RESEARCH ARTICLE

Inertial torque during reaching directly impacts grip‑force adaptation to weightless objects

T. $\text{Giard}^{1,2} \cdot \text{F}$. $\text{Crevecocour}^{1,2} \cdot \text{J}$. $\text{Mclutyre}^{3,4,5} \cdot \text{J}$. **L. Thonnard**^{2,6} · **P.** Lefèvre^{1,2}

Received: 13 May 2015 / Accepted: 31 July 2015 / Published online: 12 August 2015 © Springer-Verlag Berlin Heidelberg 2015

Abstract A hallmark of movement control expressed by healthy humans is the ability to gradually improve motor performance through learning. In the context of object manipulation, previous work has shown that the presence of a torque load has a direct impact on grip-force control, characterized by a significantly slower grip-force adjustment across lifting movements. The origin of this slower adaptation rate remains unclear. On the one hand, information about tangential constraints during stationary holding may be difficult to extract in the presence of a torque. On the other hand, inertial torque experienced during movement may also potentially disrupt the grip-force adjustments, as the dynamical constraints clearly differ from the situation when no torque load is present. To address the influence of inertial torque loads, we instructed healthy adults to perform visually guided reaching movements in weightlessness while holding an unbalanced

Electronic supplementary material The online version of this article (doi[:10.1007/s00221-015-4400-z](http://dx.doi.org/10.1007/s00221-015-4400-z)) contains supplementary material, which is available to authorized users.

 \boxtimes P. Lefèvre philippe.lefevre.uclouvain@gmail.com; philippe.lefevre@uclouvain.be

- ¹ ICTEAM, Université catholique de Louvain, Louvain-la-Neuve, Belgium
- ² IoNS, Université catholique de Louvain, Brussels, Belgium
- ³ CNRS, Centre d'Etudes de la Sensorimotricité, Université Paris Descartes, Paris, France
- ⁴ Fundacion Tecnalia Research & Innovation, San Sebastián, Spain
- ⁵ IKERBASQUE Research Foundation, Bilbao, Spain
- ⁶ Cliniques Universitaires Saint-Luc, Physical and Rehabilitation Medicine Department, Université Catholique de Louvain, Brussels, Belgium

object relative to the grip axis. Weightlessness offered the possibility to remove gravitational constraints and isolate the effect of movement-related feedback on grip force adjustments. Grip-force adaptation rates were compared with a control group who manipulated a balanced object without any torque load and also in weightlessness. Our results clearly show that grip-force adaptation in the presence of a torque load is significantly slower, which suggests that the presence of torque loads experienced during movement may alter our internal estimates of how much force is required to hold an unbalanced object stable. This observation may explain why grasping objects around the expected location of the center of mass is such an important component of planning and control of manipulation tasks.

Keywords Grip-force · Torque load · Weightlessness · Adaptation · Motor control

Introduction

With the repetition of a movement, grip force is adapted depending on the specificities of the task (Flanagan et al. [2003](#page-8-0); Nowak et al. [2004;](#page-9-0) Danion et al. [2012](#page-8-1)). For instance, during a grip-lift task, the finger forces applied on the lifted object during stationary holding decrease with practice. This decrease in grip force typically stabilizes above the minimal force needed to avoid slipping, which reflects a safety margin dependent upon contextual factors and on the mechanical properties at the interface between the skin and the manipulated object (Johansson and Westling [1984](#page-8-2); Westling and Johansson [1984](#page-9-1)). Previous work shows that the presence of a torque load has an important impact on this adaptation rate, which is much slower than in the absence of torque load (Crevecoeur et al. [2011](#page-8-3)).

Besides the level of grip force used during stationary holding in reaction to the gravitational tangential constraints, the grip force is modulated depending on the additional inertial tangential forces during the movement (Flanagan and Wing [1993,](#page-8-4) [1997](#page-8-5); Flanagan et al. [1993\)](#page-8-6). In addition to these tangential forces, torque loads are present in many situations and have an impact on the grip-force control (Goodwin et al. [1998;](#page-8-7) Kutz et al. [2009](#page-9-2); De Gregorio and Santos [2013\)](#page-8-8). These tangential forces and torques result from gravitational and inertial components. In addition, it has been shown in earlier studies that grip force is dynamically modulated according to the load force variation due to object acceleration (Flanagan and Wing [1993](#page-8-4), [1997;](#page-8-5) Augurelle et al. [2003](#page-8-9); Crevecoeur et al. [2010b;](#page-8-10) Danion et al. [2013\)](#page-8-11).

Mechanical constraints during object manipulation can be decomposed into gravitational or inertial forces. How the nervous system extracts information from these two components to adjust the overall grip force level is not fully understood. The aim of this study was to assess the influence of the inertial component of torque load on object manipulation by performing experiments in weightlessness using an asymmetrical object. In an earlier study (Crevecoeur et al. [2011](#page-8-3)), we demonstrated that the presence of a torque load on Earth slows down considerably the adaptation of grip force during static phases. However, in the laboratory condition, both gravitational and inertial components of loads are present. Therefore, performing the same experiment in weightlessness offers a unique opportunity to better understand the role of gravitational loads in this mechanism. Indeed, there are two possible hypotheses in this condition. The first hypothesis is that in weightlessness there will be no more difference in grip force adaptation between torque and no-torque load conditions; this would demonstrate gravitational constraints a necessary to slow down the adaptation in the torque load condition. The second hypothesis is that in weightlessness, there will still be a difference in grip force adaptation between torque and no-torque load conditions, and this would demonstrate inertial constraints a sufficient by themselves to show the effect (a direct consequence being that gravitational constraints are not necessary). Removing the gravitational component of the torque load allows us to extract the impact of inertial torques during reaching on grip-force adaptation. We investigated grip-force adjustments during stationary holding under weightless conditions (when the tangential forces and torques equal to 0) with or without an off-center mass attached to the manipulandum structure. Our results unambiguously favor the second hypothesis, as gripforce adaptation under zero-g condition displayed strikingly similar properties as those observed under laboratory conditions (Crevecoeur et al. [2011\)](#page-8-3), with similar adaptation rate that was much slower than when no torque comes into play. Surprisingly, although the absolute levels of static grip force (sGF) were slowly adjusted across trials, we observed a clear dynamic modulation with the inertial components of tangential loads and torques indicative of a preserved ability to anticipate the consequences of movements. Altogether, our results quantify the importance of inertial constraints on both static and dynamic components of the grip force and highlight the importance of torque loads on the learning mechanisms and internal models adaptation during object manipulation.

Methods

Subjects

Eighteen volunteers between 23 and 55 years old (17 righthanded and 1 left-handed) with no known neurological disorders gave their informed consent to take part in the experiment. Twelve subjects performed the main experiment and six subjects performed the control experiment. The subjects of the main experiment and the control experiment were different because we needed them to be naive to the purpose of the study and to microgravity conditions. They complied with the medical requirements to participate in parabolic flights (Belgian Center for Aerospace Medicine, class II medical examination). The experimental protocol was approved in terms of ethical and biomedical requirements for experimentation on human subjects by the European Space Agency (ESA) Medical Board Committee and the French Comité pour la Protection des Personnes, which reviews life science protocols in accordance with French law and the Helsinki protocols.

Parabolic flight

The experiment was performed during the 55th, the 56th and the 59th ESA Parabolic Flight Campaigns on board of the A-300 0-G aircraft (Bordeaux-Mérignac, France). Parabolic maneuvers generated sequences of 20 s of hypergravity (1.8 g) , followed by about 22 s of weightlessness (0 g) before another period of 20 s of hypergravity. Each participant performed the task during a sequence of 30 consecutive parabolas. We monitored the gravity during the data acquisition and found that gravitational levels were relatively stable (average across blocks -0.003 ± 0.0147 g; average standard deviation across blocks 0.0255 ± 0.004 g). In the following sections, one block refers to the set of trials performed during one parabola. Each parabola was followed by a break of minimum 2 min.

Experimental procedures

Main experiment (TL condition)

Subjects sat in front of four LED targets vertically aligned with respect to the aircraft floor and separated by 10 cm. The program generated a random sequence of these LED 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. Subjects held a manipulandum with a precision grip (grip aperture 4.5 cm) and were instructed to align and stabilize it with the current LED until the next target was illuminated while minimizing rotational movements of the manipulandum induced by the presence of torque loads. They received the instruction to maintain the orientation of the manipulandum such that the off-centered mass stayed at the same height as their index and thumb fingers. Head, eye and arm movements were not constrained. The subjects were allowed to manipulate the object only during the 0 g phases to reduce clues regarding its mass as well as the torque load produced by the off-centered mass. A block of 17 point-to-point movements was performed during the 0 g phase of each parabola. The manipulandum had a total mass of 340 g including the off-centered mass of 40 g placed at 10 cm (Fig. [1](#page-2-0)). Between the trials, the subjects had to maintain the manipulandum on their left knee by holding it at the top with their left hand. The subjects could clearly see the off-centered mass, but they had never held the manipulandum before the flight. Data acquisition began at the beginning of the 0 g phase of each parabola (beginning of microgravity).

Fig. 1 a Schematic representation of the instrumented object equipped with an off-centered mass that moved the center of mass away from the grip axis. The study focuses on the grip force (GF), the load force (LF), the torque load measured along the grip axis (T) and the rotation angle. **b** Photo of the manipulandum showing the off-center mass and position of the infrared markers used for motion tracking. **c** Picture of a subject before starting the first reaching movement. The manipulandum was held on participant's knee prior to reaching for the first target. The participant was maintained on the chair with two straps over the shoulders and one around the waist. The targets are depicted with four *green circles* (color figure online)

Control experiment (NoTL condition)

In the control experiment, the task was exactly the same as the main experiment, but the manipulandum was different. It was balanced with a total mass of 708 g including three masses of 136 g placed one on each hoop. This mass, called equivalent mass, was estimated based on a model of mechanical constraints to produce equivalent constraints and required the same level of GF for the same linear acceleration. We followed a theoretical approach based on the computation of the tensor of tangential constraints at the finger–object interface as in Crevecoeur et al. [\(2011](#page-8-3)). We computed the force density on the contact surface with and without the off-centered mass. On the basis of the hypothesis of linear addition, the force density tensors corresponding to a centered mass only or a torque only were summed to estimate the overall force density tensor. Then, we defined the equivalent mass as a centered mass, which would produce an identical integrated square norm of force density as the one computed in the presence of a torque. In such configuration, the integrated square norm of the force density constraint at the fingertips is identical to the one in the main experiment for the same linear acceleration (Crevecoeur et al. [2011](#page-8-3)). With such equivalence of constraints, the subjects produce similar levels of grip force in both conditions. Thus, it is possible to isolate the effect of the torque by comparing the main and the control experiment.

Apparatus and data collection

The custom manipulandum (ESAGLM, Arsalis, Louvainla-Neuve, Belgium) was equipped with two three-dimensional force and torque sensors (mini 40 F/T transducers, ATI, Industrial Automation, NC, USA). We collected the tangential and normal forces at the interface between the fingers and the manipulandum, as well as the torque loads generated by the off-centered mass along the grip axis. The sampling rate for data acquisition of the sensors was 800 Hz. Three-dimensional position signals of three infrared markers (infrared emitting diode [IRED]) placed on the manipulandum (see Fig. [1](#page-2-0)b) were sampled at 200 Hz with a motion-tracking device (Codamotion System, Charnwoods Dynamics, Leicestershire, UK).

Data processing

From the position of the three infrared markers, we computed the location of the center of the spherical structure, corresponding to the center of the line segment joining the two senors under the index and the thumb (Fig. [1](#page-2-0)). The vertical position and velocity of this point were considered. Regarding the rotation angle, the movements were first

projected onto the plane orthogonal to the grip axis which allowed us to compute the angle from the change in orientation of the vector joining the center of the spherical structure to the off-centered mass. All position signals were digitally low-pass filtered with a zero phase-lag Butterworth filter of order four with a cut-off frequency of 20 Hz. Let $(F_{\text{xr}}, F_{\text{yr}}, F_{\text{ZF}})$ and $(F_{\text{xl}}, F_{\text{vl}}, F_{\text{zl}})$ be the force components measured on the right and the left sensors, respectively, and $(T_{\rm xr}, T_{\rm yr}, T_{\rm zr})$ and $(T_{\rm x1}, T_{\rm y1}, T_{\rm z1})$ be the torque components (Fig. [1a](#page-2-0)). The normal force applied on the manipulandum by the subject is called grip force (GF) and is defined as the mean of the components of the force normal to the surface of the object for both sensors.

$$
GF = \frac{F_{zx} + F_{z1}}{2}
$$

The baseline of GF exerted before each movement was measured during each static phase (stable manipulandum) and will be defined as sGF, the mean of GF in a window of 100 ms beginning at target onset.

The difference between sGF of the first trial of a block *b* and the last trial of the same block *b* is called *sGF intrablock decrease* and represents the adaptation of the sGF during one block. The difference between sGF of the first trial of a block *b* and the last trial of the previous block *b-*1 is called *sGF inter*-*block washout* and represents the impact of the inter-block breaks on the level of sGF.

The relative GF, rGF, is the difference between GF at a specific time during a movement and sGF measured before this movement.

$$
\mathrm{rGF}_j = \mathrm{GF}(t_j) - \mathrm{sGF}
$$

The tangential force applied on the surface of the object is called the load force, LF (Fig. [1](#page-2-0)a), and is defined as the sum of the vertical component of the tangential forces, F_v , measured by both sensors. The torque load, T, is defined the same way as LF.

$$
LF = F_{yr} + F_{yl}
$$

$$
T = T_{zr} + T_{z1}
$$

Figure [2](#page-3-0) shows data from typical trials. It can be observed that there are two LF peaks during one movement. For an upward movement, the LF peak due to the acceleration is positive, whereas the one due to the deceleration is negative and vice versa for a downward movement. During the movement, three specific times are defined: t_{LEI} is the time of the acceleration peak of LF, t_{LF2} is the time of the deceleration peak of LF and $t_{LF=0}$ is the time between *t*LF1 and *t*LF2 when the LF crosses zero. Three corresponding values of rGF were defined: rGF_{LF=0} at $t_{LF=0}$, rGF_{LF1} at t_{LF1} and rGF_{LF2} at t_{LF2} .

Fig. 2 Typical traces of two consecutive movements (upward on the *left* and downward on the *right*, subject S1). The *vertical dashed lines* across all the *panels* represent target onsets. The *gray zones* are the static phases, and sGF is averaged between brackets. Three important times were used for the analyses: t_{LF1} (first peak of LF or peak of acceleration), t_{LF2} (second peak of LF or peak of deceleration) and $t_{\text{LE}-0}$ (zero acceleration or zero LF between the two peaks of LF). On the position *panel*, the *horizontal dotted lines* represent the targets position

In the present study, it is not appropriate to compare the results of the two experiments on the basis of LF since only in the main experiment a torque load is present. Indeed, both linear and rotational tangential constraints must be taken into account. In our protocol, the main experiment and the control experiment were designed in such a way that the same linear acceleration produced the same integrated square norm of the force density constraint at the fingertips in the two conditions (see appendix in Crevecoeur et al. [2011](#page-8-3)). Thus, the linear vertical acceleration was the key parameter that was related to grip force in our data analysis.

This implies that any torque due to rotational acceleration is not taken into account in this relationship. However, this approximation is reasonable since the torque induced by rotational acceleration represented less than 10 ± 8 % of the total torque estimated based on the measured linear and rotational accelerations.

Statistical analysis

We used two different statistical tests to analyze sGF. First, Student's *t* test was used to test whether the mean sGF of the first three blocks differed significantly from the mean value of sGF for the last three blocks, i.e., to test for a decrease in sGF across blocks. Then, a negative exponential, with the following equation:

$$
sGF(n) = a_0 + a_1 \exp(-a_2 n)
$$

was used to characterize the average time course of sGF adaptation across blocks. To compare the rate of adaptation with and without torque, the time constant $1/a₂$ was compared between conditions. The significance of the difference between the means of the *sGF inter*-*block washout* was also established with Student's *t* test. Deming regressions were used to compute the slopes of the correlation between rGF and acceleration as the slope of the relationship was very large, and thus, we observed a saturation of the classical least-square regression (Cornbleet and Gochman [1979](#page-8-12)). A four-way mixed-design ANOVA was used to compare the slope (averaged on three consecutive blocks) of this correlation in the different conditions with direction of movement (up or down), acceleration or deceleration and block as independent within factors and load condition (TL or NoTL) as independent between factor.

Results

Typical traces from two consecutive movements, an upward movement followed by a downward movement, are illustrated in Fig. [2](#page-3-0). The vertical dotted lines represent the target onsets, and the gray zones represent the static phases. The horizontal dashed lines on the position plot are the positions of the four LED targets. At 0 s, the LED target placed at 20 cm was turned on. The subject, who was holding the manipulandum in front of the 10 cm LED target, should have lift the manipulandum upward by 10 cm but made an overshoot of about 2.5 cm. At 1 s, the target at 20 cm was turned off and the 0 cm target was turned on. The subject subsequently moved to the latter target.

A change in angle of $+7^{\circ}$ and -10° can be observed in this example for the upward and the downward movement, respectively. These rotations around the grip axis stayed very small during the whole experiment (mean $8^\circ \pm 6^\circ$).

These changes in angle were most likely induced by different postural configurations for each target, and they had a limited influence on the torque load during the movement in comparison with the torque induced by the off-centered mass.

Indeed, the actual lever arm varies as the cosine of the changes in the joint angle, which represents a change of \leq % for angles comprised between -15° and 15°. Furthermore, variations in effective gravity during parabola had also a limited impact on the torque level as the mean of standard deviation of the gravity level represented only 5 % of the average acceleration peak during the movement.

Due to the microgravity condition, LF varied around 0 N and depended only on the acceleration of the manipulandum. The peaks of LF occurred at the peak of acceleration and deceleration, t_{LF1} and at t_{LF2} , respectively, and LF passed by 0 N at zero acceleration, $t_{\text{LE}=0}$ (vertical dotted lines).

The subject used a GF of 23.6 N during the static phase before the upward movement and 23 N before the downward movement. When the subject began the movement, the GF started to increase and kept increasing approximately until the second peak of LF. Then, it decreased to a lower level when the target was reached and the manipulandum was stabilized.

Static component of GF

Figure [3](#page-5-0) illustrates the evolution of sGF across blocks, for one representative subject (S6) in panel A and for all subjects pooled together in panel B. Each square represents the mean sGF for all seventeen trials of the block (parabola). In Fig. [3a](#page-5-0), the colored circles represent each individual trial. The black-red gradient shows the evolution within the block (black for the beginning and red for the end). Figure [3](#page-5-0)a illustrates that sGF decreased with repetition across blocks for S6. Indeed, the average sGF of the three first blocks was significantly higher than the one of the three last blocks. This difference was significant for eleven out of twelve subjects (all except S12). At this point, it is already possible to state that the GF adaptation is still possible even without any gravitational torque load.

As the range of sGF across the subjects was large (TL 13.20 ± 5.38 N; NoTL 12.56 \pm 4.88 N), the maximum of the mean of each block of each subject was used to normalize sGF before pooling the data across subjects in panel B. For subject S6, the maximum mean sGF corresponded to the mean sGF for block #2 and is indicated by the filled square in Fig. [3a](#page-5-0). In the panel B, red corresponds to the data with torque load (TL) and blue to the data without torque load (NoTL). Figure [3b](#page-5-0) clearly illustrates the significant decrease in sGF across blocks when all the subjects are pooled together (in red). We used the difference between the **Fig. 3** Evolution of sGF across blocks. **a** Data of one representative subject (S6, main experiment). The *squares* are the mean of each block $(\pm SD)$, and the *dots* are the individual trials. The *black square* is the maximum of the means across all blocks and is used for the inter-subject normalization. The *black* to *red gradient* represents the evolution within the blocks $(black = first trial, red = last$ trial). **b** Evolution of the normalized sGF across blocks (mean across subjects \pm SEM). The data collected during the main experiment are in *red*, while the data collected during the control experiment without torque are in *blue* (color figure online)

average sGF of the three first blocks and the average sGF of the three last blocks to quantify learning and found that it is about 33 % in both conditions. The asymptotic performances are also similar across conditions: 41 % in the TL condition and 51 % in the NoTL condition. The comparison of the evolution of sGF in NoTL condition (in blue) shows how much the adaptation rate was influenced by the torque load in TL condition (in red). This observation can be quantified by the difference in time constant of the negative exponential fits in each condition which was more than three times shorter when no torque comes into play (time constant with torque 11.11 blocks, 95 % confidence interval [7.74;18.34]; without torque 3.51 blocks, CI [2.64;4.72]; $R²$ 0.89 in both conditions). Qualitatively, in TL condition, about 30 blocks were necessary before sGF stabilized in comparison with only 10 blocks in the NoTL condition. This exponential fit on individual data converged only for ten subjects out of twelve on the TL condition yielding an average time constant of 15.11 blocks and for five subjects out of six on the NoTL condition yielding an average time constant of 5.27 blocks. Thus, sGF adaptation was much slower in the TL condition even though there was no gravitational component to the torque load.

In addition to this slower adaptation across the blocks, we also observed a slower sGF adaptation across the tri-als within the blocks. Figure [4](#page-6-0) shows the mean $(\pm$ SEM) of normalized sGF across all subjects for all trials plotted across the blocks. The average decrease within blocks has been computed across the first five blocks as the difference in adaptation rate was mainly present during the beginning of the experiment. This average decrease within the blocks was 40 % for the TL condition and 58 % for the NoTL condition and was significantly different between the conditions ($p = 0.01$). The effect on sGF adaptation across the blocks cannot be explained by the difference in inter-block "washout" (increase between consecutive blocks) as the difference between the two conditions was not significant (washout NoTL = 48 % vs. TL = 37 %, $p = 0.1$). Therefore, the slow down of sGF adaptation across the blocks reflected the same effect across trials due to the presence of the torque.

Dynamic component of GF

We investigated whether the presence of torque load had an impact on this GF modulation during the dynamic phase of the movement in comparison with the NoTL condition. To do so, we investigated whether the amplitude of rGF, change of GF with respect to sGF, scaled with the vertical acceleration in the same way in both conditions.

Figure [5](#page-7-0)a shows this relationship for one subject (S11) in the TL condition in the four cases (UP and DOWN, acceleration and deceleration peaks). On the panel B, the regression slopes of all subjects in both conditions are pooled together. There was a significant difference of slopes neither between conditions (TL vs. NoTL) nor between the upward versus downward movements (condition $F_{1,16} = 0.02$, $p = 0.88$; direction $F_{1,16} = 0.51$, $p = 0.48$). Moreover, there was no significant difference across the blocks, meaning that, unlike sGF, the relationship between GF and acceleration stayed stable during the whole experiment (block $F_{8,128} = 0.46, p = 0.53$).

The correlation between rGF and the acceleration was significant in all conditions (acceleration and deceleration

Fig. 4 Evolution of the sGF across blocks detailed by trial. The *thick lines* are the means across subjects, and the *shaded surface* represents the SEM. The *gray lines* are the beginning of each block. A zoom of the fifth block is shown at the *top* of the figure

peaks, upward and downward movements, NoTL and TL) and for all subjects. This correlation was still significant when movements of one amplitude (between two adjacent targets: 10 cm) were considered separately. Hence, this correlation was not due to categorical changes in movement planning across different amplitudes; instead, it reflects a fine coupling taking into account the subtle variation of movement kinematics across individual trials.

The lack of differences between the TL and the NoTL conditions in the dynamic phase supports not only that GF is still modulated even in presence of TL but also that TL is well estimated by the internal model dealing with GF modulation. Indeed, the fact that the slopes are not significantly different between TL and NoTL conditions suggests that the tangential and rotational constraints at the fingertips are taken into account and well estimated since these constraints are identical for the same acceleration in the two conditions (see ["Methods](#page-1-0)" section).

Discussion

Our results show that despite a good and stable grip-force modulation during the dynamic phase and a good correlation with the vertical acceleration, a slow down of the adaptation of the baseline of grip force is still induced by the presence of an inertial torque during object motion. Two important results will be discussed in this section. Firstly,

the baseline level of sGF still decreased with repetition, even in the presence of an off-centered mass but, more interestingly, the decrease was much slower than when no torque came into play. We also have shown that this difference in baseline of grip-force adaptation rate reflected a difference in adaptation within the blocks as the inter-block washout was similar in the torque and no-torque condition. Secondly, the difference in static grip-force adjustment rate is present despite qualitatively similar predictive gripforce modulation during the dynamic phase, with or without torque experienced by the participants. Paradoxically, the inertial component of the torque load that only impacts the constraints during the dynamic phase of the movements seems to alter mostly the control of the baseline of grip force measured during the static phases.

Static phase

In this study, we isolated the influence of the inertial torque on grip-force adjustments and we showed that it is sufficient to slow down the adaptation of baseline grip force in comparison with the adaptation observed in the control experiment and in previous reports (Crevecoeur et al. [2009,](#page-8-13) [2011\)](#page-8-3). This result unmasks the specific role of the inertial part of TL, reproducing an effect already described in the literature during a repetitive grip-lift task in the presence of both gravitational and inertial components of TL (Crevecoeur et al. [2011\)](#page-8-3). This proves that the

Fig. 5 Correlation between the rGF and the acceleration (absolute value). **a** Exemplar subjects for all the movements (S11 for the TL condition and S4 for the NoTL condition). **b** Boxplots of the regression slope for all the subjects pooled together. In the boxplots, the *thick line* represents the median and the *box* represents the interquartile range

inertial torque load is sufficient to impact the adaptation of the baseline of grip force that is applied during the whole task but highlighted during the static phases, despite the fact that there is no gravitational or inertial load during stationary holding.

The GF washout between each block directly influences the GF adaptation rate. As we have shown, this inter-block washout was substantial and likely interfered with the overall adaptation observed across the parabolas. This washout effect has already been pointed out in the literature as a potential factor influencing short-term adaptation during parabolic flights (Crevecoeur et al. [2010a,](#page-8-14) [b](#page-8-10)). The present study clearly shows the presence of washout across parabolas, but it does not explain the slower adaptation rate observed in the presence of an offcentered mass. Indeed, we observed an overall slower decrease in the static grip force with torque, despite a smaller washout across blocks.

Note that the slowdown of baseline grip force cannot be explained by an effect of the weightlessness condition as the control and the main experiments were performed in microgravity. So, we can conclude that the difference in adaptation rate in the presence of a torque was predominant due to the inertial torques generated during the movements. In addition, it is interesting to note that the slow down of the adaptation between torque and no-torque conditions was very large in the present study (time constant three times larger) and was of the same order of magnitude as in the study of Crevecoeur et al. [\(2011](#page-8-3)) (time constant four times larger) even though the experimental protocol and conditions were very different in the two studies. This shows that a dramatic increase in time constant might be a general signature of adding a torque load in object manipulation.

Dynamic phase

It is well established that there is a tight coupling between the GF and the LF when moving a grasped object (Flanagan and Wing [1993](#page-8-4), [1995;](#page-8-15) Flanagan et al. [1993](#page-8-6), [2006](#page-8-16); Flanagan and Tresilian [1994\)](#page-8-17). This modulation, which is based on a predictive model, is also present in microgravity and hypergravity (Hermsdörfer et al. [2000;](#page-8-18) Augurelle et al. [2003](#page-8-9); White et al. [2005;](#page-9-3) Crevecoeur et al. [2009](#page-8-13)) as well as between the GF and the TL (Wing and Lederman [1998](#page-9-4)). In this study, we confirmed that GF continues to be modulated as a function of the tangential loads even in the special case of weightlessness and even in the presence of an off-center mass. This was based on the observed tight coupling between GF and the vertical acceleration. Indeed, the tangential constraints can be estimated precisely from only the vertical acceleration if there is no rotation (Crevecoeur et al. [2011\)](#page-8-3). The present experiment could not assess if the subjects modulated their GF based on an estimate of tangential constraints or directly from the vertical acceleration. However, based on the vertical acceleration, our analyses showed that grip-force modulation was similar in the presence or absence of a torque load and that this modulation was stable from the first blocks.

Our results suggest that the modulation of grip force accounted for the presence of a torque. Indeed, the mass of the manipulandum differed across the experiments, which should have induced a difference in modulation gain if it were based on the net mass only (White et al. [2005\)](#page-9-3). The present experiment cannot assess whether participants were able to extract the specificity of rotational constraints induced by a torque from fingertip afferent or proprioceptive feedback. However, the similar gains across experiments suggest that the net amount of constraints, including

the effect of the torque, was taken into account in the generation of anticipatory grip-force modulations

Knowing the effect of the torque load on the baseline GF (Crevecoeur et al. [2011\)](#page-8-3), this result confirms the extension of the well-known phenomenon grip-force modulation depending on the load force to a more general gripforce modulation depending on the load force and the torque load that takes into account both gravitational and inertial torque loads (Kinoshita et al. [1997](#page-8-19); Goodwin et al. [1998](#page-8-7)).

Conclusions

We can make three important conclusions. First, the presence of an inertial torque is sufficient to slow down the adaptation of the baseline of grip force highlighted during stationary holding. Second, subjects are able to estimate rapidly and precisely the global constraints, including inertial torque, as demonstrated by the fact that GF/acceleration modulation was similar whether a torque is present or not. And thirdly, as suggested in previous studies (Augurelle et al. [2003](#page-8-9); Crevecoeur et al. [2009](#page-8-13), [2011](#page-8-3)), the difference of impact of the torque load depending on the grip-force components suggests that the adaptation of the baseline grip force and relative grip force may be distinct processes with distinct learning capabilities. It remains to be demonstrated if these two processes are implemented by distinct or overlapping parts of the CNS.

Finally, it is important to mention that the sensorimotor adaptation of the grip-force control during object manipulation is potentially a powerful tool for assessing learning capabilities in clinical as well as fundamental research. The slower adaptation due to the torque load allows assessing more precisely the learning capabilities. This adaptation measurement could be useful for clinical diagnostics or rehabilitation monitoring for example. The presence of an off-centered mass inducing a torque load provides an easy and effective way to investigate grip-force adjustments because it slows down the adaptation rate and makes learning mechanisms more apparent (Crevecoeur et al. [2011](#page-8-3)). Thus, this study is important since it helps better understanding the mechanisms of the slower grip-force adaptation in the presence of a torque.

Acknowledgments The authors thank the subjects for their participation and A. Barrea, D. Cordova Bulens, B. Delhaye and V. Théate for their help during the parabolic flight campaigns.

Grants This research was supported by a grant from the European Space Agency (ESA), PRODEX and IAP (Belspo), and ARC (Belgium). J. McIntyre is supported by Université Paris Descartes, the Centre National de la Recherche Scientifique, the Conseil Régional Ile de France and by a grant from the Centre National d'Etudes Spatiales (CNES).

Compliance with ethical standards

Disclosures The scientific responsibility for this work rests with its authors.

References

- Augurelle A-S, Penta M, White O, Thonnard J-L (2003) The effects of a change in gravity on the dynamics of prehension. Exp Brain Res 148:533–540
- Cornbleet PJ, Gochman N (1979) Incorrect least-squares regression coefficients in method-comparison analysis. Clin Chem 25:432–438
- Crevecoeur F, Thonnard JL, Lefèvre P (2009) Forward models of inertial loads in weightlessness. Neuroscience 161:589–598
- Crevecoeur F, McIntyre J, Thonnard J-L, Lefèvre P (2010a) Movement stability under uncertain internal models of dynamics. J Neurophysiol 104:1301–1313
- Crevecoeur F, Thonnard J-L, Lefèvre P (2010b) Sensorimotor mapping for anticipatory grip force modulation. J Neurophysiol 104:1401–1408
- Crevecoeur F, Giard T, Thonnard J-L, Lefèvre P (2011) Adaptive control of grip force to compensate for static and dynamic torques during object manipulation. J Neurophysiol 106:2973–2981
- Danion F, Diamond JS, Flanagan JR (2012) The role of haptic feedback when manipulating nonrigid objects. J Neurophysiol 107:433–441
- Danion F, Diamond JS, Flanagan JR (2013) Separate contributions of kinematic and kinetic errors to trajectory and grip force adaptation when transporting novel hand-held loads. J Neurosci 33:2229–2236
- De Gregorio M, Santos VJ (2013) Precision grip responses to unexpected rotational perturbations scale with axis of rotation. J Biomech 46:1098–1103
- 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, Wing AM (1993) 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, Tresilian J, Wing AM (1993) Coupling of grip force and load force during arm movements with grasped objects. Neurosci Lett 152:53–56
- Flanagan JR, Vetter P, Johansson RS, Wolpert DM (2003) Prediction precedes control in motor learning. Curr Biol 13:146–150
- Flanagan JR, Bowman MC, Johansson RS (2006) Control strategies in object manipulation tasks. Curr Opin Neurobiol 16:650–659
- Goodwin A, Jenmalm P, Johansson RS (1998) Control of grip force when tilting objects: effect of curvature of grasped surfaces and applied tangential torque. J Neurosci 18:10724–10734
- Hermsdörfer J, Marquardt C, Philipp J (2000) Moving weightless objects. Exp Brain Res 132:52–64
- Johansson R, 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
- Kinoshita H, Bäckström L, Flanagan JR, Johansson RS (1997) Tangential torque effects on the control of grip forces when holding objects with a precision grip. J Neurophysiol 78:1619–1630
- Kutz DF, Wölfel A, Timmann D, Kolb FP (2009) Dynamic torque during a precision grip task comparable to picking a raspberry. J Neurosci Methods 177:80–86
- Nowak D, Hermsdörfer J, Schneider E, Glasauer S (2004) Moving objects in a rotating environment: rapid prediction of Coriolis and centrifugal force perturbations. Exp Brain Res 157:241–254
- Westling G, Johansson RS (1984) Factors influencing the force control during precision grip. Exp Brain Res 53:277–284
- White O, McIntyre J, Augurelle A-S, Thonnard J-L (2005) Do novel gravitational environments alter the grip-force/load-force coupling at the fingertips? Exp Brain Res 163:324–334
- Wing AM, Lederman SJ (1998) Anticipating load torques produced by voluntary movements. J Exp Psychol Hum Percept Perform 24:1571–1581