F(1, 4)=9.11$ ,  $P<0.05$ ] and, to a lesser extent, that of the tibialis anterior muscles. Conversely, the anterior leg muscles were directly responsible for maintaining the backward body tilt, which meant that the tibialis [ $F(1, 4)=13.4$ ,  $P<0.025$ ] and quadriceps f. [ $F(1, 4)=9.64$ ,  $P<0.05$ ] activity increased greatly in this position, while that of the soleus decreased ( $P<0.10$ ) and that of the biceps remained unchanged.

In weightlessness, subjects were kept in the upright position owing to the additional activity of the leg flexor muscles, especially the tibialis [ $F(1, 4)=21.8$ ,  $P<0.01$ ]. They also maintained forward [ $F(1, 4)=22.4$ ,  $P<0.01$ ] and backward [ $F(1, 4)=10.2$ ,  $P<0.05$ ] inclined postures mainly by increasing or decreasing the tibialis-muscle activation and, to a lesser extent, that of the quadriceps-f. muscle, whereas the soleus and biceps activity remained unchanged in both cases. This result seems to clearly indicate that body stance in microgravity is mainly based on a modulated tibialis muscle activity, which gradually



**Fig. 1** Static EMG activities ( $\mu\text{V}$ ) recorded in stabilized standing subjects in the pre-, in-, and post-flight phases of the missions in upright (middle), inclined forward (left) and inclined backward (right) body positions. The bars give the RMS values of the soleus, tibialis, biceps femoris (f.), and quadriceps f. muscle group activity

increases from a "natural" rest position (body inclined backwards, tibialis muscles relaxed) to an "abnormal" position (body inclined forwards, sustained EMG activity in tibialis muscles), with the in-between "upright" position showing an intermediate EMG value.

On the other hand, the effects of in-flight application of elastic loads between upper trunk and foot support as well as the total absence of load under free-floating conditions were visible only in the tibialis and quadriceps muscle activity. Indeed, the level of EMG activity recorded in both muscles during flight in upright subjects before vibratory stimulation varied significantly with the load; that is, it increased with stretchers in the tibialis and quadriceps ( $P<0.05$ ), whereas it dropped by half in tibialis ( $P<0.01$ ) and clearly decreased in quadriceps f. ( $P<0.05$ ) under free-floating conditions (Table 1). As early as 1 day after the return to earth, the pre-flight static EMG patterns were restored in both standing and inclined posture. However, an increase in the mean value was observed in the activity of all the muscle groups, with a high level of significance in both biceps f. [ $F(1, 4)=27.4$ ,  $P<0.01$ ] and quadriceps f. [ $F(1, 4)=51.9$ ,  $P<0.005$ ]. This increase was especially visible in the upright position, where the difference between

**Table 1** Mean values (averages of the individual subject's trial averages in  $\mu\text{V}$ ) with standard deviations of in-flight tibialis, soleus, biceps femoris (*f.*), and quadriceps f. muscle EMG activity in upright posture before stimulation (T0) under the three following conditions: body fixed to a foot rest (1), body fixed to a foot rest plus additional elastic loads (2), and body free-floating (3)

Condition	Recorded muscle			
	Tibialis	Soleus	Biceps-f.	Quadriceps-f.
Upright position with foot rest	11.4±2.4	2.7±1.0	4.0±3.0	3.0±1.2
Upright position with additional elastic loads	13.7 ± 0.4	2.3±0.8	3.6±3.8	5.2±1.0
"Upright position" free-floating	6.1±2.3	2.2±0.6	4.1±4.1	1.9±0.2

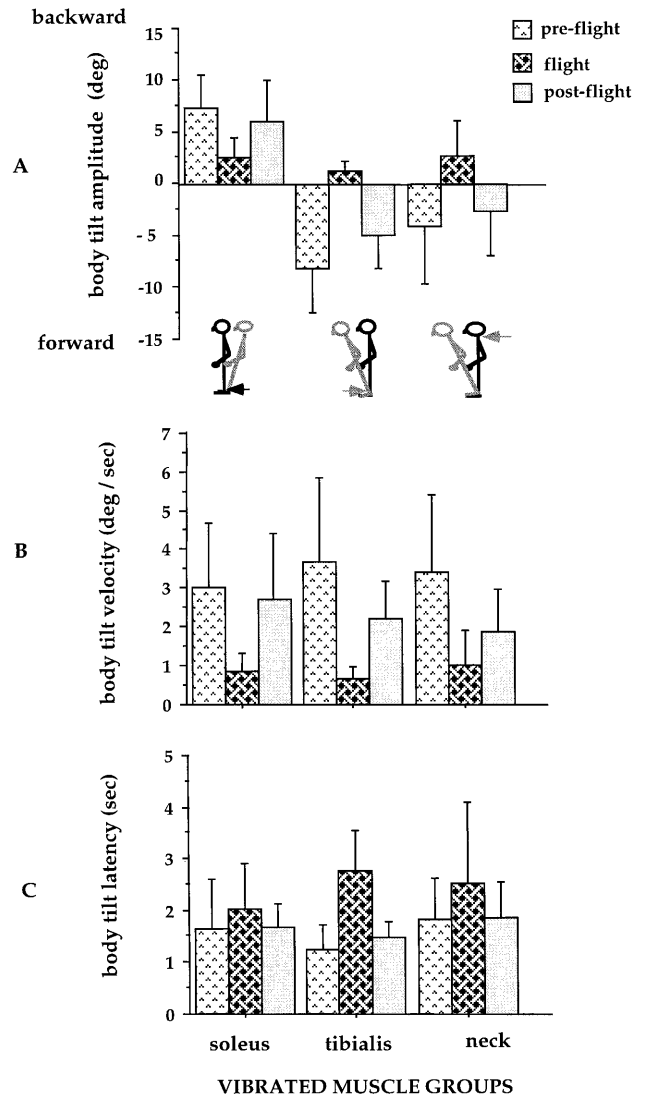
the pre- and post-flight level of each muscle activity was highly significant [soleus:  $F(1, 4)=8.94$ ,  $P<0.05$ ; biceps f.:  $F(1, 4)=28.5$ ,  $P<0.01$ ; tibialis:  $F(1, 4)=12.64$ ,  $P<0.025$ ; and quadriceps f.:  $F(1, 4)=15.6$ ,  $P<0.025$ ]

#### Dynamic postural responses to proprioceptive stimulation (Fig. 2)

Mean body-tilt amplitude (Fig. 2a). With all the data combined, the *mean amplitude* of the vibration-induced body tilt varied significantly between the pre-, in-, and post-flight periods [ $F(2, 8)=8.72$ ,  $P<0.01$ ] and between the vibrated muscle groups [ $F(2, 8)=9.75$ ,  $P<0.01$ ]. The effect of the microgravity corresponded to an in-flight decrease in the response amplitude [ $F(1,4)=21.93$ ,  $P<0.01$ ], which was associated with a change in the direction of the response with both tibialis- and neck-muscle stimulation. Indeed, only reduced backward responses occurred, whichever muscle group was vibrated. The most significant effect of the mission phase was observed with the tibialis muscle [ $F(1, 4)=39.75$ ,  $P<0.005$ ], although this effect was also visible with each of the other muscle groups stimulated [soleus:  $F(1,4)=7.86$ ,  $P<0.05$ ; neck:  $F(1,4)=7.78$ ;  $P<0.05$ ].

An in-flight partial recovery of these body-tilt amplitudes was observed with all three muscle groups vibrated when elastic loads were applied under these conditions (Table 2); this effect was significant, however, only in the case of the antigravific muscle, that is, the soleus ( $P<0.05$ ). By the first post-flight test, the direction of these postural responses was restored, whereas their mean amplitude recovered more progressively, particularly with tibialis-muscle stimulation.

Body-tilt velocity (Fig. 2b). The significant variation of the body tilt *mean velocity* during the pre-, in-, and post-flight periods resembled that of the amplitude [ $F(2, 8)=5.21$ ,  $P<0.05$ ] and no difference was observed in this respect between muscle groups. This means that the mean velocity of the postural responses decreased sharply during the flight in each of the muscle groups stimulated ( $P<0.05$ ) and failed to reach the pre-flight level after a 1 week post-flight with tibialis- and neck- ( $P<0.05$ ) muscle vibration.



**Fig. 2** Mean amplitude (A), velocity (B), and latency (C) of vibration-induced body tilts in pre-, in-, and post-flight phases of the missions. As shown by the corresponding pictograms, vibration was applied to the soleus-, tibialis-, and dorsal neck-muscle groups

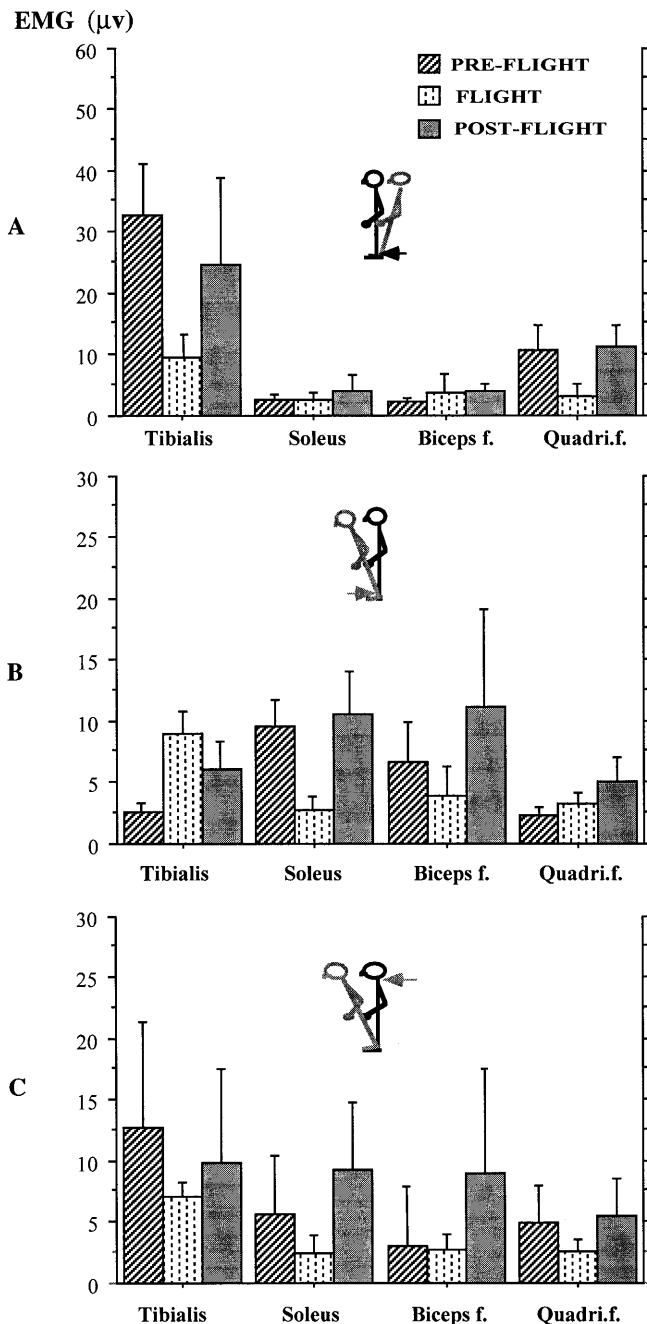
Body-tilt latency (Fig. 2c). Lastly, a significant increase in the body-tilt *latency* occurred in microgravity [ $F(2,8)=5.15$ ,  $P<0.05$ ]. This effect was especially visible when postural reactions were induced by tibialis-muscle vibration [ $F(1,4)=12.52$ ,  $P<0.025$ ]. However, a noticeable increase in the latency of the response to neck-muscle vibration was also observed. After landing, the ground postural response mean latency recovered rapidly since, in any case, the post-flight latency values did not differ significantly from the pre-flight ones.

#### Dynamic postural EMG patterns (Fig. 3)

After a 5-s period of vibration, the mean dynamic EMG activity in all four muscle groups clearly depended on the vibration site [quadriceps f.:  $F(2, 8)=8.38$ ,  $P<0.025$ ;

**Table 2** Mean values (averages of the individual subject's trial averages in degrees) with standard deviations of in-flight body-tilt amplitude after soleus, tibialis, and dorsal neck muscle group vibration with and without additional axial loads

Vibrated muscle(s)	Soleus	Tibialis	Neck
Mean body-tilt amplitude	2.6±1.9	1.2±1.2	2.6±4.0
Mean body-tilt amplitude with additional axial loads	4.6±0.5	1.7±1.7	4.6±2.2



**Fig. 3** Dynamic EMG activities induced by soleus- (A), tibialis- (B), and dorsal neck- (C) muscle-group vibration recorded in pre-, in-, and post-flight phases of the missions. Histograms giving the mean EMG values recorded in soleus, tibialis, quadriceps femoris (f.), and biceps f. after a 5-s period of vibration (T5)

tibialis:  $F(2, 8)=18.18$ ,  $P<0.005$ ; soleus:  $F(2, 8)=10.43$ ,  $P<0.01$ ; biceps f.:  $F(2, 8)=4.6$ ,  $P<0.05$ ] and the phase of the mission [quadriceps f.:  $F(2, 8)=8.53$ ,  $P<0.01$ ; tibialis:  $F(2, 8)=3.90$ ,  $P<0.10$ ; soleus:  $F(2, 8)=6.8$ ,  $P<0.05$ ], with a significant interaction between these two factors ( $P<0.01$ ) except for the biceps f. muscle.

In normal gravity, vibration-induced forward and backward body sways and the subsequent compensatory phases were accompanied by typical EMG patterns. That is, applying vibration to the soleus muscle resulted in a coactivation of the tibialis ( $P<0.001$ ) and quadriceps-f. muscles ( $P<0.01$ ) with a concomitant decrease in soleus- and biceps-f.-muscle EMG activity, which both showed exactly the same EMG pattern. The opposite EMG pattern was observed in response to tibialis-muscle vibration, which increased the activity of the soleus and biceps-f. muscles with respect to that of the tibialis and quadriceps ( $P<0.05$ ). The dorsal neck vibration, which induced forward body tilt, was accompanied by a general increase in the EMG activity in four of the leg muscles, which was particularly significant in the tibialis and quadriceps ( $P<0.05$ ).

Under weightless conditions, where the vibration-induced body tilts were all backward oriented and reduced in amplitude and velocity, the ground phasic EMG patterns disappeared almost completely and were replaced by a more tonic EMG modulation. This was particularly significant in the case of the tibialis [ $F(1, 4)=40.87$ ,  $P<0.005$ ] and quadriceps-f. [ $F(1, 4)=12.53$ ,  $P<0.025$ ] activity, where a conspicuous decrease was observed after soleus vibration. A similar effect was observed in the extensor muscles after tibialis vibration, when the soleus activity [ $F(1, 4)=15.61$ ,  $P<0.025$ ] and, to a lesser extent, that of the biceps-f. muscle group decreased sharply. Surprisingly, this effect was accompanied by a significantly higher mean activity in the tibialis flexor muscle [ $F(1, 4)=58.61$ ,  $P<0.005$ ]. Dorsal neck vibration resulted in a general decrease in the EMG activity of all the muscle groups tested ( $P<0.10$ ) except for the biceps-f. muscles, where the decrease was not significant.

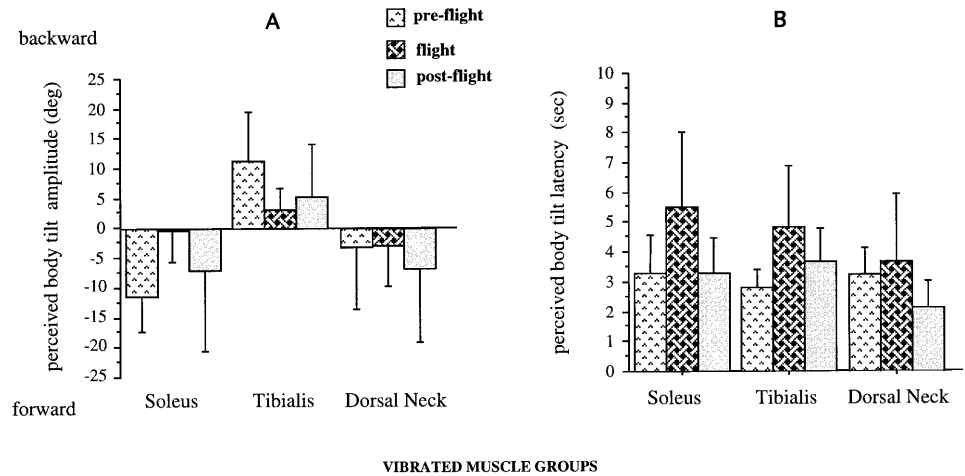
The pre-flight EMG patterns recovered as early as 2 days after landing, and a significant increase in the muscle activity occurred in most cases, whichever muscle was vibrated. This was particularly obvious in the case of the tibialis [ $F(1, 4)=7.87$ ,  $P<0.05$ ] and quadriceps-f. [ $F(1, 4)=10.40$ ,  $P<0.05$ ] muscle activity after tibialis vibration, and in that of the biceps f. [ $F(1, 4)=6.70$ ,  $P<0.10$ ] after neck vibration. After long flights, however, the data obtained on a single subject seem to indicate that the recovery took place more gradually, requiring a whole week.

#### Perceptual reorganization of proprioceptive origin

##### Perceived body-tilt amplitude (Fig. 4a)

As with the postural motor reactions, the illusory body movements in the sagittal plane, which could be easily

**Fig. 4** Mean amplitude (A) and latency (B) of whole-body postural illusions induced by applying vibration to the soleus-, tibialis-, and dorsal neck-muscle groups in pre-, in-, and post-flight phases of the missions



evoked on the ground by applying ankle- or dorsal neck-muscle vibration, tended to become less clearly perceptible in microgravity, except with the neck-muscle vibration. In fact, the perceived body-tilt amplitude varied depending on the vibrated muscle [ $F(2, 8)=7.64, P<0.025$ ], which was attested by the existence of a significant interaction between the two factors: phase of the mission and vibrated muscles [ $F(4, 16)=3.17, P<0.05$ ]. In-flight however, the only significant decrease which occurred was in the amplitude of the ankle-muscle vibration-induced illusions: the amplitude of these perceived whole-body tilts clearly decreased in weightlessness after soleus- [ $F(1, 4)=13.8, P<0.025$ ] or tibialis- [ $F(1, 4)=11.63, P<0.05$ ] muscle vibration, whereas it remained unchanged when neck-muscle vibration was applied. Moreover, no significant changes were observed in the direction of these effects. The vibration-induced virtual body movements in the specific forward and backward directions were therefore quite consistent with those evoked under terrestrial conditions.

In this case, the in-flight application of artificial loads further increased the amplitude of the whole-body movement illusions evoked by soleus- and neck-muscle vibration. As with the previously described effects of the stretchers on the motor responses, the amplitude of the perceived illusion significantly increased only in response to the soleus antigravifac muscle vibration ( $P<0.05$ ).

The post-flight values of the illusory whole-body tilt did not significantly differ from the pre-flight ones with any of the muscle groups vibrated; however, they were still below the pre-flight values more than one week after landing.

#### Perceived body tilt latency (Fig. 4b)

The latency of the perceptual effects varied with the phases of the mission [ $F(2, 8)=5.36, P<0.05$ ], without any significant interaction occurring between the two studied factors. This suggests that the in-flight latency of the perceptual illusions increased with each of the mus-

cle groups vibrated, but a significant effect was actually observed only with the tibialis ( $P<0.05$ ) muscle group. In addition, on days 12 and 13 during the first flight, atypical illusions were observed in two astronauts when vibrations were applied to the anterior lower legs (tibialis muscles). They reported a sensation of whole-body elevation along the longitudinal axis, sometimes combined with the feeling that the ankles were plantar flexed.

## Discussion

All in all, the present results show that, in a weightless environment, the processing of proprioceptive messages is greatly modified at both the sensorimotor and cognitive levels. At the sensorimotor level, if one looks at the changes observed here in the dynamic motor responses to proprioceptive stimulation, the most noteworthy finding was the decrease in their rate of occurrence with respect to the control condition. This decrease seems to vary with the duration of the flight, since it reached about 60% in two of the astronauts tested between 3 and 6 months of exposure to microgravity. When these postural responses were still observed, their amplitude was reduced with all the muscle groups stimulated, and they occurred later and more slowly. Moreover, the directional specificity of these responses, depending on the muscle group stimulated, disappeared in two of three muscle groups during the very first days of flight. Concomitantly, new EMG patterns showing a large decrease in the regulatory phasic activity occurred in the muscles involved in these behavioral changes.

At the perceptual level, the amplitude of the whole-body vibration-induced illusions was only reduced in microgravity in the case of ankle-muscle stimulation, whereas the neck-muscle sensitivity seemed to be less affected by microgravity. Nor did the orientation of the perceived body tilt change as a result of exposure to microgravity.

The main explanation which can be put forward to account for these adaptive modifications is that micrograv-

ity puts the body in a new environmental context where both erect posture and balance maintenance are no longer relevant. In fact, the changes in the body's biomechanical properties as well as the body and environment relationships imposed by this weightless context cause the brain to adapt the motor commands and the postural regulation mechanisms to these new conditions. The adaptation of the motor command took the form of a clear redistribution of motor activity from the extensor to flexor or ankle muscles. Unlike what happens on the ground, in-flight EMG recordings showed here that the static upright position was maintained, owing to a sustained tonic activity in the flexor muscles, particularly the tibialis ones. This result is quite consistent with those previously reported by Clément et al. (1984), Clément and Lestienne (1988), and Lestienne and Gurfinkel (1988). Different hypotheses are generally proposed to account for this redistribution phenomenon: on the one hand, by suppressing the vestibular influence usually exerted on the ankle muscle motoneurons, the functional otolithic deafferentation induced by these weightless conditions may result in a flexor facilitation. A more biomechanical interpretation is based on the fact that, in microgravity, the passive elastic forces developing in lower-leg extensor muscles induce a "natural" backward inclined body posture, which leads the nervous system to adapt the motor commands by increasing the flexor-muscle activity in order to counter these forces. Standing erect in microgravity, therefore, requires the opposite pattern of ankle muscle activity where the flexor-muscle activity increases considerably in comparison with the conditions on earth. Lastly, this reversal of the ankle-muscle tonic activity may also result from a change in the tactile interaction between feet and support due to the abolition of body weight. Data from Lipshits (1993) pointed to this possibility, since this author demonstrated that the EMG pattern varied depending on the nature of the foot support. In particular, when the posterior part of the foot was placed on a soft support, standing posture was kept by means of a tibialis and quadriceps-f. tonic coactivation instead of the soleus activity, which occurred alone with a firm support.

Regarding the motor command itself, the changes in postural regulation observed in weightlessness show that the sensorimotor loops linking proprioceptive afferents to motor structures underwent an adaptive process. Since balance no longer requires to be maintained in microgravity, the gain in these sensorimotor loops was greatly reduced and the vibration-induced postural responses sharply decreased or even disappeared (in particular, those from antigravific muscles). This last point is in line with data by Clément et al. (1985), showing that the amplitude of the functional stretch reflex evoked by unexpected displacement of a subject's foot support was considerably reduced in microgravity, although the cosmonaut's ability to counteract postural perturbations remained intact.

Another fact worth discussing is that the in-flight residual vibration-induced body tilts were all backward

oriented, whereas under terrestrial conditions the direction of these regulatory responses are known to be closely dependent on the muscle group stimulated (Eklund 1972; Roll and Roll 1988; Roll et al. 1989a; Gilhodes et al. 1996). The in-flight loss of the directional specificity of the vibration-induced postural responses may have directly resulted from a reversal of the ankle-muscle tonic activity. Recent studies carried out under terrestrial conditions (Gilhodes et al. 1996) support this view. They indicate that proprioceptive inhibitory influences may be sent only to ankle-muscle motor nuclei which are directly involved in maintaining erect posture. The direction of the vibration-induced postural responses would, therefore, depend on the origin (soleus or tibialis muscle) of the tonic activity mainly responsible for sustaining posture. This interpretation is consistent with the fact that the post-flight recovery of body stance was based on soleus tonic activity and that it was associated with a reorientation of the vibration-induced postural responses as early as the first day after landing.

The nature of these changes suggests that new relationships between proprioceptive sensory afferents and the motor command are set up in weightless environments, which involves a high degree of sensorimotor adaptability. The terrestrial internal model of postural regulation from proprioceptive origin seems to persist in microgravity, however, since it can be easily recalled by providing the astronauts with earth-like sensory and motor information, for instance, in the form of artificial axial forces. This "switching" effect of the sensorimotor context, whereby the appropriate mode of proprioceptive feedback processing is selected and hence the appropriate postural activity triggered, has by now been well documented under normal gravity conditions (Feldman and Latash 1982; Roll et al. 1986; Gurfinkel et al. 1993) and can probably now be extended to weightless conditions.

Two remaining facts concerning the changes observed here in the mechanisms subserving postural maintenance and proprioceptive regulation are worth discussing. First, like Kozlovskaya et al. (1981, 1982), we recorded an increase in the activity of cosmonaut's lower-limb muscles during the first week post-flight. This increase might constitute an adapted response to the considerable postural instability to which cosmonauts are subjected upon their return to earth, rather than resulting directly from the in-flight adaptation of higher level commands. A large number of data are consistent with this conclusion (Anderson et al. 1986; Kenyon and Young 1986; Collins et al. 1995). The second point concerns the finding that the proprioceptive feedback was found to contribute less efficiently to postural regulation during the early post-flight period, as demonstrated by the gradual increase in the amplitude of the vibration-induced postural responses recorded during the first week. These data are consistent with the stabilometric analyses performed by Collins et al. (1995) at the return of the SLS2 shuttle mission.

The most obvious adaptive changes undergone by the in-flight perceptual processing of proprioceptive messag-



es were the decrease in the occurrence frequency of the vibration-induced whole-body kinesthetic illusions which occurred on the very first few days of the flight. This effect was particularly visible when stimulation was applied to the soleus muscles, where only about 40% of the trials gave rise to illusory perceptions of body tilt, whereas the postural illusions of proprioceptive origin induced by dorsal neck-muscle vibration persisted in-flight and their terrestrial characteristics remained unchanged.

The fact that specific kinesthetic illusions could be still evoked under weightless conditions suggests that proprioceptors remain functional in weightlessness, and argues in favor of a central rather than a peripheral interpretation of the observed changes. The proprioceptive messages evoked in flight by vibratory stimulation might be centrally decoded as a function of the weightless context, in which new motor skills were being built up. In particular, it is worth mentioning that the need to permanently anchor the body to the ground by means of the feet disappears in microgravity, except in the case of some activities or when whole-body propulsion is necessary inside the module; ankle-muscle proprioception will therefore no longer participate in anteroposterior body-movement coding. This may explain why the ankle-muscle vibration-induced body tilt vanished. This explanation is also consistent with the finding that kinesthetic illusions could be re-evoked in flight by applying axial loads to provide foot support.

On the other hand, the in-flight persistence of the whole-body postural responses to neck-muscle vibration suggests that this body segment may play a specific role in the postural proprioceptive adaptation process. In fact, experimental reports by inexperienced cosmonauts have shown that the visual modality plays a major role in weightlessness, particularly in body orientation with respect to the environment, but also in the actual organization of body posture. Given the high degree of coupling which exists between eye and head movements and the leading role played by gaze orientation in postural control (Berthoz 1987; Roll and Roll 1988; Gilhodes et al. 1996), eye- and neck-proprioceptive information seem likely to contribute importantly to the postural adaptation to weightless environments.

**Acknowledgements** The authors are grateful to the engineering team responsible for the space missions and to the French and Russian astronauts who participated in the experiments. This work was supported by grants from the Centre National d'Etudes Spatiales (CNES). English revision of the paper by Dr. Jessica Blanc.

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