



OPEN Human position sense and the role of gravitational torque: a parabolic flight study

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An important issue in spaceflight is the loss of sensory information associated with malfunction of the proprioceptive system. Specifically, in microgravity, astronauts become uncertain about the positions of their limbs if they cannot see them. We have recently been studying limb position sense during altered gravity conditions and demonstrated that this becomes degraded, most probably because of the changed gravitational torque at limb joints. To further examine this assumption, a one-arm pointing study was conducted to investigate the effects of micro- and hypergravity created during parabolic flight. Results of six participants showed that the effects of altered gravity on position sense were particularly evident when the difference between the gravitational torque experienced under normal gravity and the torque under altered gravity was large. This suggests that a mismatch between the internal model of gravity and incoming sensory information underlies a deterioration of the sense of position. Moreover, it was explored whether the microgravity-induced loss of torque at the elbow joint can be recovered by wearing compression garments, but results revealed no beneficial effect.

Keywords Position sense, Gravitational torque, Microgravity, Hypergravity, Parabolic flight

The last time a human set foot on another celestial body was over 50 years ago. Now, NASA's Artemis space program aims to land humans on the moon again in the near future. Currently there are renewed efforts, worldwide, to revive manned space travel, with the long-term goal of a mission to Mars. The ambitious plan to explore other celestial bodies and even establish habitats there, envisages use of telerobotic systems. The intention is for humans to remotely operate robots on the surface of the moon or Mars, from the safe location of an orbiting space station. It has already been proven that this is technically possible^{1–4}, but at the same time such missions have also highlighted that human performance can be impaired due to the conditions of space travel, in particular, the microgravity effects on proprioception (see⁵ for a review). Research has repeatedly shown that human sensorimotor performance is disturbed, even with simple proprioceptive tasks under conditions of microgravity (see^{6–8} for reviews). The underlying mechanisms have not yet been fully explained and there remain several potential explanations. However, findings have been interpreted frequently in terms of disturbed proprioception in altered gravity conditions^{9–12}.

A striking example of how the human sense of position deteriorates in microgravity is the observation of astronauts who report that if they cannot see their arms in the dark, they have no sense of position in space of their arm (Schmitt and Reid, 1985, as described in⁷). The question of how limb position sense is affected by altered gravity conditions has been investigated by Lackner and DiZio¹³. Blindfolded subjects had to match the perceived position of one arm by placement of the other during hyper- and microgravity periods of parabolic flight. In other words, they carried out a two-arm position matching task. They observed that the size of vibration-induced illusory arm displacement was enhanced in hypergravity (1.8 g) and diminished in microgravity (0 g), when compared with position at normal, 1 g levels. They concluded that the changes in the illusions were a consequence of the changes in gravity, producing an altered stretch sensitivity of muscle spindles. In a more recent study¹⁴ limb position sense was measured directly, rather than from illusions evoked by vibration and using different measurement methods. In a two-arm matching task (similar to¹³ but without vibration) and a one-arm pointing task (an indicator paddle was moved to the perceived position of the hidden reference arm), the authors also found g-level dependent changes of limb position sense. During hypergravity the position of the reference arm was perceived as more extended and during microgravity as less extended than in normal gravity.

A mechanism that could underlie the gravity effects considered an interplay of muscle spindles and joint receptors. The assumption was that under normal gravitational conditions, the position signal coming from a muscle, over most of its working range was coming from muscle spindles. As the limit of movement at the joint

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was approached, the spindle signal was accompanied by activity of joint receptors^{15,16}. In hypergravity, a higher torque acting at the joint, would be expected to increase both the spindle and joint receptor components of the position signal. This would lead to an increase in the values of position sense errors compared to those measured at 1 g. A decrease in torque at the joint in microgravity would lead to correspondingly lower values for discharge rates in spindles and joint receptors, lowering the position signal and therefore leading position sense errors to lie below the 1 g values¹⁷. These observations are consistent with the findings of Bringoux et al.¹⁸, who studied subjects' arm reaching movements during parabolic flight. In hypergravity, the test subjects overshot the target, while in microgravity they undershot it.

In relation to the question of which mechanism leads to an impairment of the sense of position under altered gravitational conditions, there is also the question of whether there might be a possible countermeasure. In their parabolic flight experiment, Bringoux et al.¹⁸ used elastic bands stretched across the arm to increase the gravity-like torque at the shoulder joint during target movements, and were able to show that performance in microgravity could be restored to baseline levels in 1 g. Similar findings were made in studies on joystick-based aiming movements carried out in microgravity during space flight¹¹. While aiming accuracy fell below terrestrial performance levels during the initial phase of adaptation to microgravity, even low spring-like elasticity generated by the joystick restored aiming accuracy in microgravity¹⁶. A recent study¹⁹ investigated ankle proprioception under normal gravity and simulated lunar gravity conditions, using the active movement extent discrimination assessment (AMEDA) method for measuring proprioception. Subjects were wearing a compression sock in one experimental condition. This mainly exerts pressure on the underlying tissue, and also generates a torque during deflections about the ankle joint. For subjects who had shown poor AMEDA scores in 1 g baseline measurements, it was found that wearing the garment led to a significant improvement of position sense in simulated Moon gravity conditions.

The main objective of the present study was to further extend and verify the results of our previous parabolic flight experiment. In the previous experiment¹⁴ only one test angle in the middle of the range of possible elbow movements was examined. Assuming that torques acting on the elbow joint play a central role in the effects of micro- and hypergravity on position sense, it was thought important to investigate a wider range of test angles, since different torques act on the elbow joint at each test angle, depending on the position of the arm relative to the gravity vector. Specifically, we investigated limb position sense with five test angles that almost cover the entire elbow joint motion space. The one-arm pointing method was chosen, which, like two-arm matching, had shown g-level dependent changes in the sense of position¹⁴. In both hypergravity and microgravity, the sense of position is expected to be impaired during pointing. In both cases, greater inaccuracy in one-arm pointing should be observed compared to normal gravity. In addition, we expect greater extension errors in hypergravity and greater flexion errors in microgravity compared to the normal gravity baseline, as documented earlier¹⁴. Furthermore, we assume that the magnitude of these effects is dependent on the difference between the expected (as experienced under normogravity conditions) and actual torques on the elbow joint in altered gravity. Additionally, we explored the effect of wearing compression sleeves as a potential measure to restore limb position sense in microgravity. Conditions with sleeves worn across the elbow joint were compared with conditions without sleeve. Additional afferent input, generated by a compression garment could potentially help raise the position sensor signal and so improve proprioception²⁰. This could help to restore position sense to normal levels when receptor inputs are diminished due to microgravity conditions.

Method

Sample

For this study, six participants (1f, 5 m; 1 left-hander, 5 right-handers) with average age of $M = 40.3$ years (5.7 SD yrs.) were recruited. Participation in the experiment was unpaid and voluntary. All of the participants had taken part in a similar flight experiment, so no first flyers participated and all had similar parabolic flight experience. Inclusion criteria were that (1) none of them had reported any signs of motion sickness during previous flights, (2) they did not regularly do fitness exercises with their arms and (3) that they had not had an arm injury in the recent past or were currently suffering from one. Another prerequisite for taking part in the flights was a medical certificate from the family doctor, which had to be presented before the campaign. Their health status was again checked one day before the flight by an aviation physician. Participants were thoroughly informed about parabolic flight, safety and emergency procedures, medication, experimental tasks and procedures, and written informed consent was given by the participants. Furthermore, informed consent was obtained from two subjects to publish their image (Fig. 1a) in an online open access publication. The ethical approval from an earlier campaign¹⁴ was supplemented accordingly and approved by a French ethics committee ("Comité de protection des personnes Sud-Méditerranée I"; International ID: 23.01807.000238-MS01; national nr.: 2023-A01115-40; date: 09.01.2025). The ethical aspects of the experiment conformed with the Declaration of Helsinki. Furthermore, the experiment was approved by the data protection officer of the German Aerospace Center. All methods were performed in accordance with the relevant guidelines and regulations.

Experimental setup and equipment

The experiment was installed in an Airbus 310 (see Fig. 1a) which had been modified for parabolic flight. In a parabolic flight, the aircraft is brought to an initial altitude (approx. 6000 m) and then flies a series of parabolas, i.e. the aircraft climbs to approx. 8500 m and then falls back to the initial flight level, see Fig. 2a. This generates hypergravity (1.8G) as well as microgravity (0G) conditions (Fig. 2b). The experimental setup for the campaign consisted of a main rack carrying all technical components (PCs, electronic parts, acceleration sensor, etc.) and paddle setups. Participants sat/ leaned on seat structures to stabilise their position during the hypergravity episodes (1.8 g) of the parabolic flight. For stabilisation in microgravity, participants put their feet into straps on the bottom plate and their bodies were also strapped into the seats (see Fig. 1a). The bottom plates of the main

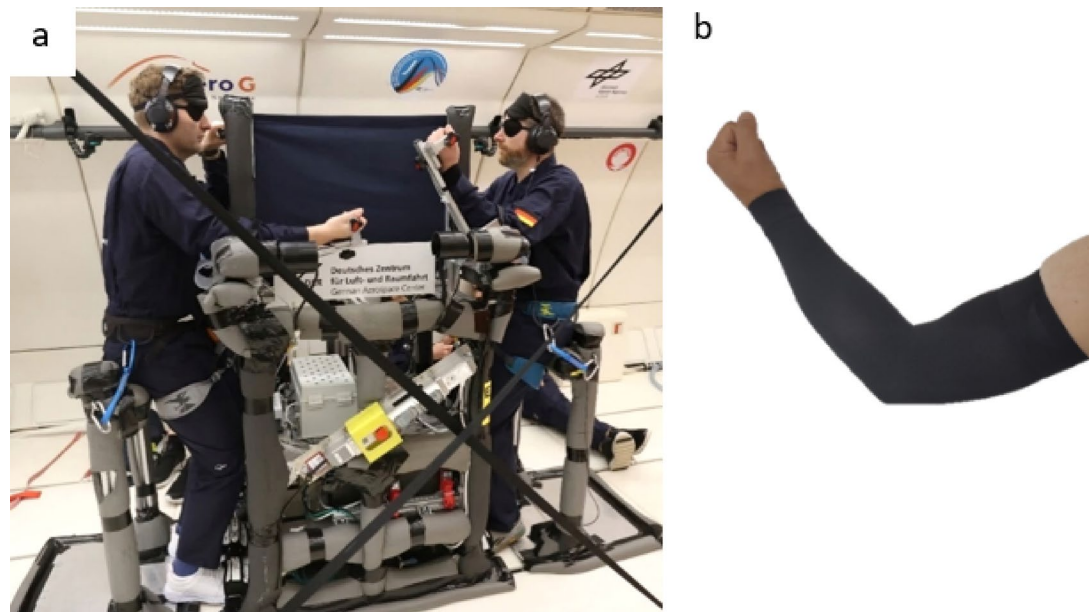


Fig. 1. (a) Experimental setup with two participants facing each other to carry out the experiment. The two persons depicted have consented to publication; (b) Compression sleeve.

rack and the two seats were firmly bolted to the airplane floor. Two paddle setups were mounted on top of the main rack in such a way that two participants could perform the experiment simultaneously. One setup consisted of two paddles which could be moved by subjects from a horizontal position (0°) to a flexed position (120°) in the sagittal plane. Movement limit stops prevented motion beyond this range. Each participant had a reference paddle (visible paddles in Fig. 1a) and a pointer paddle (hidden behind screen in Fig. 1a). The reference paddle could be moved by an integrated motor with a speed of $\sim 45^\circ/\text{sec}$. At any position the paddle could be firmly locked in place by a motor brake. The pointer paddle was used to indicate the perceived angles adopted by the reference. This paddle was additionally equipped by an electromagnetic clutch. When releasing this clutch, the motor was disconnected from the paddle and the participant could freely move the paddle without any frictional or inertial effects arising from the passively moved motor. The angles indicated by the participant were recorded by potentiometers with an angular resolution of $\pm 0.3^\circ$. Between the two arms, a cotton cloth was stretched which blocked the view of the reference arm and paddle. Paddles had a handle and a padded elbow rest with an attached Velcro strap to secure the elbow's position. The seat height and hand grips could be adjusted by the participant to make them comfortable. The paddle setup height was adjusted so that the upper arm formed an angle of about 40° relative to the horizontal, which was also considered comfortable.

Each participant wore a compression sleeve on the reference arm during one half of the experiment (see Fig. 1b). The compression sleeves selected for this study (Beister© model “BI-AS-015”) were made of thin, elastic material, and they provide a compression force of approximately of 20–30 mmHg. They had originally been designed to treat lymphoedema, arthritis or tennis elbow. Cuffs with dotted silicone bands on their inside ensured that the sleeves did not slip. Various variants of compression sleeves were compared at the start of the experiments²¹, and the most suitable material chosen did not hinder movements in the required range of motion (full elbow extension and flexion) and it was heat/ sweat-permeable. The latter was particularly important, as the sleeves had to be worn underneath flight overalls. The compression values of the garments were comparable to those used by²². Participants tried a sleeve in their clothing size, checked whether they fit tightly enough while still allowing for comfortable arm movement in the required range. If not, they chose another, better-fitting sleeve size.

Experimental software

The experimental software essentially comprised four components: (1) a module for the timing of the experimental trials, (2) the issue and timing of the experimental audio instructions during the trials, (3) the control of the paddle motors and clutches, and (4) data logging. The module for experimental timing processed the data from an acceleration sensor to detect the current g-level. This study was conducted during the hypergravity, microgravity and steady horizontal flight episodes of the flown parabolas, see Fig. 2c. The experimental trials were started in the initial hypergravity episode (HG1) after exceeding 1.5 g, in the microgravity episode (MG) after falling below 0.6 g, and in the last hypergravity phase (HG2) when exceeding 1.3 g. The normal gravity trial (NG) was initialized when g-values were below 1.15 g again, after the second hypergravity episode of a parabola. For each episode transition, a time limit was set for how long the defined g value had to be exceeded/fallen short of before a trial was started. These thresholds were fine-tuned based on g-level recordings from previous parabolic flight campaigns. The accelerometer data evaluation was implemented in Matlab/ Simulink. When a certain episode was detected, the corresponding instructions were given to the test subjects via headphones. The

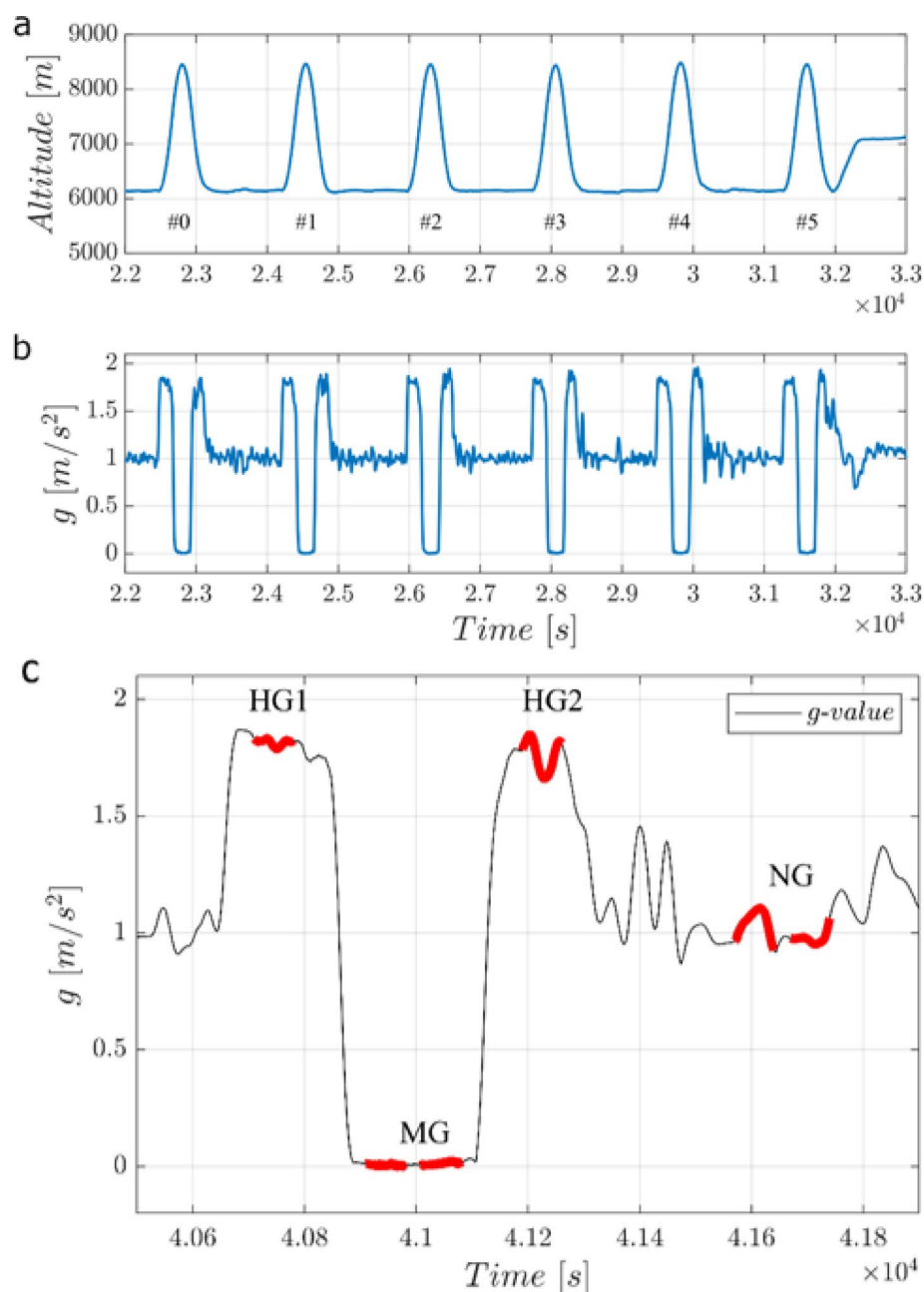


Fig. 2. Examples for the flight data of the experiment. (a) timing of parabolae and flown altitudes for the first six parabolae. (b) g -values recorded during these parabolae. (c) g -values for one parabola (#9): g values labelled in black, experimental trials red thickened.

issuing of the pre-recorded instructions was controlled by a JAVA software module. The control program was executed on a real-time Linux PC with a sampling of 1 kHz. The data recording (programmed in C++) included the presented reference angles and the indicated angles in the various g -episodes as well as the recording of the complete motion profiles.

Experimental task and design

A one-arm pointing procedure was implemented for this study. Participants wore an eye patch over the eye near the reference arm which was also hidden behind the cloth. It meant that the subject could not see either their reference forearm or the upper arm. Participants were assigned to the two sides of the experimental rack so that three participants had their dominant arm and three their non-dominant arm as reference. Like in earlier studies^{14,21,23}, all paddles were brought to a vertical starting position (90°) before the experiment began. The reference arm was positioned on the reference paddle, while the pointer paddle was grasped at the handle by the indicator arm (see Fig. 3). As soon as the experiment was started, the reference paddle moved to one of the

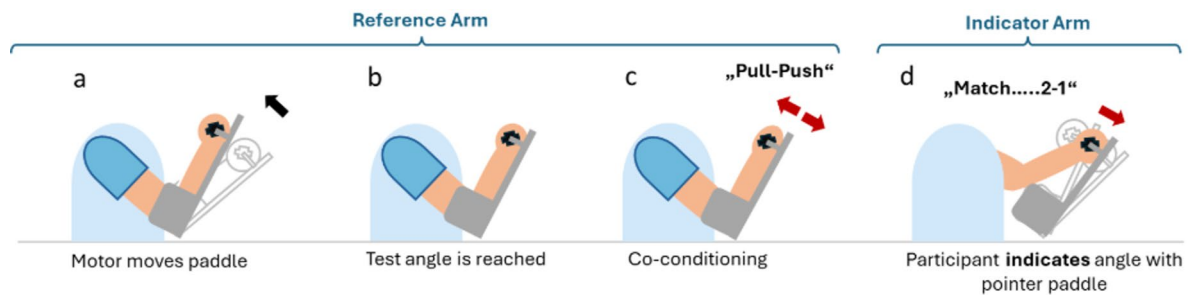


Fig. 3. Pointing procedure. The reference arm lies on a motorized reference paddle, which moves to the test angle (a). When having reached the specific angle (b), elbow antagonists are co-conditioned (c). Then, the reference arm is relaxed and the perceived position of the reference arm is indicated by the other arm by moving a pointer paddle to this position (d). Both paddles move in the same sagittal plane. Accordingly, reference arm motion only involves elbow joint rotation. The hand of the indicator arm holds the handle of the pointer paddle and the arm performs a more complex movement in space that involves multiple joints.

five test angles (10°, 35°, 60°, 85° and 110° between forearm and the horizontal) and was held there in position, see Fig. 3a and b.

In a next step, the elbow extensors and flexors of the reference arm were co-conditioned. This standard procedure involves performing isometric contractions, which ensure that the muscle spindles of the antagonists are in a clearly defined state in order to obtain reliable position signals²⁴. Elbow flexors were contracted first, followed by elbow extensors, see Fig. 3c. Participants were instructed before the experiment, that these isometric contractions should be approximately 20% of maximum voluntary contraction (MVC) and half a second in duration. Whether the exact 20% MVC was reached was not monitored, since only exceeding 10% MVC is crucial for eliminating potential slack in muscle spindles²⁵. The indicator arm was not conditioned since it acted purely to point to the reference arm. The grasped pointer paddle in the 90° starting position was unlocked and participants were asked to indicate the perceived position of the reference arm by moving this paddle, also see Fig. 3d. This procedure was repeated with each test angle. All audio instructions via headphones were pre-recorded. The isometric contractions at the new test angle were announced with “pull-push”, and when the clutch on the indicator side was released, the instruction “match” was given. The participant then had 5 s to match the position of the reference arm with a countdown “2 – 1” for the last two seconds. The angle indicated at the end of the countdown was recorded. After having finished a trial, the pointer paddle moved back to 90°, the reference paddle moved to the upcoming test angle, and the next trial was started.

Each participant completed two complete experimental sessions with data collection, first in the aircraft on ground, one day before flight (labeled as “preflight ground session”) and second during flight (labeled as “flight session”). The procedure for the experimental trials during the preflight ground session was identical to and based on the requirements of the flight session, see Fig. 4. On ground, there were 20 experimental runs that corresponded to the 20 parabolas during which the experiment was conducted in the flight session. In both sessions, there were two experimental blocks: during 10 runs or parabolas participants wore the compression sleeve on their reference arm, and during the other 10 they did not, while the order of the two experimental blocks were counterbalanced across subjects, but identical for both sessions. During each run/ parabola there were six experimental trials. One initial trial in the first hypergravity episode (“HG1”), two trials in the subsequent microgravity episode (“MG”), one trial in the last hypergravity episode (“HG2”) and finally two trials in the normal gravity episode (“NG”), see Fig. 4. For the ground session, the very same timeline was adopted as in the flight session, except that the breaks between parabolas during flight (~1 min 45 s) were shortened (40 s). For this reason, this experiment also includes “NG,” “HG,” and “MG” trials, although, of course, all of them were conducted under normal gravity conditions. Thus, $20 \times 6 = 120$ trials were completed during both experimental sessions.

For each run or parabola, two angles were randomly selected and these two angles were tested in the two trials of the HG episodes as well as in the MG and NG episodes. Yet, the full range of test angles (10°, 35°, 60°, 85° and 110°) could not be tested in HG. Our earlier campaigns^{14,23} had shown that angles down to 60° can be indicated in HG without any problems and very accurately. However, we expected stronger lever effect for angles below 60°, making it unacceptably demanding to stabilise the indicator arm - that is almost completely extended in these cases - together with the pointer paddle for the lower angles (i.e. 35° and 10°). Therefore, only three upper angles (60°, 85° and 110°) were tested during HG episodes. This resulted in an incomplete experimental design, with 5 angles in the MG and NG episodes and 3 angles in the HG episodes, see Fig. 4. For each angle in each condition this resulted in 4 repetitions, while in HG there were 4 additional repetitions for the two upper angles (85°, 110°).

Procedure

Once the participants had been selected and they had a valid medical certificate, they were prepared for the experiment with a mandatory one-hour online briefing some 1–2 months before flight. The content of this briefing was the background, the procedure and the task in the experiment as well as instructions on safety and how to avoid motion sickness during flight. In the month before flight, all participants also had to attend

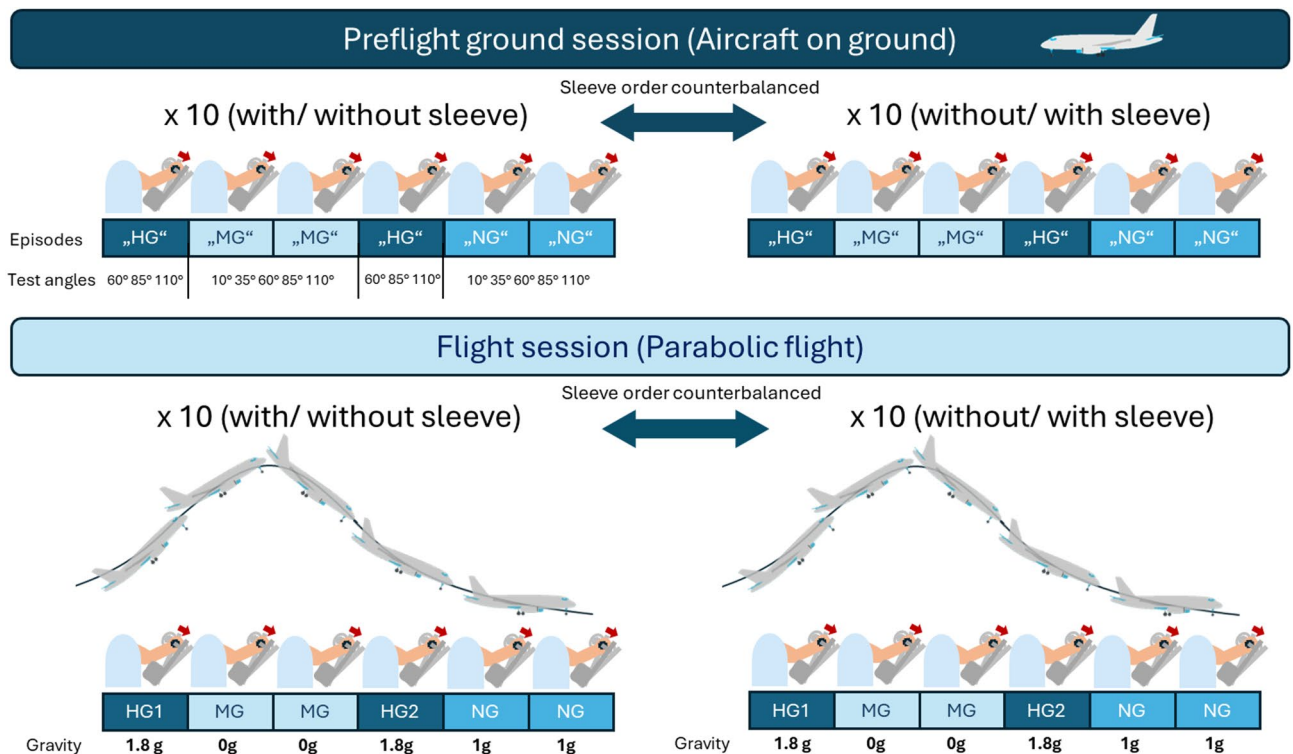


Fig. 4. The figure provides an overview of the experimental protocol. There were two experimental sessions: (1) a preflight ground session, in which the entire experiment was conducted in the aircraft on ground, and (2) the flight session during parabolic flights. The timing of both sessions was identical, and the sequences of the gravity episodes (HG = hypergravity; MG = microgravity; NG = normal gravity) were also implemented in the preflight session. Depending on the episode, different test angles could be examined, as indicated in the upper left. Ten experimental runs or parabolas were conducted with the sleeve and ten without, while the order was counterbalanced across subjects.

a meeting at the German Aerospace Center in Oberpfaffenhofen to receive a more detailed briefing about the experimental and emergency procedures. On this occasion, the participants also tried out the compression sleeve and chose a suitable size. Finally, they completed one experimental session as a training for the flight campaign. After these two briefings, all participants were also sent information material summarising all the relevant procedures of the experiment.

The flight experiments took place in Bordeaux, France, at NOVESPACE. Upon arrival at the NOVESPACE facilities, the experiment crew and participants received a general safety briefing. In each flight campaign three flights are offered on three consecutive days. In the current experiment one pair of subjects flew on one of the three flights. On the day before the flight, each pair of subjects completed the pre-flight ground session in the airplane on ground. On the morning of the flight, all passengers (experimenters and participants) received a Scopolamine injection. Depending on gender, body weight and experience in previous campaigns, a dose of 0.5–1.0 ml was administered. Scopolamine is used as standard medication for these parabolic flights to counteract motion sickness. The main side effects are dry mouth, blurred vision and drowsiness. The passengers then boarded the Airbus 310 and the plane took off. After reaching the required altitude, the passengers left their seats and went to the experimental setup. The participants took up their positions on the setup, their feet were placed in the floor straps, a climbing harness was put on which secured each participant to the seat structure, the eye patches and headphones were put on and the arms were positioned on the paddles. One of the two participants also put the compression sleeve on their reference arm. The two experimenters provided support during preparation of the participants and then took a seat on the floor in front of the experimental apparatus, securing themselves to the floor with straps.

A total of 31 parabolas were flown on each day, with the first parabola (#0) being used for familiarization, i.e. the experimental runs only started in parabola #1. This experiment was conducted during the first 20 parabolas (#1 – #20). After each 5th parabola there was a pause of 5 min and after parabola #15 a longer pause of 8 min. After parabola #10 one subject took off the sleeve and the other participant put his/her sleeve on. The time sequence of a parabola was always the same: after the airplane pulled upwards, hypergravity prevailed for ~20 s after a certain transition time, followed by ~22 s microgravity and then ~20 s hypergravity again. Then, during a phase of ~1:45 min of horizontal flight, normal gravity was established again.

Data analysis

The pointing error was calculated as the difference between the position of the reference paddle and the measured angle of the pointer paddle for each trial. This signed error can result in positive values, which indicates that the pointer was moved further in the direction of arm extension compared to the reference or negative values, indicating an error in the direction of arm flexion. The absolute error was calculated as a measure which does not take the direction of the error into account, but only the absolute deviation from the reference angle. To account for the incomplete factorial design (only three test angles in HG), the small sample size and interindividual variability, a Linear Mixed-Effects Model (LMM) analysis was conducted. Therefore, normality of data distribution was checked using Q-Q plots and the Shapiro-Wilk test. Homoscedasticity was checked using Levene’s test. The LMM analysis was conducted to analyze the effects of *Sleeve* (with vs. without), *Gravity* (MG, NG, HG), and *Angle* (10°, 35°, 60°, 85°, 110°) on the dependent variables *Signed* and *Absolute Error* in the Preflight and Flight experiment.

The model included fixed effects for all main factors and their interactions, as well as a random intercept for *Subject* to account for within-subject variability. Including repetition as a random effect was not feasible due to its systematic relationship with the fixed effects. All analyses were conducted using Restricted Maximum Likelihood (REML) estimation. Post-hoc pairwise comparisons were performed using estimated marginal means with Bonferroni correction. Directional hypotheses were tested one-tailed (1tt), all other comparisons were two-tailed tests (2tt). Finally, Hedges’ *g* was calculated as effect size.

Results

Pre-flight ground session

Signed error

As a first step, the data from the preflight session was analysed. Error values slightly deviated from normal distribution as indicated by Q-Q plots and Shapiro-Wilk test ($W = 0.99$; $p < .05$). Moreover, Levene’s test indicated significant heteroscedasticity ($W(25, 934) = 2.57$, $p < .05$). To address these violations of assumptions, robust standard errors (Huber-White-Sandwich estimator) were applied in the subsequent linear mixed model (LMM) to ensure valid inference²⁶

The LMM revealed a significant main effect of Angle ($F(4, 929) = 20.7$, $p < .001$), indicating that errors differed across test angles. No significant effects were found for Sleeve ($F(1, 929) = 0.36$, *ns.*), Gravity ($F(2, 929) = 0.61$, *ns.*), random intercepts for Subject ($\sigma^2 = 10.55$, $p = .121$) or any interactions (all $ps > 0.05$). Post-hoc pairwise comparisons showed that errors at 10° were significantly lower than at all other angles (all $ps < 0.005$, Hedges’ *g* ranging from 0.84 to 1.94, see Table 1, “Pre-flight Ground Session/ Signed Error”). Additionally, the error values for 110° were significantly higher compared to all other angles (all $ps < 0.001$; $g = 0.88–1.94$). No other pairwise comparisons reached statistical significance.

Absolute error

A similar result pattern was found when analysing the absolute error with the same LMM procedure. The only significant result was an Angle main effect ($F(4, 929) = 10.0$, $p < .001$), revealing that absolute errors were significantly smaller for the 10° test angle compared to all angles $\geq 60^\circ$ (all $ps < 0.001$). Additionally, the absolute error at 110° was significantly larger compared to the values for 35° ($p = .001$) as indicated by post-hoc comparisons (see Table 1, second row)

In summary, this baseline study showed that both the signed and absolute pointing errors varied in magnitude depending on the test angle. The errors were smallest at a 10° test angle and largest at 110°. With the exception of 10°, the signed error had a positive sign, meaning that errors were predominantly in the direction of arm extension (overshooting). There were no effects related to the sleeve, gravity or subjects.

	10°	35°	60°	85°	110°
Pre-flight ground session					
Signed error	−0.12° (1.46°)	2.90° (1.46°)	3.53° (1.40°)	3.64° (1.39°)	6.64° (1.39°)
Absolute error	3.98° (0.96°)	5.34° (0.96°)	6.31° (0.92°)	6.48° (0.91°)	7.45° (0.91°)
Flight session					
Signed error					
MG episodes	−0.36° (1.53°)	2.02° (1.52°)	4.81° (1.52°)	3.74° (1.52°)	4.33° (1.52°)
HG episodes			5.75° (1.53°)	3.88° (1.40°)	5.65° (1.40°)
Absolute error					
MG episodes	5.27° (0.97°)	6.82° (0.96°)	8.37° (0.96°)	5.97° (0.96°)	4.97° (0.96°)
HG episodes			7.77° (0.97°)	6.39° (0.86°)	6.81° (0.86°)

Table 1. Model estimated means and SE of signed and absolute pointing errors in the Pre-flight and Flight Sessions across the five test angles. To simplify presentation, data of both Sleeve conditions were merged, since no effects were observed for the Sleeve factor.

Flight session

Signed error

Two sets of NG baseline data were available for the analyses of the flight session: the pre-flight data, comprising a total of 120 trials, and the data from the NG episodes during the flight, comprising 40 trials. However, significant fluctuations in g-levels were observed in some of the NG flight episodes, which, as a confounding variable, can affect pointing errors. This mainly occurred in the 60° test angle trials with the highest average within-trial g-level fluctuations compared to the other angles ($SD(g_{10^\circ}) = 0.028 \text{ m/s}^2$; $SD(g_{35^\circ}) = 0.025 \text{ m/s}^2$; $SD(g_{60^\circ}) = 0.037 \text{ m/s}^2$; $SD(g_{85^\circ}) = 0.031 \text{ m/s}^2$; $SD(g_{110^\circ}) = 0.029 \text{ m/s}^2$). For this reason, the error values of the preflight session - conducted under stable 1 g conditions - were used as a reliable comparison baseline in the following analyses.

Again, error values deviated from normal distribution (Shapiro-Wilk $W = 1.0$, $p < .05$) and Levene's test indicated heteroscedasticity ($W(25, 1175) = 2.87$, $p < .001$). Hence, robust standard errors were again applied in the LMM. Like in the preflight session, LMM analysis yielded a highly significant Angle main effect ($F(4, 1170) = 19.0$, $p < .001$). The lowest error rates were found for 10° ($\mu = -0.24$, $SE = 1.37$) compared to all other angles ($\mu_{35^\circ} = 2.51$, $SE_{35^\circ} = 1.37$; $\mu_{60^\circ} = 4.72$, $SE_{60^\circ} = 1.33$; $\mu_{85^\circ} = 3.69$, $SE_{85^\circ} = 1.32$; $\mu_{110^\circ} = 5.56$, $SE_{110^\circ} = 1.32$; all $ps \leq 0.02$) and errors at 110° were significantly larger compared to the other angles (all $ps \leq 0.005$), except for 60°. Finally, errors at 60° were larger compared to 35° ($p = .013$). Again, no significant effects were found for Sleeve ($F(1, 1170) = 0.47$, *ns.*). Also, no significant main effects for Gravity ($F(2, 1170) = 1.09$, *ns.*) or the random intercepts for Subjects ($\sigma^2 = 9.55$, $p = .121$) were found. A non-significant trend for a Gravity x Angle interaction ($F(6, 1170) = 1.94$, $p = .071$) however indicated that the effect of gravitational load on signed pointing errors depended on test angle. Increased errors in HG compared to NG were evident for 60° test angle ($p = .047$, Hedges' $g = 0.61$, 1tt). At 110° the MG error values were significantly lower compared to NG errors ($p = .042$, Hedges' $g = 0.67$, 2tt), see Fig. 5a.

Absolute errors

As before, violations of normality (Shapiro-Wilk $W = 0.97$, $p < .05$) and homoscedasticity assumptions ($W(25, 1175) = 2.45$, $p < .001$) were detected, and thus robust standard errors were again used. Again, the LMM procedure revealed a significant effect of Angle ($F(4, 1170) = 7.8$, $p < .001$). No significant main effects of Sleeve ($F(1, 1170) = 0.02$, *ns.*), Gravity ($F(2, 1170) = 1.74$, *ns.*) or the random intercepts for subjects ($\sigma^2 = 3.33$, $p = .124$) was found, but analysis did reveal a significant Gravity x Angle interaction ($F(6, 1170) = 5.21$, $p < .001$). As regards the Angle effect, post-hoc comparisons showed the lowest absolute errors for 10° ($\mu_{10^\circ} = 4.63$, $SE_{10^\circ} = 0.83$), which was significantly smaller compared to all angles of 60° or more (all $ps \leq 0.01$; $\mu_{35^\circ} = 6.05$, $SE_{35^\circ} = 0.83$; $\mu_{60^\circ} = 7.48$, $SE_{60^\circ} = 0.81$; $\mu_{85^\circ} = 6.29$, $SE_{85^\circ} = 0.79$; $\mu_{110^\circ} = 6.41$, $SE_{110^\circ} = 0.79$). Absolute errors at 60° were significantly larger compared to all other angles except for 110° (all $ps < 0.05$).

The Gravity x Angle interaction was due to the following effects: At 10°, 35° and 60° absolute errors were larger in MG compared to NG. At 10° the absolute error was significantly larger in MG ($\mu_{MG} = 5.27$; $SE = 0.97$) compared to NG ($\mu_{NG} = 3.98$; $SE = 0.86$; $p = .04$, 1tt; Hedges' $g = 0.57$), also see Fig. 5b. At 35°, this difference also reached significance ($\mu_{MG} = 6.82$; $SE = 0.96$; $\mu_{NG} = 5.28$; $SE = 0.86$; $p = .02$, 1tt; $g = 0.69$) as well as at 60° ($\mu_{MG} = 8.37$; $SE = 0.96$; $\mu_{NG} = 6.29$; $SE = 0.83$; $p = .004$, 1tt; $g = 0.95$). Figure 6 shows the individual difference values between MG and NG for the six participants. At 110° the effect direction was opposite and absolute errors in MG were smaller compared to NG ($\mu_{MG} = 4.97$; $SE = 0.96$; $\mu_{NG} = 7.46$; $SE = 0.81$; $p = .001$, 2tt, $g = 1.98$) and compared to HG ($\mu_{HG} = 6.81$; $SE = 0.86$; $p = .04$, 2tt, $g = 0.82$). Finally, there was a non-significant trend for absolute errors at 60° to be larger in HG compared to NG ($\mu_{HG} = 7.77$; $SE = 0.97$; $\mu_{NG} = 6.29$; $SE = 0.83$; $p = .055$, 1tt; $g = 0.67$).

In sum, the parabolic flight study showed effects of the test angle on both error metrics - with generally smaller errors at 10° and a tendency toward larger errors at 60° and 110° test angles - and more importantly gravity-related effects that varied depending on the test angle. At the 60° test angle, extension errors significantly increased in hyper- compared to normal gravity. At 110° extension errors significantly decreased in micro- compared to normal gravity. Furthermore, an analysis of the absolute error revealed that, at the lower test angles (10°- 60°), significantly higher values were observed in the microgravity conditions compared to the normal gravity baseline.

Discussion

The aim of the present study was to investigate whether altered gravity impairs human limb position sense, and if so, why? The primary objective of this study was to build upon our previous study¹⁴, which, amongst other methods, also used the one-arm pointing method to measure human limb position sense in altered gravity conditions. In this study, we found evidence that, in hypergravity, the position of the arm was perceived as lying more in the direction of arm extension, and in microgravity, lying more in the direction of arm flexion, compared to normal gravity. Our explanation for this pattern of findings was based on the fact that the changes in gravitational torque acting on the elbow joint were responsible for the observed directional errors. However, one limitation of this study was that only a single angle in the middle of the elbow's range of motion (i.e. 60°) was examined, see Fig. 7a. If it is indeed the torque acting on the elbow joint then different test angles (10°, 35°, 60°, 85° and 110°), which result in different torques at the elbow joint, should be correlated with the sizes of the errors. Additionally, it was explored whether a compression sleeve can help restore the sense of position in microgravity. To measure position sense in the pointing task, two metrics were calculated. First, the signed error, which indicates whether and to what extent perceptual shifts occur in the direction of arm extension or flexion between conditions. Second, the absolute error was calculated which simply reflects the magnitude of the error regardless of its direction.

As a normal gravity baseline for the parabolic flight study, the experiment was first carried out with the aircraft standing on the ground. As expected, and consistent with earlier studies on one-arm pointing^{14,27-29}

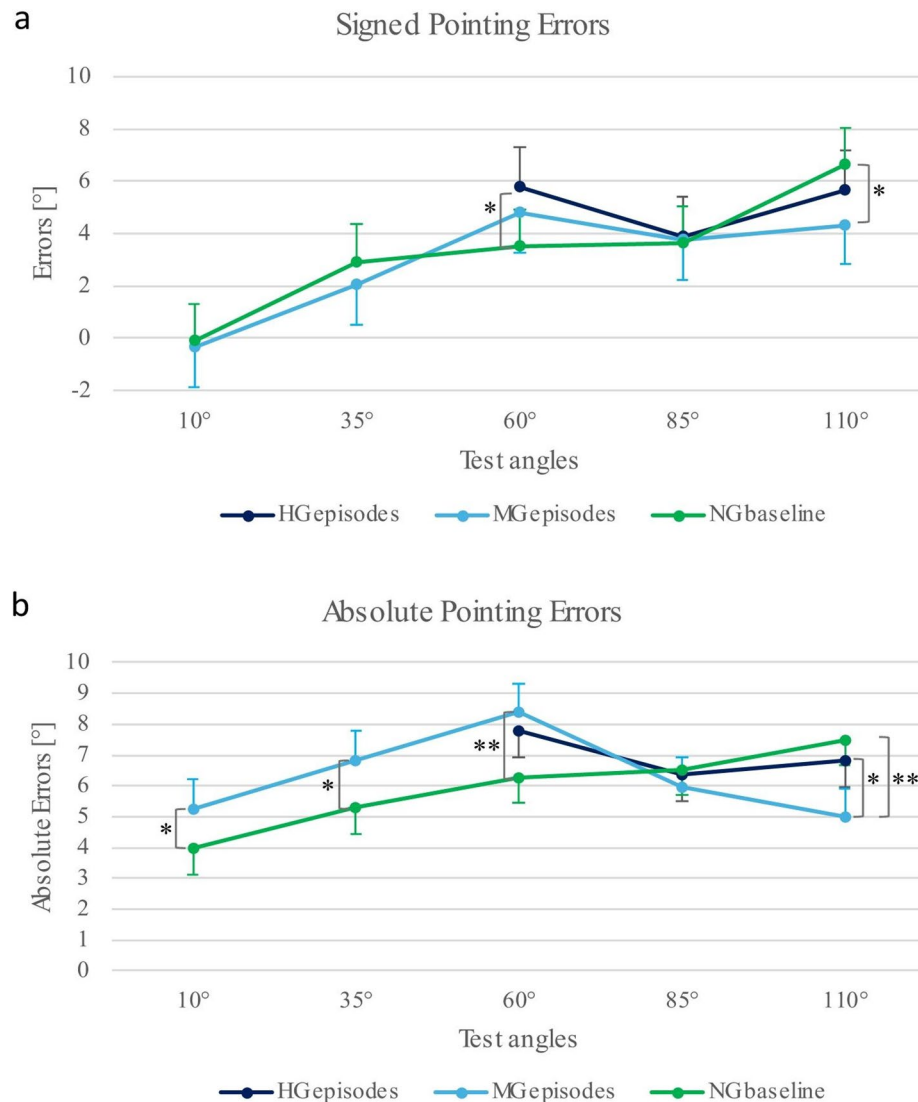


Fig. 5. (a) Estimated mean signed pointing errors and SE in the microgravity (light blue), the hypergravity (dark blue) episodes of flight and the preflight normal gravity results (green). Positive errors indicate errors into arm extension, negative errors into flexion. (b) Estimated mean absolute pointing errors and SE; same color coding as a). * $p < .05$; ** $p < .01$.

average errors lay in the direction of arm extension - except for the lowest test angle of 10° where mean pointing errors lay close to zero. It has been argued that this general tendency toward extension errors might be associated with transformation of the proprioceptive signal, coming from the hidden arm, into a visual frame of reference³⁰. In addition, it has been reported that pointing errors into extension decrease at test angles close to full arm extension or flexion, and here it has been postulated that joint receptors input increases when approaching the anatomical limits of joint movement^{15,29}. However, in our setup the elbow joint angle at the lowest test angle (10°) was about 130° (see Fig. 7b) which is still well below the joint limit at 180°. Here, it seems plausible that the extension error decreases on average because the paddles can only be moved down to 0° due to the integrated stops which of course prevent substantial extension errors from occurring. For a test angle of 110°, the exact opposite is true. First, the elbow joint is almost in full flexion³¹; see Fig. 7c), i.e. larger flexion errors are less likely to happen and are also prevented by the integrated stops at 120°. With regard to the experimental factor “Gravity” in the ground study - that is, the temporal arrangement of the various trials in the scheme as it had to be implemented for the parabolic flights - no effect was observed. Like in previous studies with the same or similar pointing tasks^{14,21,28,29} there was no evidence for any significant time effects (e.g. learning). Finally, there was also no effect of wearing vs. not wearing the compression sleeve.

The parabolic flight study was designed to test the following assumptions: We expected greater extension errors in hypergravity and smaller extension errors in microgravity compared to the normal gravity baseline. Furthermore, in both hyper- and microgravity, absolute error magnitudes should increase compared to normal gravity. These effects of altered gravity should be dependent on the reference arms position relative to the gravitational vector. Three test angles could be examined in hypergravity, ranging from near-complete flexion

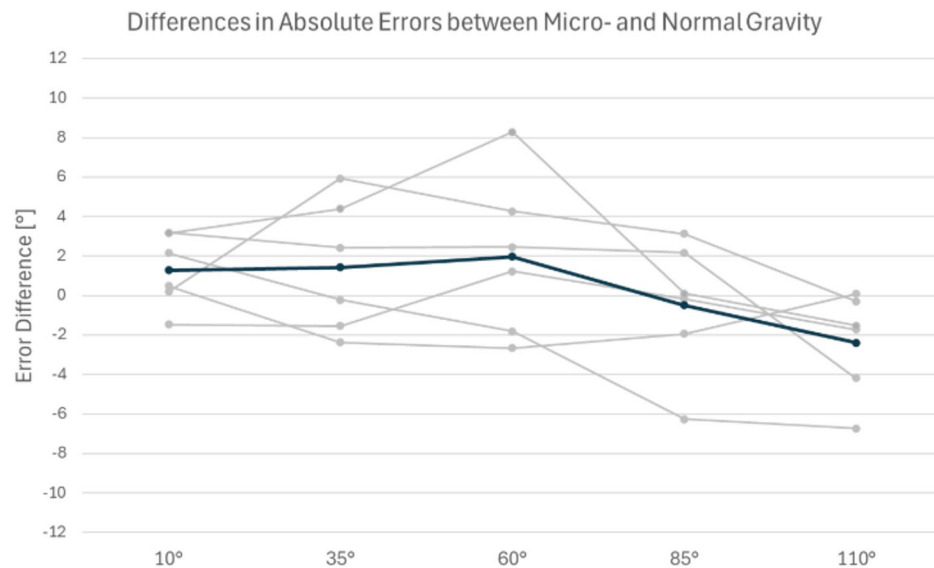


Fig. 6. Difference values between MG and NG conditions. The light grey lines show the raw data (aggregated across sleeve conditions and repetitions) of the six subjects, thick dark blue line shows mean across subjects.

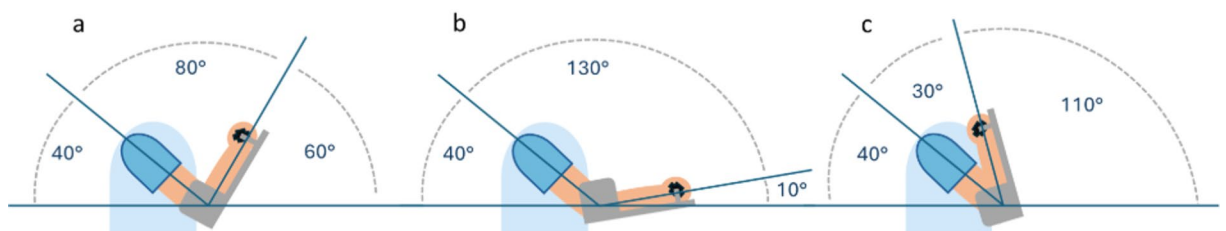


Fig. 7. Relative angles of the upper arm and forearm at test angles of 60° (a), 10° (b), and 110° (c).

(110°) to a moderate range of elbow flexion (85°, 60°). Angles beyond this extension could not be tested, as the nearly doubling of the weight of the pointer arm and paddle, which had to be held, would have required an unreasonably high amount of effort. If gravitational torque acting on the elbow does play a role in impaired position sense in hypergravity, then the expectation was, that directional errors are more evident when this torque is substantially higher compared to normal gravity conditions. Indeed, there was only an effect into the expected direction of arm extension for the 60° test angle. This increase of extension errors at the 60° test angle was comparable to the increase in our previous study (current: 2.2°; previous study¹⁴: 2.1°). The fact that no additional extension error occurred at 85° and 110° can be best explained by the fact that the torque acting on the reference arm in hypergravity at 60° is significantly greater than the expected torque in normal gravity, see Fig. 8. Consequently, the increased torque acting on the elbow joint is interpreted as a greater arm extension. At 85°, there is a slight deviation of 5° from a vertical position of the forearm. At 110°, the deviation is 20°. These acute angles do not appear to be large enough to generate sufficient additional torque in 1.8 g to have a significant effect on limb position sense, see Fig. 8. Interestingly, however, there were non-significantly lower extension errors in hypergravity compared to normal gravity for the 110° test angle, which is consistent with the change in the direction of the additional hypergravity-induced torque.

Intriguingly, at 85° - i.e. in an almost vertical forearm position - the signed and absolute errors were very close under all gravitational conditions. Apparently, neither the absence of gravity nor the near-doubling of gravity had any effect. How can that be? One might argue that using the vertical axis as a spatial reference allowed for a more accurate assessment despite changes in gravity. If that was the case, a general reduction in pointing errors should be evident for test angles near the vertical compared to other angles, but the present pre-flight study as well as other studies provide no evidence for this^{21,28,29}. Our explanation involving gravitational torque does indeed seem more plausible than using spatial axes as reference. This torque is, in fact, minimal near the vertical, since the forearm is almost aligned with the gravitational vector and perpendicular to the elbow joint. This means that there is no significant difference in gravitational torque acting on the forearm and the elbow joint between the three gravitational conditions. It is exclusively in this almost vertical configuration that the torques acting on the elbow joint are most comparable in micro-, hyper- and normal gravity (see Fig. 8), although different forearm weights are resting on the elbow.

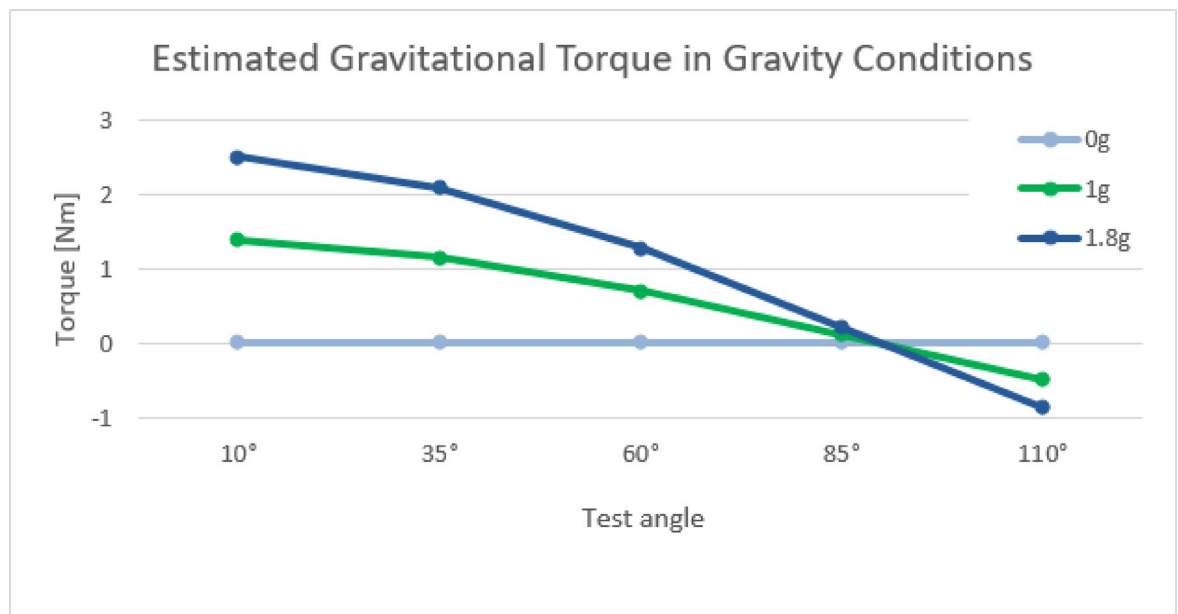


Fig. 8. Estimation of the torque acting on the forearm at the test angles under the three gravitational conditions. Here, an arm mass of $m = 1.2$ kg and a distance of $d = 12$ cm between the center of mass of the forearm and the pivot point (elbow joint) were assumed. The torque τ is calculated as the product $\tau = m \cdot d \cdot g \cdot \cos(\Theta)$; while $g = 0 \text{ m/s}^2$ in microgravity, 9.81 m/s^2 in normal gravity and 16.52 m/s^2 in hypergravity. Θ is the test angle. Since the forearm rests on a rigid lever, most of this torque is compensated by the counterforce created by the lever. However, as the arm itself is not rigid (muscles, tendons, other tissue), there will be a residual torque acting on the elbow joint.

In the earlier study¹⁴, larger signed errors in the direction of flexion were observed at 60° under microgravity conditions compared to normal gravity conditions, although this effect did not reach statistical significance. In that regard, it is not surprising that the current study also found no significant directional errors at 60°. In the previous study, co-conditioning was performed in a flexed arm position of 90°, which is known to introduce larger extension errors as e.g. co-conditioning in arm extension²⁹. The test angle co-conditioning in the present study led to an overall reduction in extension errors in normal gravity conditions and perhaps also to a lower directional error in microgravity. Like for the 60° test angle, there were no directional effects for the test angles that were more toward extension (10°, 35°) and flexion (85°), with the exception of 110°. It is difficult to explain why a significant reduction in the extension error occurred in microgravity compared to normal gravity only when the arm was almost fully flexed at 110°. The subjects were able to stabilize their bodies in microgravity very well using the foot straps. However, it is conceivable that when the arm is almost maximally flexed, and the upper arm tends to drift slightly upward in microgravity, this might result in a perception of greater arm flexion, although the forearm's position is unchanged.

Although no directional effects were observed for the other angles, a clear trend was evident in the absolute error, which reflects a higher degree of inaccuracy. At angles where a significant gravitational torque acts on the arm in normal gravity conditions - i.e., at 60° and greater toward the horizontal (35° and 10°) - significantly larger absolute errors were observed in microgravity compared to normal gravity. This means participants were significantly less able to accurately perceive their reference arm position, although these errors did not show a clear bias in any particular direction.

Overall, the expected result patterns were observed, with the exception of the 110° test angle, where the influence of artifacts cannot be entirely ruled out due to the near-complete flexion of the arm. Hence, the hypothesis that position sense is impaired by altered gravity and these impairments are moderated by test angles is partially confirmed. Altogether, the findings strongly suggest that the difference between external torque acting on the elbow joint in altered gravity compared to the torques in normal gravity plays a key role for changes in limb position sense.

The findings of this study are consistent with previous studies on limb position sense, which have documented the role of gravitational torque. For example, in a two-arm matching task, Worringham and Stelmach³² were able to demonstrate that even minimal torque differences between both arms lead to a significant, directional matching error. Ettinger et al.³³ were also able to show that the sense of position in simulated weightlessness - as induced by water immersion - was especially affected at test angles where gravitational torque is particularly high under normal gravity (horizontally outstretched arm), but not existent in conditions of simulated weightlessness. The difference between those studies and the current one, however, is that in the current study, the gravitational torque did not have to be compensated for by active muscle force, since the reference arm was resting on a stable surface. Muscular effort can therefore be ruled out as a source of information for the sense of position. A more plausible explanatory approach assumes an internal model of gravity that links perceived torque information

and limb positions³⁴. If significant deviations occur between the internal model calibrated under 1 g conditions and receptor information during altered gravity, corresponding inaccuracies or systematic directional errors arise.

While this explanatory approach mainly focuses on the role of proprioceptive information, the role of the vestibular system as a potential moderating mechanism^{7,13} remains unclear⁸. However, in the present experiment, the subjects were always in an upright position, no head movements were required, and they had tactile contact points, all of which is known to reduce vestibular disturbances in altered gravity^{7,35,36}. Moreover, if the vestibular system was the primary factor underlying gravitational effects on position sense, angle-independent effects would have been expected in altered gravity³⁴.

We also explored the potential benefits of wearing a compression sleeve in microgravity conditions. It has been argued that mechanoreceptors are stimulated by this tissue deformation, which might lead to improved proprioception (see²⁰ for a review). In current study, however, we did not find any positive effect of wearing a compression sleeve, either in normal gravity or in microgravity conditions. This may be due to the fact that the compressive forces and the torques resulting from the material's elasticity were insufficient.

Overall, this study provides further evidence for the hypothesis that the gravitational torque acting on the relevant joints of the limbs has a significant influence on the perception of their position. We were able to replicate the general pattern of results from our earlier study¹⁴ and, furthermore, demonstrate that for greater discrepancies between expected and actual gravitational torque in hypergravity and microgravity, the position sense is significantly impaired. It suggests that a prolonged adaptation process is necessary to realign internal models with sensory information. This is one of the reasons why astronauts typically do not perform tasks that require a high degree of motor precision during the first phase of their missions in space⁵. One possible reason why the compression sleeves tested here failed to achieve the desired effect is likely that, unlike in the studies by¹⁸ or^{11,12}, no active muscle force was required to counteract a resistive force; instead, only passive pressure or torque was applied to the arm. An interesting observation from the current study, however, is that due to muscle activity during co-conditioning at the test angle, significant directional effects (with the exception of 110°) were absent in microgravity. This could be an indication that the sense of position was at least partially restored by the brief fusimotor activity, even though the pointing maneuver was subsequently performed with the reference arm in a state of complete relaxation.

Limitations

One potential limitation of this study is related to the fact that the preflight session was conducted with the aircraft on ground. The parked Airbus 310 typically has a minimal nose-down pitch of ~1°, which meant that the experimental setup was not positioned exactly on a horizontal plane. However, with a discrimination threshold of 6–7° for elbow flexion angles³⁷, it is very unlikely that this had any effect on the reported results. It should also be noted that, although the respective test angles of the reference forearm were precisely set using a potentiometer, the described 40° position of the upper arm was not exactly measured. However, this is not relevant to the pointing experiment, since the pointer is intended to indicate the forearm position. Still, it may limit interpretations regarding the extent of full arm flexion.

Conclusion

For future space missions, astronauts will be required to perform tasks that demand the highest degree of sensorimotor accuracy. Reliable perception of one's own limb positions is a central prerequisite for this. In the present parabolic flight study, it was demonstrated that both hyper- and microgravity impair the sense of position as measured in a pointing task, and that the difference between expected and actual gravitational torque plays a central role in this. This can be interpreted as an indication that adaptive processes must first be completed before the internal motor programs can adjust to the altered sensory information. This must be taken into account when planning challenging astronaut missions, such as the teleoperation tasks described at the beginning. Furthermore, our study provides evidence that external torques acting on the joints are central to the human sense of position. In this regard, the use of countermeasure suits for astronauts like the “penguin axial loading suit”³⁸ - in which elastic elements are distributed according to the demands of selected antagonist muscle groups - remains a promising approach. Future studies should further scrutinise how tensile forces in such suits have to be adjusted to improve the sense of position in microgravity.

Data availability

The datasets generated during and analysed during the current study are available from the corresponding author on reasonable request.

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Author contributions

B.W. was the project manager, developed the experimental design and was responsible for organizing, conducting and analyzing the experiment. B.W. wrote a first draft of the paper. M.P. was responsible for the implementation and testing of the experimental software. B.W. and M.P. were involved in building and adapting the experimental setup. Both authors read, revised and approved the final version of the paper.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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