

Effect of gravity-like torque on goal-directed arm movements in microgravity

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Bringoux L, Blouin J, Coyle T, Ruget H, Mouchnino L. Effect of gravity-like torque on goal-directed arm movements in microgravity. *J Neurophysiol* 107: 2541–2548, 2012. First published February 1, 2012; doi:10.1152/jn.00364.2011.—Gravitational force level is well-known to influence arm motor control. Specifically, hyper- or microgravity environments drastically change pointing accuracy and kinematics, particularly during initial exposure. These modifications are thought to partly reflect impairment in arm position sense. Here we investigated whether applying normogravitational constraints at joint level during microgravity episodes of parabolic flights could restore movement accuracy equivalent to that observed on Earth. Subjects with eyes closed performed arm reaching movements toward predefined sagittal angular positions in four environment conditions: normogravity, hypergravity, microgravity, and microgravity with elastic bands attached to the arm to mimic gravity-like torque at the shoulder joint. We found that subjects overshoot and undershot the target orientations in hypergravity and microgravity, respectively, relative to a normogravity baseline. Strikingly, adding gravity-like torque prior to and during movements performed in microgravity allowed subjects to be as accurate as in normogravity. In the former condition, arm movement kinematics, as notably illustrated by the relative time to peak velocity, were also unchanged relative to normogravity, whereas significant modifications were found in hyper- and microgravity. Overall, these results suggest that arm motor planning and control are tuned with respect to gravitational information issued from joint torque, which presumably enhances arm position sense and activates internal models optimally adapted to the gravito-inertial environment.

weightlessness; motor control; arm kinematics; movement accuracy; position sense

PRODUCING ADAPTED MOTOR COMMANDS in a novel environment necessitates taking into account the moving limb characteristics and environmental dynamics within the motor planning (Davidson et al. 2005; Guillaud et al. 2011; Papaxanthis et al. 2005; Shadmehr and Moussavi 2000). However, these prerequisites are not always fulfilled, since movements performed in new force fields appear inaccurate during initial exposure, in terms of trajectory and final position. For instance, studies conducted in weightless environments have reported decreased accuracy of goal-directed arm movements performed without visual feedback compared with what is usually observed on Earth (Bock et al. 1992; Carriot et al. 2004; Fisk et al. 1993; Watt 1997; Whiteside 1961).

This decrease in performance has been mostly explained by the alteration of limb position sense in modified gravitational environments (Bock 1992; Lackner and DiZio 1992; Roll et al.

1993, 1998). Spaceflight experiments, including limb matching tasks under muscle vibration (Lackner and DiZio 1992) and perceptual estimates of limb location (Young et al. 1993) have indeed suggested that proprioception is not as effective in weightlessness as in normogravity. The origin of this proprioceptive impairment is still a matter of debate. Some studies suggested that it could result from the absence of gravity-based vestibular inputs, leading to a decreased vestibulospinal influence on muscle spindle sensitivity (Lackner and DiZio 1992, 2000). Here, the misperceived limb configuration prior to movement execution would render the motor command ill-adapted to the new gravitational environment. However, studying manual catching of falling balls by astronauts, McIntyre et al. (2001) found that slower interceptive behaviors observed in microgravity cannot be fully explained by reduced muscle tone, at least when visual feedback is available to control movements.

There is also some evidence that muscle spindle firing modifications during active contraction against a load strongly influence position sense on Earth (Allen et al. 2008; Ansems et al. 2006; Proske 2006). In addition, following Weber's intuition that “our muscles always perceive space as affected by gravity” (Weber 1922), several researchers have explored subjects' ability to match the position of their forearms submitted to differential loads in normogravity. They found that when the matching limb is differentially loaded, the error in the reference angle produced is related to the imposed external torque (Bock 1994; Worringham and Stelmach 1985). Gooley et al. (2000), also using a forearm matching task, gave further support to this hypothesis by showing that a forearm made weightless is perceived as more flexed than it actually is.

Here, we tested whether reestablishing gravity-like torque (with an elastic system) during goal-directed arm movements in microgravity can compensate for the perturbing effect of weightlessness on movement accuracy. Furthermore, as the absence of gravity is also known to alter the spatiotemporal structure of the movement (Papaxanthis et al. 2005), we also examined whether gravity-like arm loading can restore movement kinematics. Specifically, we hypothesized that providing gravity-like arm loading in microgravity would allow subjects to produce movements with similar accuracy and a spatiotemporal organization as in normogravity.

MATERIALS AND METHODS

Participants. Eight right-handed human volunteers (3 women and 5 men, mean age = 31 yr) participated in the experiment. Three had no prior microgravity experience, whereas the remaining five had participated in at least two previous parabolic flight campaigns. All subjects gave signed informed consent in compliance with the Hel-

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sinki Convention. The experiment was approved by the flight testing center of the French Army (CEV) and a local Ethics Committee.

Apparatus and experimental setup. The experiment was conducted in the A-300 ZEROg aircraft chartered by the French Centre National d'Etudes Spatiales (CNES) for parabolic flight studies during parabolic flight campaign #59. During the experiment, the plane is flown such that the resultant gravitoinertial force, when present, is normal to the aircraft floor. A parabolic maneuver is composed of three distinct phases: 20 s of hypergravity (1.8 g, pull-up phase) followed by 22 s of microgravity (0 g) before a second period of 20 s of hypergravity (1.8 g, pull-out phase). The aircraft ran a sequence of 30 parabolas per flight organized in 6 groups of 5 parabolas separated by 5- to 8-min periods of level flight. The experiment was completed in two consecutive days.

Subjects were tested on board prior to each flight in normogravity (1g condition; Fig. 1A). In this condition, they were lying prone (face down) on a padded table (2 m long \times 0.9 m wide \times 0.9 m high), with their right arm free to move off the side of the table. The right forearm was kept extended with a light rigid gutter fixed along the elbow joint. The prone orientation was adopted to match the pseudogravitational constraints induced in the 0gE condition detailed below. In this orientation, the gravity facilitated the arm movement in the shoulder's sagittal plane from 0° (i.e., arm actively oriented toward the feet along the trunk axis) to 90° (i.e., arm normal to the trunk) and acted against the movement from 90° to 180° (i.e., arm oriented toward the head-up direction). In other words, the gravitational torque at the shoulder was positive until 90° and then became negative beyond 90°.

When tested during parabolic flights, subjects were tightly restrained supine on the cabin floor with straps and pads (Fig. 1, B–D). Their right upper limb, maintained extended as in the 1g condition, was the only body segment free to move. In the microgravity condition (0g; Fig. 1B) no external force was exerted on the reaching arm, irrespective of its orientation (i.e., no gravitational torque at the shoulder). In the hypergravity condition (1.8g; Fig. 1D), always presented during the first phase of the parabola (i.e., pull-up), an external force acted against the arm movement from 0° to 90° (i.e., negative hypergravitational torque) but facilitated the movement from 90° to 180° (i.e., positive hypergravitational torque). Hence, the 1.8g condition cannot be simply considered as an “enhanced” 1g condition relative to 0g, but rather as a condition in which the gravitational constraints are also reversed with respect to 1g.

During selected microgravity episodes, hereafter referred to as the 0gE condition, two pairs of elastic bands were attached to each side of the right arm's gutter at the elbow level and fixed to a sturdy metallic frame behind and in front of the subject's shoulder (Fig. 1C). The combined strain of these elastic bands varied according to the arm orientation. The elastic configuration was determined so as to mimic the gravitational influence of the 1g condition at the shoulder level, where subjects produced arm movements in a prone position. Specifically for each subject, a neutral position (i.e., balanced strain) was reached when the arm was oriented 90°. The combined strain facilitated the arm movement from 0° to 90° (positive pseudogravitational torque) and acted against the movement from 90° to 180° (negative pseudogravitational torque). A mathematical simulation (detailed in APPENDIX) was performed to enable the selection of suitable elastics and to compare the shoulder torque evolution in both the 1g and 0gE conditions for all targeted angles. The variation of the shoulder torque across the different angular positions in this 0gE condition closely matched that observed in the 1g condition. This could only be achieved by using different body orientations relative to the cabin floor in the 1g and 0gE conditions (i.e., prone and supine orientations, respectively).

Reflecting markers were positioned at anatomical landmarks of the right upper limb (acromion, lateral epicondyle of humerus, styloid process of ulna). These markers were used for arm kinematic recordings by means of an optoelectronic system (E.L.I.T.E.) operating at a sampling frequency of 100 Hz. The corresponding local accuracy in the three-dimensional marker reconstruction was \sim 1 mm.

Procedure. In each experimental condition (i.e., 1g, 1.8g, 0g, and 0gE), subjects moved their outstretched right arm toward different sagittal orientations. All movements were performed with the eyes closed to prevent any visually based corrections. Each movement started with the arm directed toward the feet along the trunk axis (0°). This initial position, which required the arm to be actively maintained in the 1g, 0gE, and 1.8g conditions, was controlled and validated by the experimenter prior to each trial. Three egocentric orientations were defined as angular targets (i.e., spatial goals) relative to this initial arm position: 45° (i.e., midangular position between the arm down along the trunk axis and the arm normal to the trunk), 90° (i.e., the arm normal to the trunk), and 135° (i.e., midangular position between the arm normal to the trunk and the arm up along the trunk axis). Visual examples of these orientations

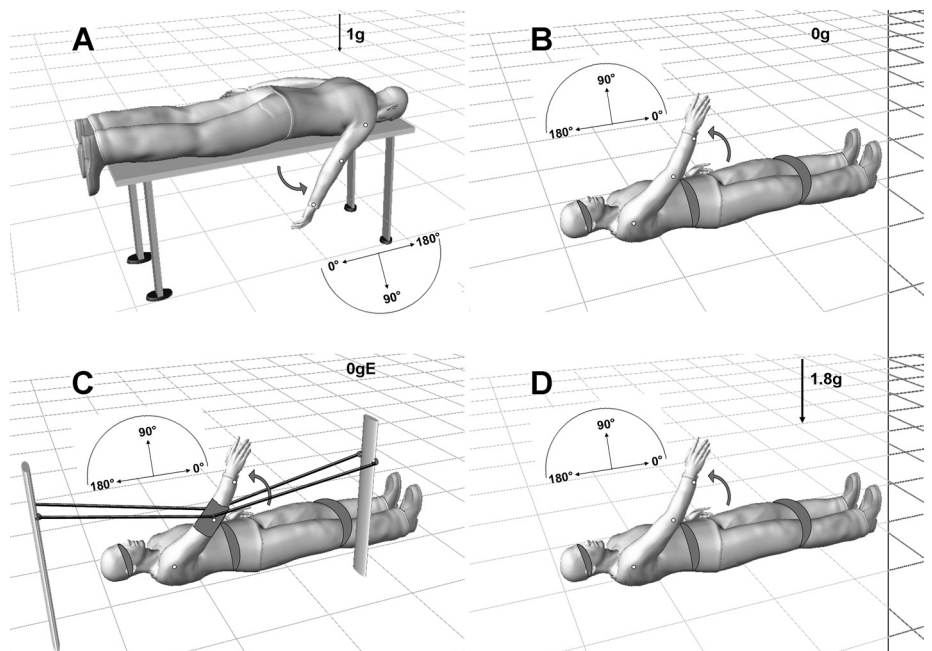


Fig. 1. Illustration of the experimental setup in the 4 environment conditions. A: in the 1g condition, subjects performed arm movements facilitated by gravity from 0° to 90° (angle referred to the arm starting position along the body) and hindered by gravity beyond 90°. B: in the 0g condition, there was no gravitational force acting on the vestibular system or on the arm. C: in the 0gE condition, although gravity was no longer present at the vestibular level, elastic bands mimicked the gravitational constraints on the arm exerted in 1g. D: in the 1.8g condition, the hypergravitational field hindered arm movements from 0° to 90° and facilitated them beyond 90°.

were given by the experimenter prior to the flights. To provide quick instructions regarding the targeted angles, we used the labels “down,” “ahead,” and “up” for the 45°, 90° and 135° orientations, respectively. During the experiment, these labels were subsequently announced by the experimenter in a pseudorandom order, prior to each trial. The goal of the subjects was to reach “as accurately as possible” toward these angular positions with the eyes closed.

Four subjects were tested per flight (2 flights were dedicated to this experiment in the campaign). During each flight, the first pair of subjects were tested from *parabola 1* to *parabola 14* and the last pair were tested from *parabola 16* to *parabola 29*. Of the first pair, only one subject was equipped with elastic bands from *parabola 1* to *parabola 7*. During the 5-min pause between *parabola 7* and *parabola 8*, the elastic bands were removed and attached to the other subject. During the 8-min pause between *parabola 15* and *parabola 16*, a new pair of untrained subjects were installed, with only one being attached to the elastic bands. Finally, the 5-min pause between *parabola 22* and *parabola 23* was used to swap the elastic bands onto the last subject. Only subjects without elastic bands were tested during the 1.8g phases.

For each parabola, both subjects received the same sequential announcement of the targets they had to reach. Prior to the flight, one subject for each pair of subjects was designated for performing the movement immediately after the announced target. When this subject returned the arm toward the initial position after the movement, she/he had to say “OK” to indicate to the second subject to start her/his movement. Such sequencing of the movements facilitated the kinematics data analyses by preventing obstructions and misattributions of kinematics markers between subjects.

Altogether, within each experimental condition, the subjects performed eight arm movements for each of the three target orientations. No feedback was given to the subjects about their final accuracy throughout the whole experiment.

Data analysis. Off-line data processing carried out with the E.L.I.T.E. software system allowed for complete three-dimensional kinematic reconstruction of marker trajectories, which were low-pass filtered with a digital second-order dual-pass Butterworth filter (10-Hz cutoff frequency). A model of arm orientation in the pitch dimension

was constructed from these markers. The arm movement onset was defined as the time when angular velocity in the sagittal plane reached 5% of its peak. Conversely, final arm position relative to the target was recorded when the angular velocity dropped under 5% of the peak velocity.

Typical outputs of this processing are illustrated in Fig. 2, representing the arm angular displacement in the sagittal plane toward the 135° target orientation and its derivative over time, for the different environment conditions.

Arm movements were analyzed by first focusing on the final accuracy, expressed as the mean angular errors obtained by subtracting the target angle from the arm angle at movement offset. Angular errors were therefore positive when the arm angle exceeded the target orientation (these errors being referred to as movement overshoots). Movement variability was analyzed by computing the within-subject standard deviations of the angular errors obtained for each condition. Movement kinematics were also analyzed by computing movement duration (MD), mean velocity (V_{mean}), peak velocity (V_{max}), the ratio $V_{\text{max}}/V_{\text{mean}}$ (C parameter; see Flash and Hogan 1985; Papaxanthis et al. 2005), as well as the relative time to peak velocity (rTPV, namely, the ratio time to peak velocity/movement duration). C and rTPV are known to respectively reflect inertial influences and gravitational constraints upon movement organization (Papaxanthis et al. 2005). Usually, C varies with movement speed under normogravity conditions, whereas rTPV essentially varies with gravity environment.

Statistics. Analyses of variance (ANOVAs) were performed to compare the means of these kinematics parameters across the experimental conditions, after having ensured that the assumptions of normality and variance homogeneity were not violated (χ^2 and Levene’s tests). Unless specified, a 3 target orientations (45°, 90°, 135°) \times 4 environment conditions (1g, 1.8g, 0g, 0gE) statistical design was used to assess the effect of the experiment conditions on the different computed variables. When significant, the effect size ($P\eta^2$) was computed to estimate the importance of the effect (α level fixed at $P < 0.05$). Post hoc comparisons (Newman-Keuls tests) were also conducted to determine significant differences between specific conditions relative to others.

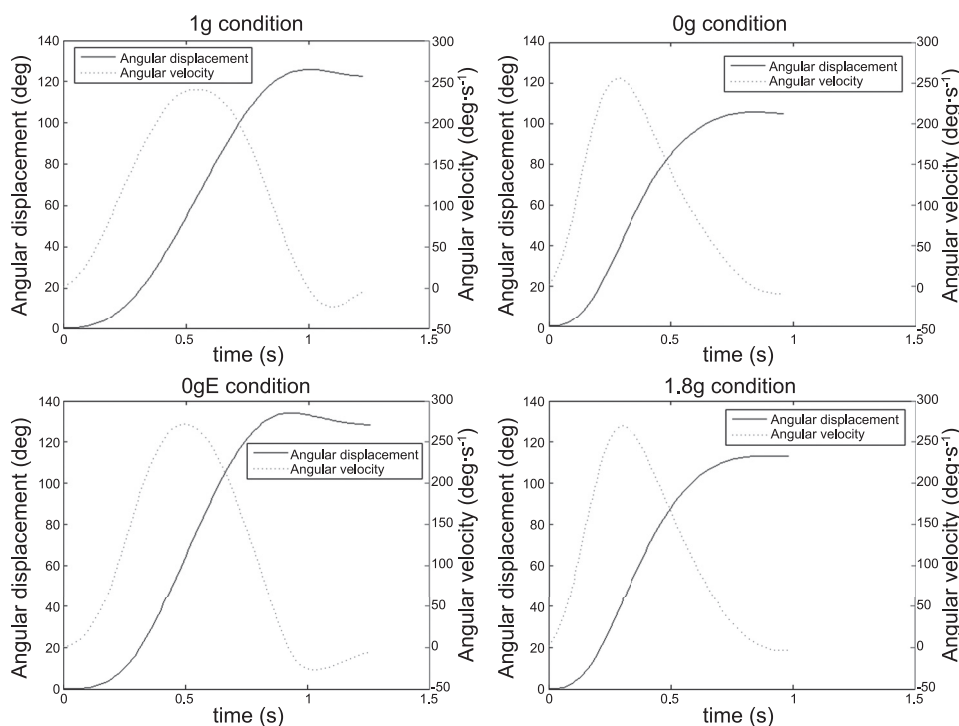


Fig. 2. Typical kinematic features of goal-directed arm movements performed toward a 135° target orientation in the different environment conditions. Angular displacement and angular velocity vs. time are represented for the 1g, 0g, 0gE, and 1.8g conditions.

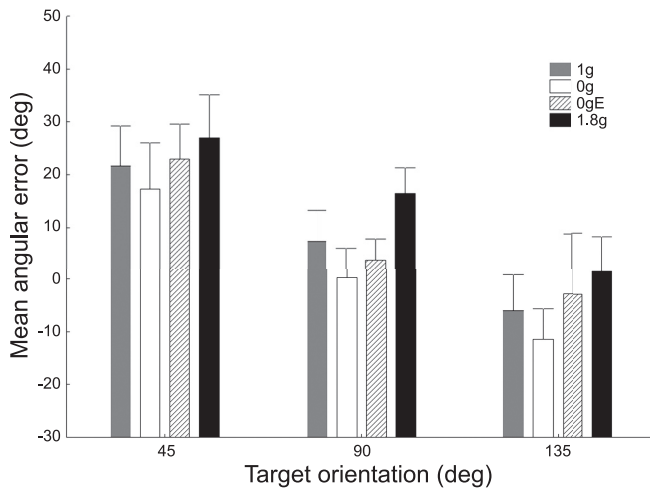


Fig. 3. Mean angular errors recorded on the final position of arm movements as a function of environment condition and target orientation. Error bars represent 95% confidence intervals.

RESULTS

First, for all measured variables, no significant differential influence of the experimental conditions was observed between subjects with and without parabolic flight experience [final position: $F(3,12) = 1.89$, $P = 0.18$; MD: $F(3,12) = 1.50$, $P = 0.27$; V_{mean} : $F(3,12) = 1.02$, $P = 0.42$; V_{max} : $F(3,12) = 0.62$, $P = 0.62$; C: $F(3,12) = 0.66$, $P = 0.59$; rTPV: $F(3,12) = 1.04$, $P = 0.41$]. Furthermore, there was no significant difference between the first and last reaching movements performed in the same experimental configuration (i.e., for each combination of target orientation and environment condition; $P > 0.05$ for all t -tests performed). This was expected because adaptive or learning effects are known to take place only in presence of an error-related feedback, for instance, from vision of the arm (Bourdin et al. 2001), which was unavailable in the present study (subjects having eyes closed throughout the experiment).

Final position. As predicted, the external forces markedly influenced the final arm orientation reached by the subjects (Fig. 3). This was confirmed by the ANOVA revealing a significant main effect of environment condition on the angular errors [$F(3,21) = 5.23$, $P < 0.01$, $P\eta^2 = 0.43$] as well as a significant target orientation \times environment condition interaction [$F(6,42) = 2.50$, $P < 0.05$, $P\eta^2 = 0.26$]. Notably, post hoc analyses showed that the angular errors measured in the 0g and 1.8g conditions always differed from the 1g condition, while no difference was found between 0gE and 1g, irrespective of the target orientation (see Table 1 for post hoc analyses).

On the other hand, the angular errors significantly differed according to the target orientation [$F(2,14) = 54.82$, $P < 0.001$, $P\eta^2 = 0.89$]. The subjects notably overshoot the 45° target orientation (global mean: +22°) and slightly undershot the 135° target orientation (global mean: -4.5°).

The variability of the reached arm orientation recorded for each condition was not found significantly different between environment conditions [$F(3,21) = 2.04$; $P = 0.14$] or between target orientations [$F(2,14) = 0.40$, $P = 0.68$]. On average, movement variability was 5.1°.

To specifically focus on the influence of the environment condition on movement accuracy, we rebased the angular errors relative to the 1g values obtained for each subject and for each target orientation. A one-way ANOVA comparing the

mean rebased angular errors among the 1.8g, 0g, and 0gE conditions was then performed, irrespective of target orientation. It revealed a main effect of environment condition [$F(2,14) = 12.11$, $P < 0.001$, $P\eta^2 = 0.63$]. The mean angular error in 0gE was significantly different from that measured in 1.8g ($P < 0.001$) and 0g ($P < 0.05$) but did not significantly differ from the 1g baseline, as shown by the statistical comparison with a standard value of 0 ($t = 0.74$, $P = 0.94$). More precisely, the mean reached position in 1g was overshoot in 1.8g (+7.3°) and undershot in 0g (-5.7°) but was not significantly different from that reached in 0gE.

Movement duration. The ANOVA conducted on movement duration did not reveal a significant effect of the environment condition [$F(3,21) = 0.96$, $P = 0.43$] or significant interaction between this factor and target orientation [$F(6,42) = 0.69$, $P = 0.66$]. This clearly indicates that the difference of final accuracy observed among environment conditions cannot be attributed to a difference in movement duration. On the other hand, movement duration was unsurprisingly affected by target orientation [$F(2,14) = 29.68$, $P < 0.001$, $P\eta^2 = 0.81$]. The greater the arm angle to be reached, the longer the movement duration (1.08 s, 1.19 s, and 1.28 s for 45°, 90°, and 135° target orientation, respectively; Fig. 4).

Mean velocity. The V_{mean} differences between environment conditions failed to reach significance [$F(3,21) = 2.96$, $P = 0.06$], and the interaction between environment conditions and target orientations was also nonsignificant [$F(6,42) = 1.75$, $P = 0.13$]. This suggests that the greater accuracy found in the 1g and 0gE conditions does not result from the slowing of the movements in these conditions (e.g., speed-accuracy trade-off). On the other hand, as generally observed, V_{mean} significantly varied with the amplitude of the movements [$F(2,14) = 107.35$, $P < 0.001$, $P\eta^2 = 0.94$]. The further the target, the greater V_{mean} (from 65°/s to 105°/s from 45° to 135° target orientations).

Peak velocity and C parameter. ANOVA revealed a significant main effect of environment condition on V_{max} [$F(3,21) = 6.03$, $P < 0.01$, $P\eta^2 = 0.46$]. Post hoc analyses revealed that the significant difference only concerned the 1.8g condition, V_{max} in 1.8g being greater than in the other conditions ($P < 0.01$). A main effect of target orientation was also found on V_{max} [$F(2,14) = 206.43$, $P < 0.001$, $P\eta^2 = 0.97$]. The larger

Table 1. Post hoc analyses

	1g	0g	0gE	1.8g
Target orientation: 45°				
1g	—	*	ns	*
0g		—	†	‡
0gE			—	*
1.8g				—
Target orientation: 90°				
1g	—	†	ns	‡
0g		—	ns	‡
0gE			—	‡
1.8g				—
Target orientation: 135°				
1g	—	†	ns	†
0g		—	‡	‡
0gE			—	ns
1.8g				—

* $P < 0.05$; † $P < 0.01$; ‡ $P < 0.001$. ns, Not significant.

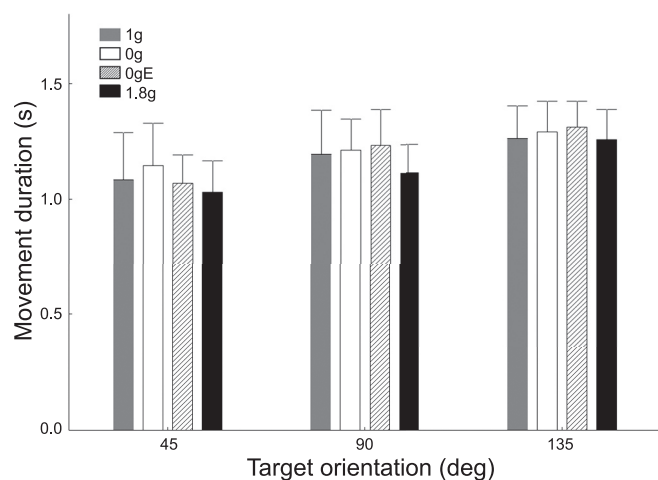


Fig. 4. Mean duration of arm movements as a function of environment condition and target orientation. Error bars represent 95% confidence intervals. Movement duration progressively increases for longer angular distances, but no significant difference appears across environment conditions.

the angle to be reached, the higher V_{\max} (from $120^{\circ}/s$ to $220^{\circ}/s$ from 45° to 135° target orientations).

As expected, the C parameter was not significantly different across the environment conditions [mean: 1.9; $F(3,21) = 1.03$, $P = 0.40$] but varied with target orientation [$F(2,14) = 4.15$, $P < 0.05$, $P\eta^2 = 0.37$]. The further the target, the greater the C value (from 1.93 for 45° to 2.18 for 135°).

Relative time to peak velocity. Analyses of rTPV showed a significant main effect of environmental condition [$F(3,21) = 21.02$, $P < 0.001$, $P\eta^2 = 0.75$]. Specifically, rTPV was found significantly greater in both 1g and 0gE conditions compared with 0g and 1.8g conditions ($P < 0.001$), while no significant difference appeared between 0gE and 1g conditions ($P = 0.82$). On the other hand, ANOVA revealed no significant effect of target orientation [$F(2,14) = 1.88$, $P = 0.18$] and no significant interaction between this factor and environmental condition [$F(6,42) = 1.99$, $P = 0.09$].

Together, these results indicate that the temporal features of goal-directed arm movements performed in the 0gE condition did not differ from those observed in normogravity, contrary to those observed in the 0g and 1.8g conditions (Fig. 5).

DISCUSSION

The main purpose of the present study was to determine whether the decreased accuracy of goal-directed arm movements observed in microgravity could be counteracted by gravity-like arm loading. Although specific to this experimental context, our results clearly demonstrate that adding shoulder joint torque in microgravity allowed subjects to perform movements that were fully comparable to those performed in normogravity. This was true in terms of both movement accuracy and movement kinematics. These two important results strongly suggest that 1) gravity-like arm torque contributes to arm estimation prior to and during reaching movements and 2) the motor planning is tuned with respect to contextual information, which primarily includes arm loading.

Gravity-like arm loading improves perceived arm location. The present experiment unambiguously validates the use of gravity-related arm loading in microgravity to preserve the accuracy of movements performed in normogravity. When

referred to the 1g baseline, the movement accuracy increased in the 0gE condition compared with the 0g condition, irrespective of the target orientation. This result provides support for arm position sense improvement due to gravity-related arm loading. To reach a specific location with the hand, the arm motor command must be tuned according to accurate estimates of the limb position prior to (Nougier et al. 1996; Rossetti 1995; Veilleux and Proteau 2011) and during (Blouin et al. 1996, Sainburg et al. 1995; Sarlegna et al. 2006) the movement. Taking this into consideration, the question then arises as to how gravity-related arm loading improves the perceived arm location.

Several studies have suggested that muscle spindle firing modifications during active contraction against a load strongly influence position sense on Earth (e.g., Allen et al. 2008; Ansems et al. 2006; Proske 2006). On the other hand, other works have insisted on the role of the central command necessary to overcome gravitational load in limb position sense (Gandevia et al. 2006; Smith et al. 2009; Walsh et al. 2009). In the framework of the present experiment, however, it proves difficult to favor one hypothesis over the other. According to the afferent explanation, the increased alpha activity required to counteract the gravity-like torque in the 0gE condition was presumably accompanied by an enhanced gamma coactivation at the fusimotor level. This higher gamma activity could neutralize the disturbing effect of microgravity on the arm movements (i.e., the decreased fusimotor drive mediated by vestibulospinal pathways; Lackner and DiZio 1992), keeping the muscle spindle sensible to muscle length changes. On the other hand, the motor command required to overcome the additional pseudogravitational torque induced by the elastic bands during arm reaching may have given rise to a better “sense of effort,” which contributes to limb position sense (Gandevia et al. 2006). Most certainly, these interpretations are not exclusive, as afferent and efferent signals might contribute both to the position sense improvement and, consequently, to the increased reaching accuracy associated with gravity-like arm loading in microgravity.

Compared with the movements they performed in normogravity, subjects undershot and overshoot the target orientations

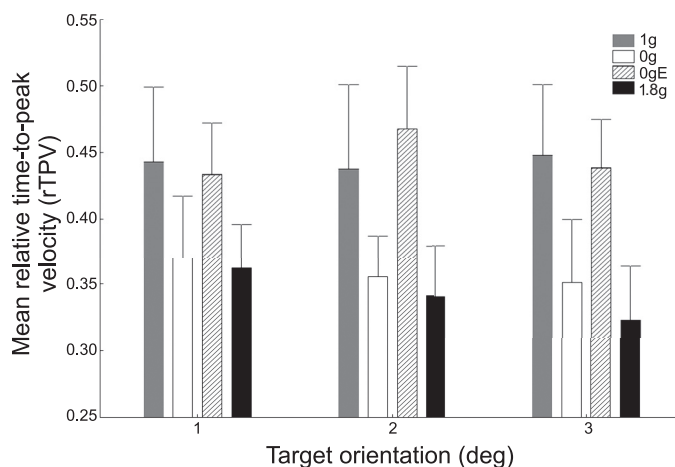


Fig. 5. Mean relative time to peak velocity (rTPV) of arm reaching movements as a function of environment condition and target orientation. Error bars represent 95% confidence intervals. If rTPV observed in 0gE significantly differs from that observed in 0g and 1.8g, it is not significantly different from rTPV observed in 1g.

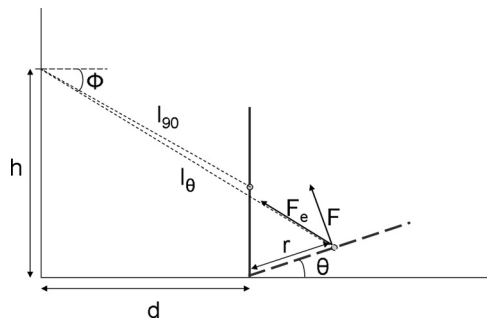


Fig. 6. Schematic illustration of the experimental setup with the parameters relevant to the calculation of the torque exerted on the subject's arm for angular positions ranging from 0° to 90° in $0gE$. See APPENDIX for definitions.

in $0g$ and $1.8g$ conditions, respectively. These observations are contrary to those one could expect when considering the simple mechanical effects due to different gravitational force fields. The pattern of errors found here may suggest that subjects overestimated the expected consequences of arm loading/unloading in hyper- and microgravity, leading to a compensatory increase of movement amplitude in $1.8g$ and, conversely, to a compensatory decrease of movement amplitude in $0g$, as already reported in a previous study (Carriot et al. 2004). The absence of visual feedback most likely decreased subjects' capacity to adapt to the new gravito-inertial fields (Lackner and DiZio 2000) and could explain the persistence of over/undershoots across trials in hyper/hypogravity. However, in line with this hypothesis, the expected motor consequences associated with the gravity-like arm loading condition might have been very close to those expected in normogravity, precisely because of a comparable shoulder torque prior to movement onset. Interestingly, the present data recorded in the gravity-like arm loading condition show that not only the final accuracy but also the movement kinematics are tuned with respect to normogravity baseline.

Gravity-like arm loading allows for 1g-adapted motor planning. The finding that arm kinematics were similar in normogravity and in microgravity when a gravity-like torque was experimentally added at the shoulder joint is a key result of the present study. In particular, the temporal structure of the movements was similar in $1g$ and $0gE$ conditions (rTPV ~ 0.45), whereas it largely differed in both $0g$ and $1.8g$ conditions (rTPV ~ 0.35). This suggests that gravity-like arm loading in weightlessness helps to preserve the organization of the arm motor command generally observed in $1g$. It has been proposed by Flash and Hogan (1985) that point-to-point movements respect the minimum jerk principle in which $C = 1.875$ and rTPV = 0.5. In that case, the hand trajectory is planned to maximize smoothness or to minimize execution variability. With $C \sim 1.9$ and rTPV ~ 0.45 , the movements produced in $0gE$ and in $1g$ conditions therefore respected the principles underlying the organization of natural movements as described by Flash and Hogan (1985).

It is worth noting that rTPV is considered to be a reliable indicator of how gravitational constraints are implemented in motor commands (Papaxanthis et al. 2003, 2005). In our experiment, rTPV largely decreased in microgravity as well as in hypergravity (~ 0.35). This contrasts with the results obtained by Papaxanthis et al. (2005) and by Crevecoeur et al. (2009), who found a significant longer acceleration phase in

microgravity and conversely an earlier rTPV in hypergravity compared with $1g$, respectively. Movements with a longer deceleration phase are frequently found when accuracy constraints require a great deal of online control (Chua and Elliott 1993; Sarlegna et al. 2003; Terrier et al. 2011). In the present study, contrary to the experiments of Papaxanthis et al. (2005) and of Crevecoeur et al. (2009), subjects did not have visual feedback of their arm. The absence of vision, which is a powerful source of information for controlling reaching movements (Sarlegna et al. 2003; Veyrat-Masson et al. 2010), may have added stress on the online control of movements performed in such unusual gravito-inertial environments and caused the lengthening of the deceleration duration. According to current models of motor control, afferent signals that arise from self-generated movements are inhibited by a mechanism that compares the internal prediction of the sensory consequences by the brain to the actual resultant sensory feedback (Roy and Cullen 2004; Voss et al. 2006). In this framework, sensory attenuation may have been minimized in both the $0g$ and $1.8g$ conditions because of the putative mismatch between expected and current proprioceptive inputs evoked by the change of gravito-inertial constraints. This process may also have increased the importance of sensory processing during the deceleration phase. By contrast, the predicted and actual afferent signals presumably matched better in the $1g$ and $0gE$ conditions. This may have decreased the importance of feedback-based online control, leading to a bell-shaped velocity curve profile of the arm (i.e., rTPV ~ 0.5).

Overall, the present study, in line with others, strongly suggests that gravitational influences are taken into account for arm movement organization and execution in a predictive manner (Bockisch and Haslwanter 2007; Crevecoeur et al. 2009; Gentili et al. 2007; Guillaud et al. 2011; Papaxanthis et al. 1998a, 1998b, 2005). For instance, while the final accuracy of upward/downward arm reaching movements is impaired during initial exposure to microgravity, typical kinematic features (e.g., curvature differences between upward and downward movements) are maintained despite the absence of gravity-related biomechanical constraints (Papaxanthis et al. 1998a, 1998b). In the framework of optimal control strategy (Berret et

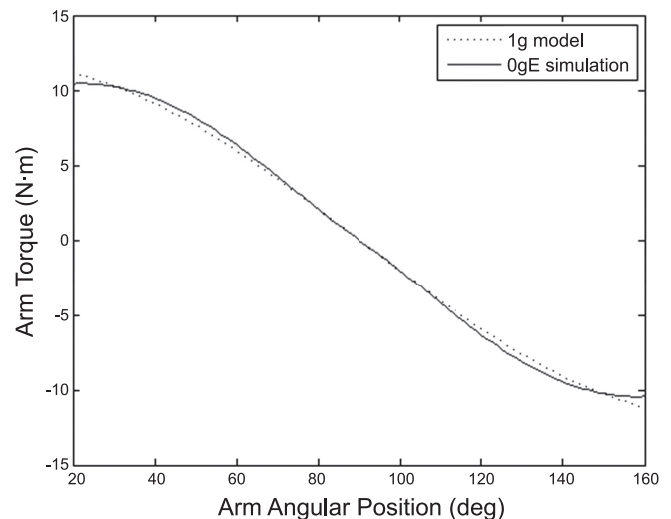


Fig. 7. Simulated torque values for the $0gE$ and $1g$ conditions within the experimental angular range for a subject of average mass (70 kg) and for an effective spring constant of 78 N-m.

al. 2008; Crevecoeur et al. 2009; Gaveau and Papaxanthis 2011), arm motor commands are optimized with respect to the action of gravity on the limb, whose consequences are integrated in motor planning and anticipated in terms of expected sensory states. It has been further hypothesized that gravity is encoded in the central nervous system and that the cerebellum may contain an internal representation of gravitational torques used for sensorimotor predictions (Gentili et al. 2009). Taking this idea further, it is tempting to hypothesize that reintroducing gravitational constraints on the moving limb by adding shoulder torque may reactivate forward internal models associated with 1g sensorimotor predictions, on the basis of an enhanced position sense. In turn, inverse dynamics of the movement could be computed in line with these sensorimotor predictions to yield a normogravity-like motor output. Here, the estimate of arm orientation could be specifically processed in proprioceptive coordinates, independently from a global state estimate of the whole-body orientation in space that may arise from a multisensory integration process (Merfeld et al. 1999).

Finally, the present data show that the additional information generated by gravity-like arm loading can be integrated in the motor commands. This integration appears effective from the very first movements performed in weightlessness, as the kinematics and accuracy of the first and last movements performed in microgravity did not significantly differ. Furthermore, the fact that gravity-related arm loading improved movement accuracy irrespective of whether participants had prior experience of microgravity suggests a wide and robust appropriateness of manipulating local torques to restore motor skills in microgravity.

Conclusions. Overall, the present study clearly shows that gravity-related constraints exerted on a moving limb may counteract the accuracy impairment observed in weightless environments in reference to normogravity baseline. This influence may be related to both position sense improvement and specific activation of a 1g-adapted motor plan. Future work is needed to question this directional effect of gravity-related arm loading, such as when gravitational constraints are not defined for prone body orientation in normogravity as in the present experiment but for supine or erect body orientation relative to the cabin floor. Other promising investigations may address the importance of gravity-related loading of body segments involved in postural control and locomotion, not only for reducing the deleterious effect of muscle atrophy during spaceflight as already considered but to help astronauts to recalibrate their motor behavior before landing back on Earth.

APPENDIX

Simulation of Torque Exerted on Arm in 0gE Condition

Extensive simulations were carried out prior to the experiment in order to ensure an acceptable correspondence between the torques exerted on the arm in the 0gE and 1g conditions. Given that the experimental setup was symmetrical about the vertical at the shoulder joint, the torques in the angular range of 90° to 180° could be determined (Fig. 6). θ is the arm angular position relative to the horizontal (starting position), Φ is the orientation of the elastic relative to the horizontal, h is the height of the attachment points of the elastic band on the metallic frame relative to shoulder joint center, d is the horizontal distance between the metallic frame and the center of the

shoulder joint, r is the distance between the center of the shoulder joint and the elastic band attachment point on the arm, l_{90} is the length of the elastic band when the arm is oriented at 90° (i.e., no extension of the elastic), and l_{θ} is the length of the elastic band when the arm is oriented at $\theta < 90^\circ$.

The torque was calculated from the elastic force F_e , which was determined with Hooke's law, $F_e = -k \cdot \text{ext}$, where ext is the extension and k the spring constant of the elastic. Equations 1–3 below show how the extension of the elastic can be derived from the geometry of the apparatus.

$$l_{90} = \sqrt{d^2 + (h - r)^2} \quad (1)$$

$$l_{\theta} = \sqrt{(d + r \cos \theta)^2 + (h - r \sin \theta)^2} \quad (2)$$

$$\text{ext} = l_{\theta} - l_{90} \quad (3)$$

$$\tau_{0gE} = r \cdot k \cdot \text{ext} \cdot \sin(\theta + \Phi) \quad (4)$$

$$\tau_{1g} = r \cdot m \cdot g \cdot \cos \theta \quad (5)$$

The spring constants of numerous elastic bands and cords were evaluated over the extension range of the arm anticipated in this experimental setup. The most linearly elastic band was selected and incorporated in such a way (bands in parallel) so as to give an appropriate mean effective spring constant over the extension range. The elastic force F_e was then resolved into its components to evaluate the actual turning force F and subsequently the total torque applied by the elastic (τ_{0gE} ; see Eq. 4). The gravitational torque on the arm in the 1g control condition (τ_{1g}) was calculated with Eq. 5, the mass of the arm (m) determined from anthropometric tables (Zatsiorsky and Seluyanov 1983). As illustrated in Fig. 7, the shoulder torque generated in the 0gE condition was very close to the torque observed in the 1g condition for the different angulations tested.

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DISCLOSURES

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AUTHOR CONTRIBUTIONS

Author contributions: L.B., J.B., H.R., and L.M. conception and design of research; L.B., J.B., T.C., H.R., and L.M. performed experiments; L.B., J.B., and T.C. analyzed data; L.B., J.B., and L.M. interpreted results of experiments; L.B. and T.C. prepared figures; L.B., J.B., and L.M. drafted manuscript; L.B., J.B., and L.M. edited and revised manuscript; L.B. approved final version of manuscript.

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