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White, Olivier ; McIntyre, Joseph ; Augurelle, Anne-Sophie ; Thonnard, Jean-Louis

ABSTRACT

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RESEARCH ARTICLE

Olivier White · Joseph McIntyre
Anne-Sophie Augurelle · Jean-Louis Thonnard

Do novel gravitational environments alter the grip-force/load-force coupling at the fingertips?

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Abstract In this experiment we examined the coupling between grip force and load force observed during cyclic vertical arm movements with a hand-held object, performed in different gravitational environments. Six subjects highly experienced in parabolic flight participated in this study. They had to continuously move a cylindrical object up and down in the different gravity fields (1*g*, 1.8*g* and 0*g*) induced by parabolic flights. The imposed movement frequency was 1 Hz, the object mass was either 200 or 400 g, the amplitude of movement was either 20 or 40 cm and an additional mass of 200 g could be wound around the forearm. Each subject performed the task during 15 consecutive parabolas. The coordination between the grip force normal to the surface and the tangential load force was examined in nine loading conditions. We observed that the same normal grip force was used for equivalent loads generated by changes of mass, gravity or acceleration despite the fact that these loads required different motor commands to move the arm. Moreover, our results suggest that the gravitational and inertial components of the load are treated adequately and independently by the internal models used to predictively control the required grip force. These results indicate that the forward internal models used to control precision grip take into account the dynamic characteristics of the upper limb, the object and the environment to predict the object's acceleration and, in turn, the load force acting at the fingertips.

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

O. White · A.-S. Augurelle · J.-L. Thonnard (✉)
Unité de réadaptation et de Médecine Physique,
Université Catholique de Louvain, 1200 Brussels, Belgium
E-mail: thonnard@read.ucl.ac.be
Tel.: +32-2-764-53-67
Fax: +32-2-764-53-60

J. McIntyre
Laboratoire de Physiologie de la Perception et de l'Action,
C.N.R.S.–Collège de France, 75005 Paris, France

Introduction

To lift an object aloft, the grip force applied normal to the object's sides (hereafter referred to as the "normal grip force") must be sufficient to counteract both the gravitational and the inertial components of the tangential load force acting on the fingertips (Johansson and Westling 1984). A tight temporal coupling between the normal grip force and the tangential load force has been documented in a large variety of tasks engaging different kinds of objects, grips, loads or modes of transport (Johansson and Westling 1984; Flanagan and Tresilian 1994; Jenmalm and Johansson 1997; Flanagan et al. 1999a, 1999b; Gysin et al. 2003). All studies to date seem to confirm that adjustments of the normal grip force anticipate tangential load changes when the movement is self-produced, provided that the physical properties of the object are predictable (Flanagan and Wing 1993, 1995). There is increasing evidence in the literature that the CNS acquires neural mechanisms called "internal models" that can simulate the behavior of our body and of the environment (Wolpert et al. 1995; McIntyre et al. 2001; Flanagan and Johansson 2002). The principle is that during object manipulation, these internal models would predict future accelerations of the arm by using a copy of the motor command that produces the intended arm movement (Flanagan and Wing 1997; Kawato 1999). From this prediction, and from visual or haptic information about the object's weight, the total tangential load force can be estimated and an appropriate normal grip force can be programmed in a feedforward manner. The loads experienced at the hand could be thus derived from the arm motor commands. Flanagan and Wing (1997) showed that normal grip force was modulated in phase with, and thus anticipated, the tangential load when moving not only inertial but also viscous and elastic loads. These results suggest that the commands for normal grip force are not simplistically linked to the commands for arm movement but are, instead, based on an internal model of the motor apparatus and external load.

In a previous study in parabolic flight, we measured how subjects adjusted the normal grip force to changes in gravity that modified the relationship between arm movement and load force (Augurelle et al. 2003). We observed that after adaptation (five trials for novice subjects) the normal grip force increased adequately in hypergravity (1.8*g*) in order to maintain the same safety margin as on the ground, even though the arm was nearly two times heavier. Hermsdorfer et al. (1999, 2000) showed that the predictive coupling between grip and load forces persisted even during transitions between gravity levels induced by parabolic flights.

In the current experiment we took this study a step further by asking two questions. First, by modifying gravitational and inertial components of the load acting on the arm, it was possible to generate different arm motor commands to accomplish the same movement. The weight of the arm was altered either by placing an external mass (200 g) around the wrist or by moving the arm in three gravity fields (1*g*, 0*g* or 1.8*g*) induced by parabolic flight. In the former case, both the gravitational torque at the joints (an increase of about 10%) and the inertia of the arm were modified whereas in the latter case, inertial torques remained unchanged. Similarly, we asked subjects to cyclically move hand-held objects of two different masses (200 g or 400 g) over two different distances (20 cm or 40 cm) in the three gravitational conditions. We asked two main questions concerning the control of normal grip force in these circumstances. First, would the subject exert a higher or smaller normal grip force for equivalent tangential loads at the fingers if the effort required to move the upper limb increased or decreased? Second, are gravitational and inertial components of the load force treated adequately and independently by the internal models used to predictively control the required grip force?

Methods and materials

Subjects

Six right-handed subjects (30–48 years old) participated in the study. They were examined in a Center for Aerospace Medicine in order to qualify for parabolic flights (medical examination type "JAR class II"). No subject reported sensory or motor deficits. They were all accustomed to parabolic flights—all had previously flown between 300 and 2000 parabolas. All participants gave their informed consent to participate in the study, and the procedures were approved by the European Space Agency Safety Committee and by the local ethics committee.

Parabolic flight

The flights originated in Bordeaux (France) using the Airbus A300 "ZEROg" aircraft. A single parabolic flight profile generates a sequence of episodes of hyper (1.8*g*), micro (0*g*), and hyper (1.8*g*) gravity of about 20 s duration each (see also Augurelle et al. 2003). Thirty parabolas were performed in each of the three flights, organized as six groups of five parabolas with 2-min pauses of 1*g* flight between each parabola plus an extra 5 to 8 min between each group. Two subjects were tested successively on each flight, during the first and last sets of 15 parabolas, respectively. A three-dimensional accelerometer fixed on the floor of the aircraft recorded its acceleration along its fore-aft axis, its lateral axis and normal to the floor. Table 1 reports the mean accelerations for all parabolic maneuvers ($n = 6$ subjects×15 parabolas = 90) along the three axes and in the three stable gravity phases.

Apparatus

Grip versus load-force coupling was examined while holding a cylindrical object (80 mm diameter, 30 mm width) during cyclic vertical arm movements (Fig. 1). The instrumented object was equipped with two brass circular grip surfaces (40 mm diameter) placed on two parallel lightweight force-torque sensors (Mini40 F/T transducer; ATI Industrial Automation, NC, USA). The mass of the object could be varied by inserting symmetrically up to six half-rings made either of tungsten carbide material (84 g each) or Ertalon (8 g each) into the cylindrical structure holding the two sensors (178 g). An opaque nylon cover (22 g) held the masses in place. The 200 g configuration was obtained by using only the empty body and cover. The 400 g was obtained with two heavy and four light half-rings plus the cover. The sensor measured the three force (F_x, F_y, F_z) components along the corresponding axes passing through the center of the corresponding grasp surface (Fig. 1A). Sensing ranges for F_x, F_y and F_z were ±40, ±40 and ±120 N with 0.02, 0.02, and 0.06 N resolution respectively.

Experimental procedure

The same procedure as in our previous experiment was followed (Augurelle et al. 2003). At a signal from the experimenter, the instrumented object was grasped between the thumb on one side and the index and middle

Table 1 Mean acceleration for all parabolic manoeuvres along the three axes and in the three gravity phases

Axis	Gravity		
	0*g*	1*g*	1.8*g*
Fore–aft	−0.01 ± 0.002	−0.03 ± 0.010	−0.07 ± 0.019
Lateral	0.00 ± 0.005	0.01 ± 0.004	0.01 ± 0.005
Normal	0.01 ± 0.020	1.00 ± 0.029	1.76 ± 0.095

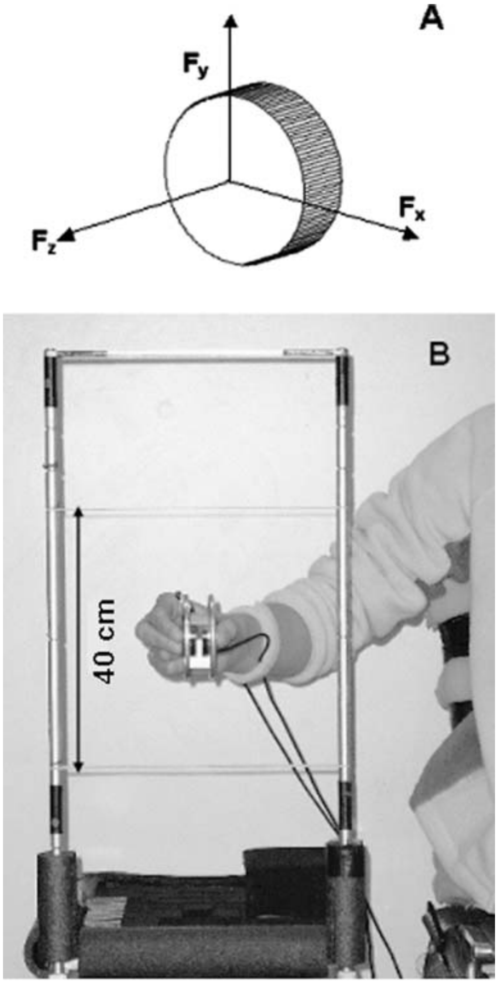

Fig. 1A–B (**A**) Reference frames for forces (F_x, F_y, F_z) measured by the force sensor placed under each grip surface. (**B**) Schematic view of the apparatus held between the thumb on one side and the index and middle fingers on the other side in the 200 g configuration. Arm displacement was limited by two rubber bands spaced 40 cm apart

fingers on the other side at about the center of the grasp surfaces. The fingers were aligned along the *X*-axis in order to place the *Y*-axis in the upward direction (Fig. 1A). The subjects were instructed to perform cyclic vertical arm movements at a frequency of 1 Hz, aided by a metronome. The amplitudes of the oscillations were maintained by lightly constraining the movement within two parallel rubber bands spaced either 20 cm or 40 cm apart, which indicated the reversal points of the movement (Fig. 1B). Subjects performed the upper limb displacement with unconstrained shoulder and elbow movements. They were instructed to maintain the *Y*-axis of the object in a vertical orientation without tilting in any direction.

The experiment was first carried out at 1*g* on the ground before the flight in order to train the subjects in the task. Then the experiment was performed at 0*g*, 1*g* and 1.8*g* during the three parabolic flight days. Each subject performed the task over 15 complete parabolas in the aircraft at a constant frequency of 1 Hz. In the five first trials (T1–T5), the task was performed with a 400 g mass displaced by a distance of 20 cm (“400g20 cm”). In the second series of five trials (T6–T10), the mass was reduced by half and the amplitude of movement was doubled (“200g40 cm”). As the frequency of movement was kept the same (1 Hz), the acceleration was also twice as great, resulting in an equivalent inertial load but a decreased gravitational load. In the last five trials (T11–T15), the 40 cm movement was performed with the 200 g mass but a ballast brace of 200 g was placed around the wrist of the subject (“ballast40 cm”). In this case the inertial and gravitational components of the load were the same as in the “200g40 cm” case, but increased for the arm. Table 2 shows that among the nine loading conditions (3 gravity fields×3 loadings), four levels of equivalent tangential load force acting on the fingertips could be reproduced while the upper limb underwent different loading and gravity environments. For simplicity sake, 2*g* is reported in Table 2 instead of 1.8*g*.

The subjects grasped the instrumented object and performed the cyclic movement during the 1*g* phase of the flight, starting approximately 30 s before the start of the 1.8*g* phase. The movement was performed throughout the entire parabola (1.8*g*, 0*g*, 1.8*g*) and continued 30 s after the return to the 1*g* phase. The

Table 2 The four levels of equivalent tangential load forces

Loading conditions	Levels	Gravity (*g*)	Mass (g)	Distance (cm)	Ballast	GL (N)	IL (N)	Tangential load force (N)
1	1	2	400	20	–	2m2*g*	2ma	2m(2*g* + a)
2	2	2	200	40	–	m2*g*	m2a	2m(*g* + a)
3		2	200	40	+	m2*g*	m2a	
4		1	400	20	–	2 m *g*	2ma	
5	3	1	200	40	–	m *g*	m2a	m(*g* + 2a)
6		1	200	40	+	m *g*	m2a	
7	4	0	400	20	–	0	2ma	2ma
8		0	200	40	–	0	m2a	
9		0	200	40	+	0	m2a	

Gravity: gravitation in g($g = 9.81$ m s^{-2}); Mass: mass of the object; Distance: object displacement; Ballast: presence (+) or absence (–) of the 200 g mass on the arm; a: object acceleration; GL: gravitational load; IL: inertial load; Tangential load force: sum of GL and IL analysis was conducted only on the data recorded during the first 1g and 1.8g phases, plus the 0g phase, of the parabola.

Data processing

The signals from the force transducers, the 3D accelerometers and the metronome were digitized on-line at 200 Hz with a 12-bit 6071E analog-to-digital converter in a PXI chassis (National Instruments, Austin, TX, USA). 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 force applied normal to each grasp surface was calculated as $-F_z$ (Fig. 1A). The total normal grip force (F_n) was calculated as the average of the normal grip forces applied by the thumb and the fingers on each transducer. The magnitude of the tangential load force (F_t) was computed as:

$$F_\mathrm{t} = \sqrt{F_x^2 + F_y^2} \tag{1}$$

where F_x and F_y are the horizontal and vertical components of the tangential load, respectively.

During the one-second baseline, the device laid with its Y-axis vertically. The artificial bias due to the mass of the two brass surfaces covering the transducers was subtracted from F_y before calculation of F_t. The total tangential load force acting on the object was calculated as the sum of the tangential load force measured by the two force transducers. The ratio $F_\mathrm{n}/F_\mathrm{t}$ between the normal and the tangential load forces was also computed.

In preliminary inspections of force traces as a function of time we noted a potential asymmetry in the grip-force and load-force profiles as a function of the direction of movement. Forces near the bottom of the movement exhibited a sharper, higher peak with respect to the mean than for the upper part of the trajectory. To quantify this effect, an index of asymmetry was computed for F_y and F_n according to:

$$|F_\mathrm{lower} - F_\mathrm{mean}| - |F_\mathrm{mean} - F_\mathrm{upper}| \tag{2}$$

where F_lower and F_upper are the forces measured at the lower and upper turning points of the trajectory, respectively.

The analysis of the force measurements was performed cycle by cycle. Seven contiguous cycles of movement were analyzed in each parabola ($n = 15$ parabolas×6 subjects×7 cycles = 630) during the steady-state portions of each gravitational phase (1g, 1.8g and 0g). For each cycle the following values were calculated: the maximum, the minimum and the average values for F_y, F_t, F_n, $F_\mathrm{n}/F_\mathrm{t}$ and the asymmetry index for F_y and F_n. A linear regression between F_y and F_n was evaluated across the seven cycles. Absolute values of F_y were computed prior to the regression to take into account only the magnitude of the force.

Inertial and gravitational components of the load

The prediction of a sufficient normal grip force depends on:

1. the ability to adjust the mean level of the normal grip force to the object's weight, and
2. the ability to modulate the normal grip force with the load force due to the object's acceleration.The vertical load force F_y can be divided into the sum of two components, inertial and gravitational:

$$F_y = F_\mathrm{g} + F_\mathrm{i} \tag{3}$$

where $F_\mathrm{g} = mg$ and $F_\mathrm{i} = ma(t)$. To maintain a constant safety margin against slip, grip force should, ideally, be proportional to load force F_y, what ever the source of the load:

$$F_n = kF_y + c \tag{4}$$

To a first-order approximation, and ignoring horizontal forces for cyclic movements in the up/down direction, grip force can be described as a linear function of the gravitational and inertial components of the vertical force load:

$$F_n = k_\mathrm{g}F_\mathrm{g} + k_\mathrm{i}F_\mathrm{i} + c \tag{5}$$

If Eq. (4) is valid, k_g should therefore be equal to k_i. To test this hypothesis we estimated k_g and k_i as follows. For each subject and each loading condition we computed the average F_n and F_y. The factor k_g was computed as the slope of the best-fit (least-squares) line passing through the three pairs of points for each of the three gravitational levels. Then for each gravitational level and each loading condition k_i was computed as the slope of the best-fit line passing through all sampled data pairs of F_n and F_y.

Statistical analysis

A three-way analysis of variance for repeated measures was performed on measurements of load force to compare the four levels of equivalent load and to test for effects of loading condition (factor 1: "400g20 cm", "200g40 cm" and "ballast40 cm"), gravity (factor 2: 1g, 1.8g and 0g) and learning across the five trials (factor 3). A Tukey pairwise multiple-comparison procedure was used to determine which treatments were significantly different. The same structure of analysis was carried out on measurements of grip force to test for the influence of the loading condition, gravity and inter-trial learning on grip-force/load-force modulation. All the statistical analyses were conducted with Statistica 6.0 (StatSoft).

Results

Figure 2 presents seven contiguous cycles of movement obtained in each stable phase of a parabola (1*g*, 1.8*g* and 0*g*) while oscillating a 200 g mass over a distance of 40 cm at a frequency of 1 Hz. The vertical aircraft acceleration was constant in each gravitational phase (Fig. 2A).

Description of the task in 1*g* (Fig. 2, left column)

When moving the object up and down at 1*g*, the tangential load force (F_t) was primarily due to its vertical component (F_y) because its horizontal component (F_x) was close to zero throughout the cycle. Tangential load force F_t fluctuated around the object weight, in proportion to the arm vertical acceleration. It reached a

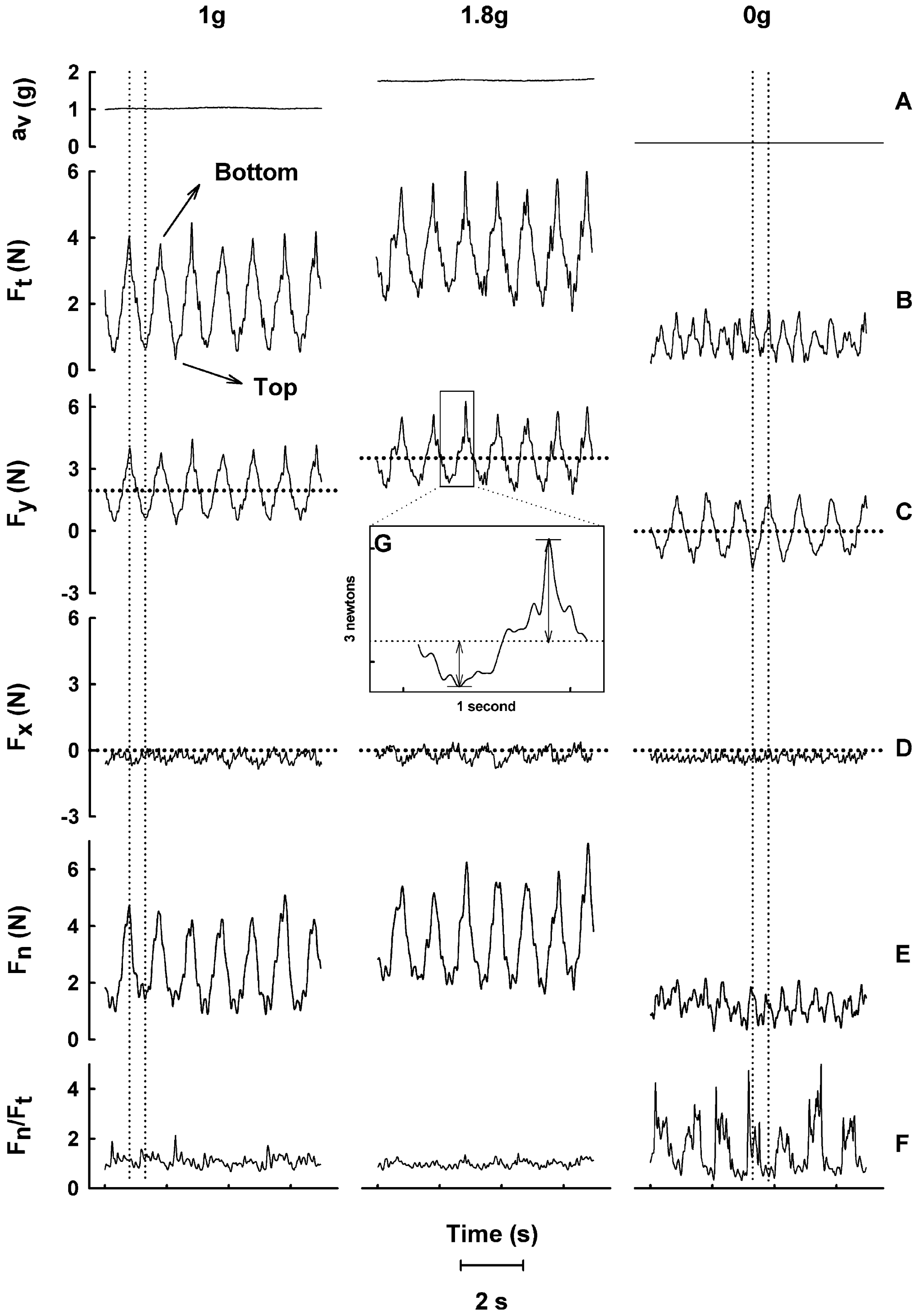

Fig. 2A–G Single records of seven typical cycles of movement in the stable period of each gravitational phase while oscillating a 200 g load a distance of 40 cm at a frequency of 1 Hz. Displayed as a function of time are: (**A**) the vertical aircraft acceleration (a_v), (**B**) the tangential load force (F_t), (**C**) the vertical (F_y) component of the tangential load force, (**D**) the horizontal (F_x) component of the tangential load force, (**E**) the normal grip force (F_n) and (**F**) the force ratio (F_n/F_t). The *vertical dotted lines* show the coordination between F_y and F_n. The inset (**G**) illustrates the asymmetry index on one particular cycle in 1.8*g* maximum at the bottom of the trajectory when the gravity and the vertical components of the object's acceleration acted in the same direction. It was minimal when the object's vertical acceleration was opposite to that of gravity. The normal grip force (F_n) oscillated continuously in parallel with the load fluctuation (F_y) (vertical dotted lines) so that the force ratio (F_n/F_t) was fairly constant across the cycles.

Description of the task in 1.8*g* (Fig. 2, middle column)

In hypergravity (1.8*g*), F_t was also principally due to its vertical component F_y (F_x remained close to zero). The mean F_t increased because the object weight was nearly doubled. The normal grip force (F_n) varied in parallel with the load fluctuation (F_t) giving a nearly constant force ratio (F_n/F_t) across the cycles, the same as in 1*g*.

Description of the task in 0*g* (Fig. 2, right column)

Because of the lack of weight in 0*g*, F_t approached zero in the middle of the trajectory, leading to very high values of the grip-force/load-force ratio in this region. On the other hand the object had to be actively accelerated twice (upwards and downwards) because gravity no longer accelerated the object downwards. In this way, the tangential load force F_t reached a maximum in both the upper and lower parts of the arm trajectory. Subjects increased normal grip force (F_n) in anticipation of the peaks of load both at the top and at the bottom of the trajectory so that the force ratio reached minimum values at these times (vertical dotted lines) comparable with what occurs in the 1*g* and 1.8*g* gravity. Note, however, that this ratio was higher when the object was at the upper turning point than at the lower one.

It is further noted that in the three gravitational conditions, F_x did not oscillate around 0 N but around a negative value, indicating a tangential stress in the antero-posterior direction. This means that the movement was not perfectly vertical in the sagittal plane but slightly curved.

Comparison between the levels of force

Four statistically different levels ($P < 0.001$) of mean tangential load force F_t emerged among the nine loading-gravity combinations, corresponding to the four levels predicted on theoretical grounds (Table 2). Within each of these levels, the mean F_t values were not significantly different ($P > 0.05$). The same analysis applied to the vertical component (F_y) of the load force gave the same results, except for the "400g20 cm" condition in 1*g* versus the "200g40 cm" and the "ballast40 cm" conditions in 2*g*. This was to be expected, because the mass was exactly doubled while the weight increased only by a factor of 1.8 in the so-called 2*g* condition. In fact, F_t showed a similar tendency towards increased values for F_t ($P = 0.105$) but this difference was not statistically significant, probably because inclusion of the small F_x component increased the variance of the F_t measure as compared to F_y.

Describing load force in terms of F_t is most appropriate, because it is the net tangential load that should determine the grip force. However, the directional characteristic of the load force is lost. In the following we consider only the vertical component F_y, because this quantity reflects the direction of the force in the upward and downward directions, making it easier to grasp the differing effects on grip force. This simplification is justified because F_x is insignificantly large compared to F_y.

Level 1 forces (mean $F_y = 7.06 \pm 0.01$ N) were generated when moving 400 g at 1.8*g* a distance of 20 cm (Fig. 3A). Level 2 forces (mean $F_y = 3.68 \pm 0.01$ N) were generated either by moving 200 g at 1.8*g* a distance of 40 cm with or without an additional mass on the wrist or by moving 400 g at 1*g* a distance of 20 cm. Note again, however, that with the 400 g mass, the mean F_y and its maximum (at the lower turning point) (Figs. 3A and 3B) were higher than in the other two conditions ($P < 0.001$). Level 3 forces (mean $F_y = 1.96 \pm 0.01$ N) were obtained with 200 g moved at 1*g* with or without the ballast on the wrist. Finally, level 4 forces occurred at 0*g* in any of the three loading conditions (mean $F_y = 0 \pm 0.01$ N). Peak F_y reached greater extremes with respect to the mean value with the 400 g mass than with 200 g ($P < 0.001$) (Fig. 3B).

Normal grip force (F_n) was measured at each level of load to test whether the same normal grip force was used for equivalent levels of load (Figs. 3C and 3D) and to test whether the same force ratio (F_n/F_t) was maintained when the level of load changed (Figs. 3E and 3F). Within each level, the normal grip forces applied for the different load conditions did not change across trials, irrespective of the mass and the gravitational context ($P > 0.23$) (Figs. 3C and 3D). In this way, similar force ratios (F_n/F_t) were maintained inside each of the four levels, at least at the reversal points of the trajectories where the load force was significant (Figs. 3E and 3F). In microgravity, however, F_t was close to 0 N in the middle of the trajectory. As the grip force never falls precisely to zero, the calculated ratio of grip force to load force is ill-conditioned, leading to very high values (infinity for $F_t = 0$ N, see Fig. 2F) that can be considered artifactual. When comparing across the four levels of load in Fig. 3F, an interesting finding was that the subjects used the same F_n/F_t ratio for the nine combinations when the load reached a maximum i.e. at the bottom of the arm trajectory ($P > 0.33$). This ratio is low and highly reproducible for each subject. The F_n/F_t ratio when the load reached a minimum was higher and more variable because the subjects did not release their grip as much as they might have while still maintaining an adequate safety margin to avoid accidental slip.

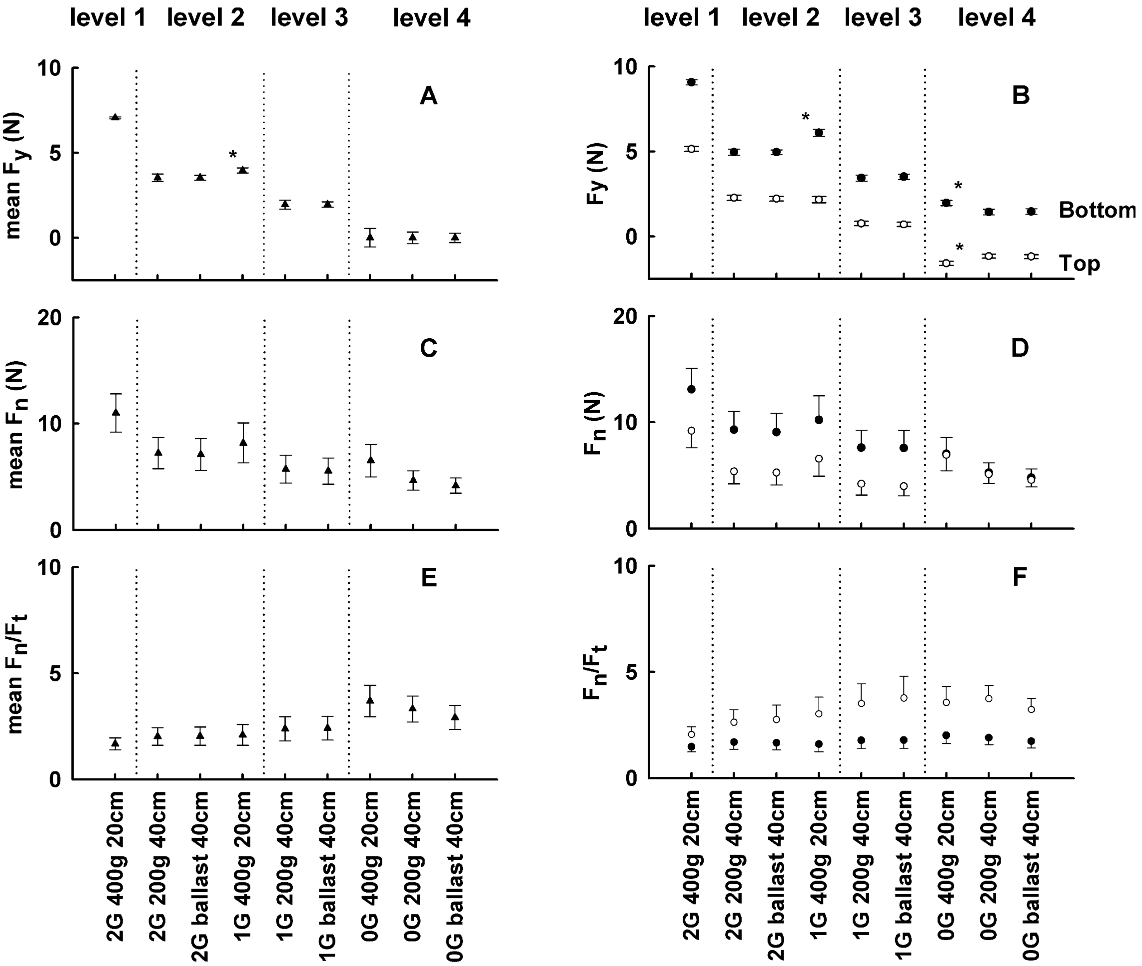

Fig. 3A–F The means and standard errors of the parameters are plotted for each load condition for all subjects and trials. The *left* graphs present the mean magnitude (*triangles*) of (**A**) the vertical tangential load force, (**C**) the normal grip force and (**E**) the force ratio. The right graphs present the values at the top (*open circles*) and at the bottom (*filled circles*) of (**B**) vertical tangential load force, (**D**) the normal grip force, and (**F**) the force ratio. *Vertical dotted lines* delimit the four levels of equivalent load. *Asterisks* signal a significant difference ($P < 0.05$) between load conditions within each level

Adaptation to inertial and gravitational components of the load

Figure 4A shows a typical scatter plot of F_n as a function of the load F_y while moving a 400 g mass in the three gravitational environments. According to Eqs. (3), (4), and (5), the gravitational gain (k_g) is given by the slope of the linear regression (dashed line) calculated between the three means of F_y and its corresponding F_n in 0*g*, 1*g* and 1.8*g*. The inertial gain (k_i) is given by the slope of each regression line (solid line) calculated between F_y and F_n within each gravity field.

Figure 4B shows the gravitational (right panel) and the inertial (left panel) gains for each loading condition. Loading conditions did not modify the gravitational gain ($P > 0.05$). When computed from finite differences between just two gravitational levels, the gravitational gain between 0*g* and 1*g* was significantly lower across subjects than the gain between 1*g* and 1.8*g* ($P < 0.05$) and lower than the gain computed from the three-point linear regression ($P < 0.05$). This indicates that the grip-force/load-force relationship for differing gravity levels is non-linear. The inertial gain was smaller in 0*g* whatever the loading condition ($P < 0.001$) and was smaller with the 400 g mass whatever the gravity field ($P = 0.002$), also indicating a non-linear relationship.

Asymmetry in load and normal grip forces

Figure 2G (inset) highlights the asymmetry between the maximum and the minimum of F_y. The asymmetry index (Eq. 2) is displayed in Fig. 5A for F_y (open symbols) and F_n (closed symbols) in the three gravity fields. All the values are positive, which means that the amplitudes of peak forces were always larger at the bottom of the trajectory, i.e. for maximum tangential load forces (in the presence of gravity). Moreover, when compared to 1*g*, this asymmetry was significantly lower for both F_y and F_n in 1.8*g* ($P < 0.015$) but only for F_n in 0*g*

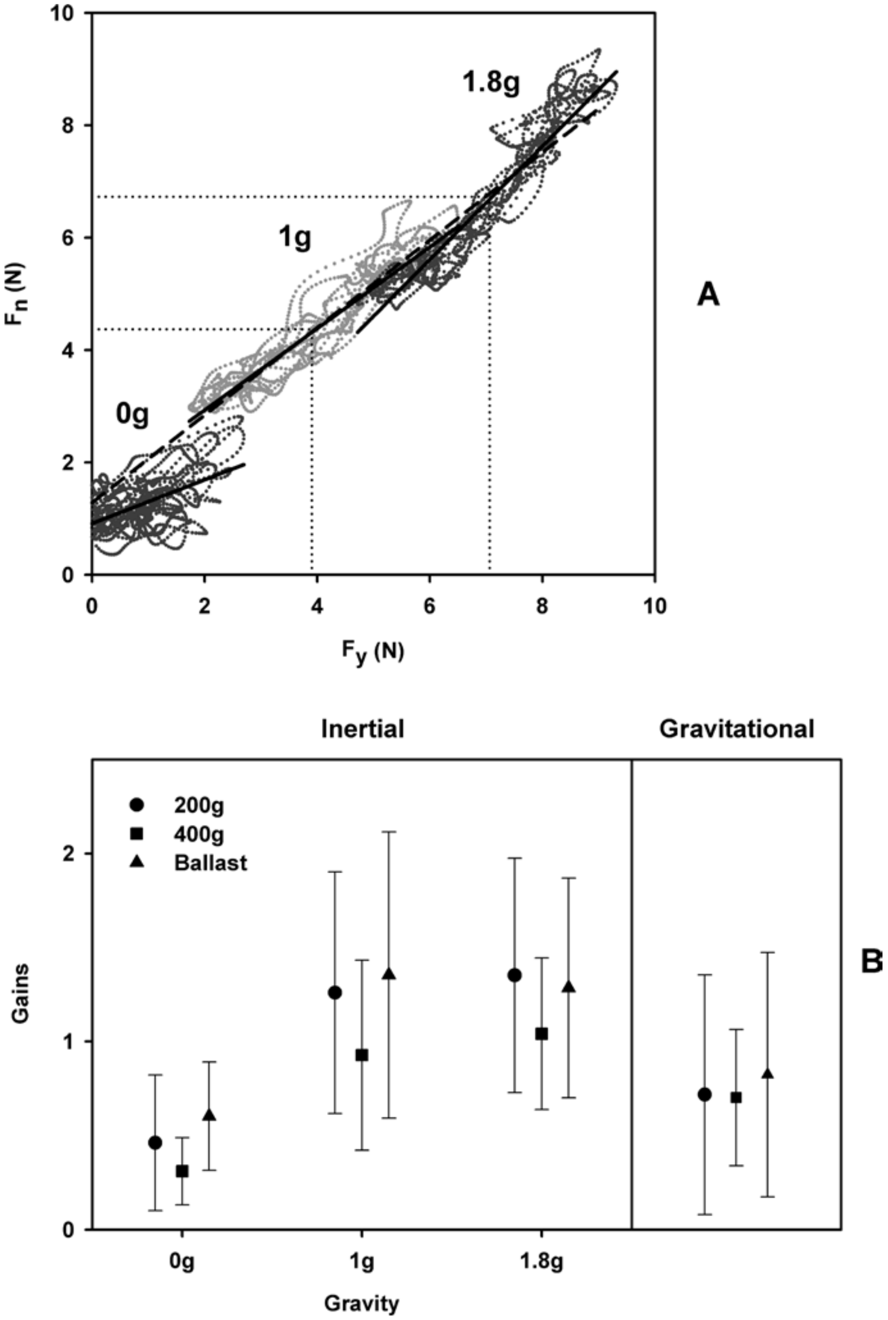

Fig. 4A–B (**A**) Typical trace of the gravitational and inertial gains of F_n as a function of the load F_y while moving a 400 g mass in the three gravitational environments. (**B**) Gravitational (*right panel*) and inertial (*left panel*) gains for each loading condition. *Error bars* represent SE

($P < 0.003$). Figure 5B shows that the asymmetry for F_n did not change across trials in 1*g* and 1.8*g* but significantly decreased in microgravity ($P < 0.025$).

Discussion

In this experiment we examined the relationship between normal grip force (F_n) and vertical component of the tangential load force (F_y) while moving an object up and down in different gravitational environments. Through a variety of test conditions we varied independently the inertial and gravitational components of the forces acting on the upper limb. On the one hand, we modified the inertial components by varying the mass of the load or the mass of the limb (ballast on the forearm). On the other hand, we varied the weight of the limb and load by adding mass and by varying the effective gravitational field. In this way it was possible to generate equivalent magnitudes of loads at the fingertips while the mechanical constraints on the upper limb and thus the motor commands required to move the arm were modified. Similarly, certain trials required similar motor commands to move the arm, but different grip forces to maintain the object safely in the grasp.

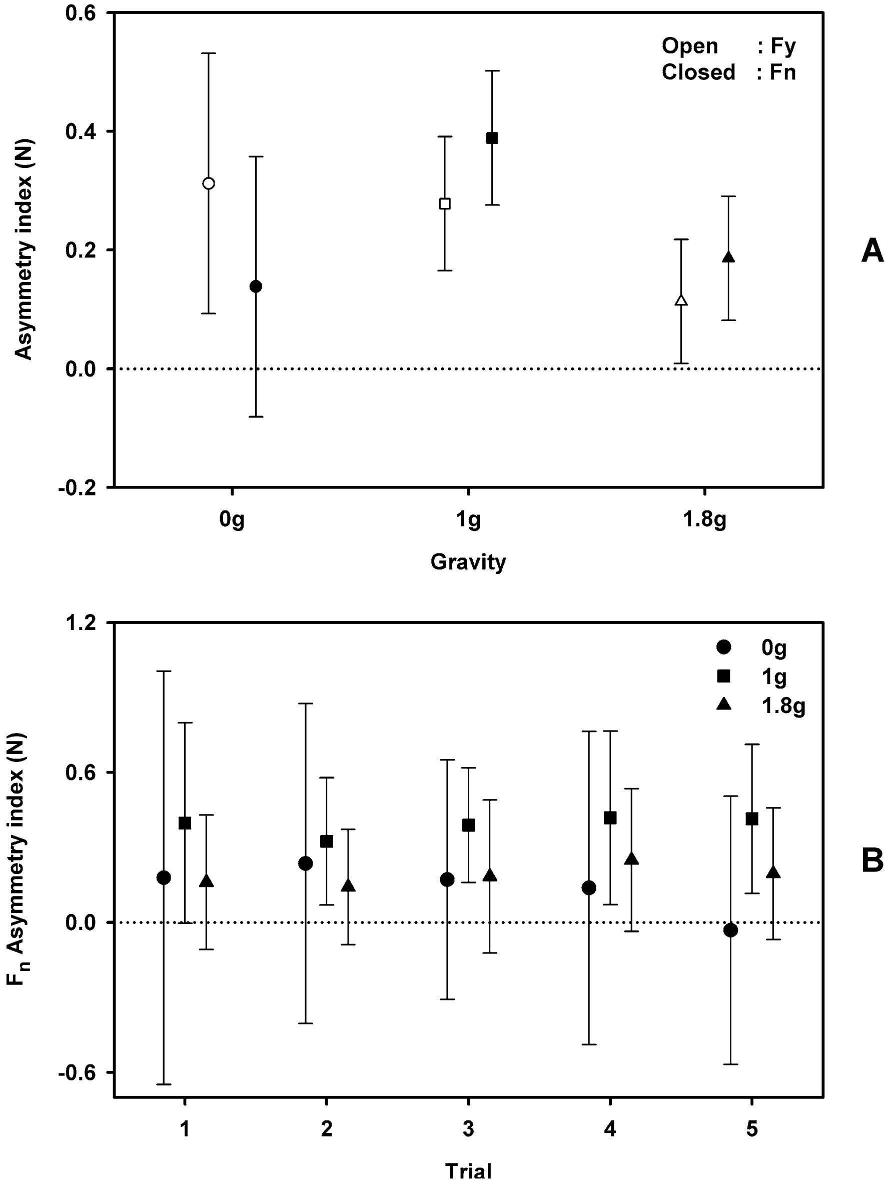

Fig. 5A–B (**A**) Asymmetry index for F_y (*open circles*) and F_n (*filled circles*) for each gravitational conditions. (**B**) The F_n asymmetry index for 0*g* (*circles*), 1*g* (*squares*) and 1.8*g* (*triangles*) is plotted in function of the trials. *Error bars* represent SE

Arm and grip force controllers are decoupled

In each loading condition, the normal grip force was modulated in phase with the load fluctuations, confirming previous results obtained in similar paradigms performed on earth and in parabolic flight (Flanagan and Wing 1995, 1997; Flanagan et al. 1999a, 1999b; Hermsdorfer et al. 2000; Augurelle et al. 2003). In microgravity, normal grip force increased at the top of the arm trajectory to prevent slip as the object was pushed downwards. The main finding was that the magnitude of the normal grip force was adequately adjusted for each maximum of load to maintain the same minimum ratio between the normal grip force and the tangential load force (F_n/F_t) in the nine loading combinations (Fig. 3F, black circles). The subjects were able to maintain this optimum ratio in different contexts of mass, gravity and upper limb accelerations. For equivalent loads at the fingertips at 1*g* or 1.8*g*, the subjects used the same normal grip force despite the fact that it required more force to displace the arm in hypergravity. These results show that normal grip force is not related to the muscle commands to the upper limb in a simplistic manner. Normal grip force is adjusted appropriately to the tangential load forces applied to the fingertips, rather than being tuned to the overall load applied to the limb.

In the experiments reported here, control of normal grip force was very stable from one parabola to the next, starting from the very first parabola. We observed no systematic evolution of the grip force as a function of trial within each loading condition. This indicates that grip force was appropriate immediately from the first trial after either a change of gravity or a change of the inertial load on the upper limb. These observations from the experienced subjects used in the current study are compatible with our previous experiment in which significant evidence of adaptation to varying gravitational levels was observed only in those subjects who were faced with altered gravity for the first time (Augurelle et al. 2003).

The two results above further extend the general framework in which the grip-force/load-force coordination is observed. Not only does this coupling reflect a general control strategy for any particular grip or mode of transport (Flanagan and Tresilian 1994; Gysin et al. 2003) but we have also shown that this strategy is used in different environmental (i.e. gravitoinertial) contexts. The similar force ratios observed in the nine loading combinations indicate that dynamic constraints such as gravitational force and inertial resistance of the arm and object were well taken into account in the control of precision grip. The precise temporal coupling between the normal grip force and the tangential load force also shows that the load was predicted correctly and that the normal grip force was calculated in a feedforward manner based on this prediction. This suggests that the forward model predicting the load can be adjusted to account for various physical contexts. In other words, subjects were able to identify the environmental context and select the appropriate motor program.

In a modular approach to the problems of motor control, it has been proposed that the brain contains multiple controllers (inverse models) associated with their corresponding predictor (forward models), with each of them suitable for one or small set of contexts (Blakemore et al. 1998; Wolpert and Kawato 1998). Based on several contextual cues such as experience from previous manipulations of the object and based on visual and tactile information about the object's physical properties, subjects can pre-select an appropriate module for, say, displacing a 400 g object a distance of 20 cm in hypergravity. The selected controller will issue the motor command and the corresponding forward model will predict its sensory consequences. If the prediction is good, the module will continue to be used. When the context estimate is wrong, the prediction will be poor and another module will be selected (Wolpert and Kawato 1998; Kawato 1999). This model fits well with our results. In this experiment, the six subjects were familiar with parabolic flights and were trained to perform the manipulative task on Earth. In flight, the nine loading conditions were thus different combinations of known environments and previously manipulated objects. The modular model of motor control also assumes that separate internal models learned for different contexts can be mixed to cope with a given task (Wolpert and Kawato 1998; Flanagan et al. 1999b). It is likely that having learned the task in 1*g* before the flight, and being already familiar with the different gravity fields in parabolic flight, the subjects could more easily execute the task after just a few trials.

Interaction between gravity and inertia to predict F_n

By decoupling the usual link present on Earth between gravity and inertia for vertical arm movements, we investigated whether the internal model could take into account this separation in order to adjust the normal grip force. Although we observed overall that grip force followed load force with a more or less common relationship (data points in scatter plots of grip force versus load force fall more-or-less along the same line within and across gravitational levels, see Fig. 4) we noted subtle differences in the gain of the grip-force/load-force relationships between different loading conditions. On the one hand, we found that the gravitational gain (k_g, Eq. 3) did not vary across loading conditions. That is, for both hand-held loads and with or without extra weight on the arm, subjects were able to adjust their normal grip force to gravity, with the same gain. On the Earth, we easily adjust our normal grip force proportional to the mass held. A pure change of gravity (no movement of the arm) induces a change of tangential load force felt by the fingertips just like that produced by a modification of mass on Earth. Therefore, subjects could easily select the appropriate model based on experience in 1*g* to predict the correct extent of F_n modulation with gravitational load.

On the other hand, we showed that the inertial gain was influenced by gravity and loading conditions. The inertial gain k_i was systematically smaller for the 400 g object than for the 200 g object, whatever the gravity level. Nevertheless, the inertial gain for the 200 g load was not affected by the additional loading of the arm (ballast). Grip force was also modulated in microgravity to account for fluctuations of the inertial load but the gain was lower in microgravity than in non-zero gravity fields. It has previously been observed that increases in average grip force, either due to an increase in the frequency of oscillation or due to voluntary effort, can lead to a decrease in the inertial gain (Flanagan and Wing 1995). This could explain the reduced inertial gain observed for 400 versus 200 g, but cannot explain the decrease of the inertial gain in microgravity. Thus, when taking into account changes in both loading and gravity, it seems that inertial and gravitational gains can be adjusted independently across conditions. This decoupling between k_g and k_i indicates that these are under high-level control and emphasizes the predictive, internal model-based character of grip force control. If the parameters of grip force modulation were based entirely on sensory feedback about the tangential force at the fingertips, it should not matter whether the source of the tangential load is gravitational or inertial; k_g and k_i should precisely co-vary. This point is further emphasized by measurements of grip-force/load-force coupling compared between novice and experienced parabolic flight subjects (Augurelle et al. 2003). Initial trials in novice subjects showed a much greater influence of gravitational than inertial load on grip force (higher k_g) during initial trials but gradually achieved a more coherent pattern of grip force regulation after practice in 0*g*.

Asymmetrical grip and load forces are preprogrammed

The results reported here showed that the load fluctuations were not symmetric around the object weight regardless of the gravitational level, as would be the case if the peaks in arm acceleration were equal and opposite at the upper and lower reversal points of the trajectory. One of two subjects showed a similar asymmetry in a related study in microgravity (Hermsdörfer et al. 2000) and asymmetry in arm kinematics has also been reported for discrete point-to-point arm movements in terms of hand-path curvature (Papaxanthis et al. 1998) and in terms of the relative time taken to accelerate and decelerate the movement (Papaxanthis et al., personal communication).

One might ask what is the source of these asymmetries? Do they reflect optimization of the motor plan with respect to the dynamic constraints imposed by gravity, or is this simply an asymmetric effect of gravity on what would otherwise be a symmetrically programmed behavior? The fact that these effects persist (at least initially) in 0*g* is the key point—variations of limb kinematics and grip force tuned to the differing effects of gravity on the limb for upward and downward movements are programmed in an anticipatory manner, otherwise they would have disappeared immediately on entry into the 0*g* environment.

As we show here, the predictive controller that regulates grip forces takes into account even the subtle asymmetry in kinematics and load forces associated with vertical arm movements. The results suggest two cooperative controls for these different processes which are, nevertheless, somewhat independent. On the one hand, the grip force controller seems to take into account the asymmetries in the tangential load forces for non-zero gravity fields. On the other hand, in microgravity, the grip force controller learned to apply symmetric patterns after five trials although the asymmetry in the kinematics persisted (Figs. 5A and 5B). We can speculate that with more trials, subjects would succeed in producing symmetric patterns of kinematics and load forces in microgravity.

Overall, we have shown that the CNS predicts load force precisely enough to program grip force in a feedforward manner, despite variations in the mass of the load, the mass of the limb and the gravitational context. We conclude that the internal models used to control precision grip are sophisticated enough to take into account the differing effects of gravitational force and inertial load on the muscular effort required to move the arm and the grip force required to hold the object.

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