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The effects of a change in gravity on the dynamics of prehension

Received: 15 March 2002 / Accepted: 22 October 2002 / Published online: 15 November 2002
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Abstract Investigating cyclic vertical arm movements with an instrumented hand-held load in an airplane undergoing parabolic flight profiles allowed us to determine how humans modulate their grip force when the gravitational and the inertial components of the load force are varied independently. Eight subjects participated in this study; four had already experienced parabolic flights and four had not. The subjects were asked to move the load up and down continuously at three different gravitational conditions (1 *g*, 1.8 *g*, and 0 *g*). At 1 *g*, the grip force precisely anticipated the fluctuations in the load force, which was maximum at the bottom of the object trajectory and minimum at the top. When gravity changed, the temporal coupling between grip force and load force persisted for all subjects from the first parabola. At 0 *g*, the grip force was accurately adjusted to the two load force peaks occurring at the two opposite extremes of the trajectory due to the absence of weight. While the experienced subjects exerted a grip force appropriate to a new combination of weight and inertia since their first trial, the inexperienced subjects dramatically increased their grip when faced with either high or low force levels for the first time. Then they progressively released their grip until a continuous grip-load force relationship with regard to 1 *g* was established after the fifth parabola. We suggest that a central representation of the new gravitational field was rapidly acquired through the incoming vestibular and somatic sensory information.

Keywords Grip-load force coupling · Microgravity · Internal model · Arm movement

Introduction

During tool handling, grasp stability is ensured by a close coordination between the grip force (GF) applied normal to the object's surface and the load force (LF) acting tangentially on the fingertips. When an object is moved, the grip force is automatically modulated in parallel to fluctuations in the load force resulting from the object weight (i.e., the product of the mass and the gravity) and the inertial object accelerations due to the arm movements (Flanagan and Wing 1995). Moreover, the grip force is always somewhat greater by a safety margin than the minimal force required to prevent slippage (the 'slip force') at any load according to the skin-object friction (Johansson and Westling 1984). The close temporal coupling between the grip force and load force is independent of the grip and mode of object transport (Flanagan and Tresilian 1994), the movement frequency, and the texture of the gripping surface (Flanagan and Wing 1993a, 1995).

The synchronous GF-LF modulation suggests that the grip force controller within the central nervous system (CNS) is provided with the load consequences of the arm movements before actual feedback from the cutaneous receptors is available (Flanagan and Wing 1993b). It is hypothesized that, with acquired experience, the CNS builds and uses internal models that capture the dynamic properties of the arm, objects (texture and weight) and external environments (e.g., gravity) in order to predict the upcoming load force (Flanagan and Tresilian 1994; Flanagan and Wing 1997; for review see Flanagan and Johansson 2002). Previous experiments argue in favor of a central representation of the gravity both as an orientation reference (vertical direction) and as mechanical load acting on the center of mass of the limbs (Papaxanthis et al. 1998; Pozzo et al. 1998). According to this theory, the consequences of the gravitational acceleration both on the load force and on the planned movement (McIntyre et al. 1998) must be taken into account in computing an adequate grip force.

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Preliminary evidence that grip force control mechanisms are able to cope with hyper- and micro-gravity during parabolic flight has been shown by Hermsdörfer et al. (1999). The grip force exerted against an object held stationary throughout a whole parabola was scaled to the weight of the object under normal and high gravity conditions. During weightlessness, although no force was necessary to stabilize the object, the subjects used a low grip force that could be seen as a pure safety margin in the event of a possible perturbation. Moreover, the grip force was also adjusted adequately in anticipation of the load fluctuations during horizontal and vertical arm movements performed during parabolic flights (Hermsdörfer et al. 2000). However, the time-course of adaptation to a new gravitational environment could not be tested because the two subjects had already experienced weightlessness before beginning the experiments.

In the present study, the grip force exerted on a hand-held object during cyclic vertical arm movements was examined at 1 g and at different simulated gravity fields (0 g and 1.8 g) attained during parabolic flight maneuvers of an airplane. A modification of the object's weight was obtained without modification of its mass, and thus its inertia was constant across the different gravitational conditions. By contrast, on earth, the weight of an object cannot be changed without changing its inertial properties. Therefore, the parabolic flight environment offered us the unique possibility to study the effect of a change in gravity on GF–LF coupling while maintaining the inertial component of the load unchanged. Eight subjects were asked to perform cyclic vertical arm movements while holding an instrumented load during ten parabolic flight maneuvers. Half of the subjects had never experienced parabolic flights. We hypothesized that the GF–LF coupling would be progressively adapted to a new gravity level in the naive subjects, whereas it would be appropriately adjusted in the experienced subjects from the first time that they executed the task in the aircraft.

Methods and materials

Subjects and experimental procedure

Eight adult subjects (six men and two women) participated in the study. They were examined in the Belgian Center for Aerospace Medicine in order to qualify for parabolic flights (NASA class III medical examination). No subject reported sensory or motor deficits; all but one were right-handed. Four subjects had no previous experience in microgravity (the non-experienced subjects, NES) whereas the other four had more than 100 parabolas each to their credit (the experienced subjects, ES). In order to prevent motion sickness, the novice subjects had taken medication (scopolamine). All participants gave their informed consent to participate in the study, and the procedures were approved both by the European Space Agency (ESA) safety committee and by the local ethics committee.

The grip–load force coupling was measured during cyclic vertical arm movements with a 164-mm high, 250-g instrumented hand-held object (Fig. 1). It was equipped with strain gauge transducers to measure the GF applied perpendicularly by the fingertips on two parallel brass disks, 30 mm in diameter and 30 mm

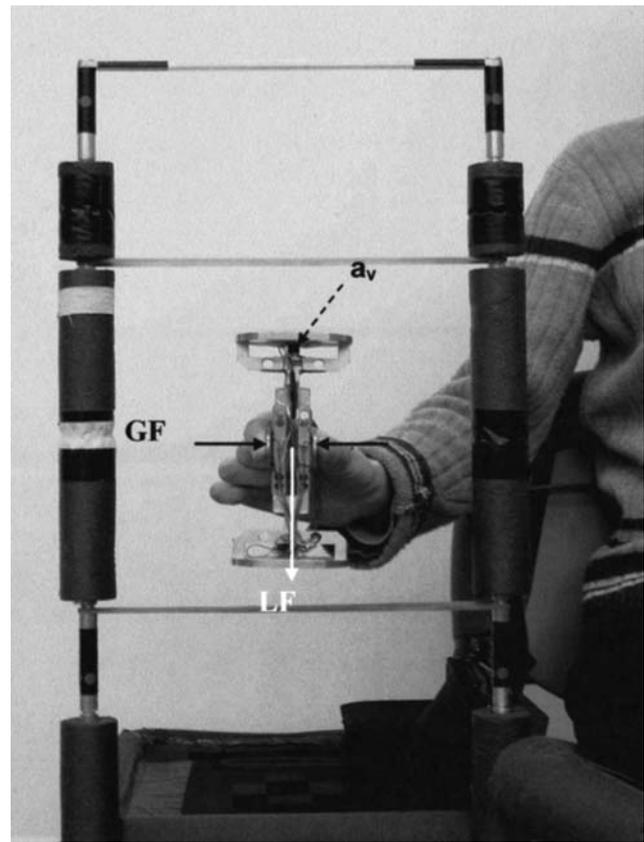


Fig. 1 Frontal view of the experimental setup. The subject moved the manipulandum up and down between the two elastic bands 20 cm apart. The grip force (GF, *black arrows*) was measured by strain gauges, the load force (LF, *white arrow*) was calculated from the vertical object acceleration measured by an accelerometer (a_v , *dashed arrow*)

apart, that served as the grasping surfaces. An accelerometer mounted on the top of the object recorded the acceleration along its vertical axis (a_v). The vertical LF resulting from the gravitational and the acceleration-dependent inertial force was calculated as the product of the mass and the vertical acceleration of the object, as measured by the accelerometer. The object center of mass was located midway between the grip surfaces to prevent rotational torque.

Each subject was seated in a chair with an attached seat belt. The right shoulder was abducted at about 30°, the elbow was flexed at 90° and the hand was resting on a horizontal surface beside the subject. At a signal from the experimenter, the instrumented object was grasped between the thumb and index finger of the right hand. The subjects were instructed to perform cyclic vertical arm movements at a frequency of approximately 1 Hz, aided by a metronome. The amplitude of the oscillations was maintained by lightly constraining the movement within two parallel rubber bands about 20 cm apart (Fig. 1), which served to guide the endpoints of the arm displacement. The upper limb displacement was performed by the subject using unconstrained shoulder and elbow movements. The subjects were required to maintain the vertical orientation of the object (i.e., no tilting) by using visual feedback. No specific instructions were provided regarding the grip force.

The experiments were first carried out at 1 g on the ground before the flight in order to familiarize the subjects with the task. Then the experiments were performed at 0 g, 1 g and 1.8 g during the parabolic flights. Each subject performed the task during ten trials of 30 s duration on earth and during ten parabolas of 120 s in the aircraft.

The flights originated in Bordeaux France using an Airbus A300 "ZEROg" aircraft. The parabolic flight profiles modified the apparent gravitational acceleration within the aircraft. Each profile started from level flight at 1 *g* and consisted of a 20-s 1.8 *g* pull-up phase during which the aircraft climbed from 6000 to 8500 m, followed by a 20-s microgravity phase (0 *g*) obtained over the top of the trajectory, followed by a 20-s symmetrical 1.8 *g* pull-out phase, which brought the aircraft back to steady horizontal flight at the original altitude; there was approximately 2 min between parabolas. These experiments were performed during four flights of 30 parabolas during the 26th and 27th ESA parabolic flight campaigns. Each flight was organized as six groups of five parabolas with a pause of several minutes between each group. A three-axis accelerometer was fixed on the floor of the aircraft to record the aircraft acceleration along the *z*-axis (normal to the floor of the airplane), the *y*-axis (lateral to the long axis of the airplane), and the *x*-axis (along the fore-aft axis of the airplane). The simulated gravity was recorded along the *z*-axis.

In the aircraft, the subjects grasped the instrumented object and started the cyclic movement during the 1 *g* phase of the flight, approximately 30 s before the start of the pull-up phase. The movement was performed throughout the whole parabola and for 30 s after the restoration of the 1-*g* condition. Thus, the grip force and object acceleration were recorded continuously for 120 s while the simulated gravity went successively from 1 *g*, to 1.8 *g*, 0 *g*, 1.8 *g*, and back to 1 *g*. Two subjects were examined per flight. On each flight, the NES performed the experiment on the first 15 parabolas and the ES was tested during the last 15 parabolas. In this way, the NES experienced microgravity for the first time when they performed the task during the first parabola. During the first 15 parabolas of each flight, the ES were not specifically involved in a manipulation task. In this study, we only analyzed the first ten trials performed by each subject.

In addition, the coefficient of static friction between the fingertips and the grip surfaces was measured, for each subject, by five lift-and-drop maneuvers performed at 1 *g* before and after each group of five parabolas. The subject was instructed to lift and hold the instrumented object stationary, then gradually release their grip until the object slipped due to the acceleration of gravity. The measure of friction was calculated as half the LF/GF ratio at onset of the slip, as detected by the accelerometer (Johansson and Westling 1984). The coefficient of friction for each trace was computed as the average of the ten lift-and-drop measurements. By assuming that the coefficient of friction was independent of the LF fluctuations during the cyclic arm movement, a theoretical slip force could be calculated as half the ratio between the LF and the coefficient of friction. When the GF dropped below the slip force, the object slipped out of the fingers. The safety margin was defined as the difference between the employed GF/LF ratio and the theoretical slip force/load force ratio. Unpublished results have shown that the coefficient of friction tends to be higher for small loads less than 200 g, and consequently the theoretical slip force was presumably overestimated at 0 *g*.

Data processing and analysis

The signals from the strain gauges and accelerometers were digitized online at 200 Hz with a 12-bit PC-LPM-16PNP National Instruments analog-to-digital converter in a personal computer. After analog-to-digital conversion, the signals were further low-pass filtered with a fourth-order, zero phase-lag Butterworth filter having a cut-off frequency of 15 Hz.

The analysis was performed during periods of constant aircraft and object accelerations. In the ground experiments, a few arm movement cycles were necessary to attain the required 1 Hz frequency and 20 cm movement amplitude, so the load force and amplitude were calculated over the last 15 cycles of the 20 obtained for each trial. The dynamics of the precision grip observed during this period were used as the control data. During the parabolic flight experiments, only six cycles could be selected as representing the

steady state of each gravitational condition for all the parabolas, when both the aircraft and the object accelerations were stable.

The analysis of the force measurements was performed cycle by cycle. The cycles were delimited between the load force maxima. For each cycle the following parameters were analyzed: the 'movement frequency' (Hz) defined as the frequency of the peak LF, the 'amplitude of LF' (N) defined as the difference between the maximum and the minimum of the load force, the 'mean GF' (N) defined as the mean level of the grip force modulation, the 'phase shift' (ms) defined as the delay between corresponding peaks of the GF and the LF (negative phase shift indicating that the GF peak preceded the LF peak), and the 'safety margin' calculated when the load force reached a maximum.

Statistical analysis

A two-way analysis of variance for repeated measures was performed on the dynamic parameters to test for the differences between the ten repeated trials (factor 1) in each gravitational condition and to test for the differences between the gravitational conditions (factor 2). The interaction between the factors was also examined. Tukey's pair-wise multiple comparison procedure was used to determine which treatments were significantly different. These analyses were performed separately for each experimental group (NES and ES). All the statistical analyses were carried out with SigmaStat 2.03 (SPSS Inc., Chicago, IL, USA).

Results

The GF-LF coupling in the different gravitational environments attained during parabolic flight is shown in Fig. 2. These signals were obtained during the last trial of an inexperienced subject. In this typical parabola, the aircraft's vertical acceleration was $9.55 \pm 0.26 \text{ m/s}^2$ at 1 *g*,

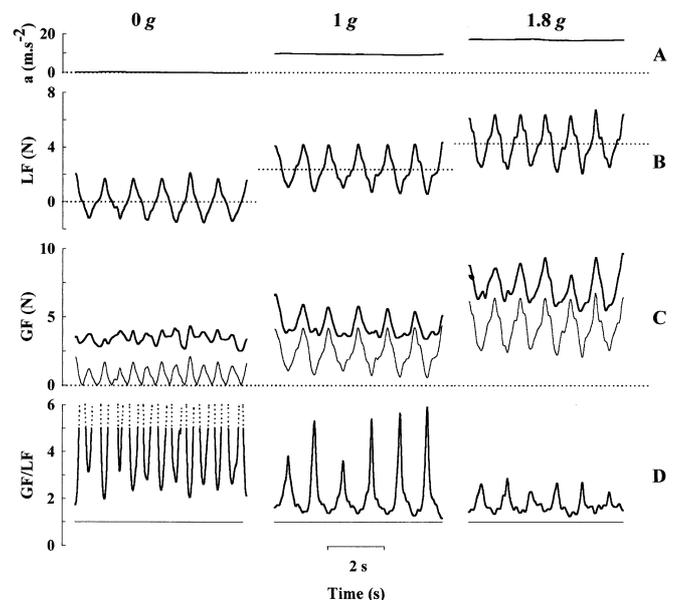


Fig. 2A–D Records of six contiguous cycles obtained during the stable period in each gravitational phase of the last trial of a non-experienced subject (NES). **A** The gravity level, **B** the load force (LF), **C** the grip force (GF, *thick line*) and the slip force (*thin line*), and **D** the GF/LF ratio (*thick line*) and the slip ratio (*thin line*). The difference between the GF/LF ratio and the slip ratio reflects the safety margin. The friction coefficient was 0.5

$17.07 \pm 0.24 \text{ m/s}^2$ at 1.8 g , and $0.11 \pm 0.17 \text{ m/s}^2$ at 0 g (Fig. 2A). The LF oscillated around the object weights of 2.5, 4.5 and 0 N at 1, 1.8 and 0 g , respectively (dotted lines in Fig. 2B). In the presence of gravity, the load force reached a maximum at the bottom of the trajectory where the gravitational and the object accelerations were acting in the same direction. The minimum load force occurred at the top of the trajectory, where the object acceleration was opposed to that of gravity. At 1 and 1.8 g , the load force was always positive because the downward acceleration of the object required by the frequency and amplitude of the movement was always less than the acceleration due to gravity. In the microgravity condition, the object had to be accelerated both upward and downward because gravity no longer accelerated the object downwards, and thus the load force was positive in the lower part and negative in the upper part of the trajectory. The amplitude of the load force fluctuations was fairly similar across gravitational environments (about 3 N), suggesting that the NES in this trial was able to maintain the constraints of the imposed movement (1 Hz and 20 cm). In each gravitational phase, the grip force (thick line in Fig. 2C) was increased and decreased when the load force rose and fell, respectively. At 0 g , the grip force was increased again at the top of the trajectory to prevent the object from slipping between the fingers when the object was accelerated downwards. The grip force was always greater than the slip force (thin line in Fig. 2C), indicating that no slippage occurred. Moreover, it was interesting to note that the mean level of the grip force modulation was great enough to prevent slip for any load, suggesting that the modulation was not obligatory. Peaks of load force were always precisely synchronized with a similar peak in the grip force so that the GF/LF ratio was minimum and highly reproducible at these times (Fig. 2D). In contrast, when the load force was minimum, the GF/LF ratio was less constant and reached its maximum because the grip was not completely released or was even further increased.

The adaptation of the GF–LF relationships in each gravitational condition is shown in Fig. 3 across four representative trials. The left panels display typical traces recorded from an experienced subject (ES), and the right panels are from a non-experienced subject (NES). Both subjects modulated their grip force in phase with the load force fluctuations induced by the object acceleration in each gravitational condition, starting from their first trial. The ES used the same GF–LF relationship from the first to their last trial in the aircraft. A nearly continuous grip–load force relationship was established across the different gravitational conditions (Fig. 3, ES). Note that the level of the GF modulation at 0 g remained slightly above that observed at 1 g . Conversely, when faced with a new gravitational field for the first time, the NES used a dramatically increased grip force at 0 and 1.8 g (Fig. 3, NES). By decreasing both the level and the variance of grip force throughout the ten trials, the NES progressively tends toward a single GF–LF relationship across the

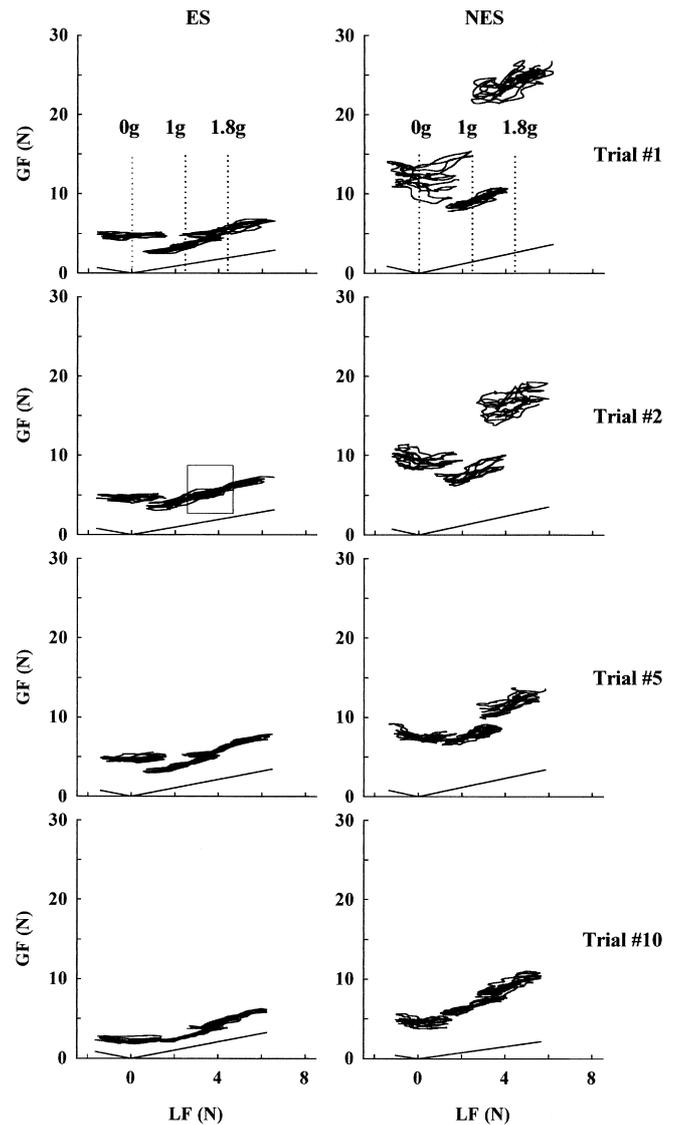
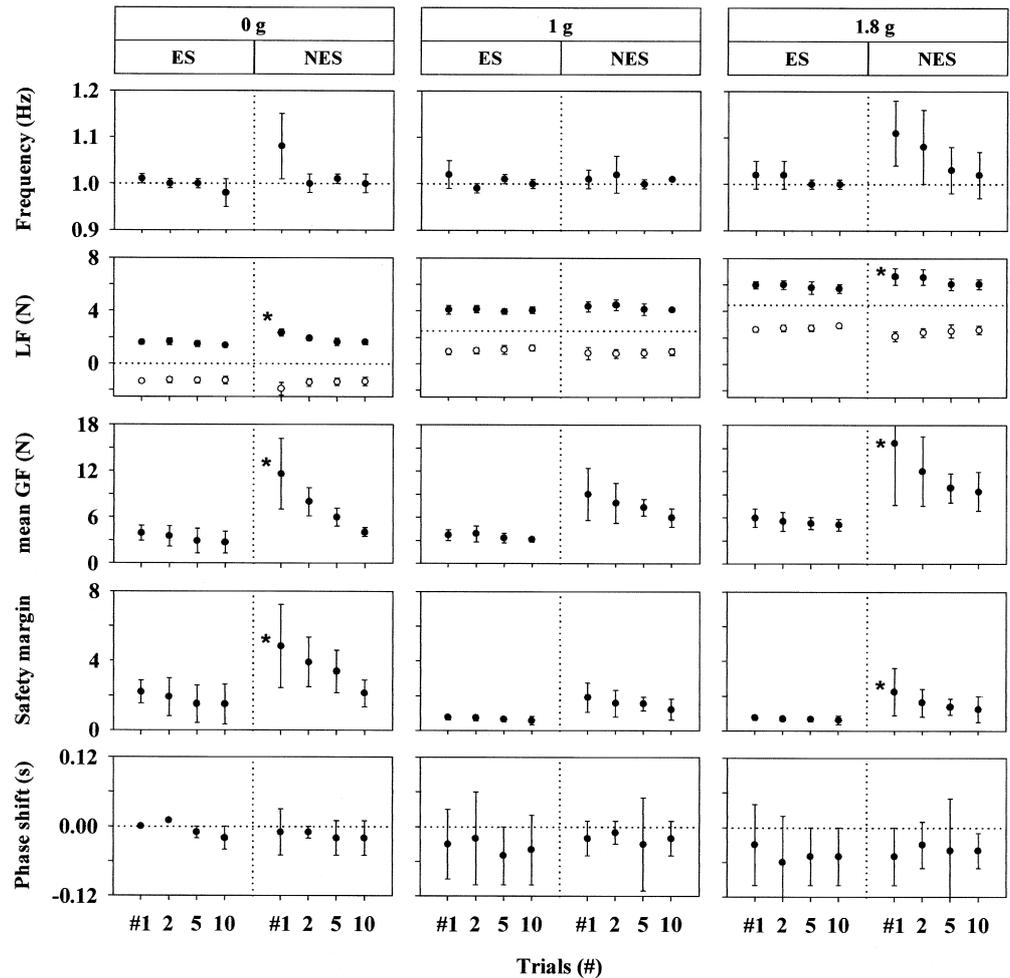


Fig. 3 The grip force (GF)–load force (LF) relationship measured during six arm cycles under three gravity levels during the first, second, fifth and tenth trials in an experienced subject (ES, left column) and a non-experienced subject (NES, right column). The dotted lines in the upper panels represent the object weight in each gravitational level. The slip force is presented by a straight line according to the friction coefficient of each trace. The inset in the left column shows the overlap between the load force ranges observed at 1 g and at 1.8 g . Trial 1 of the NES and the ES corresponded to the first and the fifteenth parabolic maneuvers of the aircraft, respectively

gravitational environments. This process started at the second trial and was achieved after the fifth.

Figure 3 (inset) also shows that same load force ranges were obtained by varying separately the acceleration of gravity and the acceleration of the object. We observed an overlap in the load force at a low gravitational acceleration (i.e., at 1 g) with a high object acceleration (i.e., at the bottom of the arm trajectory) and in a high gravitational acceleration (i.e., at 1.8 g) with a low object acceleration (i.e., at the top of the arm trajectory). Even

Fig. 4 The means and standard deviations of the dynamic parameters for first, second, fifth and tenth trials at 0, 1, 1.8 g for the four subjects with previous parabolic flight experience (ES) and the four subjects who experienced microgravity for the first time (NES). The following parameters are shown: the frequency, the minimum (*open circles*) and the maximum (*filled circles*) of the load force (LF), the mean level of the grip force (GF), the safety margin when the load is maximum, and the phase shift between the corresponding maxima of GF and LF. A significant effect of repetition between parabolas is marked by an *asterisk*. Trial 1 of the NES and the ES corresponded to the first and the fifteenth parabolic maneuvers of the aircraft, respectively



though the upper limb was in different simulated gravitational fields, the same coupling between the grip force and load force was observed after the information had been integrated, i.e., from the first trial for the ES and after the fifth trial for the NES.

Figure 4 presents the dynamic parameters of the ES and NES in each gravitational condition for four representative trials. Consider first the differences observed between the ten repeated trials in each gravitational condition within both groups of subjects. All the parameters of the ES were stable from the first trial in each gravitational condition. With NES, some adjustments occurred across the ten trials. Two-way analysis of variance for repeated measures revealed a significant interaction between the effects of repeated trials and the gravitational condition. Indeed, at 1 g on earth and in the aircraft, all the parameters were stable from the first parabola. By contrast, during the first trial at 0 and 1.8 g, the NES were generating a larger amplitude of load force ($F=1.825$, $P=0.022$), a higher level of grip force ($F=1.877$, $P=0.017$) and a greater safety margin ($F=3.95$, $P=0.002$). In the subsequent trials, these parameters progressively decreased and no further significant evolution was seen after the fifth trial. Note that although

the difference was not significant ($F=1.757$, $P>0.05$), the NES movement frequency also tended to decrease across trials at 0 and 1.8 g (Fig. 4). The phase shift between corresponding peaks of grip force and load force was constant across the ten repeated trials within each gravity level ($F=0.766$, $P>0.05$). On average, grip force peaks occurred before the load force peaks.

Consider now the differences observed between gravitational conditions when all the trials are taken into account. Firstly, the parameters of the grip-load force coordination were not significantly different when the subject performed the task at 1 g on earth or in the aircraft. A change of gravity (to 1.8 and 0 g) induced significant effects on the mean grip force (for NES $F=9.692$, $P=0.004$; for ES $F=11.941$, $P=0.002$) and safety margin (NES $F=18.78$, $P<0.001$; ES $F=5.635$, $P=0.02$). The post hoc analysis revealed that, in both groups (ES and NES), the mean grip force was identical in microgravity and in the 1 g environment but it was significantly increased in hypergravity (NES $P=0.006$; ES $P=0.007$). Consequently, the safety margin was the same in 1 g and hypergravity but it was significantly increased in 0 g (NES $P<0.001$; ES $P=0.03$). This suggests that the subjects adequately increased their GF in hypergravity

in order to maintain a safety margin equivalent to that exerted at 1 *g*. By contrast in microgravity, they were unable to decrease their GF below the level exerted in 1 *g* and the safety margin was increased.

Moreover, a change of gravity did not significantly modify the LF amplitude or the frequency of the movement, except for the first trial of the NES as seen above. The phase shift between the two force signals was not significantly different in altered gravity fields compared with those at 1 *g*.

Discussion

The GF-LF co-ordination was studied during cyclic vertical arm movements using a hand-held instrumented load across different gravitational conditions (0, 1, 1.8 *g*) induced by parabolic flight maneuvers. The transitional phases between gravitational conditions were not analyzed because the large changes in the aircraft accelerations occurring at these times were unpredictable, and would have generated inconsistent grip force reactions. The results showed that the GF was modulated in parallel with the LF fluctuations due to the arm movements, regardless of the gravity condition. In new gravity fields, the phase shift between the GF and the LF was equivalent to that observed in 1 *g*, even on the first trials of the NES. By contrast, the level of the grip force modulation was dependent upon the gravity level, and its adjustment seemed to require some adaptation for the NES. The experienced subjects (ES) adjusted the level of the grip force modulation to the new gravitational field as soon as they executed the task in the aircraft. The non-experienced subjects (NES) had some difficulty in maintaining the imposed movement and applied unnecessarily high safety margins during their first trials at 0 and 1.8 *g*. In the subsequent trials, they progressively decreased their grip force and no further evolution in the GF-LF coupling was seen after the fifth trial. In both groups of subjects, a continuous GF-LF relationship tended to be established across the different gravitational conditions although the safety margin in microgravity remained slightly above the level observed at 1 and 1.8 *g*.

In the first part of this discussion, we will consider a possible mechanism involved in the temporal coupling between GF and LF. In altered gravity conditions, the modulation of grip force with the load fluctuations was observed from the first trial. As already observed by Hermsdörfer et al. (2000), the tight coupling between the peaks of the two forces was conserved with the same phase shift as on earth (Flanagan and Wing 1995). These results suggest that the anticipatory mechanism predicting the consequences of the arm accelerations on the load force acting on the fingers is a well-tuned process that is available even in altered gravity fields. An accurate prediction of the object acceleration enables the subjects to anticipate the time at which the LF is maximal. As a result the GF is modulated in phase with the LF fluctuations whatever the gravity condition.

While the temporal coupling of the GF-LF relationship was conserved in altered gravitational fields, the mean level of grip force had to be adjusted to the gravitational component of the LF. Evidence for progressive adaptation to a new gravity level was observed in subjects with no previous experience in parabolic flights. They dramatically increased the safety margin in the first trial, both in microgravity and in hypergravity. Different interpretations of this observation can be considered. Firstly, the alterations of the limb proprioception due to the modification of the muscle spindle gain in altered gravity condition could result in altered judgment of object weight and mass (Lackner and DiZio 2000). However, the problem of mass discrimination previously observed by Ross et al. (1984, 1986) could be ruled out because in our protocol the mass could be estimated during the lift of the object during the 1 *g* period preceding the beginning of the parabola. Moreover, the information on the LF is mainly provided by the mechanoreceptors of the skin (Johansson and Westling 1991), which have not been previously reported to be affected by a change of gravity. Secondly, all novice subjects took scopolamine for motion sickness. Scopolamine may reduce sweating, which can decrease skin friction and subsequently would require a greater grip force to prevent an object from slipping. However, the mean level of NES grip force used at 1 *g* in the aircraft (with scopolamine) or on earth (without scopolamine) was equivalent, suggesting that the medication did not perturb the grip-load modulation. Thirdly and most likely, the parabolic flight experience was exciting, distracting and frightening to most novices. Therefore, the stress induced by the unusual and unexpected force circumstances was likely to contribute to the increased grip force level in order to provide a larger safety margin for the NES. Johansson et al. (1992) and Blakemore et al. (1998) have observed a similar counter strategy when manipulating an 'active' object that produced unpredictable load force. The baseline of the grip force was increased to prevent slip that might occur following a sudden increase of load.

A direct indicator of increasing subject confidence in the new gravitational surroundings was the progressive decrease of the safety margin. For the NES, a maximum of five parabolas was necessary to incorporate the effects of gravity changes into the CNS program that controlled grip forces. While no significant change in the parameters of the grip-load force coupling was observed during the subsequent trials, a decreasing trend persisted out to the tenth trial. These results suggest that after a few repetitions the NES have acquired a better internal representation of the new gravitational field through the incoming vestibular and somatic sensory information. This supports the results of Papaxanthis et al. (1998), which provided evidence that gravity is centrally represented in an anticipatory fashion as a driving force during vertical arm movement planning. This also confirms the hypothesis that adaptation of the human motor system to new force environments generating changes in the

dynamics of the arm occurs rapidly over a limited number of trials (Lackner and DiZio 1994).

Evidence of such internal representation of the gravity can be seen in the results obtained for the experienced subjects. Subjects with previous participation in parabolic flights (long-term experience) and passively submitted to 15 parabolas before the experiment (short-term experience) adequately adapted the mean grip force to the new gravity fields when performing the task for the first time in these environments. This supports the hypothesis of Flanagan et al. (1999) that the brain maintains internal models of the kinematics and dynamics of different environments and has some ability to combine and decompose them as called for by the situation. Nevertheless, as the ES were only tested after 15 parabolas, it is unknown whether they would also exhibit an adaptation during the first parabola of the aircraft. The present results do not allow us to differentiate the effects of long- or short-term parabolic flight experience on the dynamics of prehension. Yet, it is obvious that the ES subjects took advantage of their experience to manipulate the objects with an adapted safety margin from their first trial.

The fast adaptation to different gravity conditions and the ability to maintain the gravity representation in internal CNS models probably explain why Hermsdörfer et al. (2000) did not observe learning in a similar experiment. In their study, only two subjects were examined, the first one had a previous parabolic flight experience 4 years earlier, and the second one was a novice. Both subjects participated in the two flights and the novice subject was tested on the second flight. During the five first parabolas, the subject had to maintain an object stationary across the different gravity phases. The cyclic vertical arm movements with a hand-held load were only performed during the three subsequent parabolas. Consequently, neither of the two subjects were really naïve with respect to micro- and hyper-gravity before starting the oscillatory task that was similar to our experiment. Actually, simple passive exposure to parabolic flight maneuvers leads to rapid perceptual adaptation in terms of magnitudes of apparent force experienced (Lackner and Graybiel 1982).

We have also observed that once the subjects were familiar with new gravity conditions they tended to establish a single GF-LF relationship across the gravitational environments. Ideally, the subjects should increase and decrease their GF at 1.8 g and 0 g, respectively, in order to keep the same safety margin as in the 1-g condition. Our results showed that even with the ES after ten parabolas, the GF in microgravity remained the same as in 1 g, inducing a greater safety margin. We cannot rule out the possibility that further adaptation would occur on longer periods of microgravity or it may be that the subjects did not want to reduce their GF below the level experienced on earth.

Previous studies have shown that a change in gravity perturbed the arm movement kinematics in target pointing, manual tracking (for review see Bock 1998) and arm movement control (Fisk et al. 1993). In our study, despite

an imposed amplitude (20 cm) and frequency (1 Hz) of movement, we have observed an increase in the load force amplitude when subjects were faced with a new gravity environment for the first time. Since the frequency was not perturbed, this suggests that the peak-to-peak object acceleration was modified by a change of the arm trajectory. Further study will be performed to investigate this hypothesis using a three-dimensional movement tracking system.

Acknowledgements The technical assistance of R. Lemaire for the design of the instrumented grip object is gratefully acknowledged. The authors are grateful to Dr Norman Heglund for reviewing an earlier version of the manuscript. This research was supported by a grant to Prodex, OSTC (Belgian Federal Office for Scientific, Technical and Cultural Affairs).

References

- Blakemore SJ, Goodbody SJ, Wolpert DM (1998) Predicting the consequences of our own actions: the role of sensorimotor context estimation. *J Neurosci* 18:7511–7518
- Bock O (1998) Problems of sensorimotor coordination in weightlessness. *Brain Res Brain Res Rev* 28:155–160
- Fisk J, Lackner JR, DiZio P (1993) Gravitoinertial force level influences arm movement control. *J Neurophysiol* 69:504–511
- Flanagan JR, Johansson RS (2002) Hand Movements. In: Ramshandran VS (ed) *Encyclopedia of the human brain*, vol 2. Academic Press, San Diego, pp 399–414
- Flanagan JR, Tresilian JR (1994) Grip-load force coupling: a general control strategy for transporting objects. *J Exp Psychol Hum Percept Perform* 20:944–957
- Flanagan JR, Tresilian J, Wing AM (1993a) Coupling of grip force and load force during arm movements with grasped objects. *Neurosci Lett* 152:53–56
- Flanagan JR, Wing AM (1993b) Modulation of grip force with load force during point-to-point arm movements. *Exp Brain Res* 95:131–143
- Flanagan JR, Wing AM (1995) The stability of precision grip forces during cyclic arm movements with a hand-held load. *Exp Brain Res* 105:455–464
- Flanagan JR, Wing AM (1997) The role of internal models in motion planning and control: evidence from grip force adjustments during movements of hand-held loads. *J Neurosci* 17:1519–1528
- Flanagan JR, Nakano E, Imamizu H, Osu R, Yoshioka T, Kawato M (1999) Composition and decomposition of internal models in motor learning under altered kinematic and dynamic environments. *J Neurosci* (online) 19:RC34
- Hermsdörfer J, Marquardt C, Philipp J, Zierdt A, Nowak D, Glasauer S, Mai N (1999) Grip forces exerted against stationary held objects during gravity changes. *Exp Brain Res* 126:205–214
- Hermsdörfer J, Marquardt C, Philipp J, Zierdt A, Nowak D, Glasauer S, Mai N (2000) Moving weightless objects. Grip force control during microgravity. *Exp Brain Res* 132:52–64
- Johansson RS, Westling G (1984) Roles of glabrous skin receptors and sensorimotor memory in automatic control of precision grip when lifting rougher or more slippery objects. *Exp Brain Res* 56:550–564
- Johansson R S, Westling G (1991) Afferent signals during manipulative tasks in man. Afferent signals during manipulative tasks in man. In: Franzen O, Westman J (eds) *Somatosensory mechanisms*. Macmillan Press, London, pp 25–48
- Johansson RS, Riso R, Häger C, Bäckström L (1992) Somatosensory control of precision grip during unpredictable pulling

- loads. 1. Changes in load force amplitude. *Exp Brain Res* 89:181–191
- Lackner JR, DiZio P (1994) Rapid adaptation to Coriolis force perturbations of arm trajectory. *J Neurophysiol* 72:299–313
- Lackner JR, DiZio P (2000) Human orientation and movement control in weightless and artificial gravity environments. *Exp Brain Res* 130:2–26
- Lackner JR, Graybiel A (1982) Rapid perceptual adaptation to high gravito-inertial force levels: evidence for context-specific adaptation. *Aviat Space Environ Med* 53:766–769
- McIntyre J, Berthoz A, Lacquaniti F (1998) Reference frames and internal models for visuo-manual coordination: what can we learn from microgravity experiments? *Brain Res Brain Res Rev* 28:143–154
- Papaxanthis C, Pozzo T, Popov KE, McIntyre J (1998) Hand trajectories of vertical arm movements in one-G and zero-G environments. Evidence for a central representation of gravitational force. *Exp Brain Res* 120:496–502
- Pozzo T, Papaxanthis C, Stapley P, Berthoz A (1998) The sensorimotor and cognitive integration of gravity. *Brain Res Brain Res Rev* 28:92–101
- Ross H, Brodie E, Benson A (1984) Mass discrimination during prolonged weightlessness. *Science* 225:219–221
- Ross HE, Brodie EE, Benson AJ (1986) Mass-discrimination in weightlessness and readaptation to earth's gravity. *Exp Brain Res* 64:358–366