

Sensorimotor Mapping for Anticipatory Grip Force Modulation

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Crevecoeur F, Thonnard J-L, Lefèvre P. Sensorimotor mapping for anticipatory grip force modulation. *J Neurophysiol* 104: 1401–1408, 2010. First published June 23, 2010; doi:10.1152/jn.00114.2010. During object manipulation, predictive grip force modulation allows compensation for inertial forces induced by the object's acceleration. This coupling between grip force (GF) and load force (LF) during voluntary movements has demonstrated high levels of complexity, adaptability, and flexibility under many loading conditions in a broad range of experimental studies. The association between GF and LF indicates the presence of internal models underlying predictive GF control. The present experiment sought to identify the variables taken into account during GF modulation at the initiation of a movement. Twenty subjects performed discrete point-to-point movements under normal and hypergravity conditions induced by parabolic flights. Two control experiments performed under normal gravitational conditions compared the observed effect of the increase in gravity with the effects of a change in movement kinematics and a change in mass. In hypergravity, subjects responded accurately to the increase in weight during stationary holding but overestimated inertial loads. During dynamic phases, the relationship between GF and LF under hypergravity varied in a manner similar to the control test in which object mass was increased, whereas a change in movement kinematics could not reproduce this result. We suggest that the subjects' strategy for anticipatory GF modulation is based on sensorimotor mapping that combines the perception of the weight encoded during stationary holding with an internal representation of the movement kinematics. In particular, such a combination reflects a prior knowledge of the unequivocal relationship linking mass, weight, and loads under the invariant gravitational context experienced on Earth.

INTRODUCTION

The ability to predict and anticipate the consequences of one's actions is a robust and general component of the processes involved in motor control (Wolpert and Flanagan 2001). Motor predictions and anticipatory control are evidenced in various contexts, such as the remapping of the visual field prior to a saccade completion (Duhamel et al. 1992), the compensation of self-generated Coriolis acceleration in pointing during active trunk rotation (Pigeon et al. 2003), and the synchronized modulation of grasping forces with inertial loads during object manipulation (Flanagan and Wing 1993). In the latter context, the grip force (GF) normal to the surface of the manipulated object is modulated with self-induced variations of the load force (LF) resulting from inertial and gravitational constraints between the fingertips and the object.

GF depends on many variables, including the object's weight, the mechanical properties of the skin–object interface (André et al. 2010; Johansson and Westling 1984), the sensory

feedback provided by cutaneous afferents (Augurelle et al. 2003b; Monzee et al. 2003; Nowak et al. 2001a; Witney et al. 2004), and the manipulated object's internal model of dynamics (Flanagan and Wing 1997).

The coupling between GF and LF exhibits high levels of complexity and flexibility relative to distinct loading conditions. For instance, Flanagan and Wing (1995) demonstrated that the slope and intercept of the GF/LF relationship were independently adjusted in response to increased frequency of movement during rhythmic cycles. A similar result was reported in the context of multidigit grasp with distinct conditions of movement acceleration and object mass (Zatsiorsky et al. 2005), yielding the hypothesis that gravitational and inertial constraints could be treated separately. Moreover, the flexibility of the coupling between GF and LF allows adaptation to changes in load profiles induced by changes in gravity, for both rhythmic and discrete types of movements (Augurelle et al. 2003a; Nowak et al. 2001b).

The possible dissociation between gravitational and inertial constraints encouraged us to decompose GF into static and dynamic components to investigate the adaptation of GF in zero-gravity conditions (Crevecoeur et al. 2009a). This approach revealed a distinct timescale of adaptation for each component, giving further support to the hypothesis that each outcome could adapt and evolve independently.

The dissociation of static from dynamic components yields the hypothesis that gravitational and inertial constraints may be independently controlled. Under this assumption, the internal representation of the manipulated object's weight should be the primary factor influencing the adjustment of GF during stationary holding, whereas the GF modulation should be primarily based on the prediction of inertial loads. It is therefore necessary to estimate weight and inertial load to produce adequate GF levels. To date, however, the physical variables taken into account during these estimations and the sensorimotor strategies underlying the prediction of inertial loads have not been thoroughly investigated.

To this purpose, this study used a hypergravity environment to induce changes in weight without changing the mass of the manipulated object. We show that the factors underlying the GF modulation are based on a combination of the object weight encoded during stationary holding and an internal representation of the intended movement. In particular, this combination reflects a sensorimotor mapping between the object weight and a prior knowledge of the life-long experienced physical laws linking mass, weight, and loads on Earth.

METHODS

Twenty healthy subjects (11 males and 9 females) without neurological disorders participated in this experiment. All subjects gave

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informed consent and the experimental protocol complied with the ethical requirements observed by the Medical Board of the European Space Agency (ESA) and the French Committee for the Protection of Persons. The latter organization is responsible for life-science experiments performed in France.

Each subject was seated in front of three vertically aligned visual targets (green light-emitting diodes) placed 18 cm apart, with the central target at shoulder height. Subjects were asked to grasp a manipulandum (4.5 cm grip aperture; 250 g mass) with a precision grip and to align it in front of the central target. Each subject's arm was thus in a horizontal position. A random sequence of targets was then generated and the subject was asked to align the manipulandum with the current target by means of outstretched-arm rotation around the shoulder in the sagittal plane. After each upward or downward movement (from center to the top or bottom target, respectively), the subject returned the arm to central alignment prior to the next movement.

Each subject performed the experiment in a training session under laboratory conditions (normal gravity, 1 g) to learn the task and become familiarized with the experimental protocol. The training session was composed of 10 blocks of 16 to 20 movements. The first group of subjects ($n = 10$) then performed the experiment under the hypergravity conditions induced in parabolic flights. We used the 47th and 48th ESA Parabolic Flight Campaigns. One parabolic flight was composed of a sequence of 31 parabolic maneuvers. The gravity was increased to 1.8 g over a period of about 20 s during the first phase of each parabola. The second phase consisted of roughly 22 s of zero gravity, followed by another 20 s phase of hypergravity. The subjects performed the experimental task during the second hypergravity phase of each parabola. Two subjects were evaluated per flight and each subject performed the task during ≥ 14 consecutive parabolas.

The 10 remaining subjects were involved in two control experiments. After the training session, the first control group ($n = 5$) performed another series of eight blocks under normal laboratory conditions. This control experiment allowed only 1 s to complete each movement, instead of the 1.25 s allowed in the training session. In addition, the subjects were explicitly requested to perform faster movements. The second control group ($n = 5$) performed a second series of eight blocks without changes in movement timing or instructions regarding the velocity of the movement, but the manipulandum was loaded with an additional mass of 220 g (470 g in total). The increase in weight for this control group was similar to that experienced by the group tested under hypergravity conditions. For each control session performed under 1 g conditions, the data from the first block were systematically removed from the sample to avoid transient effects due to learning the task. Based on visual inspection, the second block was removed for three of the control subjects for similar reasons.

The manipulandum was equipped with force and torque sensors located under each finger (Mini 40 F/T Transducers; ATI Industrial Automation, Apex, NC), and with a low-g accelerometer sensitive to acceleration changes in a range of ± 3 g (ADXL330; Analog Devices, Cambridge, MA). Another accelerometer of the same type was used during the flights to sample the gravity inside the aircraft and to verify that the movements were performed during stable gravitational phases. Trials performed during unstable gravitational phases were discarded. The three-dimensional position of the manipulandum was sampled at 200 Hz with a motion-tracking device (Codamotion; Charnwood Dynamics, Leicestershire, UK) to measure the movement accuracy across the different gravitational conditions. Given that the movement amplitude depended on subjects' arm length, the analysis of movement variance was based on the amplitude coefficient of variation (CV; the SD was normalized to the mean amplitude).

The data collected from the sensors and accelerometers were digitally low-pass filtered with a fourth-order zero-lag Butterworth filter and a cutoff frequency of 50 Hz. Position data of the manipulandum were low-pass filtered at 20 Hz. GF was defined as the mean of the absolute force components normal to the sensor surfaces. Variation in LF was collected from the accelerometer signal and multiplied by the object's mass.

Representative trials performed under both gravitational conditions are shown in Fig. 1, with the variables for the hypergravity trials illustrated (Fig. 1, *right column*). GF was decomposed into a static component (GF_S , dashed horizontal line), measured prior to movement when the arm was stable, and a dynamic component (GF_I , gray arrow), measured as an increment of GF at the peaks of LF relative to the static component. The increment of LF (LF_I , black arrow) is the difference between maximum LF and the weight of the object. During hypergravitational conditions, weight was computed using the actual gravity measured during each trial. The decomposition was computed for each trial at maximum LF, corresponding to the acceleration phase (for upward movements) or the deceleration phase (for downward movements). This decomposition of GF is similar to the method that we used previously (Crevecoeur et al. 2009a). It is a convenient approach to examine the combined estimation of object mass during static phases and dynamic modulation during dynamic phases that produce the grip motor command. By measuring the increments of grip force at the load force peaks, we address the capability of subjects to anticipate the actual variation of load force, taking into account the trial-to-trial variability. The temporal coupling between the GF and LF was measured as the time lag between the GF peak and the LF peak for each individual trial.

A one-way ANOVA was used to test the presence of a main effect on the tested variables across the parabolas. The comparisons between the hypergravity and normal gravity conditions, and between the normal and fast or loaded conditions for the control experiments, were

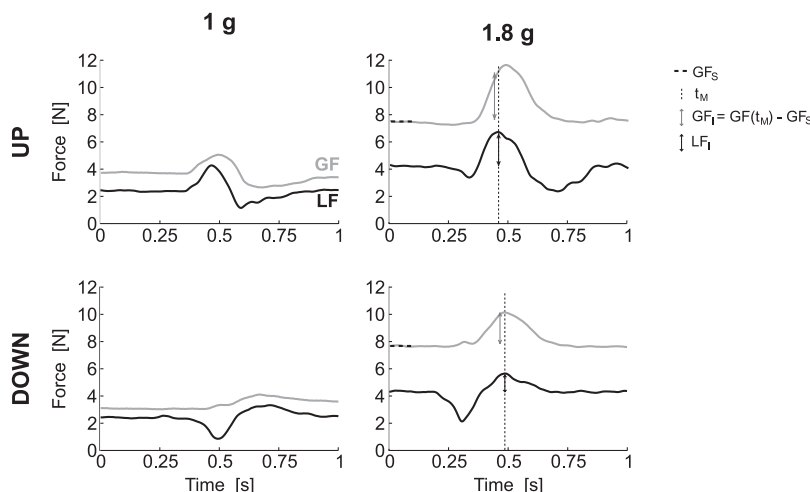


FIG. 1. Typical traces of grip force (GF) and load force (LF) in the 2 gravitational conditions (1 g, left; 1.8 g, right) and in the 2 movement directions (upward, up; downward, down). The variables are represented on the examples selected from hypergravity: the static grip force measured during stationary holding prior to the movement (GF_S), the increment of GF (GF_I) measured at the time of load force peak (t_M) relative to GF_S , and the increment of LF (LF_I) measured at the difference between the peak of LF and the weight of the held load.

realized with Wilcoxon rank-sum test. The relationship between GF_I and LF_I was addressed by means of classical least-square linear regressions and the R^2 statistics reported in the following text indicate the square of the linear correlation coefficient estimated from the linear regression.

RESULTS

Hypergravity experiment

The accuracy of movements was generally similar across the two gravitational conditions. For the upward movements, there was no significant effect of gravity on the endpoint variance (Wilcoxon rank-sum test, $P > 0.1$): the CV of the movement amplitude ranged between 0.07 ± 0.016 and 0.085 ± 0.024 in normal and hypergravity conditions, respectively (mean $\pm$ SD across subjects). For the downward movements, however, the movement CV was significantly greater in hypergravity ($P < 0.01$): we measured 0.068 ± 0.01 in normal gravity, against 0.1 ± 0.02 in hypergravity. In this gravitational condition, there was no significant evolution of the CV across the parabolas (one-way ANOVA, $F < 1.3$, $P > 0.2$). A detailed analysis of the movement kinematics was reported in our previous study (Crevecoeur et al. 2009b).

The temporal coupling between GF and LF was similar under hyper- and normal gravity conditions. The time lag between the GF and LF peaks did not show a significant tendency across the parabolas for both upward and downward movements (one-way ANOVA, $F < 1.4$, $P > 0.16$). The time lag in hypergravity was 17 ± 9 ms (average $\pm$ SD across subjects). These values are similar to the time lag measured under normal gravity for these subjects, where the average was 19 ± 17 ms. There was no effect of the change in gravity on the time lag (Wilcoxon rank-sum test, $P > 0.5$).

Under normal gravity conditions, GF_S varied across subjects. The individual means during the training session ranged between 2.5 and 9.6 N (with a mass of 250 g). Under 1.8 g conditions, GF_S increased in response to the weight increase induced by the change in gravity: the individual means ranged between 4.87 and 9.83 N. Figure 2A shows the mean GF_S , normalized for each subject to his/her normal gravity mean, and the time course of GF_S across the parabolas. There was no significant evolution of GF_S across the parabolas (one-way ANOVA, $F = 0.22$, $P > 0.9$). Despite some variability, the relative increase in GF_S under hypergravity corresponded to the relative increase in object weight, as evidenced by the increase in gravity shown on the same plot (gray line). Both GF_S and gravity data were averaged across subjects in each block (one block corresponds to one parabola). The low variability in the gravity data (Fig. 2A) confirms the stability and reproducibility of experimental conditions across parabolas.

The absolute ratio between GF and maximum LF during upward and downward movements (measured at LF peaks) significantly increased under hypergravity (Wilcoxon rank-sum test, $P < 0.001$). This effect was significant for seven subjects (individual $P < 0.005$). The dynamic phase was analyzed to address the origin of the increase. Figure 2B shows that increments of GF increased under hypergravity for a given variation of LF, as evidenced by a greater ratio between the two variables than that observed under normal gravity conditions (Fig. 2B, left). There was no significant main effect of the parabola number on the GF_I/LF_I ratio for both upward and

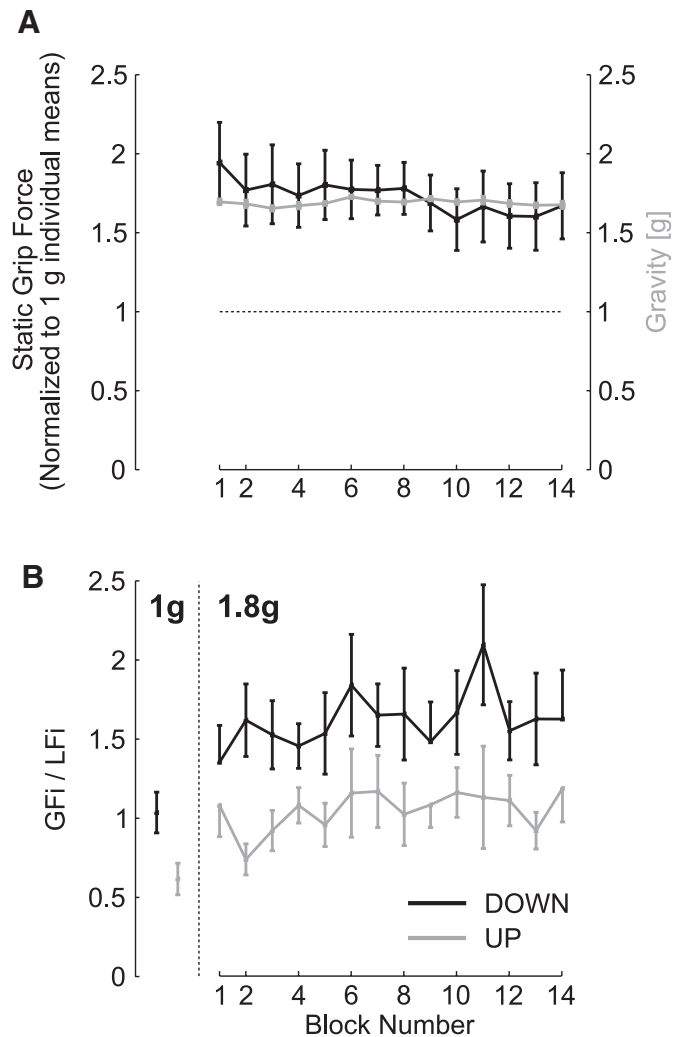


FIG. 2. A: evolution of the GF_S across the parabolas. The data were normalized to the individual means measured under the 1 g condition. The average gravity during the measurement of GF_S is shown on the same plot (gray trace). B: ratio between GF_I and LF_I in 1 g and in hypergravity across the parabolas in each movement direction. Data from up and down trials are represented in gray and black, respectively. In A and B, the vertical bars indicate the SE computed across subjects.

downward movements (one-way ANOVA, $F < 0.44$, $P > 0.9$). The ratio between increments of GF and LF increased an average of 0.44 for upward movement and 0.62 for downward movement.

The origin of this effect was investigated using the following linear model for increments of GF (GF_I) as a function of the variation of LF (LF_I)

$$GF_I = a_0 + a_1 LF_I \quad (1)$$

As shown in Fig. 3, A and B, GF_I was significantly correlated with LF_I in both gravitational conditions among all subjects (all subjects pooled, $F > 174$, $P < 0.001$, R^2 range 0.289–0.621 for each regression). The upward and downward movement data were separated since the linear regression parameters were distinct. This difference in parameters between the two movement types was consistent under both gravitational conditions. The linear regressions were significant for all individual subjects (individual $F > 5.71$, $P < 0.05$), except for the downward movements of one subject in hypergravity ($P =$

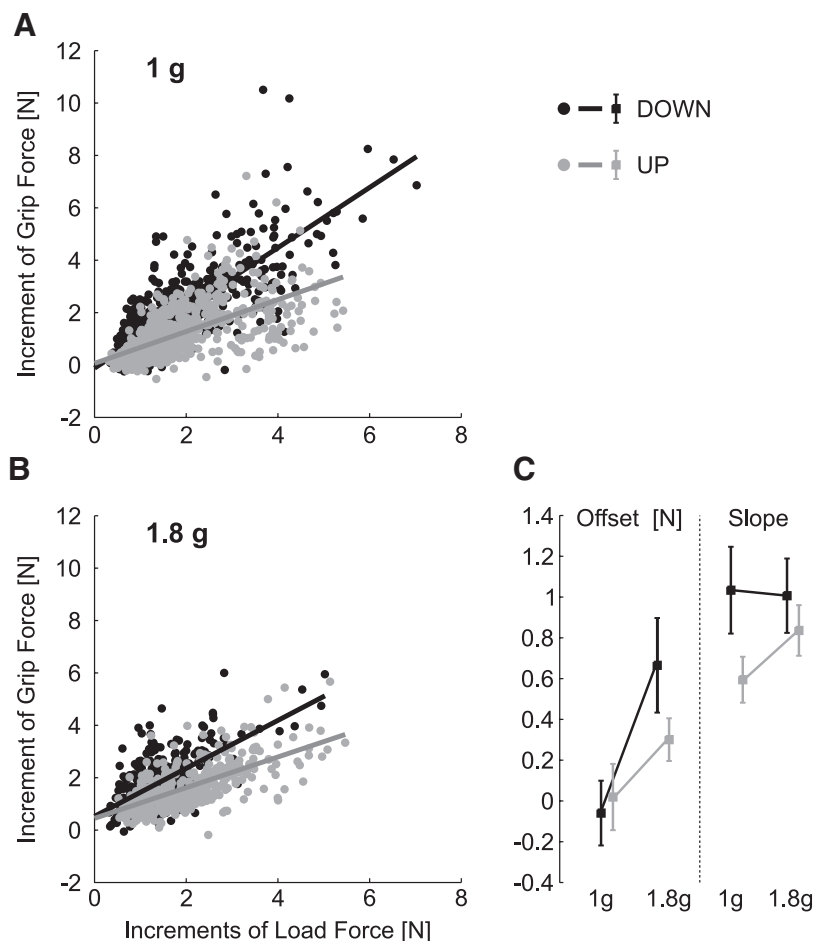


FIG. 3. A: linear regressions of GF_1 as a function of LF_1 under the 1 g condition. The regressions were computed on up (gray) and down (black) data separately. The data from all subjects were pooled for the illustration. B: same plot as in A with the data collected in hypergravity. C: effect of the change in gravity on the regression parameters. The vertical bars indicate the intersubject SE on the estimation of the regression slope and offset in each direction and gravitational condition.

0.69). Individual R^2 values in both movement directions ranged between 0.08 and 0.53 under normal gravity and between 0.1 and 0.63 under hypergravity conditions. Figure 3C shows the effect of the increase in gravity on the parameters of the linear regression computed for each subject. The offsets (a_0) and slopes (a_1) were averaged across subjects for each movement direction and gravitational condition. The offsets significantly increased in hypergravity for both the upward and downward movements (Wilcoxon rank-sum test, $P < 0.05$). The estimated offsets increased an average of 0.31 and 0.7 N for the upward and downward movements, respectively. It can be observed that the slope of the linear regressions for the upward movements tended to increase in hypergravity, although this tendency did not reach the level of statistical significance ($P = 0.1$). Thus the default increment of GF (a_0) increased under hypergravity for both movement directions to compensate for the increase in LF. The two control experiments presented in the following text aimed to reproduce this increase in a_0 by changing the movement kinematics (first control experiment) or the object's mass (second control experiment).

Control experiments

Several factors could underlie the above-described effect on anticipatory GF modulation. The first control experiment tested whether the change in GF adjustment could be induced by a change in movement kinematics (Crevecoeur et al. 2009b). Indeed, the movements were faster in both directions under

hypergravity conditions. The average peak inertial load in the training session performed under normal gravity was 1.61 N for the 10 subjects who performed the hypergravity experiment and 1.34 N for the control group. The control group showed a significant increase in LF peaks between the training session (first eight blocks) and the session in which they were requested to perform faster movements (eight subsequent blocks; Wilcoxon rank-sum test, $P < 0.001$). The average increase in LF_1 between the two sessions was 1.2 N, reflecting greater variation in the kinematics profile than that observed for the hypergravity group (average 0.05 N increase in LF_1). When the control subjects performed rapid movements, there was a significant increase in the ratio between GF_1 and LF_1 in both movement directions (Wilcoxon rank-sum test, $P < 0.01$). The average increase in the ratio was 0.05 for upward movements and 0.31 for downward movements.

The increments of GF correlated with the increments of LF in both movement directions and movement speed conditions in 18 of 20 computed regressions for the first control group (2 directions $\times$ 2 speed conditions $\times$ 5 subjects, $F > 4.26$, $P < 0.05$). The remaining nonsignificant regressions were for downward movements in the training session of one subject and upward movements in the rapid session of another subject ($P > 0.25$). Individual R^2 values ranged between 0.06 and 0.69. Figure 4A shows the mean effect of the increase in peak acceleration (and therefore LF) on the parameters of the linear regressions. Indeed, there was no strong effect of the change in

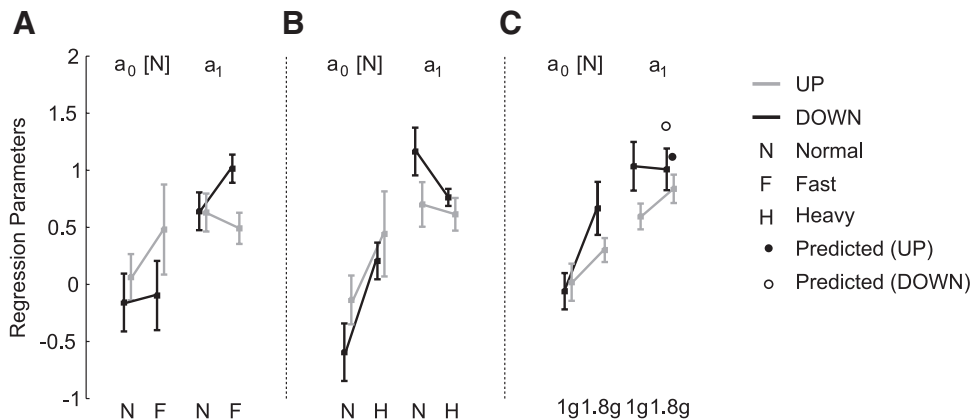


FIG. 4. A: effect of the change in movement kinematics on the parameters of the coupling between GF_I and LF_I in the first control group with identical mass across the 2 testing sessions. B: effect of the change in object weight on the parameters of the coupling between GF_I and LF_I in the second control group, with an additional mass on the held load and similar instruction relative to the movement speed across the 2 testing sessions. C: same plot as in Fig. 3C for comparison with the results of the control experiments. The open and filled circles show the results of the second control experiment in the heavy condition multiplied by the average relative increase in gravity across subjects and parabolas in each movement direction.

movement kinematics on the offset of the linear regressions (Wilcoxon rank-sum test on the offsets of upward and downward movements pooled, $P > 0.9$), which suggests that a change in movement kinematics cannot account for the increase in a_0 measured under hypergravity for both movement directions.

The second control group revealed that the subjects' strategy during exposure to hypergravity could be attributed to the effect of the change in weight on anticipatory GF modulation. The average peak inertial load during the first eight blocks performed by the second control group was 1.6 N, similar to the average of 1.61 N observed during training sessions for the group that performed the task in hypergravity. The peak inertial loads were logically greater due to the change in the object's mass but the peak acceleration was reduced in the session performed with the heavier manipulandum (Wilcoxon rank-sum test, $P < 0.001$). The average decrease in peak acceleration for both directions in this session was 0.57 ms^{-2} and the average increase in peak inertial loads was 1.14 N. Thus the increase in inertial loads represented 81% of the increase in loads that would correspond to movements realized with identical peak acceleration across the two sessions. This suggests that the change in movement kinematics for this control group had a limited effect relative to the variation in inertial loads induced by the change in mass. This control experiment also produced a significant increase in the ratio between GF_I and LF_I for upward (0.12) and downward (0.13) movements (Wilcoxon rank-sum test, $P < 0.001$).

GF_I correlated with LF_I for all subjects ($F > 6.02$, $P < 0.05$), excepting upward movements in the loaded condition of one subject. The relationship approached significance in this case ($P = 0.06$). Individual R^2 values ranged between 0.08 and 0.71. In this control experiment (Fig. 4B), the change in mass produced a significant increase in the regressions offset (Wilcoxon rank-sum test on the offsets of upward and downward movements pooled, $P < 0.05$), consistent with the effect of hypergravity on these parameters (Fig. 3C). The offsets of the linear regressions increased an average 0.61 and 0.84 N for the upward and downward movements, respectively. Thus qualitatively the effect of the change in mass on the regressions offsets was similar to the effect of hypergravity, although the average increases were greater in this second control experiment.

The results of the second control experiment suggest that the increase in a_0 could be due to the change in the object's weight. However, although the two control experiments reproduced the

increase in the ratio between GF_I and LF_I , neither was in quantitative agreement with the increase in this ratio measured under hypergravity conditions. This suggests that inertial loads may be overestimated in hypergravity. In the following text we show that such overestimation is consistent with the application in hypergravity of the strategy revealed by the second control group.

Under normal gravity conditions, a change in weight is necessarily due to a change in mass. However, the 10 subjects who performed the experiment in hypergravity faced an increase in weight that was due to gravity rather than to mass. By erroneously attributing the increase in weight to mass under hypergravity conditions, the subjects would expect an inertial load equal to

$$LF_I \cong \alpha m a(t_M) \quad (2)$$

where α is the increase in gravity, m is the mass of the manipulated object, and $a(t_M)$ is the peak acceleration of the intended movement. Based on the static GF developed under hypergravity (Fig. 2A), we can hypothesize that the subjects had a good internal estimate of α . However, the actual inertial load for this movement would be equal to $ma(t_M)$. Consequently, if the predicted inertial load is equal to α times the actual inertial load, then we expect that Eq. 1 becomes

$$GF_I = a_0 + a_1 \alpha LF_I \quad (3)$$

where a_1 corresponds to the gain of modulation applied to the internal estimate of the upcoming LF_I when manipulating an object of mass αm .

The second control experiment provided us with an estimate of a_1 applied by the subjects who experienced a change in weight due to mass. By multiplying this value (average a_1 in the heavy condition of the second control experiment) by α (average increase in gravity), we estimated the slopes of the modulation in hypergravity that corresponded to a strategy based on estimation of weight combined with an internal representation of movement kinematics. Figure 4C shows the slopes obtained in this situation for upward (solid circle) and downward (open circle) movements. The increase of GF modulation in hypergravity showed a consistent tendency toward these values, under the assumption that the subjects who experienced the increase in gravity used a similar strategy as the subjects tested during the second control experiment.

DISCUSSION

Our results describe the GF adjustments to LF variation during voluntary movements realized under hypergravity conditions. First, the increase in weight was properly compensated for by an increase in the level of GF developed during stationary holding. Second, the increase in the ratio between the increments of GF and LF revealed that the magnitude of the predicted inertial loads could be overestimated. The control experiments determined that such changes were likely due to the increase in weight that could be treated as an increase in mass in agreement with the invariant relationship between mass and weight on Earth.

These results reflect a coherent sensorimotor strategy under the hypotheses of optimal feedback control (Izawa et al. 2008; Liu and Todorov 2007; Todorov and Jordan 2002) and Bayesian integration of state and parameter estimation in motor control (Kording and Wolpert 2004). Optimal feedback control posits that the state estimate is mapped into motor commands in a way that optimizes a performance index. In the present study, the observed increase in GF modulation following an increase in object weight is fully compatible with the presence of a sensorimotor loop in which the anticipatory control of GF is modulated by the sensory inflow that conveys information about the object's weight. Under these assumptions, the persistent overestimation of the inertial loads may reflect that the on-line state estimate of the load force based on internal models and sensory feedback is biased by the internal prior that changes in weight are usually due to changes in mass. This could explain the overproduction of grip force since, by erroneously attributing the increase in weight to the mass, subjects would predict greater inertial loads for a given movement acceleration. Such persistent overestimation of inertial loads mapped into grip motor commands possibly generated the overproduction of grip force under hypergravity. Although it is not in itself an optimal behavior, the overproduction of grip force increments is compatible with the assumption that internal prior and sensory feedback are integrated in a Bayesian way and continuously mapped into motor commands.

A possible mechanism for such modulation is that the neural structures controlling the grip force receive proprioceptive input from the fingers, in addition to the arm, and that the encoding of weight is based on the force developed to maintain a stable grip. This proposed mechanism is based on the overlapping of sensory and motor representations of a given body part. This local sensorimotor association forms the basis for the default strategy or prior estimate used by the CNS during motor learning (Asanuma 1981; Singh and Scott 2003).

The exchange of modulation gain for a constant offset under an increased load is compatible with the motor system's tendency to minimize motor output variability in the presence of signal-dependent noise (Harris and Wolpert 1998; Todorov 2002). Higher loads are necessarily associated with higher arm or grip motor commands. Thus the internal prediction of inertial loads suffers from greater uncertainty in these situations, which is compensated for by applying a constant increment of grip force and a lower modulation gain based on prediction. We suggest that this strategy minimizes the variability in grip modulation when the magnitude of the inertial load increases.

Several factors could influence grip force outcome and produce the increase in the ratio between the grip force and load force increments. For instance, variability in the gravity level during the task execution potentially disrupted subjects' estimates of the object mass. However, these variations were rather limited and the possibility that this produced consistent overestimation is not straightforward.

A change in muscular cocontraction and grip stiffness control is another possible origin of excessive grip force modulation under hypergravity. In the present experiment, such an effect could be due to stiffness adjustment while subjects learned to move in a novel force field (Franklin et al. 2003, 2008), given that the greater variability observed for the downward movement could indicate that the acquisition of internal models adapted to hypergravity was not totally completed. However, this possibility fails to explain the persistent overestimation of load force variation observed for upward movements, for which movement accuracy was comparable in hyper- and normal gravity conditions and movement kinematics were stable across parabolas (Crevecoeur et al. 2009b).

Changes in grip stiffness can also be due to the amplification of muscle spindle activity under hypergravity, which could influence the motor behavior (Fisk et al. 1993). In the context of isometric force production, Mierau and colleagues (2008) observed in a similar experimental context that the change in tonic input at a segmental level could not account for the exaggerated forces produced under hypergravity and suggested that the impairment of force estimation was a consequence of higher neural processing. In addition, Mierau and colleagues demonstrated that it was not due to deficient proprioceptive feedback, in agreement with the observation that the impairment of isometric force estimation found its origin in central motor commands and partially corrected by sensory feedback (Girgenrath et al. 2005).

In several ways, these findings are similar to the present findings: we observe an overestimation of the self-generated inertial loads measured at the load force peaks, precluding the possibility that altered proprioceptive feedback misled the estimation of load force variation. Why was the load force overestimated at a central level? We suggest an alternative hypothesis based on Bayesian inference for state estimation (Kording and Wolpert 2004). Our results suggest that the encoding of weight is combined with an internal representation of the intended movement and that this combination is based on a Bayesian prior corresponding to the unequivocal relationship between weight, mass, and inertial loads experienced on Earth. However, in hypergravity, the sensory feedback must inform the CNS that the actual loads are smaller than expected, compared with the expected load while assuming only an increase in mass. Under the assumption of Bayesian integration, we hypothesize that the adjustments in grip modulation parameters are based on whether the difference between the expected and actual loads is most likely due to a change in the body or in the environment. Indeed, such Bayesian inference for estimating the origin of motor errors was demonstrated to be a very powerful model for motor adaptation and generalization (Berniker and Kording 2008). We suggest that a similar inference was processed in hypergravity and that the persistent overestimation of inertial loads reflects the strength of our internal prior knowledge of an environment in which gravity never changes.

The Bayesian inference allows one to interpret the distinct aspects of movement and force control. Indeed, a sensorimotor map based on the arm's weight could also yield excessive arm motor commands for upward acceleration since the inertial force would be overestimated. Such an effect would counter the overestimation of actual inertial force, since acceleration would be underestimated even when mass was overestimated. However, this factor could not account for the effect of hypergravity on the kinematics of downward movements; these movements were faster and there was a sharp reduction in target overshooting (Crevecoeur et al. 2009b). These results contradict the suggestion that arm motor commands were calibrated to overcome a force that was smaller than expected. We may thus conclude that the internal models of arm dynamics were adapted and that the internal representation of movement kinematics was reliable. This is further supported by the good correlations (similar to 1 *g* conditions) between increments of the grip force and the load force in hypergravity and by the synchronization of grip force with load force that did not change across the two gravitational conditions. These results are also similar to the results of a previous experiment in which isometric force production was exaggerated under hypergravity, whereas hand displacements were similar to the normal gravity condition (Guardiera et al. 2007). In the context of Bayesian integration, these and our results are compatible with the fact that visual feedback—providing good estimates of the effector's position and velocity—comes into play in the context of movement control, whereas force estimation is mostly based on prior experience and on proprioceptive signals, the latter being directly influenced by the force background.

Our hypothesis that gravitational forces are used to calibrate the internal models is compatible with the observation that under the 0 *g* condition, the mass discrimination threshold is impaired (Ross et al. 1984). This suggests that the loss of information provided by the object weight alters the internal estimates of its mass. Similarly, we have proposed in a recent study that the control strategy under 0 *g* was modulated by a greater uncertainty affecting the internal representation of arm and held objects dynamics (Crevecoeur et al. 2010). The present paper gives an interpretation of this phenomenon under 0 *g*, there is no weight information that can be mapped onto grip motor commands at movement initiation.

The Bayesian inference model also provides a theoretical framework in which the variation in regressions parameters can be explained. The first control experiment revealed that the effect of a change in movement kinematics may contribute to the hypergravity results because the regressions offsets tended to increase in the fast condition. Indeed, the hypothesis that subjects exchange gain for offset to minimize grip output variability under higher loads also applies to faster movements. However, this tendency was weaker than that in the heavy condition, where the increase in regressions offsets was significant. In addition, the fast versus normal experiment produced a change in movement kinematics that was greater than the changes in kinematics observed under hypergravity. Thus although the effect of a change in movement kinematics should not be rejected, our data indicate that it had a limited impact on the increase in regression offsets observed under hypergravity. Based on the second control experiment, we interpreted that the load force prediction was based on a combination of the perception of the object weight and a reliable representation of

the movement kinematics. Thus the overestimation of the inertial loads may be a consequence of the fact that inferring inertia from weight uses a Bayesian prior assumption that the gravity was constant. According to the hypothesis of Bayesian integration, the prior expectation should be partially corrected by the sensory feedback that conveys information about the actual load variations. The partial feedback correction gives further understanding about the fact that, in comparison with the strategy observed in the loaded condition of the second control experiment, the regressions parameters in hypergravity increased by a smaller amount than that if the sensorimotor mapping used for the anticipation of inertial loads was exclusively based on the prior assumption that gravity was constant.

Despite this bias, our results demonstrate that arm and grip motor commands are dissociated. Similar results were reported in the context of oscillatory movements by White et al. (2005) who showed that the grip force was adjusted to the actual load despite the fact that the variation of load force resulted from a distinct combination of object mass, movement acceleration, and gravity. In the present context of discrete movements, independent prediction must be estimated for each trial, which presumably hardens a fine GF adjustment relative to the actual load. In addition, our subjects were experiencing a change in gravity for the first time, whereas the subjects tested by White and colleagues (2005) had extensive experience with parabolic flights (>300 parabolas). Another factor that possibly alters the adjustment of internal prior estimate corresponding to the hypergravity condition is the alternation of gravitational phases to which subjects were exposed in parabolic flights. This alternation between different gravitational phases can induce washout between parabolas and motor variability, rendering the process of early adaptation occurring during the first trials quite hard to observe. Our sample did not allow observing such an early adaptation effect and we therefore concentrated on the main effect and the evolution across the blocks, which could be reliably addressed. Under more stable exposure to hypergravity, the investigation of isometric force production revealed that practice under hypergravity (3 *g*) improves the force scaling (Gobel et al. 2006). Thus regarding precision grip control, we expect that after a longer and more stable exposure, humans are able to learn an unbiased prior mapping between weight and loads that corresponds to a novel gravitational context.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

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