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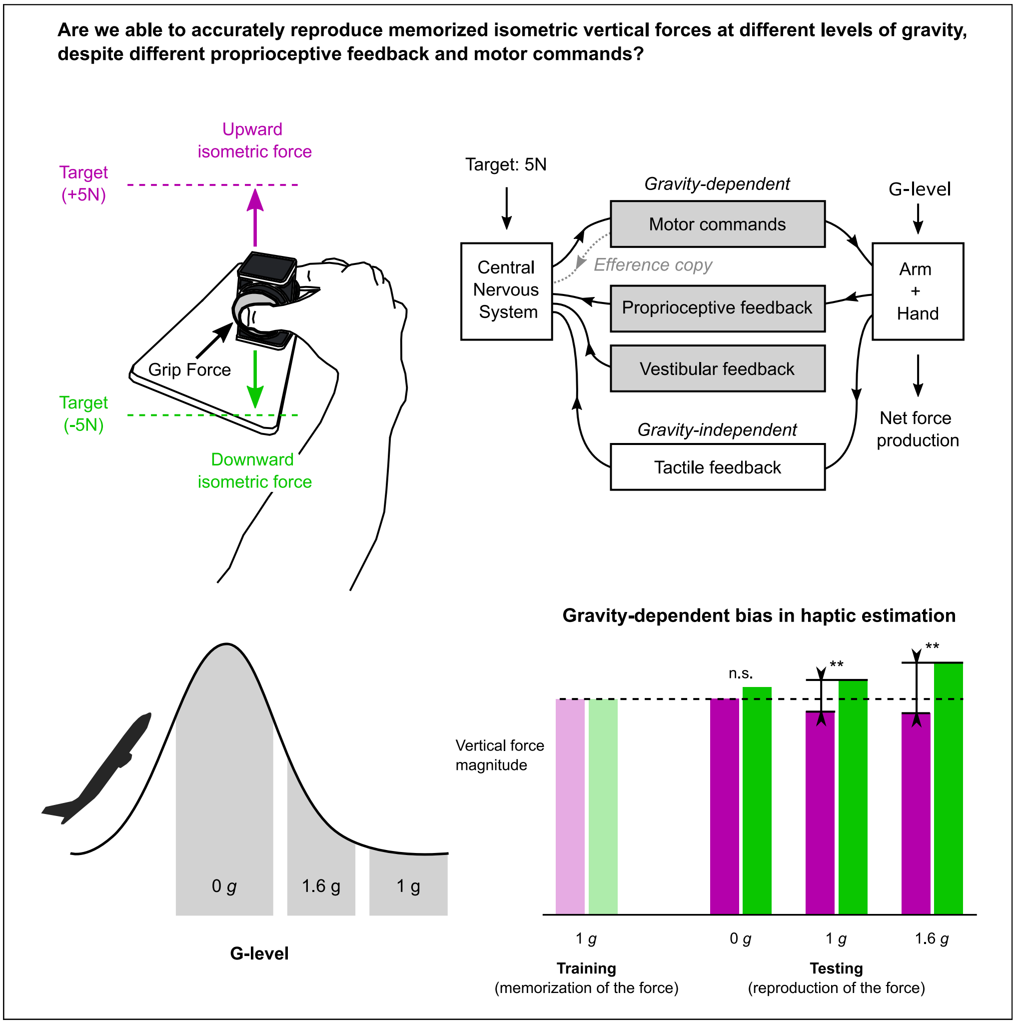

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Highlights

Gravity biases the haptic estimation of isometric vertical forces

Gravity creates the illusion that upward forces are larger than downward forces

The illusion disappears in microgravity and is increased in hypergravity

The illusion also impacts the control of prehension

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A haptic illusion created by gravity

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SUMMARY

Human dexterity requires very fine and efficient control of fingertip forces, which relies on the integration of cutaneous and proprioceptive feedback. Here, we examined the influence of gravity on isometric force control. We trained participants to reproduce isometric vertical forces on a dynamometer held between the thumb and the index finger in normal gravity and tested them during parabolic flight creating phases of microgravity and hypergravity, thereby strongly influencing the motor commands and the proprioceptive feedback. We found that gravity creates the illusion that upward forces are larger than downward forces of the same magnitude. The illusion increased under hypergravity and was abolished under microgravity. Gravity also affected the control of the grip force employed to secure the grasp. These findings suggest that gravity biases the haptic estimation of forces, which has implications for the design of haptic devices to be used during flight or space activities.

INTRODUCTION

Fine manual force control is a fundamental aspect of dexterity, enabling humans to accomplish complex and eloquent tasks, from delicate surgeries to the teleoperation of a gigantic robotic arm while floating on board the International Space Station. Achieving such high-precision dexterity requires one to estimate the forces applied by the fingers to the tools they manipulate. Questions remain regarding how the nervous system combines tactile, proprioceptive, and internal efferent feedback to estimate these forces. In particular, it is not clear whether gravity, which impacts the motor commands and proprioceptive feedback associated with the production of a specific force, influences the haptic estimation of forces. Answering this question is of primary importance for the design of haptic devices to be used in environments experiencing highly variable gravito-inertial accelerations, such as fighter jets or spaceships.

During object manipulation, grasping forces must be finely controlled to prevent accidental slips while minimizing muscle fatigue. Slips occur when the tangential component of the contact force (a friction force) exceeds some threshold proportional to the normal component of the contact force (Coulomb's law). When holding an object in precision grip (i.e. between the thumb and the index finger), one can ensure that this threshold is not exceeded by tuning the grip force (GF), which is applied perpendicularly to the contact surfaces, to the load force (LF), which is produced by the tangential forces applied by each finger.[1,2] Many studies have examined the coordination between LF and GF during object manipulation to probe human dexterity. In a large variety of tasks (arm movements,[1,3,4] locomotion,[5] controlled collisions,[6–8] etc.), tight coupling between LF and GF is observed, suggesting that the nervous system estimates LF online with good accuracy during voluntary movements, which allows precise anticipative and reactive adjustments of GF.

A key player in GF-LF coordination is the tactile feedback transmitted by cutaneous mechanoreceptors.[1,9–13] These receptors are sensitive to skin deformation, and their input allows precise estimation of tangential and normal contact forces.[14–17] Abolishing tactile feedback using anesthesia greatly impairs GF-LF coupling,[1,11,12] and recent studies have shown that stretching the skin artificially during object manipulation can alter the perception of LF and thus the control of GF.[18,19] But the nervous system also estimates forces based on the activities of hand and arm muscles via proprioceptive receptors (muscle spindles and tendon organs)[20–22] or based on motor commands sent to the muscles.[23–25] Importantly, producing a force against versus in the direction of gravity, or in normal versus altered gravity, will require very distinct arm muscle activities. The main objective of the present study was to test whether the nervous system is able to reproduce memorized isometric LFs and maintain an adequate GF-LF coupling in different gravito-inertial environments, despite very distinct proprioceptive feedback and arm motor commands.

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The influence of gravity on GF-LF coordination has received much attention in the last 30 years. It has been shown that the nervous system anticipates the effects of gravity when predicting the consequences of arm movements on LFs[4,26] and when reacting to unpredictable perturbations.[27] Later studies have reported that an adequate GF-LF coupling can be maintained across the various gravito-inertial levels experienced during parabolic flight after a short adaptation period, during arm movements[28–32] or when holding an object stationary.[33] Thus, the nervous system is able to adapt motor commands and predictions adequately to microgravity and hypergravity in order to maintain a safe and efficient grip control. However, manipulating an object that is free to move is fundamentally different from producing isometric forces on a haptic interface. In the first case, inaccurate load force productions lead to inappropriate movements of the object, which are picked up rapidly by the visual and proprioceptive systems and can help adjust and estimate manipulation forces and update internal representations of limb and object dynamics.[34,35] In microgravity, for instance, motor commands adjust rapidly to reproduce movements learned in normal gravity.[36–39] The new internal representation of limb dynamics can then be used to update the feedforward mechanisms participating in LF estimation.[11,40,41] When using an isometric interface, motion feedback and movement errors are not available to aid in LF estimation or to update internal models. In this context, the nervous system can rely only on tactile and proprioceptive force feedback and on "sense of effort" based on efference copies.[21,23,42] Therefore, adaptation of the GF-LF coordination to altered gravity may be more challenging in that context.

To answer these questions, we studied the ability of human participants to reproduce memorized isometric load forces during exposure to various gravito-inertial levels (G-levels) induced by parabolic flight. Participants were trained on the ground to produce upward and downward isometric LFs of 5 N on a static dynamometer held in precision grip. They were asked to reproduce these vertical forces without explicit feedback during parabolic maneuvers producing distinct G-level phases, which constituted microgravity (0 *g*) and hypergravity (1.6 *g*) conditions. We found that gravity was associated with LF production bias such that the magnitude of LF reproduced was consistently larger in the downward direction than in the upward direction in normal gravity. Importantly, this bias was reduced in microgravity and more pronounced in hypergravity. In contrast, GF values were similar in both LF directions regardless of G-levels, leading to a decoupling between GF and LF magnitudes that persisted until the last parabola. We suggest that gravity biases force estimation during isometric force production, creating a haptic illusion.

RESULTS

Establishment of the experimental model

Participants (N = 11) were trained to apply upward and downward isometric LFs of 5 N on a dynamometer fixed to a support (see STAR Methods). They held the dynamometer in a precision grip (Figure 1A) and applied an isometric LF by pulling the dynamometer upward or downward. At regular intervals, the target LF was communicated via an auditory feedback cue, namely a beep that was emitted whenever the LF magnitude was within the range of 4–6 N. The participants were then asked to reproduce the memorized LF when the auditory feedback was off. No explicit instruction was given to the participants regarding grip force, but they were asked to avoid slips during the production of the vertical force. Upward and downward trials were always performed in alternance. LF was computed as the absolute value of the resultant force applied by both fingers along the vertical axis, tangentially to the contact surfaces. Applied GF was computed as the mean of the normal forces applied by each finger.

Trained participants reproduced the learned LF, first on the ground ($\leq$24 h before the flight) and then on board the aircraft during level flight in a steady 1-g environment, before undertaking the experiment during parabolic maneuvers (Figure 1B). On the ground and during level flight, they performed two sequences of 20 trials without auditory feedback (test trials, Figure 1C), alternating between downward and upward LFs. They performed 6 additional trials with auditory feedback after each such sequence to remind them of the target (practice trials, Figure 1C). Each trial lasted 2 s with a 1-s intertrial break. The force data were averaged within the plateau phase of each trial (Figure 1D; see STAR Methods).

Isometric LF reproduction is asymmetric in normal gravity

We focus here on data obtained during level flight (Figure 2), which were similar to the ground data (see Figure S1). During the test trials, LF remained on average within the target bounds yielding a mean LF ($\pm$SD) of 4.98 $\pm$ 1.15 N (Figure 2A). LF decreased gradually across the 20 trials of each sequence, by about 18% on average. A concomitant decrease in GF of similar magnitude was observed (Figure 2B). We

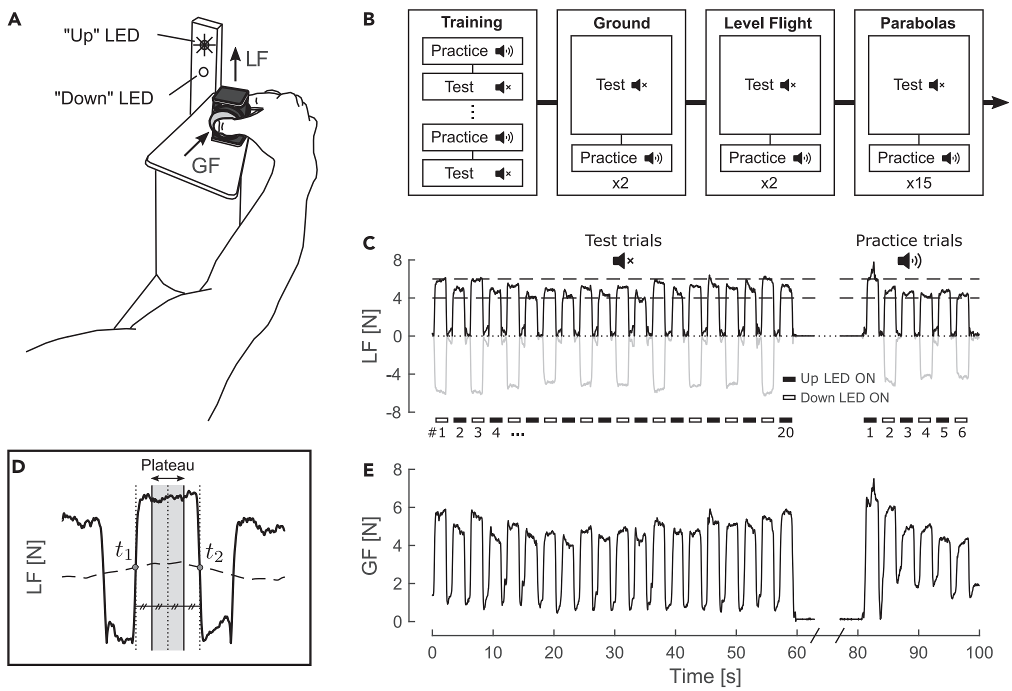

Figure 1. Experimental design and data analysis

(A) Task: Participants held a static dynamometer between their thumb and index finger and were instructed to produce upward and downward isometric load forces (LFs) of 5 ± 1 N. An LED display indicated the direction of LF to produce.

(B) Protocol: Participants were first trained on the ground to produce the desired LF. During practice trials, a beep was emitted when the produced LF was within the target bounds ([4 N, 6 N]). During test trials, no auditory feedback was given. They were asked to reproduce the memorized forces on the ground, during level flight, and during parabolic maneuvers producing phases of microgravity and hypergravity.

(C) LF during a typical sequence of test and practice trials performed on the ground. The gray line shows the signed values of LF (negative for downward forces). The dashed horizontal lines indicate the target LF (5 ± 1 N).

(D) Magnified view of LF during one trial from panel C. Individual trials were delimited by the points t_1 and t_2 defined as the intersections between LF (plain line) and a downscaled moving average of LF computed with a 3-s sliding window (dashed line). For each trial, the plateau phase was defined as a window centered between t_1 and t_2 (shaded gray area).

(E) Grip force (GF) measured in the trials shown in panel C.

observed a strong temporal correlation between GF and LF for all test sequences ($r = 0.93 \pm 0.05$, mean ± SD) consistent with the GF-LF coupling typically observed in object manipulation tasks.

Strikingly, up/down asymmetry in LF was observed. LF was significantly larger in the downward direction than in the upward direction, by 19% (0.86 N) on average ($t_{10} = -3.56$; $p < 0.01$). Despite tight temporal coupling between LF and GF, GF remained similar for the two LF directions (Figure 2B; $t_{10} = -1.06$; $p = 0.31$). During the practice trials performed with auditory feedback, both LF ($t_{10} = -0.74$; $p = 0.48$) and GF ($t_{10} = 0.94$; $p = 0.37$) were similar in the two directions, as expected.

G-level affects LF asymmetry but not GF symmetry

When the participants repeated the same task during parabolic maneuvers, during which the G-level varied from 0 g to around 1.6 g (Figure 3A), they reproduced the LF that had been learned in 1 g in both the microgravity (0 g) and hypergravity (1.6 g) conditions with good accuracy (Figure 3B), even though auditory feedback was not given during the parabolas. Nevertheless, a clear effect of G-level on up/down LF asymmetry was observed. During microgravity phases (trials 1–6), when G-level (and thus arm weight) was close to zero, LF asymmetry was reduced compared with LFs produced in 1 g during level flight. Subsequently, as G-level increased from 0 to 1.6 g (trials 7–12), the difference between downward and upward LFs increased substantially, approaching a 30% difference on average after the transition from 0 to 1.6 g. This asymmetry decreased progressively as the G-level returned to 1 g (trials 12–20). This pattern was observed from the first to the last parabola (see Figure S2 and STAR Methods) and was observed for experienced participants

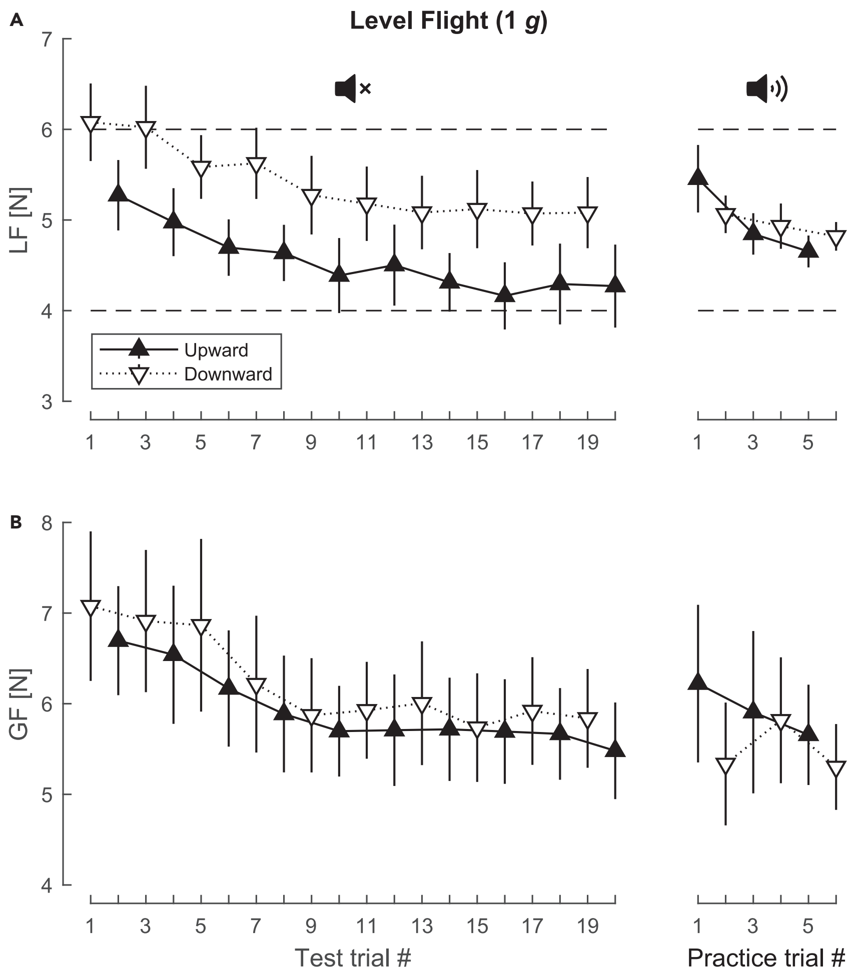

Figure 2. Average force data during level flight
Evolution of LF (A) and GF (B) across test and practice trials performed during level flight. The two sequences were averaged by participant and trial number. The Fig shows the means (upward/downward pointing triangles for upward/downward LF) ± 1 standard error of the mean (SEM; error bars) across participants (N = 11). The horizontal dashed lines in panel A show the LF target zone. See also Figure S1.

(N = 6, see STAR Methods) as well as for inexperienced participants (N = 5) who were being exposed to parabolic maneuvers for the first time (see Figure S3).

In contrast to LFs, GFs remained symmetrical at all G-levels, being similar for upward LFs and downward LFs (Figure 3C), resulting in a decoupling between LF and GF magnitudes. GF appeared to follow LF inter-trial variations well for downward trials, but less so for upward trials. Notwithstanding, a strong temporal correlation was maintained between GF and LF and the mean correlation coefficient (±SD) during the parabolas was 0.90 ± 0.05. This coefficient was stable across parabolas. Similar to the behavior observed during level flight, participants adjusted GF as a function of LF, but they failed to account for the directional bias in LF production modulated by G-level.

To quantify the effects of G-level and direction on LF and GF, we divided the test trials into three distinct bins corresponding to 0-, 1-, and 1.6-g gravito-inertial accelerations (see STAR Methods). The mean LF, GF, and GF/LF ratio values obtained are shown in Figure 4 (upper panels) together with the mean differences in values between upward and downward trials (lower panels). There was no main effect of G-level on LF ($F_{2,20}$ = 0.59, p = 0.57). However, LF was globally significantly greater in the downward direction than in the upward direction ($F_{1,10}$ = 26.5, p < 0.001; Figure 4A) and this asymmetry was modulated by G-level, as indicated by a significant interaction effect between G-level and direction ($F_{2,20}$ = 5.34, p = 0.01;

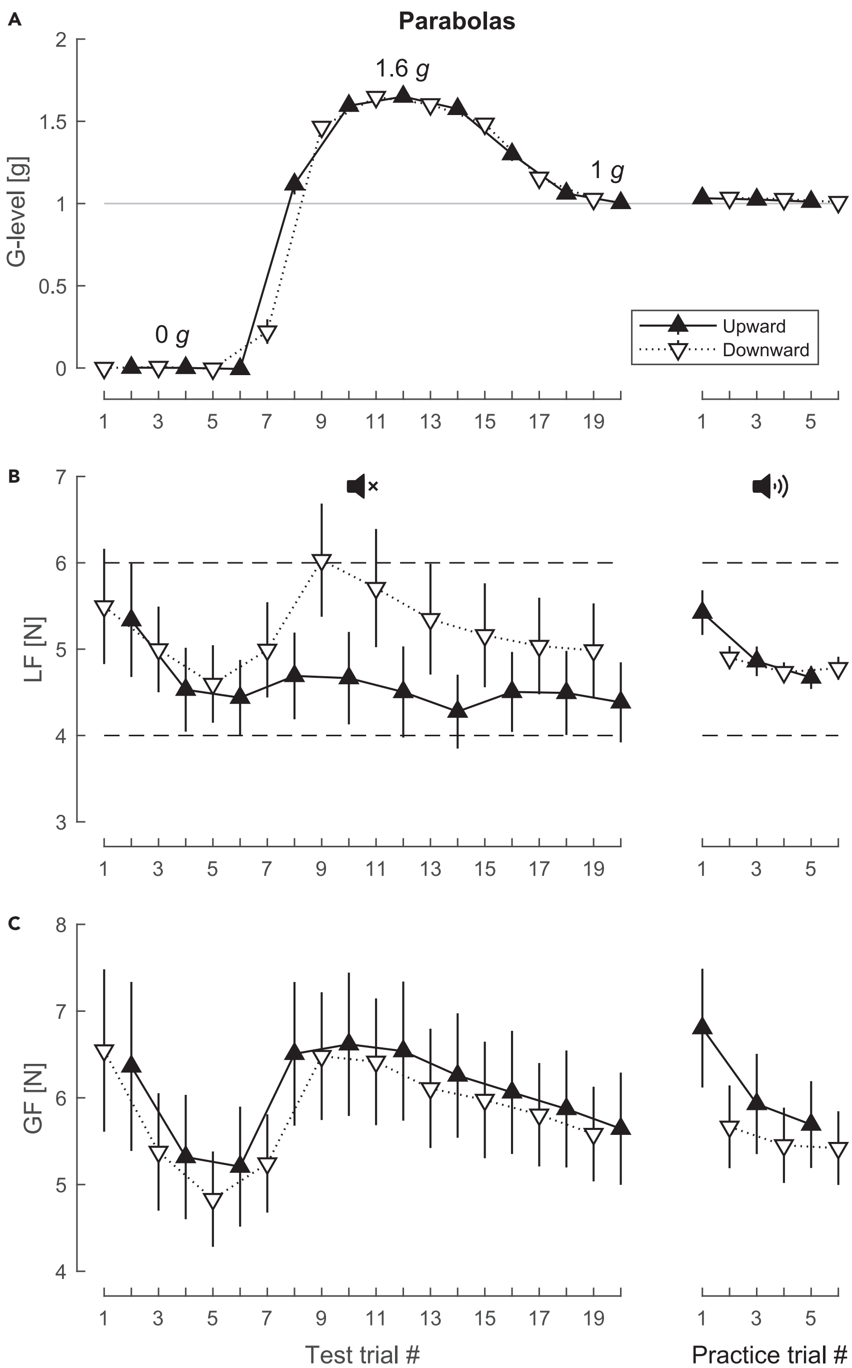

Figure 3. Average force data during the parabolas

Evolution of G-level (A), LF (B), and GF (C) across test and practice trials. The data obtained in 15 parabolas performed by each participant were averaged by participant and trial number. The Fig shows the means (upward/downward pointing triangles for upward/downward LF) ± SEM (error bars) across participants (N = 11). The horizontal dashed lines in panel B show the LF target zone. See also Figure S2.

Figure 4B). Downward LF increased significantly with G-level ($F_{2,20}$ = 3.87, p = 0.038), while the decrease of upward LF with G-level was not significant ($F_{2,20}$ = 1.30, p = 0.30). As a consequence, the difference between downward and upward LF increased with G-level (Figure 4B), being non-significantly different from zero in 0 g (t_{10} = 2.09, p = 0.06) while being significantly positive in 1 (t_{10} = 3.42, p < 0.01) and 1.6 g

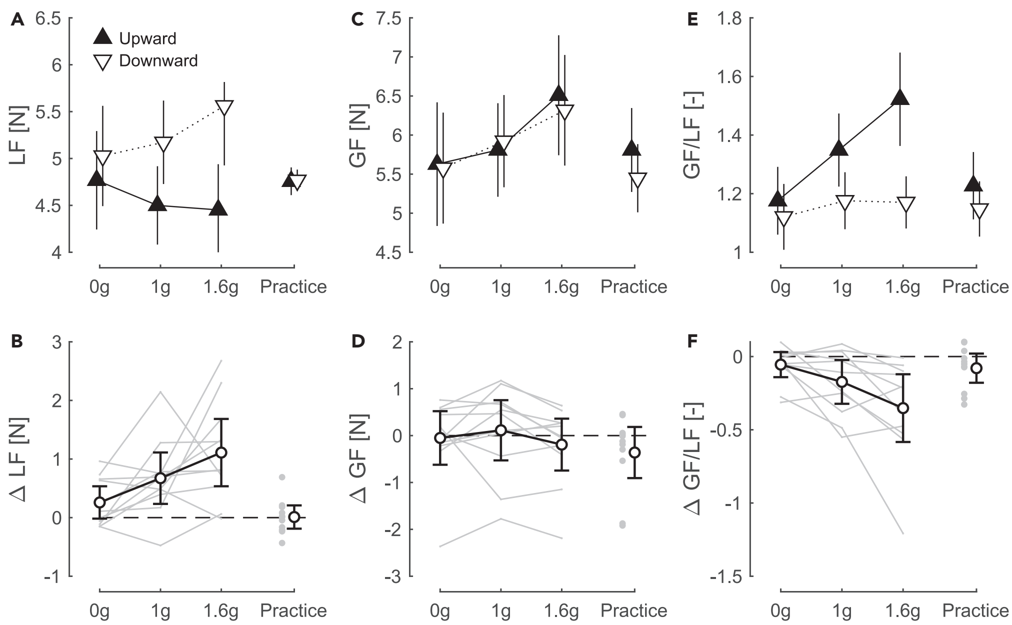

Figure 4. Up/down asymmetry as a function of G-level

(A, C, and E) Mean LF, GF, and GF/LF values in each G-level bin during practice and test trials. Triangle markers and error bars show the mean ±1 SEM across participants (N = 11).

(B, D, and F) Mean differences between downward and upward trials for LF, GF, and GF/LF ratio. Error bars with caps show the 95% confidence intervals. Gray lines show data from each participant. The 1 g and practice bins include the level-flight data shown in Figure 2.

See also Figure S3.

(t_{10} = 4.31, $p < 0.005$). Conversely, GF did not differ significantly between upward and downward trials (Figures 4C and 4D; $F_{1,10}$ = 0.03, p = 0.87). GF tended to increase with G-level, but the effect was not significant ($F_{2,20}$ = 2.54, p = 0.10) and there was no significant interaction between G-level and direction for GF ($F_{2,20}$ = 1.33; p = 0.29). Due to decoupling between LF and GF magnitudes, the GF/LF ratio was not constant across directions and G-levels (Figure 4E). Rather, we observed significant main effects of both G-level ($F_{2,20}$ = 9.33, $p < 0.005$) and direction ($F_{1,10}$ = 10.2; $p < 0.01$) on the GF/LF ratio, as well as significant interaction between G-level and direction for GF/LF ratio ($F_{2,20}$ = 7.84, $p < 0.005$; Figure 4F). Scaling between GF and LF was thus gravity dependent.

DISCUSSION

The present study shows that gravity biases isometric force production, as reflected by a gravity-dependent up-down asymmetry of reproduced LF. Unexpectedly, when participants were instructed to reproduce a vertical LF that had been practiced on the ground (1 *g*) with symmetry relative to zero (±5 N), they failed to reproduce the symmetry practiced in training, even in the exact same gravity condition. Reproduced LFs had consistently larger downward magnitudes than upward magnitudes in a 1 *g* condition. This asymmetry increased in hypergravity and disappeared in microgravity during parabolic maneuvers, and thus we deduce that it was directly related to arm weight. Strikingly, GF, which is supposed to be scaled to LF to prevent accidental slips, had always similar magnitudes whether LF was produced upward or downward. In other words, GF was not accurately tuned to LF. We propose that our data reflect a haptic illusion—an overestimation of upward forces and/or an underestimation of downward forces—that is caused and modulated by gravity and that can affect grip control.

Contribution of gravity-dependent muscular effort to LF estimation

The present results are compatible with the hypothesis that the nervous system estimates load forces by combining tactile feedback with a sense of effort related to arm or hand muscle activity.[23,43,44] Had the participants relied solely on tactile feedback to memorize and reproduce the force, we would not have observed any influence of G-level on LF reproduction. By detecting skin deformations at the fingertips, tactile feedback alone should indeed provide accurate tangential force feedback unbiased by gravity.[14,16,45–47] But tactile feedback is also subject to uncertainties. For instance, a given tangential force can in general lead to distinct patterns or amplitudes of skin deformations (and thus afferent responses) depending on the normal component of the contact force as well as on the frictional properties of the contact interface.[45,47,48] Combining tactile feedback with proprioceptive feedback and motor commands associated with the hand and/or arm muscles should reduce these uncertainties to some degree.

However, muscular effort is necessarily biased by gravity: producing a 5-N LF in opposition to gravity (upward) requires more effort than producing the same LF in the direction of gravity (downward). If muscular effort contributes to force estimation, upward LFs would be expected to be overestimated relative to downward LFs. This may be why we observed asymmetric LFs in 1 g, and why these asymmetries were reduced in 0 g. Although participants were not explicitly told to match upward and downward forces, they knew that both forces were the same magnitude. Alternatively, they may simply have failed to account correctly for the weight of their arm. Background G-level modulates the tonic muscle activity required at the shoulder joint to compensate for limb weight. Underestimating this tonic activity in hypergravity would lead to an under-compensation of arm weight, which would increase the asymmetry between upward and downward LFs, as observed in our data. Note that the sense of effort is also influenced by muscle fatigue,[21,23] which may be one reason explaining the progressive force decline observed across trials during level flight and on the ground, although the forces produced were relatively low compared with MVC values (see STAR Methods and[11,49]).

Muscular effort can be sensed via internal feedback about motor commands (efference copies) or via proprioceptive feedback conveyed by muscle spindles and tendon organs. In line with our data, both motor commands[23,50] and proprioception[20–22] have been shown to influence the conscious perception of forces. Additionally, anisotropies in haptic force perception have been observed in the horizontal plane previously, with manual forces produced in directions requiring larger effort (due to larger limb impedance) being perceived as larger.[43,44] The present data reveal an anisotropy in haptic force estimation in the vertical plane (up/down asymmetry) caused by gravity and consistent with a role of muscle activity in force estimation.

GF-LF coupling is affected by G-level in isometric conditions

Our data showed a tight temporal correlation between GF and LF that was maintained during parabolic maneuvers, consistent with the robustness of the GF-LF coordination that has been reported in past parabolic flight studies involving arm movements.[28–32] Such fine synchronization between GF and LF can be explained by the hypothesis that the nervous system predicts the consequences of motor commands sent to the arm and hand muscles and uses tactile and proprioceptive feedback to calibrate these predictions and respond to unexpected perturbations.[1,11,25,51]

Interestingly though, our results highlighted a decoupling between GF and LF in terms of force magnitude across the various G-levels, in contrasts with the results of several past studies involving active arm movements. In those studies, the authors observed a constant scaling between GF and LF during rhythmic arm movements in altered gravity[29,30] or when the arm was loaded with a ballast[30] or an elastic band,[52] indicating that GF can be tuned accurately to LF independently of the muscle activity generated to move the arm. This dissimilarity relative to our results suggests that the additional visual and kinesthetic feedback available during arm movements may improve grip control significantly. For instance, the nervous system could use internal inverse models to infer manipulation forces from the kinematics of the manipulated object.[53,54] In agreement with this hypothesis, altered visual feedback of object motion has been shown to affect the GF-LF coupling.[55–57] In addition, movement errors can be used to enable rapid adaptation of motor commands to the novel dynamics of an unfamiliar environment. In parabolic flight, a few parabolas are typically required to adapt movement kinematics[39,58] and to stabilize GF-LF coupling.[28,29,32,33] The absence of movement errors might be one factor explaining the absence of significant learning in our paradigm, apart from a direction-independent, non-significant decrease in LF and GF magnitudes that corrected the slight initial overshoots. Note that similar direction-independent overshoots have been described previously during isometric force production in parabolic flight and in human centrifuge in both the horizontal and vertical planes.[59–61]

The decoupling between GF and LF magnitudes was characterized by a larger GF-LF ratio upward than downward in 1 g, and this asymmetry was modulated by G-level. For a stable grasp, the GF to LF ratio must be tuned to the static coefficient of friction of the finger-object interface to avoid slip.[1] Friction anisotropies between upward and downward directions have been documented previously,[27,62] which could affect GF-LF ratio. However, friction is not expected to be affected by G-level, and thus cannot explain the impact of microgravity and hypergravity on GF-LF ratio.

All things considered, we believe that the impact of G-level on GF-LF scaling reflects the influence of gravity on LF estimation. In other words, we propose that the haptic illusion that we describe not only affects LF reproduction but also GF control.

Application to haptic device design

The presently demonstrated gravity-dependent haptic illusion could be considered when designing haptic devices used to support telesurgeries[63] or other remote operations, or haptic supports aimed at improving sensorimotor performance in astronauts.[64] One could implement direction-dependent gains, such that the force output would reflect more accurately the intention of the user, rather than following the actual force produced. For haptic devices to be used in aircraft, in rockets, or on board the International Space Station, these gains could be adjusted as a function of the G-level given that our results indicate that gains optimized for 1-*g* conditions on the Earth's surface may not be optimal in reduced or increased gravity settings. Gravity-dependent gains could help minimize errors in force production when visual feedback about performance is unavailable or unreliable—errors that can have dramatic consequences in these contexts.

Limitations of the study

This study does not distinguish the respective contributions of hand and arm muscles to the illusion that we describe. Future work could test the contributions of shoulder, elbow, wrist, and finger muscles to LF estimation using ballasts, elastic cords, and counterweights attached to different points of the arm during isometric force production. Additionally, performing a similar experiment with the arm supported should allow testing whether the weight of the arm is truly a key factor influencing load force perception. One could also test the impact of hand posture (e.g., flipping the hand 180°) on LF reproduction to control for biomechanical asymmetries. These experiments can be performed on the ground and allow the effects of muscle activity to be distinguished from other effects specific to the conditions of microgravity and hypergravity, conditions that also affect vestibular inputs, postural control,[37,38] spatial orientation,[65–67] limb position sense,[68–70] and stress.[71] Besides, our protocol did not allow us to probe the participants' conscious perception of forces. Studying how gravity influences force perception, and how force perception influences grip control, could improve our understanding of the phenomenon. Although GF control has been shown to be unaffected by some perceptual illusions, such as the size-weight[72,73] or material-weight[74] illusions, we showed here that GF control can be perturbed by gravity-dependent haptic illusion. In the same vein, GF control can be affected by illusions of increased stiffness caused by artificial skin stretch.[19]

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- MVC experiment

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2023.107246.

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AUTHOR CONTRIBUTIONS

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DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

We support inclusive, diverse, and equitable conduct of research.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Raw and analyzed data	This paper	https://doi.org/10.5281/zenodo.7937536
Software and algorithms		
MATLAB R2018a	MathWorks	https://nl.mathworks.com/
RStudio 2022.02.3	RStudio, Inc	https://posit.co/download/rstudio-desktop/
LabView 2013	NI Instruments	https://www.ni.com/fr-be/shop/labview.html
Other		
GLM	Arsalis, Belgium	ESAGLM MEv2; GLM-BOX 1
Airbus A-300 zero-g	Airbus, Novespace	N/A

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Philippe Lefèvre (philippe.lefevre@uclouvain.be).

Materials availability

This study did not generate new unique reagents.

Data and code availability

The data and the scripts used for post-processing and creating the figures are publicly available in the following repository[75]: Zenodo Data: https://doi.org/10.5281/zenodo.7937536.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Subjects

A group of 12 healthy adult volunteers (age, 23–58 years; 9 males, 3 females) participated in this experiment; 6 participants had participated in at least one parabolic flight prior to this study, while the other 6 participants had never experienced parabolic flights before. Data from one participant was excluded (explanation below in the Experimental procedure section). All participants gave their informed consent and received approval for parabolic flight in a National Center for Aerospace Medicine class II medical examination. The experiment complied with the European Space Agency ethical and biomedical requirements for experimentation on human subjects (ESA Medical Board Committee) and was approved by the local French ethics committee (CPP) in charge of reviewing life science protocols in accordance with French law.

Parabolic flight

The experiment was performed during the 58th ESA parabolic flight campaign on board the A-300 zero-*g* aircraft. Each parabolic maneuver began with 20-s of hypergravity (pull-up phase) followed by 22-s of microgravity (0 *g*), before another 20-s period of hypergravity (pull-out phase; 1.6 *g*) and then a progressive transition back to a 1-*g* gravito-inertial level. The beginning and end of each microgravity phase were announced by the pilot as the "injection" and "pull-out" phases, respectively. One flight was performed each day for three consecutive days; a sequence of 31 parabolas was performed in each flight.

METHOD DETAILS

Task

The experimental task consisted of applying the LF, an isometric tangential vertical force of a specified magnitude (5 ± 1 N) and direction (upward or downward), on a static dynamometer held in precision grip. Participants were instructed to grasp the dynamometer in precision grip and to pull it either upward or downward, vertically with respect to the aircraft reference frame (and therefore always aligned with the gravito-inertial force). The force had to be maintained for 2 s. No explicit instruction was given to the participants regarding grip force, but they were asked to avoid slips during the production of the vertical force. A load force magnitude of 5 N was chosen because it is a moderate force that is very commonly produced in everyday-life object manipulation: it corresponds to the force required to hold a 500-g object. Pilot testing indicated that such force is below 10% of MVC in healthy participants (see Section *MVC experiment* below). The tolerance of $\pm$1N was chosen as a compromise between precision and difficulty of the task.

Training

Between 1 and 14 days prior to flight, the participants were trained to memorize and reproduce the desired upward and downward LFs on the dynamometer. The training consisted of sequences of *practice* and *test* trials. During practice trials, auditory force feedback was given as a beep that was emitted whenever the LF magnitude was within the target bounds (4–6 N). During test trials, the participants were asked to reproduce the memorized upward or downward LF, and no feedback was given. The participants were told that the magnitude of the force was the same in the two directions (but were not explicitly instructed to match upward and downward forces). Each participant performed at least four training sequences of 60 trials divided into blocks of 6 practice trials followed by 6 test trials, always alternating between an upward trial and a downward trial. Each trial lasted 2 s (time interval between the onset and offset of the LED target) and the time interval between successive trials was 1 s. A short break was imposed every 30 trials.

Experimental procedures

Once properly trained, participants performed the actual experiment, segmented into sequences of 26 trials. Each sequence started with 20 test trials and ended with 6 practice trials after a 20-s break to maintain good memorization of the forces to be reproduced. Trials always alternated between an upward and a downward force, as illustrated in Figure 1C. As during training, every trial lasted 2 s, with an inter-trial interval of 1 s. The participants performed at least two of these sequences on the ground, then performed two additional sequences on board the aircraft during level flight (1 *g*). Finally, they performed identical sequences during 15 consecutive parabolas. During the parabolas, the sequence started at the injection point (onset of 0-*g* phase) and ended in 1-g after the pull-out phase. On average, participants performed 6 test trials in 0 *g*, ~5 test trials at >1.5 *g*, as well as ~3 test trials in 1 *g* per parabola. The other test trials were performed during the transition phases of the parabolas. All practice trials were performed in 1 *g*.

We rejected the trials that were performed in the wrong direction and those for which the standard deviation of the LF exceeded 20% of the mean during the plateau phase (<1% of trials). Due to technical issues, data could not be acquired during three parabolas for four participants and during five parabolas for two other participants. Furthermore, data could not be acquired during one level-flight block for two participants. In addition, the auditory feedback did not work for one participant on board the aircraft during the practice trials; this participant was removed from the data set.

QUANTIFICATION AND DATA ANALYSIS

Data collection

Duplicate experimental setups allowed data to be acquired from two participants simultaneously during each flight. Because each participant performed the experiment during 15 consecutive parabolas, four participants were tested per flight. The participants were seated and restrained in pairs of side-by-side chairs. In front of each participant, a dynamometer was fixed on a horizontal platform sitting vertically with respect to the aircraft floor. Each dynamometer (GLM, Arsalis, Louvain-La-Neuve, Belgium) was equipped with two force-torque sensors (40 mm diameter, Mini 40 F/T transducers, ATI Industrial Automation, Apex, NC, USA), one for the thumb and one for the index finger. The final distance (50 cm) and orientation of the dynamometer relative to the chair were chosen such that all participants could comfortably grasp the device in precision grip with the arm extended (Figure 1A). The arm used for grasping (right arm) was not supported during the experiment. Two LEDs indicated the direction of the LF to be applied on the dynamometer (upward or downward).

On board the aircraft, G-level was measured with a three-dimensional accelerometer (ADXL330, Analog Devices). Force and acceleration signals were all sampled at 1000 Hz and synchronized thanks to a signal conditioner (Arsalis, Louvain-La-Neuve, Belgium) and a data acquisition system (National Instruments, USA). Offsets of force signals were cancelled before each test sequence so that they were at zero when no force (other than gravity) acted on the sensors. LF was computed as the absolute value of the sum of the vertical component of the tangential forces applied by each finger. GF was computed as the mean of the normal component of the forces applied by each finger.

Data analysis

The data were processed in custom software written in Matlab (Mathworks, USA). Because force offsets were cancelled in a 1 *g* setting (see previous paragraph), force signals obtained during parabolas were corrected to avoid a bias induced by the weight of the sensor plate varying as a function of G-level. This correction consisted in subtracting a G-level-dependent offset, $C = m_s \times (9.81 - G)$, from the vertical component of the force measured by each sensor. In this equation, m_s is the mass of the sensor plate (0.023 kg) and G is the gravito-inertial level, in m/s^2 (9.81 in 1 *g*). Force and accelerometer data were digitally low-pass filtered with a zero phase-lag Butterworth filter of order four with cut-off frequencies of 40 Hz and 5 Hz, respectively.

Because participants were instructed to apply a vertical force and auditory feedback was related to that vertical component during practice trials, we did not consider the horizontal component of tangential forces applied to the dynamometer. The vertical component of the tangential force constituted the LF and accounted for, on average, 98.0 ± 2.6% of the total tangential force.

LF was used to segment the data into individual trials, as illustrated in Figure 1D. A moving-average of LF was computed using a 3-s sliding window and then down-scaled by a factor of 0.8. This down-scaling was performed such that the moving-average crossed the LF signal at around half the value reached by LF during the plateau phase of each trial. The crossing points of this down-scaled moving-average with the LF signal (see t_1 and t_2 on Figure 1D) were used to define the plateau phase in each trial: the plateau phase was defined as a time window located halfway between t_1 and t_2 and having a duration of $0.5 \times (t_2 - t_1)$. On average, the duration of the resulting plateau phases was 971 ± 123 ms (mean ± SD). Mean LF and GF values were computed within each plateau phase.

Statistical analyses

Statistical analyses were performed in R using the *ez* package. For analyses of ground and level-flight data, two-sided paired t-tests were used to compare upward and downward test trials. We also used two-sided paired t-tests to compare upward and downward practice trials (the 1st and 2nd practice trials of each sequence were not included in this analysis to focus on stable performance with explicit auditory feedback). For analyses of the parabola data, the test trials were divided into three bins: a 0-*g* bin for trials performed at a mean G-level between −0.05 and 0.05 *g*; a 1-g bin for trials performed during level flight and at the end of each parabola at a mean G-level between 0.9 and 1.1 *g*; and a 1.6-*g* bin for trials performed at a mean G-level greater than 1.5 *g*. The trials performed during the transition phases of the parabolas were not included in these bins. We checked whether GF and LF changed across parabolas by comparing the first parabola to the last five parabolas in a 3-way repeated-measures ANOVA with factors of Parabola (first/last five), Direction (upward/downward) and G-level (0 *g*/1 *g*/1.6 *g*). During the first parabola, the participants tended to produce greater LFs (and GFs) compared with subsequent parabolas. Because the effect was marginal ($F_{1,10}$ = 3.86, p = 0.07) and independent from G-level ($F_{2,20}$ = 0.81, p = 0.41) and direction ($F_{1,10}$ = 2.91, p = 0.08), all parabolas were pooled together. The effects of direction (upward/downward) and G-level (0 *g*/1 *g*/1.6 *g*) on LF and GF were then tested in 2-way repeated measures ANOVAs. The assumption of sphericity was verified with Mauchly's test. When this assumption was violated ($p < 0.05$), p values were subjected to Greenhouse-Geisser correction.

To study GF-LF temporal coupling, we computed the correlation coefficient between GF and LF signals taken between the onset of the first test trial and the offset of the last test trial of each 20-trial sequence. The correlation coefficient was computed with the Matlab function *corrcoef*.

MVC experiment

In a complementary pilot experiment, we measured the maximum load force that can be produced upward and downward by human participants during maximum voluntary contraction (MVC). Six participants (5 males, 1 female; age, 24–58 years) took part in this experiment. While seated, they were asked to push downward or upward with maximum force on a force sensor (Mini 40 F/T transducers, ATI Industrial

Automation, Apex, NC, USA) located on a table approximately 50 cm in front of them. They used a hand posture similar to the precision grip employed by the participants of the parabolic flight study but applied the vertical force normally to the contact surface instead of tangentially, so that we could isolate the maximum vertical force from the grip force. They performed 3 trials in each direction, and we took the maximum force measured during those 3 trials as the MVC force. The order of the directions (upward/downward) was counterbalanced across participants. We found that the maximum force was >50N in all participants and directions (Downward: Mean = 98.9 N; Min = 71.2 N; Max = 120.0 N. Upward: Mean = 91.0 N; Min = 52.7 N; Max = 117.2 N).