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Short review

The sensorimotor and cognitive integration of gravity

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Abstract

In order to demonstrate that gravity is not only a load acting locally and continuously on the body limbs, but is also used by higher levels of the nervous system as a dynamic orienting reference for the elaboration of the motor act, a review of several experiments conducted both in 1 *g* and 0 *g* are presented. During various locomotor tasks, the strategy that consists of stabilizing the head with respect to gravity illustrates one of the solutions used by the CNS to optimize the control of dynamic equilibrium. A question which remains to be solved when considering experimental results obtained in weightlessness concerns, however, the maintenance of motor schema that has evolved under normal gravity. Results have suggested that the concept of conservative processes, that would adapt postural control to weightlessness by using previously learned innate strategies, must be reconsidered during goal-oriented tasks. In fact, it is proposed that when conservative processes and existing solutions derived from a repertoire of terrestrial postural strategies do not provide efficient output, the CNS has to create novel strategies through a slow learning process. As with the study of postural control, three-dimensional arm reaching movements also illustrate the central representation of gravity. Indeed, gravity can be regarded as either initiating or braking arm movements and, consequently, may be represented in the motor command at the planning level. Finally, from a prospective point of view, there is a need to determine new experimental paradigms in order to study the specific motor control of man in space. It is suggested that the formulation of experimental paradigms should not consider man in space simply as a terrestrial biped.

Keywords: Posture; Gravitational force; Sensorimotor adaptation; Central representation; Planning; Kinematics

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Contents

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1. Introduction

As the passage from day to night, the gravitational field created by the mass of the earth makes up one of the ethological constraints that permanently act upon living organisms. Resulting perhaps from such a continuity, gravity has, thus, become a natural phenomenon somewhat taken for granted which has rarely figured among the list of questions frequently posed by neuroscientists. Within this perspective, the role of gravity has remained confined either to stimulating vestibular organs or a force exerted locally upon body segments. However, cognitive processes must account for the presence or absence of gravitational force. Indeed, our mode of locomotion reflects and is the product of a successful adaptation to the terrestrial environment. In the same way as the development of communication skills, bipedal walking has become one of the decisive criteria of humanity.

Gravity can essentially be considered as a force acting both on the vestibular and proprioceptive systems. The consequence of this separate action has resulted in a common distinction in studies of sensorimotor adaptation to changing gravitational conditions. Gravity has been studied either, as an orienting reference leading to the development of related experiments examining spatial orientation and eye–head coordination [7,34], or it has been considered both (i) as an orienting reference and (ii) a mechanical constraint (load) which may in some situations, result in the subjects' disequilibrium. These questions have commonly been studied through the examination of equilibrium functions [30] or posture and movement coordination [19].

This paper will focus upon the coordination between posture and movement, and more specifically, will attempt to show that gravity affects cognitive functions related to spatial orientation, as well as playing an important role in motor planning.

2. Gravity provides a reference frame for the estimation of body movements

The representation and efficient guidance of a body segment in space would be impossible if the CNS is unable to use a reference frame within which the external objects' positions and displacements in terms of the whole body could be estimated. A question asked frequently in behavioral neuroscience surrounds the problem of the existence of a stable reference frame used to control posture and voluntary movement [2].

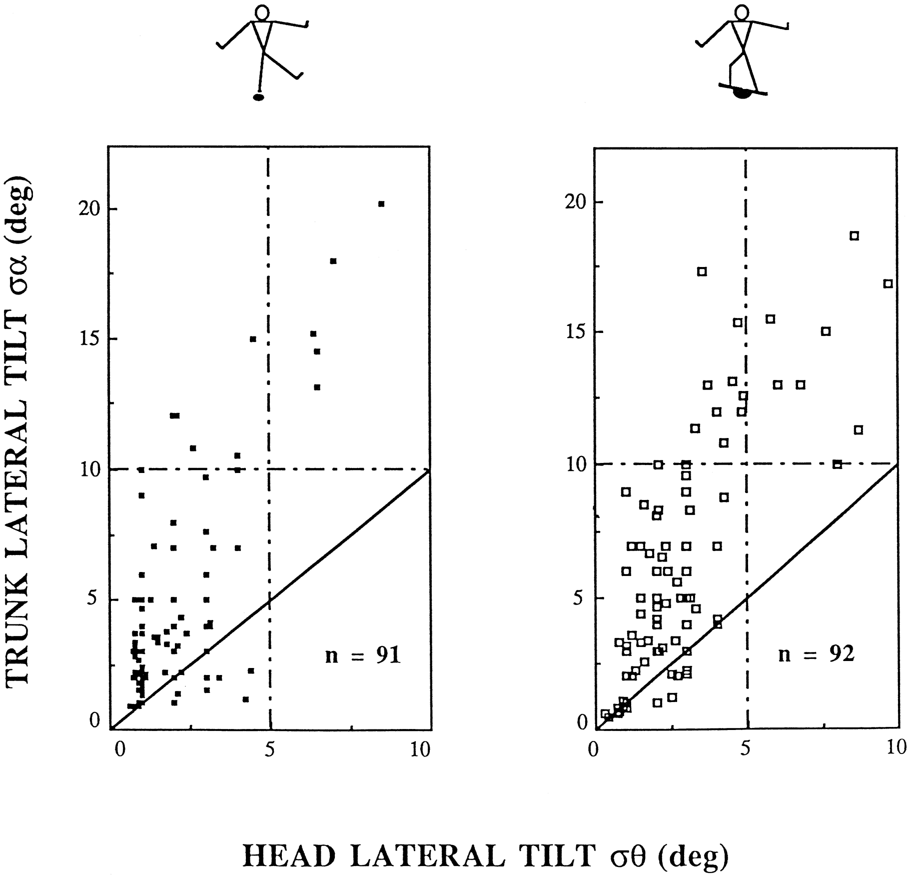

Fig. 1. Head rotation vs. trunk rotation in the frontal plane. Standard deviation of head rotation (σ_θ) is plotted as a function of the standard deviation of the rotation of the trunk (σ_α) in the frontal plane on the beam (left) and on the rocking platform (right) for the eight subjects in all experimental conditions. Note that the data points are mainly distributed above the diagonal indicating that head rotation is less than trunk rotation (n = number of samples).

During various locomotor tasks, the cephalic segment may constitute a stabilised reference. Even though the task imposed upon the subjects does not require the orientation of the head in any one particular direction (such as is the case during walking), head stabilisation made upon a geocentric reference provided by the gravitational vertical has the advantage of simplifying incoming information processing. Signals from the vestibular system, received at a cranio-topic landmark, provide direct information as to the movements of the head in space, in other words, as an exocentric reference, without the need for signal transformation [3]. If the landmark at which accelerometers are found is supplied with information from another landmark where certain calculations are made, the problem of coordinate transformation disappears [10]. Experimental results [32] have confirmed this theory and have shown that during unstable equilibrium in the frontal plane, regardless of the supporting base, head angular displacements are reduced to a few degrees (Fig. 1). These and similar results found in a variety of voluntary tasks [29,30,32] have permitted the generalisation of the hypothesis that head stabilisation, around the direction determined by gravitational force, constitutes a strategy used by the subjects to optimize the control of dynamic equilibrium. Other studies have also demonstrated that gravity strongly determines kinematic patterns during human locomotion. Borghese et al. [5], for instance, have recently demonstrated that invariant kinematic patterns are related to gravity. They found a planar co-variation of limb orientation with respect to the vertical, contrasting to a large variability of interlimb angular displacements. They also concluded that gravity-based frames would allow the registration of spatial information derived from multiple sensors and directed to multiple effectors.

3. The modification of postural strategies in conditions of weightlessness: operative or conservative processes?

A question which remains to be solved when one studies experimental results obtained in weightlessness (0 *g*), concerns the maintenance of motor schema that have evolved under normal gravity (1 *g*) conditions, or the acquisition of a new repertoire of postural strategies. Previous studies have demonstrated that postural processes remain in conditions of 0 *g* after a few days of adaptation, in the absence of equilibrium constraints [8]. Anticipatory postural adjustments (APA's) that precede voluntary movements in 1 *g* conditions minimizing forthcoming disequilibrium of the center of mass (CM), have also been recorded in 0 *g* [2]. Massion et al. [20,21] have demonstrated that CM projection remains inside the foot support area during forward and backward trunk bending movements conducted in 0 g. These authors proposed that axial synergies (a coupling between hip, knee and ankle joints) and the resulting CM stabilisation are independent of gravity constraints. Finally, Mouchnino et al. [24] have shown that during leg raising movements conducted during parabolic flights, the CM remains the stabilized reference, confirming ideas previously formulated in 1 *g* [23].

Thus, until now, all these findings agree with the suggestion that CM regulation is independent of modifications to the gravitational environment [18]. Results that somewhat contradict these suggestions have been obtained from goal-directed whole body reaching movements [31]. A large majority of previous studies have imposed voluntary movements upon erect postures, only examining resulting constraints placed upon equilibrium. During a whole body reaching task executed towards a target located on the ground, the CNS has to simultaneously solve constraints of both spatial trajectory formation and equilibrium. Correct hand trajectory towards a target in extracorporal space has to be defined, whilst at the same time preserving the entire body's CM within the supporting foot area. In addition, all body segments are involved in the movement towards an object in extrapersonal space and, consequently, multiple joint configurations and trajectory solutions of distal limbs are used. Recent results [36] have concluded that the execution of whole body reaching under 1 *g* conditions is achieved by an anticipated backward displacement of the CP (under neuromuscular control of ankle muscles) [41], leading to a separation of projections of the CP and CM. The resulting moment arm produces external torque which induces forward whole body angular momentum [39]. Such processes result in body segment acceleration and significant horizontal displacements of the CM which can move up to 65% of foot length [38]. Interpreted alternatively, results showed that anticipatory postural adjustments initiate CM displacement, not directly ensuring their minimization.

CM displacements during whole body reaching in 0 *g*, collected from four cosmonauts during the Franco-Russian spatial missions ALTAIR (1993) and EUROMIR (1994) aboard the Russian Space Station MIR, deviated from CM displacements recorded in 1 *g* conditions [37]. In Fig. 2, it can be seen that cosmonaut C1 shows the most surprising modifications to horizontal CM displacements, values increasing three-fold on various flight days, compared to pre-and post-flight tests. Slightly less striking differences were recorded for C2. Although at least two-fold increases in CM horizontal displacements were recorded early during spaceflight (FD6), C2 demonstrated CM amplitudes that had returned to below pre-flight values by FD20.

Furthermore, in contrast to previous results obtained during standing postures [8,21], data from whole body reaching movements [31] have shown an initial backward posture inclination immediately preceding movement onset in 0 *g*. This backward leaning posture, previously unreported, was present in all testing sessions throughout prolonged space flight and may be interpreted by considering the whole sequence of the movement. Under 1 *g* conditions, similar squatting movements have been shown to be

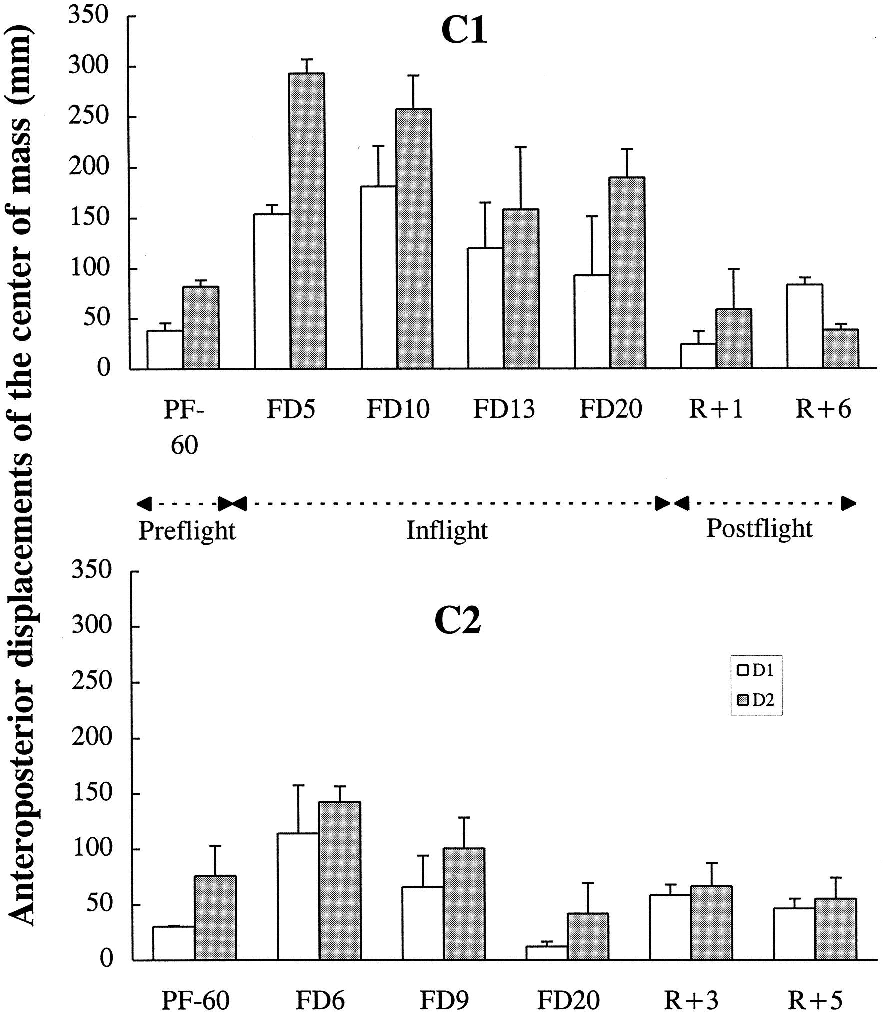

Fig. 2. Mean values and S.D. of the displacement of the center of mass along the anteroposterior axis during pre- (PF-60), in- (FD-5,9,10,13,20) and post-flight (R + 1,3,5,6) tests for cosmonauts C1 and C2. Grey and white bars indicate the two different target distances ($D_1 = 5$ cm and $D_2 = 45$ cm), respectively.

facilitated by gravity force [6]. In 0 g, gravitational torques are lacking. Making use of active and passive elastic forces of lower leg muscles remains the only means of generating joint torques for movement production, especially the distal joints which are attached with footstraps to the 'floor' of the cabin. A backward body tilt stretches ankle flexor muscles in order to obtain adequate net joint torques in the absence of gravitational components. Fig. 3 shows the evolution of muscular dorsi-flexor ankle torque when cosmonauts C1 and C2 reached objects placed at two distances. What is most important to note is the significant increase in values acquired during all flight days as compared to pre- and post-flight measures for the distant target condition.

Otherwise, such a backward-leaning posture which results in an initial and final displacement of the CM out of the foot area, contradicts the idea of an invariance of the strategy aimed at maintaining the CM position within the foot area under conditions of weightlessness. The results outlined above suggest that the theory may hold for some tasks such as arm lifting [8] or axial bending movements [20], but must be reconsidered for whole body, goal-oriented tasks.

Hand trajectory shapes in the sagittal plane remained approximately the same both in 1 g and 0 g, but did not, however, result from joint angular displacement invariance [31]. A minimization of trunk angular displacement, coupled with larger knee joint flexion were recorded in four subjects in conditions of weightlessness, compared to movements made in normal gravity conditions.

These findings lead to several speculations. In weightlessness, the CNS cannot use a gravitational reference to compute the displacement of body segments. It seems that it uses principally a geocentric reference derived from the establishment of an internal body axis reference, called an 'idiotropic vector'. Fredérici and Levelt, [13] have demonstrated that in weightlessness, subjects have a tendency to localize object position in space by means of an egocentric reference. Consequently, movements could be estimated within a body-related reference situated at the head/trunk

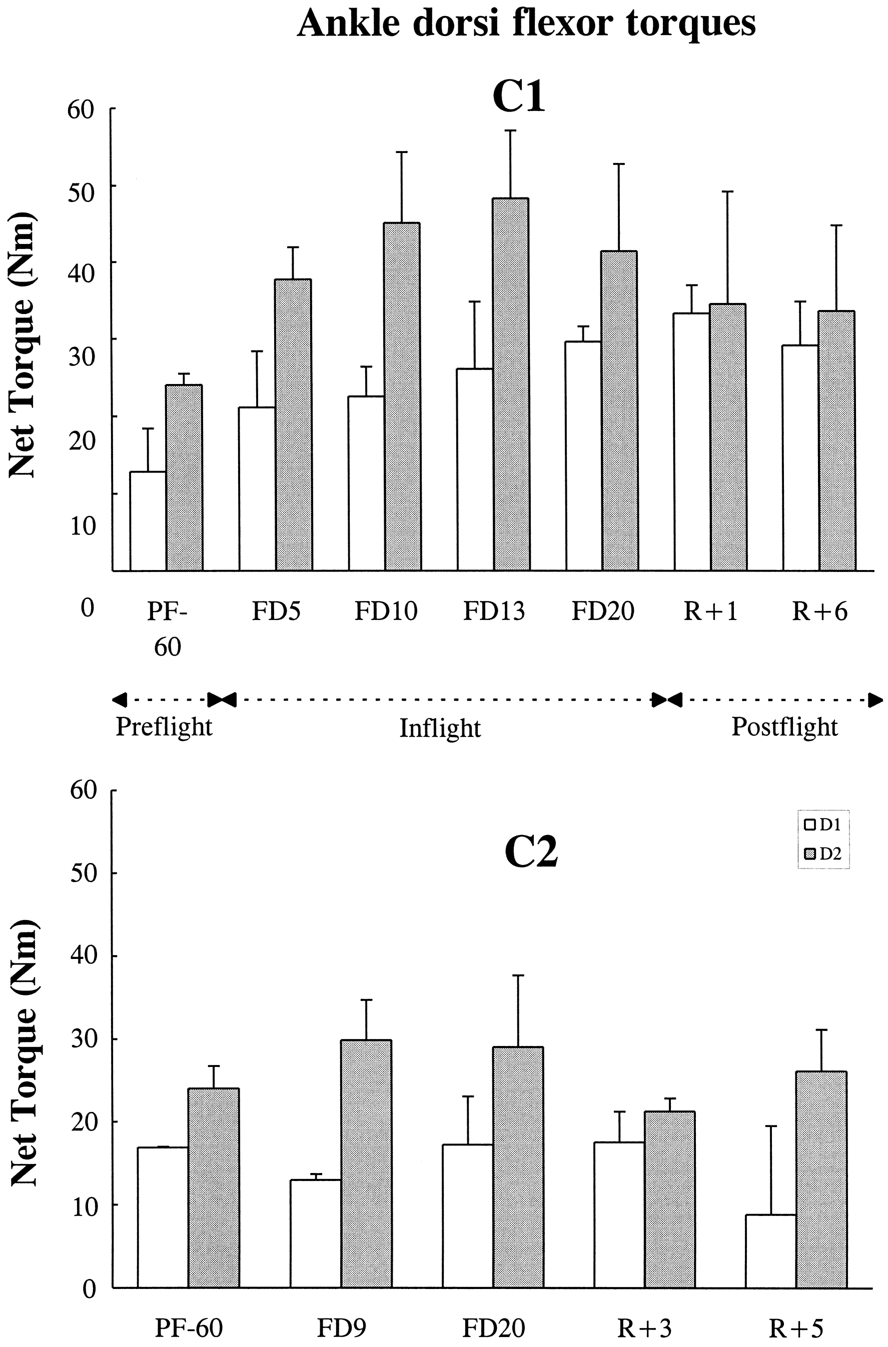

Fig. 3. Mean values and S.D. of net ankle torques calculated from pre- (PF-60), in- (FD-5,9,10,13,20) and post-flight (R + 1,3,5,6) tests for cosmonauts C1 and C2. Grey and white bars indicate the two different target distances ($D_1 = 5$ cm and $D_2 = 45$ cm), respectively.

level. This hypothesis may be confirmed through sensations experienced by cosmonauts during leg flexion movements. Attached by footstraps, they reported a feeling that the ‘floor’ was approaching the body, and not the habitual feeling of descending towards the floor. Furthermore, Gurfinkel et al. [15], studying the determinant of spatial orientation during ellipse drawing, have concluded that the egocentric reference system ensures the normal performance of sensorimotor tasks in the absence of a gravitational reference. Therefore, in our experiment, the strategy which consists of stabilizing the trunk during rotation provides a substitute (egocentric) frame of reference used to calculate target position in extracorporal space, as well as necessary limb trajectory to reach the target.

Overall, these results suggest that the concept of conservative processes that would adapt postural control to weightlessness by using previously learned and innate strategies [18] must be reconsidered during complex postural goal-oriented tasks. The discrepancy between previous studies which have suggested a general tendency to use similar motor solutions in 0 *g* and 1 *g* conditions may often be explained if the mechanics or task goals are taken into account. During whole body reaching movements, trunk angular displacement with respect to the vertical is approximately 70°. In contrast, during the trunk forward bending paradigm [20], this angle never exceeds 30°. Thus, simple mechanical modelling would reveal that during whole body reaching movements, hip gravitational torque is twice that calculated for trunk bending movements. Additionally, during arm raising movements [8], the effects of gravitational torque upon the whole body may be neglected, as modifications to vertical trunk orientation are minimal. Therefore, it might be expected that when gravity is absent, movements will remain unchanged. Additionally, if subjects are asked to maintain an erect posture, what would be the need to develop new solutions if those used in 1 *g* function perfectly in 0 *g*? Finally, if the goal of an experimental task is to stabilize the CM along the anterior–posterior axis, as may be the case during trunk bending for example, why modify this objective in 0 *g*? In contrast, however, when the goal of the task is to reach a target located in extracorporal space, under normal gravitational conditions, gravity seems to play a considerable role in movement execution. Therefore, when confronted with modified surroundings, subjects must turn to alternative strategies to successfully execute whole body reaching movements.

Finally, we propose that when conservative processes and existing solutions derived from a repertoire of terrestrial postural strategies do not provide efficient output, the CNS has to create novel strategies through a slow learning process, for example, aquatic locomotion. In Fig. 3, cosmonaut C2 (three previous spaceflights) clearly demonstrated similar increases in muscular ankle torque to C1 (first spaceflight), but was able to reduce CM displacement by FD20. These inter-subject differences may further cast doubt upon conservative highly stable pre-established strategies, built up by experience. Data on CM displacements in C2 which initially increase under 0 *g* conditions and then reduce towards FD20, may indicate rather than a recovery of CM control per se, a novel strategy, whereby subjects make use of their only supporting point of contact (the foot in footstraps). Using their attachment to the floor of the cabin, subjects place a greater dependency upon knee flexion [33] to attain the target. This would induce a straighter CM trajectory towards the floor of the cabin and in turn, may explain lower CM horizontal displacements with experience of spaceflight.

4. Evidence for a central representation of gravitational force: arm kinematics in normal gravity and weightless environments

The previous section has considered the effects of gravity in spatial orientation and dynamic equilibrium during whole body movements. In this section, the question of sensorimotor integration of gravitational force by the CNS will be discussed for vertical arm movement.

Numerous theories have been forwarded concerning the way in which the CNS plans arm movements. Several authors [11,22,42] have proposed that the planned variable by the CNS is hand trajectory in space (extrinsic coordinate frame). Other authors [16,35] have suggested that movements are planned in joint space (intrinsic reference frame). Finally, the equilibrium point hypothesis proposes, however, that the CNS may profit from mechanical features of the musculoskeletal system in order to produce arm movements [4,9]. In addition to considering the coordinate systems in which a movement could be planned (Cartesian, joint or muscular), an interesting question would concern the relationship between gravitational force and arm movement control. Gravity can be regarded as either initiating or braking arm movements and, consequently, may be represented in the motor command. Atkeson and Hollerbach [1] have shown how different components of joint torques (including gravity torques) might be represented by the CNS during vertical arm movements. For elbow flexion/extension in the sagittal plane, Virji-Babul et al. [40], concluded that the CNS modulates a basic pattern of activation by using gravitational force. In contrast, Fisk et al. [12], analyzed sensorimotor adaptations to changing gravito-inertial environments, and inferred that adaptations are easier for rapid than for slow movements due to the high influence of micro and hyper-gravity on proprioceptive information.

The question as to how gravity is represented by the brain for arm movement production remains, however, unresolved. Does the CNS treat gravitational force as a simple external load or does gravity have a unique status in the motor command? We have hypothesized that gravitational force is centrally represented in an anticipatory fashion during vertical arm movement planning. To test this hypothesis, we asked subjects to perform vertical movements in two directions (against and with gravity) with two different loads (unloaded and with a 0.5-kg mass).

Our principal results from 1 *g* experiments [25–28] have revealed curved paths in the sagittal plane for all subjects (Fig. 4). It is important to note that movements against gravity showed greater maximum deviation ($D_{\max}$) from straightness than movements with gravity, for both weight conditions (Table 1). ANOVA analysis gave a significant main effect of movement direction ($F_{1,7} = 7.92$, $p = 0.025$) and no significant effects of weight and interaction between weight and direction ($p > 0.05$). Despite these differences, however, subjects executed arm movements for both directions and weights with approximately the same movement times (Table 1).

We also looked for modifications in finger paths as the result of exposure to 0 *g* conditions. Here, ANOVA analysis (two directions × two weights × five days) gave

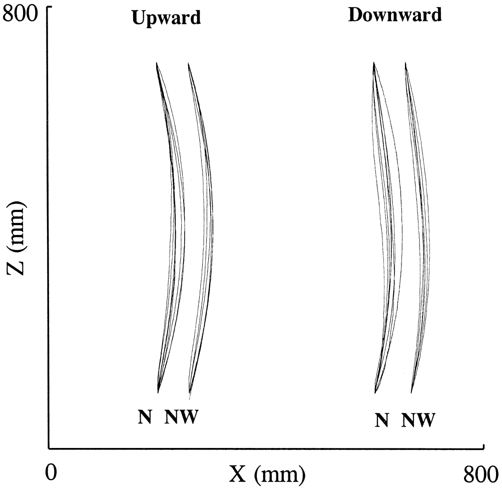

Fig. 4. Averaged paths from each subject ($n = 8$) in the sagittal plane for both directions and weights. Paths have been superimposed for each experimental condition and artificially offset to the right along in the X axis. N: normal speed without weight, NW: normal speed with a 0.5-kg weight.

an interaction effect of the three factors upon D_{max}, ($F_{4,4} = 10.35$, $p = 0.021$), while no single factor had a significant main effect ($p > 0.25$). The difference in curvature between upward and downward 1 g movements persisted in weightlessness, even until the 18th flight day. In the absence of added mass, downward movements were straighter on flight days 12 and 18, in comparison to pre-flight measurements. Upward movements were also slightly straighter on FD-12 and FD-18.

Hand paths for early post-flight tests (R + 1) without mass were also straighter than pre-flight paths, for both direction movements. Later post-flight tests (R + 7) revealed that paths had a tendency to return to pre-flight curvature levels (not statistically different from pre-flight values). Compared to trials without mass, weighted movements tended to be straighter even for pre-flight tests, maintaining a relatively constant level of curvature throughout all pre- and in-flight tests. The effects of weightlessness upon the path's form, are qualitatively illustrated in Fig. 5.

Curved paths for vertical hand movements, observed in this study, were in contrast to the virtually straight hand paths previously recorded in horizontal arm movements [11,14,22]. Furthermore, the significant effect of movement direction upon path curvature also disagrees with previous experimental results that have reported invariant hand paths for different directions, speeds and loads in both horizontal and sagittal planes [11,17,35].

Therefore, what seems clear from our results, is that movements against gravity are not performed in exactly the same manner as movements with gravity or as movements in the horizontal plane. Nevertheless, the cause of these differences remains to be elucidated. Are the changes in kinematic features between upward and downward movements an indication of a difference in planning? Equally, do variations in hand paths result from a misrepresentation of the effects of gravity in the programming of a movement that would ideally possess usual invariant characteristics?

The fact that movement time in normal gravitational environments, remained constant regardless of movement direction and weight, argues in favor of a central representation of gravitational force within the motor command. If the CNS had planned equivalent hand trajectories, without correctly taking into account gravitational torques, movements executed with the aid of gravity should have shown shorter movement times than movements executed against gravity.

What then can be concluded about differences in hand paths recorded between the two movement directions? Data from experiments in micro-gravity support the idea that direction-specific hand path differences are included in the planning process. If the CNS in a 1 g environment plans straight-line hand paths for vertical movements, but is unable to produce these paths due to deficiencies in the programming of gravitational torques, hand paths should become straighter immediately upon exposure to weightlessness. At least, differences between upward and downward movements should have disappeared. No such effect was seen during space flight. Hand paths were curved for both directions, pre-flight and early in-flight.

Furthermore, downward movements remained consistently straighter than upward movements throughout the flight. Thus, it would appear that curved hand paths for vertical arm movements and differences between upward and downward movement directions are included at the

Table 1
Mean and standard errors from all subjects and conditions, of movement time (MT) and the greatest perpendicular distance from the path to the straight line (D_{max})

	Experimental conditions			
	UN	UW	DN	DW
D_{max} (mm)	38.25 (8.49)	36.31 (7.02)	33.5 (8.46)	28.80 (6.80)
MT (ms)	911.42 (277.19)	913.95 (229.92)	925.31 (226.30)	956.75 (271.03)

UN: upward direction without weight, UW: upward direction with a 0.5-kg weight. DN: downward direction without weight, DW: downward direction with a 0.5-kg weight.

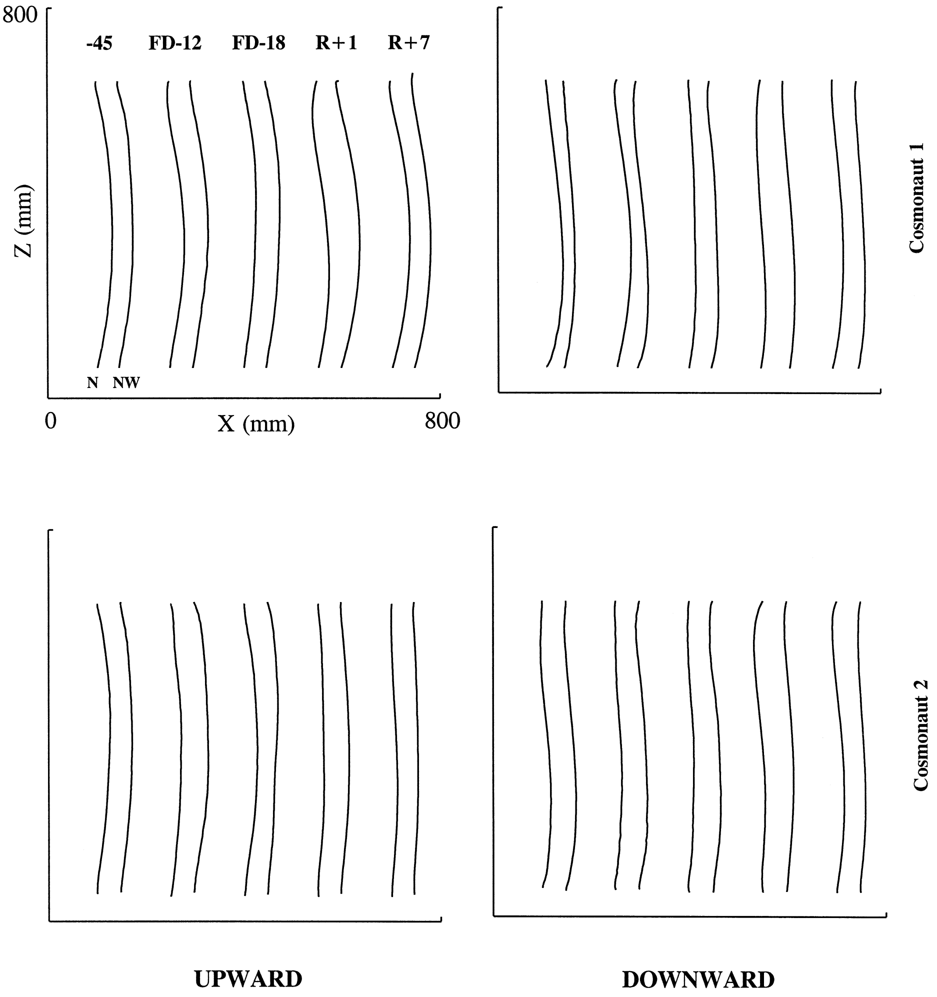

Fig. 5. Mean paths from both cosmonauts, directions and weights. D-45: pre-flight, FD 12: 12th flight day, FD 18: 18th flight day, R + 1: first-post flight day, R + 7: 7th post-flight day. N: normal speed without weight, NW: normal speed with a 0.5-kg weight.

planning level. The fact that hand paths remained curved early in-flight, and that hand paths conserved their straightness shortly after the return to earth would argue for a gradual adaptation of the internal movement template, rather than a transient perturbation brought on by the sudden lack or addition of a constant bias force. This argument is further strengthened by the fact that hand path curvature returned to pre-flight levels, at least in one subject, after several days of adaptation to a normal gravitational environment.

5. Conclusion

Results from the experiments presented in this paper argue in favor of a central integration of gravitational force during locomotor, dynamic postural and arm movement reaching tasks. Growing-up in a gravito-inertial environment, subjects learn to perform movements by representing gravity at higher levels within the motor command. We propose that integration and central representation means that gravitational force has not only the status of a load, acting on the limbs' center of mass, but also constitutes an orientation reference (the vertical direction), the basis upon which body orientation in space, proprioception and motor commands are referred to. Such a central representation of gravity can facilitate sensorimotor transformations for postural control, whole body and arm reaching movements, and calibrate different spaces of movement representation (head-centered, arm-centered or retinotopic).

Until now, a vast majority of studies have replicated 1 *g* experimental designs in weightlessness. This makes it possible to study adaptation and readaptation processes through pre-, in- and post-flight records. Nevertheless, the fact remains that when gravity is lacking, subjects must develop new motor strategies to execute certain motor tasks. Indeed, locomotion in weightlessness, because of it's specificity, can only be studied in weightlessness. Surprisingly, little is known about manual non-rhythmic locomotion, commonly used by astronauts during spaceflight. Thus, from a prospective point of view, there is a need to determine new experimental paradigms in order to study the specific motor control of man in space. Moreover, a new scientific approach to this question must be conducted without considering man in space only as a terrestrial biped. Any such research must be conducted to more fully understand motor solutions developed in weightlessness.

Acknowledgements

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