"Forward models of inertial loads in weightlessness."

Crevecoeur, Frédéric ; Thonnard, Jean-Louis ; Lefèvre, Philippe

ABSTRACT

In this experiment, we investigated whether the Central Nervous System uses internal forward models of inertial loads to maintain the stability of a precision grip when manipulating objects in the absence of gravity. The micro-gravity condition causes profound changes in the profile of tangential constraints at the finger-object interface. In order to assess the ability to predict the micro-gravity-specific variation of inertial loads, we analyzed the grip force adjustments that occurred when naive subjects held an object in a precision grip and performed point-to-point movements under the weightless condition induced by parabolic flight. Such movements typically presented static and dynamic phases, which permitted distinction between a static component of the grip force (measured before the movement) and a dynamic component of the grip force (measured during the movement). The static component tended to gradually decrease across the parabolas, whereas the dynamic component was rapidly modulated with the micro-gravity-specific inertial loads. In addition, the amplitude of the modulation significantly correlated with the amplitude of the tangential constraints for the dynamic component. These results strongly support the hypothesis that the internal representation of arm and object dynamics adapts to new gravitational contexts. In addition, the difference in timescales of adaptation of static and dynamic components suggests that they can be processed independently. The prediction of self-induced variation of inertial loads permits fine modulation of grip force, which ensu...

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FORWARD MODELS OF INERTIAL LOADS IN WEIGHTLESSNESS

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Abstract—In this experiment, we investigated whether the CNS uses internal forward models of inertial loads to maintain the stability of a precision grip when manipulating objects in the absence of gravity. The micro-gravity condition causes profound changes in the profile of tangential constraints at the finger–object interface. In order to assess the ability to predict the micro-gravity-specific variation of inertial loads, we analyzed the grip force adjustments that occurred when naive subjects held an object in a precision grip and performed point-to-point movements under the weightless condition induced by parabolic flight. Such movements typically presented static and dynamic phases, which permitted distinction between a static component of the grip force (measured before the movement) and a dynamic component of the grip force (measured during the movement). The static component tended to gradually decrease across the parabolas, whereas the dynamic component was rapidly modulated with the micro-gravity-specific inertial loads. In addition, the amplitude of the modulation significantly correlated with the amplitude of the tangential constraints for the dynamic component. These results strongly support the hypothesis that the internal representation of arm and object dynamics adapts to new gravitational contexts. In addition, the difference in time scales of adaptation of static and dynamic components suggests that they can be processed independently. The prediction of self-induced variation of inertial loads permits fine modulation of grip force, which ensures a stable grip during manipulation of an object in a new environment.

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Key words: precision grip, adaptation, internal models, microgravity.

Motor actions are a fundamental mode of interaction between the human body and the external world. The mechanisms that underlie movement control are commonly described in terms of internal inverse and forward models (Wolpert and Kawato, 1998; Kawato, 1999; Wolpert and Ghahramani, 2000). Inverse models invert the dynamics of the limb in order to map a desired trajectory onto a motor command, whereas forward models predict the sensory consequences of a motor command (Miall and Wolpert, 1996; Davidson and Wolpert, 2005). The modulation of grasping forces with self-induced loads is an example of predictive control mechanisms based on forward models. When the object is held in a precision grip, i.e. between the thumb and the index finger, the grip force (GF) is synchronously modulated with variations in tangential constraints due to the sum of the object's weight and inertial forces (LF, load force). In this case, the absence of a delay in the response of GF to changes in LF is the signature of a predictive mechanism that is conceptualized as a forward model. Adaptation of motor control in general can be seen as an acquisition of appropriate internal models (Wolpert et al., 2001). To date, adaptation of forward models of inertial loads in the absence of gravity has not been demonstrated. Therefore, to address specifically the adaptation of forward models, this study focuses on the GF response to a variation of LF in a micro gravity condition (0×g).

The tight coupling between GF and LF has been thoroughly studied on Earth in various paradigms, such as grip lift (Johansson and Westling, 1984; Westling and Johansson, 1984), horizontal and vertical point-to-point movements (Flanagan and Wing, 1993), and cyclic arm movements (Flanagan and Wing, 1995; Blank et al., 2001; Descoins et al., 2006). Modulation of GF with LF is also very efficient in other contexts such as multi digit grasp (Zatsiorsky and Latash, 2008), or when variations of LF are induced by locomotion (Gysin et al., 2003). In the context of precision grip, the coupling between GF and inertial, elastic and viscous loads induced by linear motors has provided evidence for a forward model of the manipulated object dynamics (Flanagan and Wing, 1997; Flanagan et al., 2003). Similarly, previous studies on the coupling between GF and LF in altered gravity have shed light on the adaptability of GF control in a new gravitational context. Stationary holding (Hermsdorfer et al., 1999) and cyclic arm movements (Hermsdorfer et al., 2000; Augurelle et al., 2003a; White et al., 2005) were performed under a 0×g condition induced by parabolic flights. Under the normal gravity condition, a downward acceleration usually does not produce a negative peak of LF (except in very fast movements where the held load is accelerated faster than gravity); however, it does generate a decrease in tangential constraints resulting from the weight of the manipulated object. Consequently, there is no increase in GF in phase with the downward acceleration. In contrast, under the 0×g condition, grip force is modulated with a negative peak which is delayed with respect to the peak of LF. This modulation is strongly correlated with the amplitude of the tangential constraints. Under microgravity, this coupling is greatly increased. When the object is held in a precision grip, the grip force is synchronously modulated with variations in tangential constraints due to the sum of the object’s weight and inertial forces (LF, load force). In this case, the absence of a delay in the response of GF to changes in LF is the signature of a predictive mechanism that is conceptualized as a forward model. Adaptation of motor control in general can be seen as an acquisition of appropriate internal models (Wolpert et al., 2001). To date, adaptation of forward models of inertial loads in the absence of gravity has not been demonstrated. Therefore, to address specifically the adaptation of forward models, this study focuses on the GF response to a variation of LF in a micro gravity condition (0×g).

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0×g condition, negative acceleration produces a negative LF since the weight of the held load equals zero. Therefore, the risk to lose grip stability associated to both positive and negative peaks of LF is specific to the 0×g condition. In a preliminary study, Nowak et al. (2001) performed point-to-point movements in combination with other protocols in micro-gravity and emphasized a change in the pattern of GF in response to LF variations. This finding proves that an adaptation occurs in 0×g condition, but the nature of the adaptive mechanism remains unknown. In particular, the ability to predict the positive and negative peaks of LF was not addressed and it remains unanswered whether the amplitude of the GF modulation is based on a prediction of the inertial loads. There is, to date, no formal proof that such changes in GF modulation in weightless condition rely on internal forward models of inertial loads adapted to the novel gravitational context. The aim of the present study was to provide a quantitative analysis of GF adjustments to variations of LF under the 0×g condition in order to elucidate whether the adaptation is due to an internal forward model.

To this end, we varied the amplitude and direction of discrete point-to-point movements (see Hogan and Sternad (2007) for a definition) and investigated both the time course of GF responses to the variations of LF and the amplitude of the response with respect to the amplitude of LF. In the previous studies investigating oscillatory movements in changed gravity, the change in GF reflected a fine adaptive control, but sensory feedback continuously drove the GF modulation through the repeated cycles of identical amplitude. In addition, the mechanisms controlling rhythmic and discrete movements in altered gravity are different (White et al., 2008). In the context of point-to-point movements performed in 0×g, if the LF was predicted in a time-varying fashion and the GF was adjusted accordingly, we expect to uncover distinct GF responses to positive and negative peaks of LF leading to biphasic GF profiles with appropriate timing and amplitude for each individual movement.

**EXPERIMENTAL PROCEDURES**

**Subjects**

Eight healthy human subjects (24–37 years old), naive to the purpose of the study and to 0×g conditions, participated in this experiment. All subjects gave their informed consent and received the approval to participate in parabolic flights from their National Center for Aerospace Medicine (class II medical examination). The experiment complied with the European Space Agency (ESA) ethical and biomedical requirements for experimentation on human subjects (ESA Medical Board Committee) and was approved by the local French CPP Committee (Comité pour la Protection des Personnes) in charge of reviewing the life science protocols in accordance with the French law.

**Parabolic flight**

These experiments were performed during the 43rd and 44th ESA Parabolic Flight Campaigns on board the A-300 0-G aircraft (starting from Bordeaux–Mérignac, France). A parabolic maneuver is composed of three distinct phases: 20 s of hypergravity (1.8×g, pull-up phase) followed by 22 s of weightlessness (0×g) before another period of around 20 s of hypergravity (pull-out phase). The beginning of each 0×g phase is announced by the pilot as the injection point. The aircraft ran a sequence of 30 parabolas per flight organized in six groups of five parabolas separated by 5–8 min pauses. Each subject typically performed the task during 15 parabolas, but due to the unforeseeable nature of the experimental conditions, data could be collected during only eight parabolas for subject S6.

**Experimental procedure**

The task, illustrated in Fig. 1A, was performed only in the 0×g phases. Four target light emitting diodes (LEDs) were placed along a structure that was vertically aligned with respect to the aircraft floor. The target LEDs were positioned every 15 cm. Data acquisition began at the injection point. The program generated a random sequence of targets at a frequency of 1 Hz. The target sequence was generated such that, at any time, the transition probability from the current target to any of the three remaining targets was equal to 1/3. The subjects were seated in front of the target axis and, during data acquisition, held a manipulandum in a precision grip (mass 800 g, grip aperture 4.5 cm). They were asked to align and stabilize the manipulandum with the current target as fast as possible until the next target was illuminated.

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![Fig. 1.](image-url) (A) A subject performing the task. The white disks represent the position of the targets. (B) The subjects held the manipulandum in a precision grip between the thumb and the index finger. Fx, Fy, and Fz are the normal and tangential constraints between the fingers and the manipulandum measured by the left and right sensors (R and L). The four IREDs used to track the position and orientation of the manipulandum are represented by black disks.
Head, eye, and arm movements were not constrained. The subjects were allowed to touch the manipulandum only during the 0×g phases to reduce cues to its mass. On return to normal gravity condition, all the subjects were very surprised when they lifted the manipulandum and felt the actual weight. It appeared that their estimation of object mass from experienced LF variation was much smaller than the actual mass. The randomized sequence of targets yielded 12 possible movements. For the purpose of this analysis, the movements were separated into six different categories: upward or downward movements of one, two, or three steps, regardless of the initial hand position. A block of 18 point-to-point movements was performed during each parabola. In the following text, one block refers to the set of trials performed during one parabola. The subjects tested in the second half of each flight were not involved in tasks involving object manipulation during the first half of the flight.

Apparatus and data collection

The manipulandum was equipped with two force-torque sensors, one under each finger (40 mm diameter, Mino 40 F/T transducers, ATI Industrial Automation, NC, USA). The contact surface between the fingers and the manipulandum were disks of brass pasted on each sensor. These sensors measured the forces and torques in three dimensions, as illustrated in Fig. 1B. The sampling rate for acquisition by the sensors was 800 Hz. Three-dimensional position signals of four infrared markers (infrared emitting diode [IRED]) placed on the manipulandum as shown in Fig. 1B were sampled at 200 Hz with a motion-tracking device (Codamotion System, Charnwoods Dynamics, Leicestershire, UK).

Data postprocessing

Forces and position signals were digitally low-pass filtered with a zero phase-lag Butterworth filter of order four with a cutoff frequency set to 15 Hz. Let \((FX_L, FY_L, FZ_L)\) and \((FX_R, FY_R, FZ_R)\) be the force components in the three directions of space, measured in the right and left sensors’ reference frame, respectively (Fig. 1B). The GF was defined as the mean of the components normal to the sensors’ surfaces:

\[
GF = \frac{|FZ_R| + |FZ_L|}{2},
\]

(1)

The LF was defined as the projection of the resulting tangential constraint \((\hat{T}_{C})\) on the vertical axis of the aircraft’s reference frame \((\hat{t}_{y})\). More precisely, \(\hat{T}_{C}\) and LF were computed as follows:

\[
\hat{T}_{C} = \left( (FX_R + FX_L)e_x + (FY_R + FY_L)e_y \right) e_z,
\]

(2)

\[
LF = \hat{T}_{C} \cdot \hat{t}_{y},
\]

(3)

where \(e_x\) and \(e_y\) represent the unit vectors of the sensors’ reference frame, in which \(FX_L, FY_L, FY_R\) and \(FY_R\) were measured. Given that the norm of \(\hat{t}_{y}\) is equal to 1, the dot product comes down to the product of the norm of \(\hat{T}_{C}\) and a correction term equal to the cosine of the angle between this vector and \(\hat{t}_{y}\). This procedure allowed for correction of cases in which the manipulandum was slightly tilted or when the trajectories were not strictly vertical. We verified that this correction did not exceed 5% of the norm of \(\hat{T}_{C}\) across all blocks and subjects. The onset of the movement was detected when the arm velocity exceeded 5% of the peak velocity computed on each trial. The end of the movement was defined similarly when the arm velocity dropped below the same threshold. The movement duration and amplitude (i.e. the displacement between the movement onset and end), as well as the peak velocity, were used to characterize the subject’s performance with respect to the arm trajectory.

Data analysis

According to Newton’s second law, the resulting tangential constraints at the finger–object interface when the manipulandum is held and moved vertically is equal to the sum of the weight and the inertial load:

\[
LF = m(g + a(t)),
\]

(4)

where \(m\) is the mass of the manipulandum, \(a(t)\) is its acceleration and \(g\) is gravity. Since \(g\) equals zero in this experiment, LF is directly proportional to the acceleration (Fig. 2C and 2D), provoking positive and negative peaks of LF corresponding to acceleration and deceleration phases of the movements in both directions. Therefore, we distinguished four different types of tangential constraints, in accordance with the profile of LF. For upward movements (Fig. 2D, left), LF first reached a maximum and then a minimum. These two extrema were defined as \(U^-\) (Up-Negative) and \(U^+\) (Up-Positive) constraints, respectively. Similarly, the constraints \(D^-\) (Down-Negative) and \(D^+\) (Down-Positive) were defined for the extrema of LF that occurred during a downward movement (Fig. 2D, right). In the analyses, the sign of LF was preserved to allow differentiating phases of the movement: presenting negative tangential constraints usually not experienced on Earth, and which are different in up (final phase) and down movements (initial phase). For each trial, the static level of grip force (\(GF_S\)) was defined as the average GF in a 100 ms time window after the target onset. It represents the level of GF exerted by a subject when the arm was at rest. The increment of GF was defined as the difference between GF and \(GF_S\) measured at the time of LF extrema. Thus, for each trial, there was one measurement of \(GF_S\) and two measurements of increments, one relative to the positive maximum of LF (\(U^+\) or \(D^+\)) and the other relative to the negative minimum of LF (\(U^-\) or \(D^-\)). Fig. 2D illustrates these parameters. The brackets represent the time window in which \(GF_S\) is computed and the dotted vertical lines joining LF and GF illustrate that grip force increments (\(GF_I\)) were measured with respect to \(GF_S\) at the extrema of LF.

Statistical analysis

The values of \(GF_S\) inside each block were pooled after verifying that there was no effect of initial hand position for any of the subjects, and no significant tendency within the blocks (ANOVA, \(P > 0.05\)). This observation motivated the analysis of the evolution of \(GF_S\) across the blocks. When ANOVA revealed significant effect across the blocks, classic least squares linear regressions were computed on raw data from individual trials to identify the nature of the effect based on the sign of the slope. The ratio between GF increments and corresponding extremum of LF was utilized to address the stabilization of the dynamic component. The analyses were performed across the blocks for consistency with the analysis of the adaptation of the static GF. The stabilization across the blocks was assessed for each subject by comparing the data obtained from a sliding window that contained three blocks with the data obtained in the next block. The non-parametric Wilcoxon rank-sum test was employed to test the hypothesis that block i was not significantly different from blocks i-1 to i-3 pooled together. A lack of any significant difference indicates that the four blocks under examination could be considered as stable. This method permits one to assess the stabilization of static and dynamic components of GF with an identical criterion without any hypothesis on the learning curve. The Levene test was used to assess variance homogeneity. The analysis of the modulation of GF during the dynamic phase of the movement is based on classic least-square linear regression. For all statistical tests, a \(P\) level
inferior to 0.05 was considered to be statistically significant. Finally, cross-correlations between the GF and the absolute LF were used to provide an index of synchrony.

RESULTS

Two typical trials are shown in Fig. 2, three steps upwards (Fig. 2, left) and three step downwards (Fig. 2, right). In both directions, the subjects performed trajectories with bell-shaped velocity profiles (Fig. 2B). The arm trajectories performed by the subjects were rapidly adapted. Indeed, subjects had continuous visual feedback and could therefore correct the movement and stabilize the manipulandum accurately. For the movements of one step in both directions corresponding to movements of 15 cm, the average absolute amplitude after four blocks was 15.17 cm with a standard deviation of 1.71 cm (averaged across subjects), which shows that subjects performed accurate movements. The movement duration, amplitude, and peak velocity did not show any significant trend across the trials and blocks, suggesting a fast adjustment of internal inverse models. It can be observed that GF profiles shown in Fig. 2D are synchronously modulated with positive $U^+$ and $D^+$ constraints and also with the negative $U^-$ and $D^-$ constraints. Therefore, GF has two distinct peaks for one single point-to-point movement. The following sections separately assess the evolution of the static and dynamic components of GF.

Static component of GF

The static component GF$_s$ represents the baseline of GF exerted when the subject’s arm is at rest for each trial. The following analysis investigates the evolution of GF$_s$ across the blocks. There was no evidence that the performance of subjects tested during the last 15 parabolas was different from the performance of the subjects tested in the first 15 parabolas. The tendency for a decrease in GF$_s$, shown in Fig. 3A for one subject, was significant for seven out of eight subjects (linear regressions, $R$ ranged between 0.38 and 0.65 across subjects). Fig. 3A also shows the result of the sliding window analysis (see Experimental procedures) revealing that, for this subject, the last four blocks surrounded by the grey rectangle may be considered stable. It
should be emphasized that the values of GFS shown for this subject are already rather low from the first block, at least with respect to the minimum GF required to hold an object of 800 g in normal gravity condition. However, low GFS were not observed for all the subjects and some of them developed static GFS up to 20 N. Similar analyses of the remaining subjects revealed that six out of eight subjects showed stabilization for at least the last four blocks. The earliest stabilization across the subjects was observed for the last seven blocks (subject S7). It is worth mentioning that one of the two subjects who did not show any stabilization was S6, who performed only eight blocks. The decrease in GFS was accompanied by a significant reduction of variance inside the blocks, as shown in Fig. 3B for the same subject. This significant reduction of variance across blocks was observed for all of the subjects. Given the variability of the range of GFS across the subjects, the means were normalized for each subject with respect to the largest mean across all of the blocks before the data were pooled for illustration. Fig. 3C and 3D clearly show for all subjects that adaptation of the static component could be characterized by a decrease across the blocks, a stabilization around the 10th block, and a reduction of variance across the blocks.

**Dynamic component of GF**

The analysis of the dynamic component of GF in response to LF variations describes firstly the time course of the modulation and secondly the amplitude of the modulation. Particular interest is given to the negative LF for the update of internal models, since the risk that the object slips due to a negative LF is specific to the 0g condition. Fig. 4A shows LF traces of two typical up (left) and down movements (right). Three events, which correspond to the vertical dotted lines, were defined with respect to the profile of LF: first extremum occurring at $t_1$, zero of LF occurring at $t_2$ and second extremum occurring at $t_3$. The solid traces in Fig. 4B show the dynamic component of GF (GF-GFS) for the corresponding trials. The events defined above were used to compute the slopes of linear fits of GF-GFS as a function of time for the periods between $t_1$ and $t_2$ and between $t_2$ and $t_3$ (see $\alpha_1$, $\alpha_2$, $\alpha_3$, and $\alpha_4$ in Fig. 4B). It is important to mention that there is no increment of GF with a negative LF under the normal gravity condition. For the sake of illustration, the dashed lines represent the putative profiles of GF that are expected on earth (freehand sketch, see Flanagan and Wing (1993) for real data). Therefore, for upward movements, a $1 \times g$ strategy would produce negative $\alpha_1$ and $\alpha_2$ slopes, whereas $\alpha_3$ and $\alpha_4$ would be positive for downward movements. In contrast, double peak responses of GF, such as those shown in Fig. 4B, change the signs of $\alpha_2$ and $\alpha_3$ with respect to the normal gravity condition: $\alpha_2$ becomes positive and $\alpha_3$ becomes negative. As a consequence, the change in the signs of slopes provides evidence for a biphasic GF response. The analyses revealed that $\alpha_2$ was significantly positive for seven subjects out of eight (all but S6, individual values between 0.21 and 0.84) and $\alpha_3$ was significantly negative for all of the subjects (individual values between −0.72 and −0.04). As expected, $\alpha_1$ and $\alpha_4$ remained significantly
negative and positive, respectively, for all the subjects. As illustrated in Fig. 4C, \( \alpha_2 \) and \( \alpha_3 \) had opposite signs with respect to those in the \( 1 \times g \) profiles from the first bin of four blocks, and the slopes and correlations (Fig. 4D) were relatively stable across the blocks. These findings suggest that biphasic responses of GF to the variations of LF can be observed very early and that this tendency is already significant within the first four blocks.

Following our analysis of the time course of the modulation, we investigated whether the amplitude of GF was scaled with the amplitude of LF variations. To this end, we computed the relationship between the increments of GF (i.e. GF-GFs in Fig. 4B measured at \( t_1 \) and \( t_3 \)) and the corresponding maximum or minimum of LF, namely \( U^+ \), \( U^- \), \( D^+ \), and \( D^- \). The increments significantly correlated with the \( D^- \) constraint for all of the subjects and for all but one subject (S6) with the \( U^- \) constraint. Slopes and \( R \) statistics of the linear regressions for each subject are listed in Table 1. More importantly, the significant correlation between the increments of GF and the maximum or minimum of LF remained significant when we considered only the movement of one amplitude in each direction (\( R \) ranged between 0.24 and 0.83 across subjects). This was observed for all the subjects but S6 who did not significantly modulate GF with the \( U^+ \) and \( U^- \) constraints, as was already observed for correlations computed on the data including all the movement categories (see Table 1).

Fig. 5 shows the relationship between GF and the corresponding extremum of LF for one subject (S5). Only the movements corresponding to one step upwards and downwards are represented. This significant relationship within one single movement category (\pm 15 cm) demonstrates...
that the actual motor command of each individual movement is taken into account for the generation of an increment of GF.

Previous analyses demonstrate a time varying prediction of the inertial loads and a significant modulation of GF with the actual LF. In order to assess when the predictions were stabilized, indicating that the dynamic component was adapted, we computed the ratio between the increments of GF and the corresponding maximum or minimum LF and applied the same sliding window analysis as for the stabilization of GFS. The ratio is stable from the 3rd block for \( U^+/H_11001 \), from the 6th block for \( U^-/H_11002 \) and \( D^-/H_11001 \), and from the 5th block for \( D^-/H_11002 \) (all movements pooled, averaged across subjects). Again, there was no difference between the subjects evaluated during the first 15 parabolas and the subjects evaluated during the second 15 parabolas.

Finally, in order to test the synchrony between LF and GF profiles, the cross-correlations were computed on the trials performed during the last four blocks when both static and dynamic components could be considered stable. The average time shift corresponding to the maximum correlation was very close to zero (LF lead of \( 19\pm30 \) ms on average). The corresponding maximal correlations were equal to \( 0.83\pm0.06 \) (mean±standard deviation, averaged across subjects).

This section provides evidence for biphasic profiles of GF in response to the positive and negative LF and demonstrates that the amplitude of the GF response of each movement is scaled with the amplitude of LF. The predictions are stable from the fifth block on average and the GF modulation is synchronized with the LF variations.

**DISCUSSION**

Our results describe the adaptation of static and dynamic components of GF. On the one hand, the static component decreases slowly, tends to stabilize late, and the variance of GFS decreases across the blocks. On the other hand, the dynamic component is quickly modulated by the tangential constraints, and the modulation is significantly correlated with the positive and negative peaks of LF.

Our results appear to be fully compatible with those reported in earlier studies. In an analysis of stationary holding of an object under the 0g condition, Hermsdörfer and colleagues (1999) observed a continuous decrease of GF during the first five parabolas dedicated to this task (subsequent parabolas were dedicated to other protocols). They concluded that longer exposure is needed in order to observe stable performance. The results of the present study indicate that around 10 parabolas are required before stabilization of GFS occurs. In a previous study, which investigated oscillatory movements performed in parabolic flights by naive subjects, Augurelle and colleagues (2003a) reported stabilization of the baseline of GF in 0g from the 5th parabola. The nature of the movement (rhythmic oscillations) probably facilitates this earlier stabilization of the baseline GF. In addition, the subjects performed the task in different gravitational contexts during the flight (in particular in 1g), which could contribute to provide the subjects with a good estimate of the object mass and help producing an adequate GF.

Our main finding is that GF modulation reflects a fine prediction of the specific inertial loads experienced under the 0g condition. The double-peak responses of GF (see Table 1. Slopes and R statistics of the linear regression of GF as a function of the corresponding peak of LF

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**Fig. 5.** Modulation of GF as a function of the corresponding extremum of LF, data from subject S5. The grey lines correspond to linear regressions computed on raw data. Only the data corresponding to movements of one amplitude are represented. (A) Upward movements. (B) Downward movements.
Fig. 2D and Fig. 4) and significant correlations between GF, and the extrema of LF (Fig. 5) demonstrate a predictive control mechanism, which takes into account the variation of LF as a function of time for each particular movement, and produces an increment of GF that is proportional to the predicted constraint. Analysis of the one-step category (Figs. 5C and 5D) confirms that the prediction is realized on a trial-by-trial basis. This implies that the prediction takes the actual motor command sent to the limb into account in order to produce an appropriate grip response. This mechanism, which is well characterized under the normal gravity condition for point-to-point movements (Flanagan and Wing, 1993), is rapidly adapted to the zero g condition and allows for fine prediction of positive and negative constraints, as well as prediction of their amplitude. In zero g, Nowak and colleagues (2001) reported that GF remained elevated during the whole movement in order to counteract both peaks of LF. They concluded that the control of GF was highly flexible and able to integrate changes in load profile that were induced by changes in gravity. However, their study involved only two subjects with different experiences of weightlessness who performed the task during only two parabolas. The protocol consisted of movements of one amplitude (corresponding to two steps in our experiment) without randomization. Their preliminary data permitted enhancement of a change in GF control but fell short of explaining the mechanism that underlies the adaptation to micro-gravity. In contrast, we provide evidence for a biphasic response of GF proving a time-varying prediction of LF, and we demonstrate that the amplitude of the modulation of GF is scaled as a function of the predicted LF. Altogether, our results permit us to conclude that LF is predicted in a time varying fashion and GF is adjusted accordingly, proving the existence of a forward model of inertial loads adapted to weightless condition.

The point of performing this experiment in weightlessness is that the nature of the perturbation (the change in gravity) obliges the subjects to learn appropriate arm motor control through sensory signals of force and motion from muscles and tendons (Lackner and Di Zio, 2005). This is due to the fact that there is no external contact point between the limb and a perturbing device like a robot. This distinction in the nature of the perturbation led Lackner and Di Zio to emphasize distinct adaptation processes when identical forces were applied on the limb, depending on the nature of the perturbing force: Coriolis in one case (without contact) and induced by a robot in another case. Concerning object manipulation, it was previously demonstrated that the CNS can predict the effect of various force fields induced by linear motors (Flanagan and Wing, 1997), which proves that a forward model of inertial loads is available when the manipulated object presents altered dynamics experienced through contact between the object and the fingers, whereas the arm is moved in normal condition. In addition, performing horizontal movements on Earth generates a similar profile of LF in the direction of the movement (Flanagan and Wing, 1993), but the relative variation of the total LF for an acceleration in the range observed in the present study would be small in comparison with the constant offset due to the object weight (less than 8% variation of total LF for an acceleration of 4 m/s2). On Earth, the weight of the object can be counterbalanced by an external support, leading to pure acceleration dependent loads for horizontal movements. A fine coupling between normal and tangential forces can be observed in such contexts (Flanagan and Lolley, 2001; Descoins et al., 2006) providing evidence for a good anticipation of inertial loads related to the manipulated object dynamics. However, similar range of LF variation as observed under zero g condition cannot be experienced in normal gravity without artificially neutralizing the object weight. Moreover, the whole system (arm–object) undergoes the perturbation induced by a change in gravity without contact on the limb or on the object. Therefore, the forward models must take into account the change in arm dynamics in addition to changes in the object dynamics.

The main difference between the adaptation processes uncovered by Lackner and Di Zio concerned the time course of adaptation and the presence of an aftereffect, which was greater after the Coriolis perturbation than after the robot’s perturbation. It was not possible to investigate the presence of an aftereffect in our experiment given the context of parabolic flight (short exposure separated by hyper- and normal gravity phases with short pauses), thus the question of de-adaptation after longer exposure remains an open question and would provide further indication of the nature of the adaptive process. Indeed, it has been shown that context-specific adaptation to an expected Coriolis force field does not require de-adaptation upon return to normal condition (Cohn et al., 2000). The investigation of subjects’ performances after a long-term flight should indicate whether a similar kind of adaptation would occur in zero g condition. In particular, the presence (or absence) of aftereffect should allow dissociating whether the internal forward models of inertial loads are adapted to the weightless condition, or whether a new context specific internal model is built in absence of gravity.

Based on the hypothesis of distinct control processes for posture and movement (Kurtzer et al., 2005), our results confirm that GF can be decomposed into static and dynamic components with different time scales of adaptation. Indeed, the dynamic component of GF was found to be stable from the fifth blocks on average, whereas the static component gradually decreased across the blocks. This finding suggests that the two components of GF can independently adapt and evolve. This additive model for static and dynamic components of GF is in accordance with previous hypotheses that gravitational and inertial loads are treated separately in order to program GF (Hermsdorfer et al., 2000; Nowak et al., 2001; White et al., 2005; Zatsiorsky et al., 2005). A dissociation between static and dynamic components has also been reported in trunk postural and bending adjustments under prolonged exposure to weightlessness (Baroni et al., 2001). In precision grip, the decoupling between static and dynamic components can also be related to the observation made by...
Flanagan and Wing (1995) that the intercept and gain of GF as a function of LF during oscillatory movements independently adapt in response to an increase in the movement frequency. However, the analogy must be considered with caution because there are known differences between rhythmic and discrete movements (Ronssse et al., 2008a,b,c). In particular, it has been shown that neural circuitries underlying the control of rhythmic and discrete tasks are distinct (Schaal et al., 2004).

More generally, we propose that the static component is the output of a mechanism that depends on the context and on an internal estimation of the object mass. In our experiment, the sensory feedbacks contributing to the general perception of a change in the environment (e.g. blood pressure variations and vestibular signals) probably encouraged the subjects to apply high levels of GF in the beginning in order to face stress, excitement or uncertainty. Cutaneous feedback is also crucial to the generation of the static GF as well as for the adjustments of GF modulation and calibration of forward models through an estimation of skin–object coefficient of friction (Johansson and Westling, 1984; Westling and Johansson, 1984; Augurelle et al., 2003b; Witney et al., 2004). Concerning the modulation of GF, we showed that LF is continuously predicted in order to generate the grip modulation, which must take into account the estimation of the mass and frictional properties of the held load in addition to an estimation of the arm acceleration. In this framework, the modulation of the increment may differ depending on the nature of the movement and its specific underlying mechanism (rhythmic, discrete, reflex, etc.). Our data suggest that the static component and the increment are additively combined to produce the grip motor command.

Further studies should investigate the neural circuitry of both components. It is tempting to speculate that GFs based on cutaneous feedback and subject to volitional control would result from high-level cortical control, including the primary sensorimotor cortex, ventral premotor cortex, supplementary and cingulated motor area, and inferior parietal cortices (Kuhtz-Buschbeck et al., 2001), whereas the increments, which are unconsciously adapted and highly automated, would result from lower level control, including the cerebellum (Miall et al., 1993; Kawato et al., 2003; Nowak et al., 2007). Indeed, accumulating evidence in the literature suggests that this region could store forward models underlying the control of precision grip.

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