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Humans underestimate their body mass in microgravity: evidence from reaching movements during spaceflight

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eLife Assessment

This paper undertakes an **important** investigation to determine whether movement slowing in microgravity is due to a strategic conservative approach or rather due to an underestimation of the mass of the arm. The experimental dataset is unique, the coupled experimental and computational analyses comprehensive, and the effect is strong. However, the authors present **incomplete** results to support the claim that movement slowing is due to mass underestimation. Further analysis is needed to rule out alternative explanations.

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Abstract

Astronauts consistently exhibit slower movements in microgravity, even during tasks requiring rapid responses. The sensorimotor mechanisms underlying this general slowing remain debated. Two competing hypotheses have been proposed: either the sensorimotor system adopts a conservative control strategy for safety and postural stability, or the system underestimates body mass due to reduced inputs from proprioceptive receptors. To resolve the debate, we studied twelve taikonauts aboard the China Space Station performing a classical hand-reaching task. Compared to their pre-flight performance and to an age-matched control group, participants showed increased movement durations and altered kinematic profiles in microgravity. Model-based analyses of motor control parameters revealed that these changes stemmed from reduced initial force generation in the feedforward control phase followed by compensatory feedback-based corrections. These findings support the body mass underestimation hypothesis while refuting the strategic slowing hypothesis. Importantly, the sensory estimate of bodily property in microgravity is biased but immune from sensorimotor adaptation, calling for an extension of existing theories of motor learning.

Introduction

Successful space exploration fundamentally depends on efficient sensorimotor control under microgravity conditions, where both movement accuracy and speed are critical (Strangman et al., 2014). A consistently observed phenomenon is that astronauts exhibit slower movements during routine activities in space stations (Kubis et al., 1977). This general movement slowing persists even in controlled experimental settings where astronauts are securely fastened without concerns for postural stability or safety. Indeed, fast movements in microgravity can be disadvantageous, potentially destabilizing posture, complicating the arrest of accelerated body segments, and increasing collision risks in confined spacecraft environments (Bock, 1998; Layne et al., 2001; Paloski et al., 1999; Reschke et al., 1998; Tafforin et al., 1989). Yet even when body stability is ensured, well-practiced goal-directed actions consistently show prolonged movement durations across various tasks, from hand pointing to visual targets (Berger et al., 1997; Bock et al., 2001, 2003; Mechtcheriakov et al., 2002) to step tracking with joysticks (Newman & Lathan, 1999; Sangals et al., 1999). This slowing manifests as reduced peak speeds in hand pointing (Mechtcheriakov et al., 2002; Sangals et al., 1999; Weber & Stelzer, 2022). Despite extensive documentation of this phenomenon, the underlying sensorimotor mechanisms remain unclear (Bock et al., 1996b; Weber et al., 2019), presenting a significant challenge for optimizing human performance in space.

Two primary hypotheses have emerged to explain the slowing of goal-directed actions in microgravity. The conservative control hypothesis suggests that the sensorimotor system adopts a generalized strategy prioritizing safety and postural stability over speed (Berger et al., 1997; Bock et al., 2010; Mechtcheriakov et al., 2002). This adaptation may arise from the novel challenges of movement control in microgravity, where even simple actions can propagate unexpected forces through body segments. The persistent application of this conservative strategy, as a generalized adaptation to the novel environment, could explain the movement slowing in microgravity. Alternatively, the body mass underestimation hypothesis builds on observations that humans consistently underestimate the mass of handheld objects in microgravity (Ross & Reschke, 1982), suggesting that similar perceptual biases might extend to the estimation of body segment properties (Bock et al., 1996b). Such misperception would directly impact the feedforward control of movement, potentially leading to systematic under-actuation of initial movements (Elliott et al., 2010, 2017).

Both hypotheses predict reduced peak speed and acceleration in microgravity, but they diverge in their predictions about movement kinematics. First, typical reaching movement exhibits a symmetrical bell-shaped speed profile, which minimizes energy expenditure while maximizing accuracy or smoothness according to optimal control principles (Flash & Hogan, 1985; Todorov, 2004). The conservative control hypothesis suggests a maintained temporal symmetry as longer durations are strategically planned for optimal performance, the peak speed and acceleration are thus delayed in time (Figure 1A). In contrast, the body mass underestimation hypothesis predicts that insufficient initial force generation, resulting from a systematic sensory bias in internal models that predict movement dynamics, would lead to earlier occurrence of peak speed and acceleration (Elliott et al., 2010, 2017). Previously, the timing of these peaks has shown mixed results, with some studies reporting earlier peaks (Sangals et al., 1999), others finding delays (Fowler et al., 2008), and some showing no temporal shifts (Berger et al., 1997; Mechtcheriakov et al., 2002). Second, the hypotheses make distinct predictions about feedback-based corrections during late reaching. The conservative control hypothesis suggests that movements are optimally adapted for the microgravity environment, thus requiring no additional corrections. Instead, the mass underestimation hypothesis predicts that initial underactuation would necessitate subsequent feedback-based corrections to reach the target (Chua & Elliott, 1993; Smeets & Brenner, 1995). These corrections would manifest as additional submovements, contributing to asymmetric speed profiles (Figure 1A). Current evidence for increased feedback-based corrections in microgravity remains inconsistent: while some studies support their presence (Sangals et al., 1999), others show conflicting results (Mechtcheriakov et al., 2002) or opposite effects (Fowler et al., 2008). If present, these corrective submovements should predict movement duration prolongation, serving as crucial evidence for the mass-underestimation account for the general slowing in microgravity.

To resolve the theoretical debate, we leveraged a unique biomechanical property of arm movements: the natural variation in effective limb mass across movement directions, known as anisotropic inertia (Mussa-Ivaldi et al., 1985). Based on a two-joint arm model (Li & Todorov, 2004), reaching movements toward targets in the frontal-medial direction involve greater

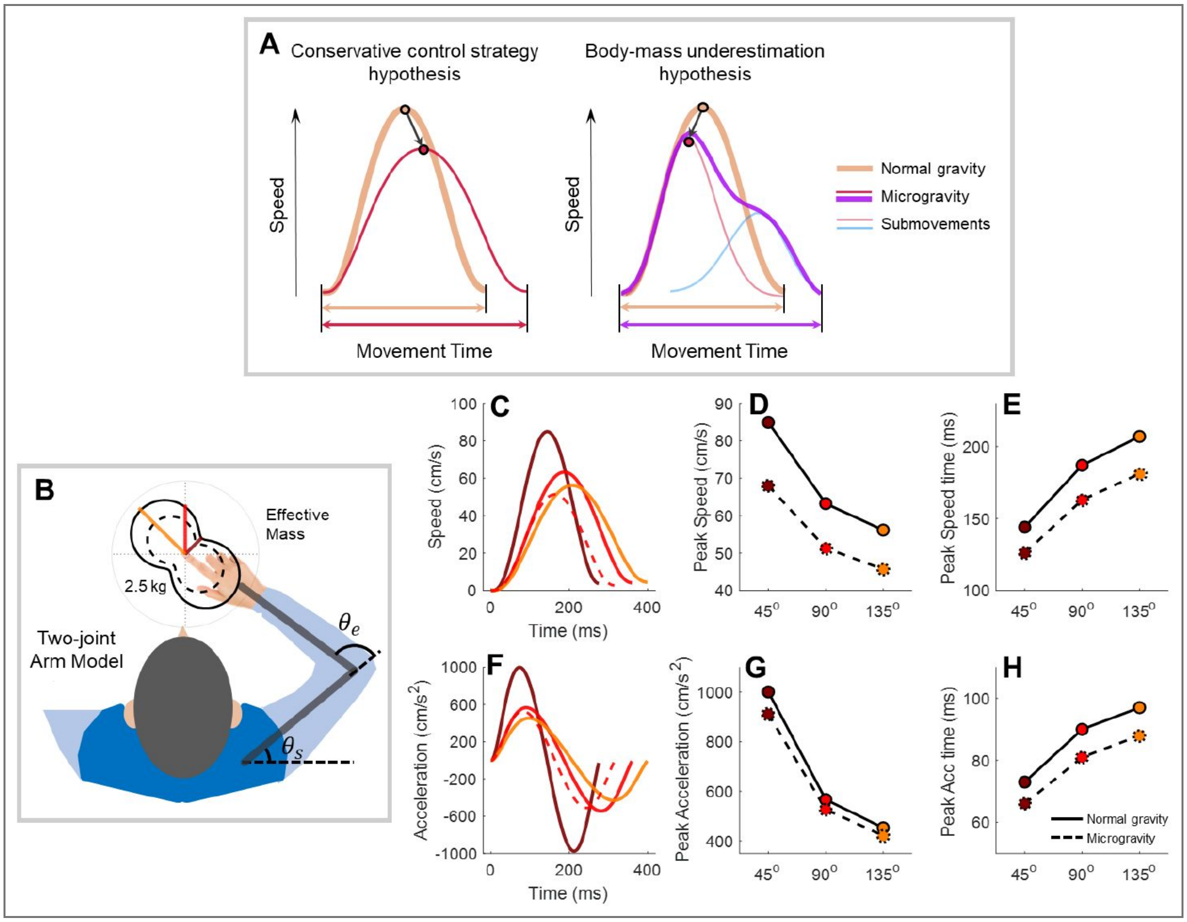


Figure 1. **Model simulations revealing characteristic kinematic features of reaching movements.**

A) Speed profile predictions under two competing hypotheses. Under normal gravity, hand speed follows a typical profile (bold apricot lines). According to the body mass underestimation hypothesis (left panel), initial underactuation produces a lower, earlier peak speed (light red), necessitating a corrective submovement (light blue) that results in an asymmetric, prolonged profile (purple). The conservative strategy hypothesis (right panel) predicts symmetric slowing with delayed peak speed (red). **B)** Two-joint arm model and its simulated effective mass. The spatial distribution of effective mass is shown by black curves (solid: normal gravity; dashed: 30% mass underestimation in microgravity). Colored lines indicate effective mass values for our three experimental target directions (45°, 90°, 135°). **C & F)** Representative speed and acceleration profiles simulated using effective masses from B. Profiles shown for normal (solid) and underestimated (dashed) body mass in the 90° direction demonstrate reduced, earlier peaks with mass underestimation. **D-E & G-H)** Simulated kinematic parameters across movement directions under normal (solid) and underestimated (dashed) mass conditions. Mass underestimation consistently leads to reduced amplitude and earlier timing of speed/acceleration peaks across all directions. Model simulation details are provided in the Methods.

effective mass compared to those in the frontal-lateral direction. Based on the motor utility theory, both the magnitude and timing of peak speed and acceleration should be systematically modulated by target direction (Shadmehr et al., 2016). Similarly, if astronauts underestimate their limb mass by approximately 30% in microgravity (Crevecoeur et al., 2014), we would expect reduced peak speed/acceleration and earlier occurrence of these peaks across all the directions. Here we examined twelve taikonauts before, during, and after their 3- or 6-month missions on the China Space Station (CSS) and compared their performance to age-matched ground controls. Participants performed rapid reaching movements to targets specifically chosen to engage different effective masses. Our approach allows us to dissociate the effects of mass underestimation from strategic control by examining how movement kinematics vary with direction-dependent effective mass.

Results

We compared the performance of 12 taikonauts to that of age-matched ground controls across multiple test sessions (Figure 6B and Table S1). Participants performed rapid reaching movements toward one of three targets on a tablet, presented in pseudorandom order to minimize movement automation and ensure active planning for each reach. Participants were instructed to reach the target with both speed and accuracy, pausing briefly before initiating the return. The emphasized requirement of moving fast would critically test whether movement slowing is ubiquitous in microgravity. The three target directions (45°, 90°, and 135°) were chosen to vary the effective mass of the moving limb, as verified through biomechanical simulations based on the two-joint arm model ((Li & Todorov, 2004); Figure 1B). Our model simulations not only demonstrated the direction-dependent variation in limb mass but also predicted how actual and misperceived limb mass would affect reaching kinematics (Figure 1C-H). These predictions were derived by combining the movement utility framework for estimating planned movement duration ((Shadmehr et al., 2016); Figure S1A-B) with a forward optimal controller for simulating reaching trajectories ((Todorov, 2005); Figure 1-figure supplement 1C-D). Notably, the model predicted that underestimating limb mass would lead to reduced and earlier peak speed/acceleration across directions (Figure 1C-H).

Movement Accuracy and Reaction Time Remain Intact in Microgravity

All participants successfully completed the task. Invalid trials, comprising early initiation (RT < 150 ms), late initiation (RT > 400 ms), or measurement failures, accounted for only 1.87% of trials in the experimental group and 0.70% in the control group. The percentage of invalid trials remained stable across the pre-in and post-flight phases (Friedman's tests, all $p > 0.1$).

Reaching accuracy remained high despite the stringent speed requirement of completing movements within 650 ms after target appearance (Figure 2-figure supplement 2). Analysis of endpoint error using a 3 (target direction) × 3 (phase) repeated-measures ANOVA revealed no significant differences across phases for either group. While the experimental group showed slightly better accuracy for the 45° target, this difference was minimal (0.04 cm over a 12 cm reach distance).

To introduce sufficient variability in reaction times for assessing speed–accuracy trade-offs (Sutter et al., 2021), a beep sound was played upon the target appearance in half of the trials. The random auditory signal tended to accelerate responses, thereby widening the distribution of reaction times in our dataset. The beep effectively reduced median reaction times by approximately 38 ms (242 ± 49 ms vs. 281 ± 50 ms; Figure 2A; see control group data in Figure 2-figure supplement 1A). To evaluate microgravity effects, we pooled data from both beep conditions and conducted a 3 (direction) × 3 (phase) repeated-measures ANOVA. The experimental group showed significant main effects of direction ($F(2,22) = 25.260$, $p < 0.001$, partial $\eta^2 = 0.697$) and phase ($F(2,22) = 5.820$, $p = 0.014$, partial $\eta^2 = 0.346$), without interaction ($F(4,44) = 2.246$, $p = 0.111$). Post-hoc analyses revealed slower reaction times for the 45° direction compared to both 90°

($p < 0.001$, d = 0.293) and 135° ($p = 0.003$, d = 0.284). Contrary to the conservative-strategy hypothesis, taikonauts did not show generalized slowing in reaction time; they actually had faster reaction times during spaceflight, incompatible with a generalized slowing strategy. Reactions were faster during the in-flight phase compared to pre-flight ($p = 0.037$, d = 0.333), with no significant difference between in-flight and post-flight phases ($p = 0.127$). Similar effects were observed in the control group (Figure 2-figure supplement1A), suggesting that the reduced reaction times likely reflect practice effects rather than microgravity influence. Thus, participants maintained, and even improved, their ability to rapidly initiate movements in microgravity with reaching accuracy.

Microgravity leads to slower movement

Although showing no decrement in movement accuracy or RT, the taikonauts exhibited prolonged movement durations (MD) during the in-flight phase compared to both pre- and post-flight phases (Figure 2B). A two-way repeated-measures ANOVA reveals significant main effects of direction ($F(2,22) = 62.555$, $p < 0.001$, partial $\eta^2 = 0.850$) and phase ($F(2,22) = 6.761$, $p = 0.015$, partial $\eta^2 = 0.381$), with no significant interaction ($F(4,44) = 1.413$, $p = 0.263$). Post-hoc comparisons showed that MD was significantly prolonged during the in-flight phase (vs. pre-flight: $p = 0.014$, d = 0.333; vs. post-flight: $p = 0.013$, d = 0.181). MD was also significantly greater for the 90° and 135° directions—those associated with larger effective mass—compared to the 45° direction (all $p < 0.001$ in pairwise comparisons). In contrast, the control group showed a similar directional effect but, importantly, did not show a phase effect (Figure 2—figure supplement 1), suggesting that movement slowing is specific to spaceflight.

Microgravity leads to reduced peak acceleration/speed and advanced timing of these peaks

The initial movement exhibited signs of underactuation during spaceflight, consistent with the body mass underestimation hypothesis (Figure 2—figure supplement 6). Peak acceleration and peak speed, established measures of feedforward control (Elliott et al., 2010, 2017), both showed significant decreases during the in-flight phase (Figure 3). For peak acceleration, there were significant main effects of phase ($F(2,22) = 6.401$, $p = 0.015$, partial $\eta^2 = 0.368$) and direction ($F(2,22) = 75.516$, $p < 0.001$, partial $\eta^2 = 0.873$), along with an interaction effect ($F(4,44) = 4.548$, $p = 0.016$, partial $\eta^2 = 0.293$). Consistent with model simulations, the 45° direction, associated with a lower effective mass, showed significantly higher peak acceleration than the other two directions (Figure 3A; all $p < 0.001$ in pairwise comparisons). Peak acceleration decreased significantly during spaceflight across all three directions (simple main effects: 45°, $p = 0.020$, $\eta^2 = 0.543$; 90°, $p = 0.004$, $\eta^2 = 0.673$; 135°, $p = 0.005$, $\eta^2 = 0.657$). Planned contrasts further indicated lower peak acceleration in the in-flight phase compared to pre-flight (45°, $p = 0.006$, $\eta^2 = 0.516$; 90°, $p = 0.008$, $\eta^2 = 0.485$; 135°, $p = 0.003$, $\eta^2 = 0.560$), with marginal recovery in the post-flight phase for two directions (45°, $p = 0.071$, $\eta^2 = 0.267$; 90°, $p = 0.062$, $\eta^2 = 0.282$) and significant recovery for one direction (135°, $p = 0.029$, $\eta^2 = 0.363$). In contrast, the control group displayed only the direction effect (Figure 3—figure supplement 1A-B), confirming that the underactuation was specific to microgravity.

Peak speed showed parallel changes during spaceflight (Figure 3B). Analysis revealed significant main effects of phase ($F(2,22) = 7.043$, $p = 0.009$, partial $\eta^2 = 0.390$) and direction ($F(2,22) = 114.420$, $p < 0.001$, partial $\eta^2 = 0.912$), without interaction ($F(4,44) = 1.929$, $p = 0.161$). Peak speed was significantly reduced during the in-flight phase compared to both pre-flight ($p = 0.004$, d = 0.331) and post-flight phases ($p = 0.046$, d = 0.199), with evidence of recovery post-flight (pre-vs. post-flight: $p = 0.483$, d = 0.132). Target direction systematically modulated peak speed (all pairwise comparisons, $p < 0.001$), with the 45° direction showing highest speeds and 135° lowest—matching predictions based on the movement utility theory. The control group showed only direction effects without phase-related changes (Figure 3—figure supplement 1B), confirming the specificity of these changes to microgravity exposure.

Figure 2. Reaction time and movement duration in the experimental group.

A) Median reaction times plotted by experimental phase (x-axis) and target direction (different colors). Dashed lines and dot lines represent the "beep" and "no beep" conditions. **B)** Average movement durations shown in the same format. Data are combined across beep conditions due to no significant differences between them. In both panels, error bars denote standard error across participants. Asterisks indicate significance levels for post-hoc phase comparisons ($^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$).

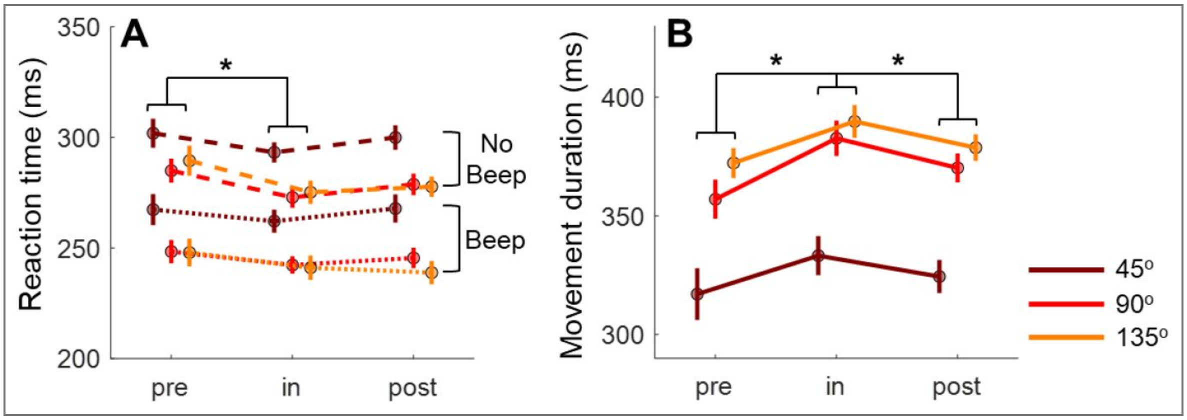
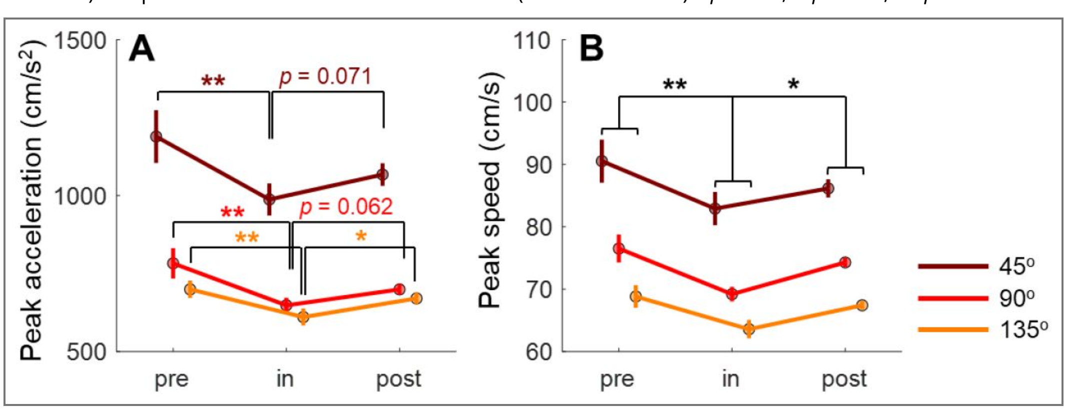


Figure 3. Magnitude changes of peak acceleration and speed during spaceflight.

A) Peak acceleration across experimental phases and movement directions, showing systematic decreases during the in-flight phase. **B)** Peak speed data presented in the same format, demonstrating parallel changes to peak acceleration. Error bars indicate standard error across participants. Statistical significance levels are shown for both overall phase comparisons (black asterisks) and planned contrasts within each direction (colored asterisks): $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.



The critical test for the competing hypotheses of movement slowing lies in whether peak acceleration and peak speed occur earlier or later in microgravity. The body mass underestimation hypothesis predicts earlier timing, whereas the conservative control strategy hypothesis predicts delayed timing. We observed an overall timing advance of these two measures. For peak acceleration time in the experimental group (Figure 4A), two-way repeated-measures ANOVAs revealed significant main effects of phase ($F(2,22) = 5.189$, $p = 0.024$, partial $\eta^2 = 0.321$) and direction ($F(2,22) = 30.375$, $p < 0.001$, partial $\eta^2 = 0.734$), along with an interaction effect ($F(4,44) = 4.503$, $p = 0.013$, partial $\eta^2 = 0.290$). In line with predictions, peak acceleration appeared significantly earlier in the 45° direction than other directions (45° vs. 90°, $p < 0.001$, d = 0.304; 45° vs. 135°, $p < 0.001$, d = 0.271). The phase effect emerged only for directions with higher effective mass (simple main effects, 90°: $F(2,10) = 6.660$, $p = 0.015$, $\eta^2 = 0.571$; 135°: $F(2,10) = 8.411$, $p = 0.007$, $\eta^2 = 0.627$). Planned contrasts confirmed earlier peak acceleration during spaceflight compared to post-flight (90°, $p = 0.005$, $\eta^2 = 0.530$; 135°, $p = 0.004$, $\eta^2 = 0.537$), with marginal differences versus pre-flight (135°, $p = 0.065$). The control group showed only directional effects without phase effect (Figure 4—figure supplement 1A).

Given that overall movement duration is prolonged in microgravity, a more direct way to assess the symmetry of the speed profile is to compute the relative timing of speed/acceleration peaks as a percentage of MD. Indeed, the relative timing of peak acceleration showed the same reduction in microgravity with a more pronounced effect than absolute timing (Figure 4C). A two-way repeated-measures ANOVA revealed significant main effects of phase ($F(2,22) = 15.414$, $p < 0.001$, partial $\eta^2 = 0.584$) and interaction ($F(2,22) = 7.223$, $p = 0.002$, partial $\eta^2 = 0.396$), while the main effect of direction was marginally significant ($F(2,22) = 3.374$, $p = 0.053$, partial $\eta^2 = 0.235$). Phase effects were significant for directions with higher effective mass (simple main effects: 90°, $F(2,10) = 13.327$, $p = 0.002$, $\eta^2 = 0.727$; 135°, $F(2,10) = 24.574$, $p < 0.001$, $\eta^2 = 0.831$) but not for 45° ($F(2,10) = 0.609$, $p = 0.563$). Planned contrasts confirmed significantly earlier timing during spaceflight compared to both pre- and post-flight phases (all $p < 0.002$ for 90° and 135° directions). None of these effects appeared in the control group (Figure 4—figure supplement 1C).

Peak speed also showed a timing advance, but only for relative timing. For absolute timing (Figure 4B), a two-way repeated-measures ANOVA revealed a significant main effect of direction ($F(2,22) = 57.428$, $p < 0.001$, partial $\eta^2 = 0.839$) and a marginal interaction ($F(4,44) = 2.233$, $p = 0.095$, partial $\eta^2 = 0.169$), without a phase effect ($F(2,22) = 0.093$, $p = 0.864$). In contrast, relative timing analysis (Figure 4D) showed significant effects of phase ($F(2,22) = 8.941$, $p = 0.004$, partial $\eta^2 = 0.448$), direction ($F(2,22) = 4.991$, $p = 0.030$, partial $\eta^2 = 0.312$), and their interaction ($F(4,44) = 4.755$, $p = 0.015$, partial $\eta^2 = 0.302$). The phase effect appeared only for directions with higher effective mass (90°: $F(2,10) = 17.278$, $p = 0.001$, $\eta^2 = 0.776$; 135°: $F(2,10) = 6.189$, $p = 0.018$, $\eta^2 = 0.553$). Planned contrasts revealed significantly earlier relative timing during spaceflight versus pre-flight for both 90° ($p < 0.001$, $\eta^2 = 0.770$) and 135° ($p = 0.007$, $\eta^2 = 0.496$) directions, with significant post-flight recovery in 90° ($p = 0.003$, $\eta^2 = 0.575$). The control group showed only directional effects (Figure 4—figure supplement 1B & 1D). Thus, after accounting for the prolongation of movement duration, we observed a temporal advance of peak acceleration and speed during spaceflight.

Movement slowing is associated with corrective submovements

The feedforward component of movement, captured by our model simulations, accounts for only the initial phase of reaching. With peak acceleration and speed occurring at approximately 80 ms and 150 ms after movement onset, and total movement duration spanning 300-400 ms, participants had ample opportunity for feedback-based corrections (Dimitriou et al., 2013). These corrections, if present, would manifest as secondary submovements (D. E. Meyer et al., 1988). While optimal reaching movements typically show symmetrical speed profiles (Flash & Hogan, 1985), the presence of corrective submovements creates characteristic right-skewed speed profiles (Elliott et al., 2010; D. E. Meyer et al., 1988; Woodworth, 1899). To identify such corrections, we employed an established decomposition method (Rohrer & Hogan, 2006) to detect trials containing both primary and secondary submovements (two-peak trials; Figure 5A).

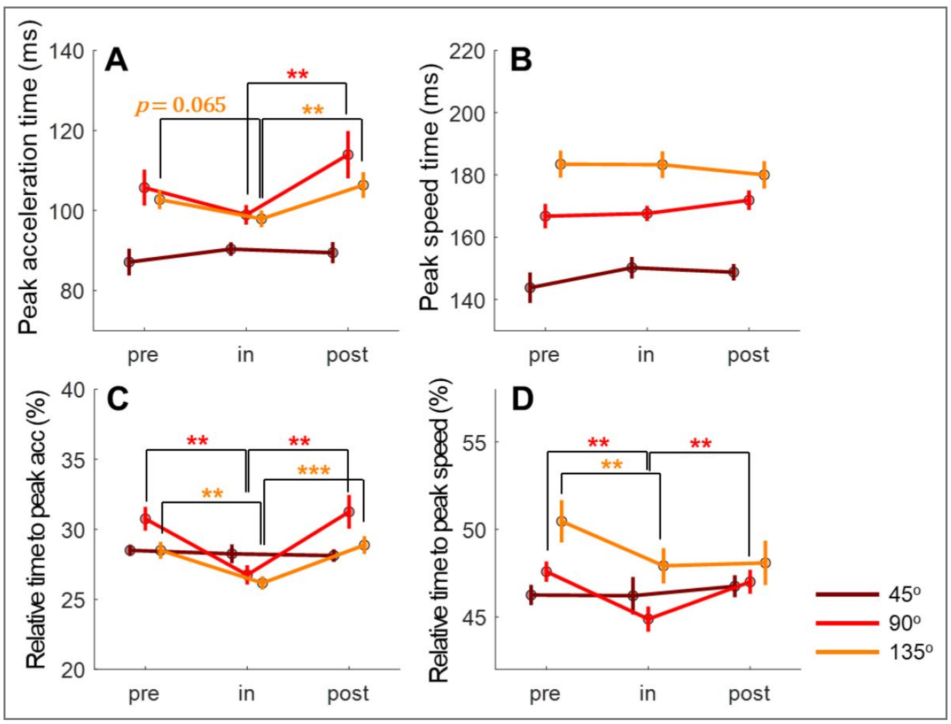


Figure 4. **Temporal analysis of peak acceleration and peak speed during spaceflight.**

A-B) Time to peak acceleration and peak speed across experimental phases and movement directions. **C-D)** Relative timing analysis showing these same peaks as a percentage of total movement duration, revealing more pronounced microgravity effects than absolute timing measures. Error bars indicate standard error across participants. Asterisks denote significance levels for planned phase comparisons ($^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$). Note the systematic modulation of timing by phase, particularly for high effective mass conditions.

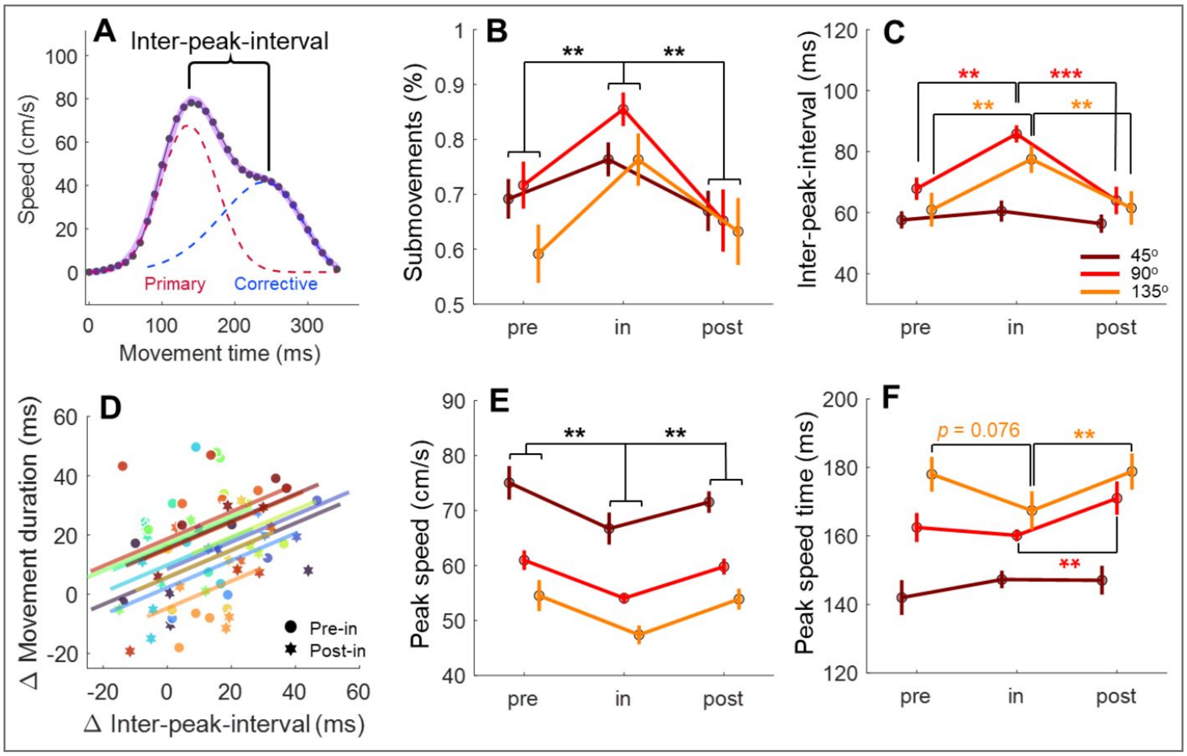


Figure 5. **Submovements analysis revealed changes in corrective movements during spaceflight.**

A) Decomposition of a representative two-peak speed profile, illustrating primary and corrective submovements separated by the inter-peak interval (IPI). **B)** Proportion of movements showing corrective submovements across phases and directions. **C)** Magnitude of feedback corrections quantified by IPI, showing direction-dependent increases in microgravity. **D)** Linear relationship between feedback correction changes (ΔIPI) and movement slowing (ΔMD). Each participant (shown in different colors) contributed multiple data points from different phases and directions. **E-F)** Primary submovement characteristics: peak speed amplitude and timing. Error bars denote standard error across participants; asterisks indicate significance ($^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$).

Analysis revealed a striking increase in corrective movements during spaceflight. The percentage of trials showing two distinct submovements increased significantly during the in-flight phase (Figure 5B), evidenced by a main effect of phase (F(2,22) = 13.969, $p < 0.001$, partial $\eta^2 = 0.559$) and a marginal phase-by-direction interaction (F(2,22) = 2.642, $p = 0.054$, partial $\eta^2 = 0.194$). This effect was specific to microgravity exposure, as the control group showed no significant changes across phases (all $p > 0.05$; Figure 5—figure supplement 1A). Notably, the increase in corrective movements was most pronounced for directions with higher effective mass (simple main effects: 90°, F(2,10) = 11.426, $p = 0.003$, $\eta^2 = 0.696$; 135°, F(2,10) = 7.292, $p = 0.011$, $\eta^2 = 0.593$).

To understand how feedback corrections contribute to movement slowing, we analyzed the inter-peak interval (IPI) between primary and corrective submovements, an established measure of feedback-based control (Craik, 1947; D. Meyer et al., 2018; D. E. Meyer et al., 1988). The taikonauts showed markedly longer IPIs during spaceflight (Figure 5C), with a two-way ANOVA revealing significant effects of phase (F(2,22) = 11.150, $p = 0.001$, partial $\eta^2 = 0.503$), direction (F(2,22) = 4.721, $p = 0.026$, partial $\eta^2 = 0.300$), and their interaction (F(2,22) = 6.559, $p = 0.002$, partial $\eta^2 = 0.374$). Critically, IPI increases were confined to directions with greater effective mass (90°, F(2,10) = 11.573, $p = 0.002$, $\eta^2 = 0.698$; 135°, F(2,10) = 13.371, $p = 0.001$, $\eta^2 = 0.728$). The control group exhibited only directional effects (F(2,22) = 19.277, $p < 0.001$, partial $\eta^2 = 0.637$; Figure 5—figure supplement 1B) without phase-related changes (all $p > 0.13$).

To establish whether these enlarged corrective movements explain the overall movement slowing, we examined how changes in IPI (ΔIPI) predict changes in movement duration (ΔMD) during spaceflight (Figure 5D). A Linear Mixed Model analysis incorporating ΔIPI, phase transition (pre-to-in and post-to-in), and direction revealed that ΔIPI significantly predicted ΔMD (β = 0.458 [0.144, 0.771], t(67) = 2.915, $p = 0.005$, partial-$R^2 = 0.103$). Phase transition also showed significance (β = -0.01 [-0.017, -0.001], t(67) = -2.696, $p = 0.009$, partial-$R^2 = 0.086$), with stronger effects for pre-to-in versus post-to-in transitions, indicating incomplete recovery post-flight. Movement direction showed no significant effect (all $p > 0.42$), suggesting that the relationship between corrective movements and duration slowing generalizes across reaching directions.

The analysis of primary submovements revealed even stronger evidence for feedforward control changes in microgravity. By focusing on just the primary submovement in two-peak trials, we found more pronounced effects than when analyzing the overall movement (comparing Figure 5E to Figure 5—figure supplement 1C). The primary submovement showed a robust reduction in peak speed during spaceflight (main effect of phase: F(2,22) = 10.363, $p = 0.001$, partial $\eta^2 = 0.485$) that was consistent across directions (interaction: F(4,44) = 0.382, $p = 0.711$; Figure 5E). More tellingly, while the overall movement showed timing changes only in relative measures, the primary submovement exhibited earlier peak speed timing in absolute terms (phase-by-direction interaction: F(2,22) = 4.264, $p = 0.012$, partial $\eta^2 = 0.279$). This temporal advance was most evident in directions with higher effective mass (planned contrasts vs. post-flight: 135°: $p = 0.008$, $\eta^2 = 0.615$; 90°: $p = 0.076$, $\eta^2 = 0.403$) but absent in the 45° direction ($p = 0.188$, $\eta^2 = 0.284$). The selective nature of the primary submovement in both magnitude and timing (comparing Figure 4B and Figure 5F) provides compelling evidence for mass-dependent changes in feedforward control. The control group showed only the expected directional variations (F(2,22) = 46.259, $p < 0.001$, partial $\eta^2 = 0.808$; Figure 5—figure supplement 1D) without any phase effects (all $p > 0.13$), confirming these changes as specific to microgravity exposure.

The microgravity effects on movement kinematics are directionally dependent

Reaching movements are inherently directionally dependent due to anisotropies in limb dynamics (Gordon et al., 1994; Shadmehr et al., 2016). Even before microgravity exposure, key kinematic variables—peak speed, peak acceleration, and their timing—exhibited consistent directional differences, as shown in Figure 1C–H. This baseline direction-dependency suggests that effective mass varies across movement directions and influences movement execution under normal gravity. Building on this observation, we tested whether microgravity-induced changes would also follow a direction-specific pattern, as predicted by the mass underestimation hypothesis.

To assess microgravity-induced changes, we quantified the directional differences (Δ) in peak speed, peak acceleration, and their timing, comparing in-flight measurements to pre-flight baselines. The comparison between in-flight and post-flight was not included in this analysis since post-flight recovery was not complete (see peak speed and peak acceleration changes in Figure 3). As shown in Figure 6, these directional effects were evident across all kinematic metrics. For both Δ peak speed and Δ peak acceleration, the magnitude of change followed a consistent ranking across directions, with the largest effects at 45°, intermediate at 90°, and smallest at 135° (i.e., 45° > 90° > 135°). Similarly, for timing metrics—Δ peak speed time and Δ peak acceleration time—the shortest delays occurred at 45°, while 90° and 135° showed comparably larger shifts. Note the 45° did not show significant timing advance, as previously shown in Figure 5F.

Overall, the direction-dependent changes were roughly consistent with model predictions based on the mass underestimation hypothesis (Figure 1 D, E, G and H). The model simulation similarly indicates that amplitude changes (Δ peak speed, Δ peak acceleration) and timing advances are rank ordered by movement directions. To quantify the correspondence between model predictions and experimental measurements, we performed repeated-measures correlation analyses between simulated and observed Δ values across directions (Bakdash & Marusich, 2017). Significant within-subject correlations were found for Δ peak speed time (r_{rm} = 0.627, p < 0.001), Δ peak acceleration time (r_{rm} = 0.591, p = 0.002), and Δ peak acceleration (r_{rm} = 0.573, p = 0.003), while Δ peak speed did not reach significance (r_{rm} = 0.334, p = 0.103). Together, these results demonstrate that the microgravity effect is direction-specific and the rank ordering of directions is broadly aligned with the predictions of the mass underestimation model.

Speed-accuracy trade-offs remain intact during spaceflight

The speed-accuracy trade-off, a fundamental indicator of motor control efficiency, remained largely intact during spaceflight. We evaluated this trade-off using two complementary approaches. First, following the traditional Fitts' framework =, we examined the relationship between movement duration and endpoint dispersion, which was not negatively affected by microgravity (Figure 2—figure supplement 3). Second, we analyzed the trade-off between reaction time and initial movement variance (Figure 2—figure supplement 4), which reflects the quality of movement planning (Sutter et al., 2021). This relationship persisted across all phases in both groups. Thus, while microgravity altered movement execution through mass underestimation, it did not fundamentally disrupt the sensorimotor system's capacity to regulate the speed-accuracy trade-off. Additionally, in both groups, we found a significant negative correlation between movement duration (MD) and reaction time (RT), both across and within individuals (Figure 2—figure supplement 5). This finding indicates that participants moved faster when their RT was slower, and vice versa. This flexible motor adjustment, likely in response to the task requirement for rapid movements, remained consistent during spaceflight.

Discussion

Long-term exposure to microgravity presents a unique environment that cannot be replicated on Earth, offering invaluable insights into human sensorimotor adaptation. Understanding how microgravity affects motor performance is crucial both for ensuring successful space exploration and for advancing our fundamental knowledge of motor control principles. Our study elucidates the mechanisms underlying one of the most distinctive motor signatures in microgravity: the slowing of goal-directed actions during spaceflight. While taikonauts maintained reaching accuracy and rapid reaction times, their movements exhibited systematic changes in microgravity characterized by reduced peak speed and acceleration, along with advanced timing of these peaks. These kinematic alterations persisted across repetitive trials within a session and also persisted across multiple sessions during spaceflight (Figure 4—figure supplement 2), contradicting the

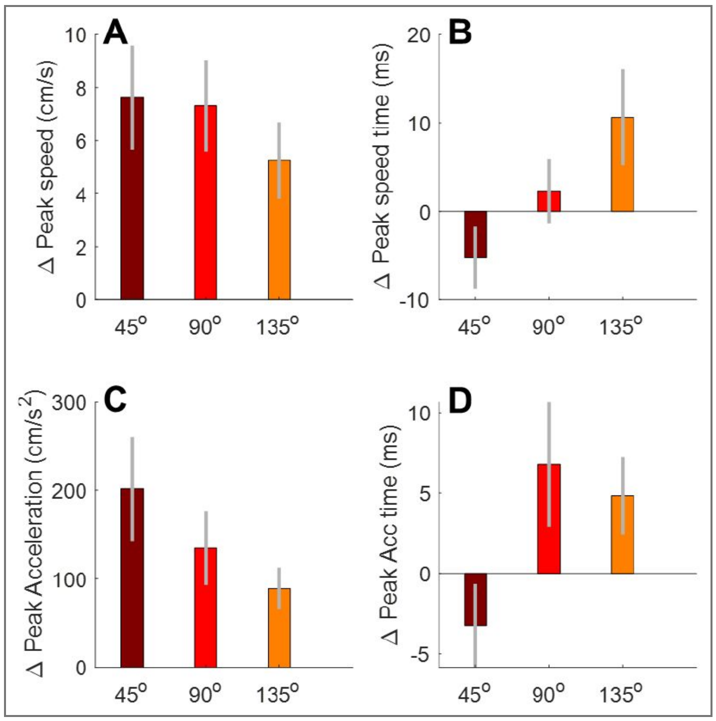


Figure 6. Direction-dependent effects of microgravity on peak kinematics and their timing.

Each panel shows the change (Δ) relative to the in-flight session. Colors represent movement directions consistently across panels. Panels A–D show, respectively: (A) change in peak speed (cm/s), (B) change in peak speed time (ms), (C) change in peak acceleration time (ms), and (D) change in peak acceleration (cm/s^2). Bars represent group means; error bars denote standard errors across participants.

hypothesis that astronauts adopt a conservative control strategy to maintain stability. Instead, they align precisely with our hypothesis that individuals underestimate limb effective mass, leading to underactuated initial movements.

These changes followed model predictions across movement directions with varying effective masses due to limb biomechanics, confirming that the representation of body mass indeed affects movement control during spaceflight. Beyond the initial underactuation caused by altered feedforward control, we observed increased feedback-based corrective submovements that predicted movement duration prolongation in spaceflight. These effects were specific to microgravity exposure, occurring only during spaceflight with marked recovery post-flight, while ground controls showed no comparable changes. Notably, the taikonauts' fundamental motor control capabilities remained largely intact, as evidenced by preserved movement accuracy, reaction time, and speed-accuracy trade-offs.

The underactuation observed in initial movements under microgravity extends findings from parabolic flight studies (Crevecoeur et al., 2014; Papaxanthis et al., 2005). When individuals performed reaching movements with handheld weights during parabolic flight-induced gravity alterations, their reaching trajectories and grip forces showed systematic changes suggesting mass misperception (Bock, 1998; Bock et al., 1996a, 1996b; Crevecoeur et al., 2014; Papaxanthis et al., 2005). In zero-gravity conditions, goal-directed arm movements were slower (Papaxanthis et al., 2005), and grip-load force coordination was altered (Crevecoeur et al., 2010, 2014), consistent with mass underestimation. Conversely, hypergravity (1.8g) induced increased peak acceleration and speed in reaching movements, along with elevated grip force during object manipulation, suggesting mass overestimation (Bock, 1998; Bock et al., 1992, 1996a, 1996b). Notably, modified grip-load force coordination reflects changes in feedforward control (Flanagan & Wing, 1997; Johansson & Edin, 1993), indicating that mass misestimation influences action planning. However, while parabolic flight studies capture only transient adaptations to rapid gravity transitions, our study targets general slowing during spaceflight and reveals the enduring effects of sustained microgravity exposure.

We also considered alternative explanations beyond mass underestimation. First, we tested whether a change in the cost-function of our optimal control model, which simulates a more conservative control, could account for movement slowing. This was implemented as a uniform rescaling of the state and control weights (Q and R) in the cost function (Crevecoeur et al., 2010). Increasing the scaling factors (α) will simulate the increase in control effort penalty and a more conservative control. However, while this manipulation reduced peak velocity and acceleration, it also delayed their occurrence, a pattern opposite to the observed effect. Thus, changing the cost function alone is unable to explain away the movement slowing. Details of the cost-function simulations are provided in the Supplementary Materials (Supplementary Notes 1 and Figure 1—figure supplements 2 and 3). Second, muscle weakness, a common effect during prolonged spaceflight, might also contribute to movement slowing. However, recent large-sample studies suggest that muscle strength reduction is mainly in lower-limb muscles that counter gravitational pull, not in upper-body muscles (Scott et al., 2023). Furthermore, the torques required in our task (~2 N·m for ~12 cm reaches) are relatively small, it is unlikely that muscle weakness alone accounts for the observed kinematics. Third, finger-screen friction might slow down the reaching movements. However, during typical interaction with a touch screen, frictional forces are modest, generally ranging from 0.1 to 0.5 N (Ayyildiz et al., 2018), and directional variations are likely even smaller. These values are minimal compared to the 10–15 N required to accelerate the arm during reaching, making frictional anisotropy an unlikely source of the directional kinematic changes. Fourth, body stabilization in microgravity might also contribute to movement slowing in space. In fact, our participants were securely strapped at the feet and used the non-reaching hand to grasp a fixed bar for support. Importantly, the primary effects—reduced peak acceleration and earlier timing—emerged within the first ~90–100 ms of movement onset, well before any instability-related corrections could occur. Thus, insufficient stabilization is unlikely to account for the observed movement changes. Finally, Coriolis and centripetal torques, omitted from our simplified model, might also contribute to movement slowing or direction effect we observed.

Previous work has suggested that such effects may be non-negligible in fast planar reaching (Hollerbach & Flash, 1982). To examine their potential contribution, we incorporated Coriolis and centripetal torques terms in our extended model (see Supplementary Notes 2 and Figure 1—figure supplement 4 and 5 for details). These torques were also directionally anisotropic, but their magnitudes were too small to meaningfully affect movement utility or effort computation in our model. Thus, Coriolis and centripetal torques are unlikely to explain the large and systematical effects we observed.

Our results strongly challenge the conservative control strategy hypothesis, which posits that movement slowing reflects a generalized adaptation to address stability or safety concerns during spaceflight (Bock, 1998). Contrary to this hypothesis, taikonauts demonstrated faster reaction times during spaceflight—incompatible with a generalized slowing strategy. More critically, if the sensorimotor system adopted a conservative strategy with pre-planned longer movement durations, the speed profile should maintain symmetry with delayed peak acceleration and speed. Instead, we observed left-skewed speed profiles with earlier peak occurrence, directly contradicting the predictions of strategic slowing. This temporal change was more pronounced if primary submovement is isolated to pinpoint the feedforward control of the reaching since the overall speed profile is affected by the later feedback-based corrections. Previous studies reported inconsistent findings regarding speed profile symmetry, including advanced (Sangals et al., 1999), delayed (Fowler et al., 2008), or unchanged (Berger et al., 1997; Mechtcheriakov et al., 2002) peak speed timing during spaceflight. These discrepancies likely reflect methodological differences, including task variations and technical limitations. For example, two studies used joystick-based pointing tasks without involving limb movement (Fowler et al., 2008; Sangals et al., 1999), which arguably makes them less suitable for examining mass underestimation effects. Mechtcheriakov and colleagues used an outstretched arm task, but their limited sampling rate of 25 Hz may have hindered precise quantification of peak speed, preventing submovement analysis. Additionally, our larger sample size (n = 12) may have enhanced detection of microgravity effects compared to previous studies with typically 3-7 participants (Berger et al., 1997; Bock et al., 2001, 2003, 2010; Fowler et al., 2008; Mechtcheriakov et al., 2002; Papaxanthis et al., 1998; Weber & Stelzer, 2022) or single-participant designs (Heuer et al., 2003; Manzey et al., 1998; Sangals et al., 1999).

The underestimation of body mass in microgravity likely arises through two complementary mechanisms: degraded proprioceptive feedback and misinterpretation of weight-related cues. Microgravity impairs proprioception by reducing both muscle spindle sensitivity (Lackner & DiZio, 1992) and joint receptor responsiveness (Proske & Weber, 2023)—inputs that are crucial for weight perception (Proske & Gandevia, 2012). Furthermore, the sensorimotor system may interpret weight unloading as reduced body mass rather than environmental change (Bock et al., 1996b). Recent studies demonstrate that the sensorimotor system probabilistically infers body-versus-environment causality based on available sensory cues (Berniker & Kording, 2008; Fercho & Baugh, 2014; Kluzik et al., 2008; Kong et al., 2017; Wilke et al., 2013). In normal gravity, consistent mass-weight relationships lead to heavy reliance on weight-related cues for mass estimation (Bock, 1998; Bock et al., 1996b; Sangals et al., 1999). In microgravity, however, reduced weight cues become misleading and may systematically bias mass perception, affecting feedforward control of movement.

The persistence of deviant feedforward control and the subsequent within-movement corrections appears intriguing from the theories of human motor learning. Humans demonstrate remarkable ability to adapt to environmental changes in terrestrial studies. For experimentally-applied visual or force perturbations, individuals can recalibrate their sensorimotor control and restore baseline performance within minutes (Krakauer et al., 2019), a process often theorized as forming internal models of the new environment (Kawato, 1999; Wolpert et al., 1995). Relatedly, even when the body mass is perturbed by attaching a weight on the forearm, individuals can fully adapt their reaching movements within tens of trials (Wang & Sainburg, 2004). Previous studies on parabolic flights have also shown that the control of arm movements exhibited rapid adaptation to gravitational changes over the course of several parabolas. (e.g., Gaveau et al., 2016). In contrast, our in-flight sessions were scheduled at least three weeks post-launch—even well beyond the 2-3 weeks window typically considered critical for sensorimotor adaptation in spaceflight (Kanas & Manzey, 2008), but the participants still exhibited un-adapted feedforward control and internal model.

We believe this contrast stems from distinct natures of perturbation effects in microgravity when compared to in terrestrial environments. Previous studies on sensorimotor adaptation simulated environmental changes by imposing a perturbation to alter the relationship between motor commands and sensory consequences of motor commands. For reaching adaptation here, visuomotor perturbations changes the spatial mapping between hand motion and its visual representation's motion (Krakauer et al., 2000; Wolpert et al., 2011); force perturbations change the dynamic mapping between actual force outputs and hand motion (Lackner & Dizio, 1994; Shadmehr & Mussa-Ivaldi, 1994). These mapping changes, though novel, are consistent thus the sensorimotor system is capable of approximating them and adapting accordingly. Theories of sensorimotor adaptation conceptualize the formation of the new mapping as acquiring internal models, which links motor command and efference copy to sensory consequences of motor commands (Flanagan & Wing, 1997; Kurtzer et al., 2008; Wolpert et al., 1998; Wolpert & Miall, 1996). However, the novel environment of microgravity alters the sensory estimate of motor apparatus (i.e., the body mass here), not merely the sensorimotor mapping. In normal gravity, weight-related sensory cues—mostly proprioceptive feedback—accurately represent body mass. In microgravity, however, these weight-related cues are substantially reduced due to the absence of gravitational pull, providing persistently biased information about body mass. In other words, the microgravity environment failed to provide veridical sensory cues for mass estimation, and reduced gravitational and proprioceptive cues persistently misinform the controller about body mass. Since body mass is a parametric input to the internal models, its bias would affect motor actions even when the internal models are well adapted. Hence, the unique environment of microgravity reveals a fundamental constraint of the sensorimotor system, i.e., its quick adaptability is restricted to learning a novel sensorimotor mapping, not to persistent sensory bias of bodily property.

The discrete nature of our reaching task may contribute to the persistence of sensory bias. Within-movement corrections indicates that the sensorimotor system learns about sensory bias of mass estimation (Dimitriou et al., 2013), possibly via kinesthetic feedback during movement (Papaxanthis et al., 2005; Proske & Weber, 2023; Weber & Stelzer, 2022). However, movement-related cues only become available after movement initiation. Once a movement ends and the hand returns to rest, microgravity continues to elicit misleading sensory cues that bias mass estimation between trials. This lack of between-trial adaptation parallels findings from a manual interception study aboard the International Space Station, where astronauts persistently initiated movements too early when attempting to intercept an object moving at constant speed (McIntyre et al., 2001). Although astronauts corrected their movements online within each trial, their initial timing error persisted across multiple trials and sessions during a 15-day spaceflight. Hence, discrete motor tasks, such as manual interception and reaching, rely heavily on feedforward control, and are susceptible to sensory biases induced by microgravity. This explains why continuous reaching between targets, without stopping, shows quicker adaptation to zero gravity in parabolic flights (Papaxanthis et al., 2005) and does not exhibit prolonged movement duration during spaceflight (Fowler et al., 2008).

What are the potential consequences of body mass underestimation beyond the simple reaching movements examined here? The implications may be particularly significant given two key considerations. First, the majority of human movements are not deliberately controlled (Brooks, 1986; Marsden et al., 1976), suggesting that underactuated initial movements may be pervasive in microgravity—especially for actions involving larger body masses such as whole-body movements or object manipulation. Without the controlled conditions and explicit speed requirements of our experimental task, such underactuation might manifest even more prominently in natural movements during spaceflight. Second, our finding of increased reliance on feedback-based corrections points to a potentially costly compensatory mechanism. As feedforward control becomes systematically biased by mass underestimation, the sensorimotor system must depend more heavily on feedback control to achieve adequate performance. This increased reliance on feedback processes may demand additional cognitive resources for action regulation (Bock et al., 2010), potentially contributing to the non-specific stressors that have been shown to impair human performance in space (Tian et al., 2024). The cognitive cost of these compensatory adjustments might be particularly relevant for complex motor tasks or situations requiring divided attention during spaceflight operations.

The preservation of speed-accuracy trade-offs in our study extends previous findings from Fitts' task experiments performed during spaceflight (Fowler et al., 2008). Both the traditional speed-accuracy trade-off and action planning-dependent trade-off remained intact in microgravity (Figure 2—figure supplement 3 and 4), suggesting preserved fundamental motor control capacity. Motor performance during spaceflight typically degrades in tasks with high cognitive demands (Eddy et al., 1998; Manzey et al., 1998; Strangman et al., 2014), particularly those requiring sustained attention (Tian et al., 2024). Our findings suggest that while mass underestimation affects movement execution, the underlying motor control capabilities remain robust in microgravity when cognitive demands are modest.

Our study presents three methodological limitations that warrant consideration. First, despite matching for age and gender, our ground controls exhibited faster movements than the taikonauts. This systematic difference, reflected in higher peak acceleration and speed, may stem from differing experience with the touchpad device used for movement recording. While taikonauts used touchpads regularly, 9 of 12 control participants had minimal experience, potentially leading to compensatory faster movements to avoid overtime errors. Second, the temporal evolution of mass underestimation effects remains unclear. Our earliest measurements occurred three weeks post-launch, though parabolic flight studies suggest these effects may emerge within hours of microgravity exposure (Crevecoeur et al., 2014; Papaxanthis et al., 2005). Additionally, incomplete post-flight recovery in some kinematic measures suggests either a mass overestimation due to exaggerated weight-related cues or neuromuscular deficiency typically observed shortly after returning to earth (Tays et al., 2021). Third, while our hand-reaching task enabled us to use well-established analytical frameworks for studying motor control aspects of movements, the generalizability of mass underestimation effects to other movements, particularly whole-body actions, remains to be determined. Future research should address these limitations by implementing matched device training protocols, adding early- and post-flight measurements, and extending investigations to diverse motor tasks. We also notice that the microgravity effect was less consistent for the 45° reaching direction. This direction engages more single-joint, elbow-dominant reaches, whereas the 90° and 135° targets require greater multi-joint (shoulder + elbow) coordination. Consistent with this, an exploratory analysis of hand-path curvature (cumulative curvature; positive = counterclockwise) showed larger curvature at 45° (6.484° ± 0.841°) than at 90° (1.539° ± 0.462°) or 135° (2.819° ± 0.538°). The significantly larger curvature in the 45° condition suggests that these movements deviate more from a straight-line path, supporting a more elbow-dominant movement in this direction. Importantly, this curvature pattern was present in both the pre-flight and in-flight phases, indicating that it is a general movement characteristic rather than a microgravity-induced effect. We postulate that single-joint movements, more so than we considered in our ideal two-link model, made effective mass rather small in the 45° direction, hence the mass underestimation and underactuation in feedforward planning had smaller effect, compared to model simulations, in this direction.

In conclusion, our study provides compelling evidence that movement slowing in microgravity stems from systematic underestimation of body mass, rather than a conservative control strategy. By leveraging the direction-dependent variation in limb effective mass, we demonstrated that reaching movements in microgravity exhibit kinematic signatures—reduced and earlier peak speed/acceleration—that precisely match the predictions of mass underestimation. The persistence of these effects throughout long-duration spaceflight, coupled with increased feedback-based corrections, reveals how altered sensory inputs fundamentally impact both predictive and reactive components of motor control and evades sensorimotor adaptation. While basic motor control capabilities remain intact, as evidenced by preserved speed-accuracy trade-offs, the consistent underactuation of movements may have significant implications for the theorization of sensorimotor learning and for practical considerations of motor performance during space operations. These findings not only advance our understanding of how the sensorimotor system adapts to novel gravitational environments but also reveal fundamental principles of sensorimotor integration, particularly the central role of gravitational cues in shaping our perception of body dynamics.

Methods

Participants

Twelve taikonauts (2 females, 10 males; mean age 49.5 ± 6.5 years) from the first four missions of the China Space Station (CSS) served as the experimental group (Table S1). The control group consisted of 12 right-handed residents from Beijing (2 females, 10 males; mean age 49.9 ± 6.5 years). Control group received monetary compensation. All participants were provided with written informed consent forms, approved by the Ethics Committee of the China Astronaut Research and Training Center and the Institutional Review Board of Peking University. The experimental group was exposed to microgravity for 92–187 days during manned missions in China's Shenzhou Program. Due to operational constraints, the number of test sessions varied among taikonauts: one completed 4 sessions, five completed 6, and six completed 7 (Table S1). All control sessions were conducted at Peking University.

Task and experimental design

The task was conducted using a tablet (Surface Pro 6, Microsoft, Redmond, Washington) with 100Hz sampling frequency and noise-canceling earphones (FiiO FA7, FiiO Electronics Technology, Guangzhou, China). During in-flight sessions, participants wore earphones and assumed a neutral posture with feet secured by foot straps in front of a foldable tabletop, positioned 0.9 meters above the cabin floor. They held the tabletop edge with their left hand, allowing their right hand to move freely on the tablet (Figure 7A). The foot straps and left-hand grip provided body stabilization. The tablet, attached to the tabletop with Velcro, was placed ~35 cm in front of participants and 30 cm below chest level (Figure 7A). At the start of each trial, an orange circle (0.5 cm radius) appeared at the bottom of the screen, signaling participants to move their right index finger to this start circle. After a random delay (500–1000 ms), a target appeared at one of three possible locations, 12 cm from the start circle at 45°, 90°, or 135° counterclockwise from the horizontal axis (Figure 7A). Participants were instructed to reach the target quickly and accurately, pausing briefly before returning to the start. If the time from target appearance to movement end (finger speed <10 cm/s) exceeded 650 ms, a "too slow" message prompted faster movement. In half of the trials, a 50 ms "beep" sound was played at target appearance. Each session included 120 trials, with 3 target directions and 2 beep conditions balanced and randomized (Figure 7B). The x-y position of the index finger was recorded continuously at 100 Hz.

All experiments aboard the China Space Station were monitored in real time by experimenters at the Beijing Control Center. Task instructions were displayed on the opening screen of the data-acquisition application, and participants were given ample time to read them. The same team of experimenters administered all pre-, in-, and post-flight sessions using identical instructions. Consistent with standard practice, the astronauts served as both participants and on-orbit experimenters and were extensively trained for this role on the ground. Multiple pre-flight sessions were conducted to familiarize them with the task. These safeguards were implemented to ensure high-quality data.

The control group was included to assess a potential confounding effect of repeated measurements. The interval between successive test sessions was 6–9 days, which was shorter than those of the taikonauts (1–2 months) to conservatively evaluate potential practice effects. Despite the shorter intervals, no significant differences were observed across sessions for most measures (except reaction time), confirming minimal practice effects and providing a robust

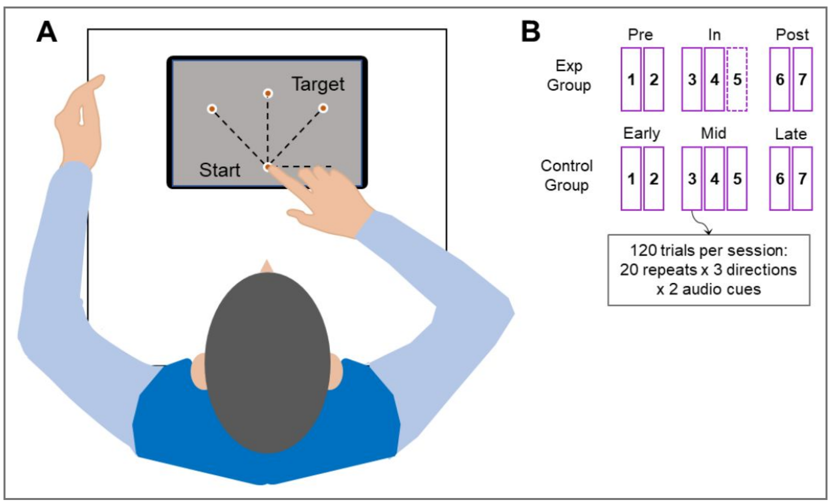


Figure 7. Experimental Setup and Design.

A) Top-down view of a participant performing the reaching task with the right hand on a tablet. The start position and all possible target locations are shown as orange dots on the tablet screen. **B)** Experimental design. Both groups completed 4–7 sessions, with each session consisting of 120 trials. Some taikonauts missed 1 or 2 in-flight sessions.

baseline for evaluating microgravity's impact on the taikonauts. All ground tests, for both groups, were conducted using identical devices and software. The layout of the table and tablet was kept consistent across sessions. The only difference was that, in ground tests, participants sat in a chair approximately 90 cm above the ground without foot straps and did not need to hold the edge of the tabletop with their left hand for stability.

Model simulation

We simulated the peak speed, peak acceleration, and their corresponding times for reaching movements in different directions. We employed the classical two-joint arm model to demonstrate the effect of biomechanics (Li & Todorov, 2004; Figure 1B). This was combined with a movement utility model to estimate planned movement time (Shadmehr et al., 2016; Figure S6A and S5B) and a forward optimal controller to simulate reaching movements (Todorov, 2005; Figure 1C and F, Figure S6C-D). Our simulation is briefly outlined below in steps.

We used a two-joint planar arm model to estimate the effective mass of the hand moving in different directions (Figure 1B). The parameters of the upper arm (length l_1, mass m_1, center of mass lc_1, inertia I_1) and the lower arm (length l_2, mass m_2, center of mass lc_2, inertia I_2) are based on values from Shadmehr et al., 2016:

$l_1 = 0.33 \quad l_2 = 0.43$ m

$m_1 = 1.93 \quad m_2 = 1.52$ kg

$lc_1 = l_1/2 \quad lc_2 = 2l_2/3$ m

$I_1 = 0.014 \quad I_2 = 0.019$ kg.m^2

The elbow and shoulder angles are denoted by θ_e and θ_s, respectively. The initial arm configuration is set by $\theta_s = 0.785$ rad, and $\theta_e = 1.571$ rad, following the experimental conditions from Gordon et al., 1982. With a particular joint angle configuration, the end-point hand position is:

$$x = \left[l_1 cos\,\theta_s + l_2 cos\left(\theta_s + \theta_e\right);\ l_1 sin\,\theta_s + l_2 sin\left(\theta_s + \theta_e\right)\right]. \qquad \text{(eq.1)}$$

The arm's inertia matrix is:

$$I(\theta_s, \theta_e) = [I_{11}, I_{12}; I_{21}, I_{22}], \qquad \text{(eq.2)}$$

where:

$$I_{11} = a_3 + a_1 l_1^2 + a_4 + 2a_2 l_1 cos\theta_e,\ I_{12} = I_{12} = a_2 + l_1 cos\theta_e + a_4,\ I_{22} = a_4,$$

with:

$$a_1 = m_2,\ a_2 = m_2 lc_2,\ a_3 = m_1 lc_1^2 + i_1,\ a_4 = m_2 lc_2^2 + i_2$$

The joint torques at the shoulder and elbow are represented as:

$$\tau = I(\theta)\,\ddot{\theta}, \qquad \text{(eq.3)}$$

and the forces at the hand are:

$$f = M(\theta)\ddot{x}. \qquad \text{(eq.4)}$$

We use the Jacobian matrix $\Lambda = \frac{dx}{d\theta}$ to relate force and torque, based on virtual work principle:

$$\tau = \Lambda^T f, \qquad \text{(eq.5)}$$

$$\dot{x} = \Lambda\dot{\theta}, \qquad \text{(eq.6)}$$

$$\ddot{x} = \dot{\Lambda}\dot{\theta} + \Lambda\ddot{\theta}. \qquad \text{(eq.7)}$$

Put S3 into S5:

$$f = \Lambda^{-1^T} I(\theta)\ \ddot{\theta}, \quad \text{(eq.8)}$$

then combine S7 and S8:

$$f = \Lambda^{-1^T} I(\theta)\Lambda^{-1}\left(\ddot{x} - \dot{\Lambda}\dot{\theta}\right). \quad \text{(eq.9)}$$

Since the hand speed at the beginning of the movement is zero, according to S4 and S9, the mass matrix of hand $M(\theta)$ is:

$$M(\theta) = \Lambda^{-1^T} I(\theta)\Lambda^{-1}, \quad \text{(eq.10)}$$

The mass matrix $M(\theta)$ is a 2 x 2 matrix, and the effective mass $m(\theta)$ is determined by the length of the force vector when $M(\theta)$ is subjected to a unit acceleration.

In Figure S6A, the solid curve illustrates the effective mass across various directions under normal gravity, while the dashed curve represents the effective mass with a hypothetical 30% ($m_{0g}(\theta) = 0.3m(\theta)$)mass underestimation in microgravity. The colored lines indicate the effective mass amplitudes for the three target directions used in our experiment: 45°, 90°, and 135°.

Movement time determined by optimal utility

Following Shadmehr et al., 2016, the utility of an reaching action is given by:

$$J_{ut} = \frac{\alpha - amT - bmd^i/T^2}{1+\gamma T} \quad \text{(eq.11)}$$

where α is the reward, m is mass, d is the distance to be moved, T is the planned duration of the movement, and a, b and i are scaling factors of the effort cost. γ represents a temporal discounting factor. The optimal movement time (T_{opt}) is the time that maximizes the utility J_{ut}:

$$T_{opt} = arg_T max\ (J_{ut}). \quad \text{(eq.12)}$$

The parameter values used in the simulation of Figure S6B were taken from Shadmehr et al., 2016: α = 1000, a = 15, b = 100, i = 1. 1, γ = 1. The movement distance d is set as 0.12 m, the target distance in the experiment. Figure 1—figure supplement 1B illustrates how the utility curves change with planned movement time in three experimental directions (45°, 90°, and 135°) under normal gravity, with colored dots indicating the optimal movement durations.

Movement kinematics simulated by optimal control theory

After setting the movement time T_{opt}, the position, speed and acceleration over time can be simulated based on an optimal control model (Todorov, 2005). The arm's control operates as a second-order low-pass filter:

$$u_t = \tau_1\tau_2\ddot{f}_t + \left(\tau_1 - \tau_2\right)\dot{f}_t + f_t, \quad \text{(eq.13)}$$

with the time constants $\tau_1 = \tau_2 = 40ms$.

The system state vector is [x= p (t); p (t); f (t); g (t); p^*], where p is position of hand, f is force acting on the hand, and g is an auxiliary state variable, p^* is the target position. The control law is given by:

$$u_t = \tau_1\dot{g}_t + g_t,\ g_t = \tau_2\dot{f}_t + f_t.$$

The system dynamics are:

$$x_{t+1} = Ax_t + B\left(u_t + \xi_t\right), \quad y_t = Hx_t + \omega_t \quad \text{(eq.14)}$$

With the sensory feedback carries information about position, velocity and force:

$$y_t = \left[p(t); \dot{p}(t); f(t)\right] + \omega_t.$$

ξ_t is signal-dependent noise $\xi_k \sim N(0, (\sigma_c u_t)^2)$. ω_t is sensory noise $\omega_k \sim N(0, \Omega^\omega)$, where

$$\Omega^\omega = diag\left(\sigma_p^2, \sigma_v^2, \sigma_f^2\right)$$

We define the sampling interval Δt, and the number of steps is $N = T_{opt} / \Delta t$, the discrete-time dynamics of the above system are:

$$p(t + \Delta) = p(t) + \dot{p}(t)\Delta$$
$$\dot{p}(t + \Delta) = \dot{p}(t) + f(t)\Delta/m$$
$$f(t + \Delta) = f(t)\left(1 - \frac{\Delta}{\tau_2}\right) + g(t)\Delta/\tau_2$$
$$g(t + \Delta) = g(t)\left(1 - \frac{\Delta}{\tau_1}\right) + u(t)(1 + \sigma_c \varepsilon_t)\Delta/\tau_1$$

Which is transformed into the matrices as:

$$A = \begin{bmatrix} 1 & \Delta & 0 & 0 & 0 \\ 0 & 1 & \Delta/m & 0 & 0 \\ 0 & 0 & 1 & \Delta/\tau_2 & 0 \\ 0 & 0 & 0 & 1-\Delta/\tau_1 & 0 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

$$H = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \end{bmatrix}$$

$$B = [0; 0; 0; \Delta/\tau_1; 0].$$

The controller seeks to minimize the cost function J by optimizing the command u:

$$J = \sum_t \left(x_t^T Q x_t + u_t^T R u_t\right), \qquad \text{(eq.15)}$$

$R = w_u$, $Q = pp^T + vv^T + ff^T$, $p = [w_p; 0; 0; 0; -w_p]$, $v = [0; w_v; 0; 0; 0]$, $f = [0; 0; w_f; 0; 0]$

Here, we used the penalty values from Todorov (2005) for each state and control variable: $w_u = 0.00001$, $w_p = 2$, $w_v = 0.2$, $w_f = 0.02$, $\sigma_c = 0.5$, $\Omega^\omega = \left(0.5 diag[0.02m; \frac{0.2m}{s}; 1N]\right)^2$. . We first estimated the time-varying gains $\{L_k, K_k\}$ correspond to the feedforward mapping and the feedback correction gain, respectively. The control law can be expressed as: $u_k = u_k^{ff} + u_k^{fb} = -L_k x_k^{nom} - K_k(\hat{x}_k - x_k^{nom})$, where u_k is the control input, x_k^{nom} is the nominal planned state, $\hat{x}_k$ is the estimated state, L_k is the feedforward (nominal) control associated with the planned trajectory, and K_k is the time-varying feedback gain that corrects deviations from the plan. To define the motor plan for comparison with behavior, we then simulate the deterministic open-loop trajectory by turning off noise and disabling feedback corrections, i.e., $u_k = u_k^{ff} = -L_k x_k^{nom}$ We then obtain the peak speed, peak acceleration, and their respective times.

In summary, we apply the movement utility theory to calculate the optimal movement time for a simplified two-joint arm moving in a 2D plane. This movement time is primarily determined by the effective mass and temporal discounting of reward. Next, we employ the optimal control theory to model the kinematics of hand movement, including its position, speed, and acceleration. This approach also enables us to estimate the peak speed and acceleration, as well as their respective times, for reaches performed toward different target directions. To simulate the effect of microgravity, we introduce a mass underestimation factor to account for the kinematic changes associated with this perceptual error.

Data analysis

Kinematic analysis

A Butterworth low-pass filter with a 20 Hz cutoff frequency was applied to the positional data. Movement distance at each time point was computed as the Euclidean distance between the finger's current position and the center of the start circle. Speed was estimated by performing linear regression over a moving window of five consecutive positional data points, and acceleration was calculated similarly from the speed data. Movement onset was defined as the first time point at which acceleration exceeded 50 cm/s^2, while movement offset was the first time point at which acceleration fell below 50 cm/s^2. Reaction time was defined as the interval between target onset and movement onset, and movement duration as the interval between movement onset and offset. Movement endpoint error was computed as the Euclidean distance between the target and the finger's position at movement offset. Peak speed and peak acceleration were identified as the maximum speed and acceleration occurring between movement onset and offset, respectively. The times of peak speed and peak acceleration were measured as their respective time intervals from movement onset, and their relative times were calculated by dividing each by the movement duration.

Submovement extraction

To separate the primary submovement from the secondary corrective submovement, the speed profile of each reaching movement was decomposed into a sum of submovements. Following the optimization algorithm described by Rohrer and Hogan (2006), the speed profile was fitted as a sum of support-bounded lognormal (LGNB) curves. Each LGNB curve is defined as:

$$B(t) = \frac{(T_1 - T_0)D}{\sigma\sqrt{2\pi}(t - T_0)(T_1 - t)} exp\left\{\left(\frac{-1}{2\sigma^2}\right)\left[ln\left(\frac{t - T_0}{T_1 - t}\right) - \mu\right]^2\right\},$$

where T_0 and T_1 represent the start and end times of the movement, D is a scaling parameter, and the parameters μ and σ determine the skewness and kurtosis of the underlying lognormal function. These five parameters enable each LGNB submovement to vary across a wide range of possible shapes.

In theory, the number of submovements could be treated as a free parameter. However, to avoid overfitting, we limited each movement to two submovements, given the brevity of the movement (average duration approx. 350 ms). For each trial, we initially fit the data using both one and two LGNB curves and then determined the optimal number of submovements using the "greedy" method from the previous study (Rohrer & Hogan, 2006). Briefly, the fitting error for each movement with one and two LGNB curves was calculated as:

$$\varepsilon = \frac{\int |F(t) - G(t)| dt}{\int |G(t)| dt},$$

where G(t) is the actual movement speed profile, and F(t) is the fitted speed profile (the sum of the submovements). If the fitting error for a single submovement was below a 2% threshold, or if adding a second submovement reduced the fitting error by less than 2%, a single submovement was considered adequate. Otherwise, two submovements were included. Trials with large fitting errors (>10%) were discarded, accounting for 3.60% and 4.83% of trials in the experimental and control groups, respectively. The percentage of trials with two submovements was calculated for each movement direction and phase. The time difference between the peaks of the two submovements was also computed, and set to zero if only one submovement was detected. Data fitting was performed using Matlab's *fmincon* function (MathWorks, Natick, MA, USA), and the robustness of fitting was confirmed by testing 20 random sets of initial parameters.

Statistical analysis

First, invalid trials were excluded from further analysis, with three possible causes: early initiation (RT < 150 ms, indicating guessing of the target direction), affecting 0.74% and 0.70% of trials in the experimental and control groups, respectively; late initiation (RT > 400 ms, indicating inattention), affecting 1.13% and 0%; and measurement failures, affecting 1.16% and 0.70%. The proportion of invalid trials did not differ significantly across testing phases (Friedman's tests, all p > 0.1).

Most dependent measures—including movement duration, peak acceleration, peak speed, time to peak acceleration/speed, relative time to peak acceleration/speed, the percentage of submovements, and inter-peak intervals—were analyzed using two-way repeated-measures ANOVAs with a 3 (phase) × 3 (movement direction) design. Reaction time was analyzed using three-way repeated-measures ANOVAs with a 3 (phase) × 3 (movement direction) × 2 (beep/no beep) design. Greenhouse-Geisser corrections were applied when sphericity was violated (Kirk, 1968). Normality was assessed with Shapiro-Wilk tests, and if more than 10% of tests for a dependent variable violated normality, the Aligned Rank Transform (ART) procedure was applied before conducting repeated-measures ANOVA. Tukey's HSD tests were used for pairwise comparisons.

To examine the relationship between submovement and movement duration, a Linear Mixed Model (LMM) was used to analyze the association between changes in the inter-peak interval of submovements (ΔIPI) and changes in movement duration (ΔMD). The dependent variable $y_{\Delta MD}$ represents the mean change in movement duration across two adjacent phases (pre-to-in and post-to-in transitions) for each target direction. Target direction (45°, 90°, 135°) and phase transitions (pre-to-in and post-to-in) were treated as within-subject factors. The predictors included three fixed factors: ΔIPI, phase transition (x_{pha}), and direction (x_{dri}). An intercept term (u_{par}) was included as a random factor to account for individual differences in movement duration. The resulting LMM is as follows:

$$y_{\Delta MD} = \beta_0 + \beta_1 x_{\Delta IPI} + \beta_2 x_{pha} + \beta_3 x_{dir} + Zu_{par} + \varepsilon,$$

where β_0 denotes the overall intercept and ε denotes a Gaussian residual error.

All statistical analyses were performed using MATLAB's Statistics and Machine Learning Toolbox. The significance level was set at $\alpha = 0.05$, and all tests were two-tailed unless otherwise specified.

For the directional dependent effects (Figure 6), we applied repeated measures correlation to quantify within-subject associations (Bakdash & Marusich, 2017). Each participant contributed three repeated measurements under different directions. The predictor variable was identical across conditions, and the outcome variables were the measured responses of interest. Repeated measures correlations were computed separately for each of the four metrics, controlling for between-subject differences by including subject-specific intercepts and estimating a single common slope across participants.

Data availability

All data supporting the findings of this study are included in the main text and supplementary materials.

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Additional information

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Authors contributions

Conceptualization: KW, YT, ZZ; Data curation: YT, ZZ; Formal analysis: ZZ; Funding acquisition: KW, CW, YT, ZZ; Methodology: KW, ZZ; Software: YT, CW, CJ, BW, HY, RZ; Supervision: KW; Visualization: ZZ; Writing: KW, ZZ.

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Additional files

Supplemental materials

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Peer reviews

Reviewer #1 (Public review):

The authors have conducted substantial additional analyses to address the reviewers' comments. However, several key points still require attention. I was unable to see the correspondence between the model predictions and the data in the added quantitative analysis. In the rebuttal letter, the delta peak speed time displays values in the range of [20, 30] ms, whereas the data were negative for the 45{degree sign} direction. Should the reader directly compare panel B of Figure 6 with Figure 1E? The correspondence between the model and the data should be made more apparent in Figure 6. Furthermore, the rebuttal states that a quantitative prediction was not expected, yet it subsequently argues that there was a quantitative match. Overall, this response remains unclear.

A follow-up question concerns the argument about strategic slowing. The authors argue that this explanation can be rejected because the timing of peak speed should be delayed, contrary to the data. However, there appears to be a sign difference between the model and the data for the 45{degree sign} direction, which means that it was delayed in this case. Did I understand correctly? In that regard, I believe that the hypothesis of strategic slowing cannot yet be firmly rejected and the discussion should more clearly indicate that this argument is based on some, but not all, directions. I agree with the authors on the importance of the mass underestimation hypothesis, and I am not particularly committed to the strategic slowing explanation, but I do not see a strong argument against it. If the conclusion relies on the sign of the delta peak speed, then the authors' claims are not valid across all directions, and greater caution in the interpretation and discussion is warranted. Regarding the peak acceleration time, I would be hesitant to draw firm conclusions based on differences smaller than 10 ms (Figures R3 and 6D).

The authors state in the rebuttal that the two hypotheses are competing. This is not accurate, as they are not mutually exclusive and could even vary as a function of movement direction. The abstract also claims that the data "refutes" strategic slowing, which I believe is too strong.

The main issue is that, based on the authors' revised manuscript, the lack of quantitative agreement between the model and the data for the mass underestimation hypothesis is considered acceptable because a precise quantitative match is not expected, and the predictions overall agree for some (though not all) directions and phases (excluding post-in). That is reasonable, but by the same logic, the small differences between the model prediction and the strategic slowing hypothesis should not be taken as firm evidence against it, as the authors seem to suggest. In practice, I recommend a more transparent and cautious interpretation to avoid giving readers the false impression that the evidence is decisive. The mass underestimation hypothesis is clearly supported, but the remaining aspects are less clear, and several features of the data remain unexplained.

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Reviewer #2 (Public review):

This study explores the underlying causes of the generalized movement slowness observed in astronauts in weightlessness compared to their performance on Earth. The authors argue that this movement slowness stems from an underestimation of mass rather than a deliberate reduction in speed for enhanced stability and safety.

Overall, this is a fascinating and well-written work. The kinematic analysis is thorough and comprehensive. The design of the study is solid, the collected dataset is rare, and the model adds confidence to the proposed conclusions.

Compared to the previous version, the authors have thoroughly addressed my concerns. The model is now clear and well-articulated, and alternative hypotheses have been ruled out convincingly. The paper is improved and suitable for publication in my opinion, making a significant contribution to the field.

Strengths:

- Comprehensive analysis of a unique data set of reaching movement in microgravity

- Use of a sensible and well-thought experimental approach

- State-of-the-art analyses of main kinematic parameter

- Computational model simulations of arm reaching to test alternative hypotheses and support the mass underestimation one

This work has no major weakness as it stands, and the discussion provides a fair evaluation of the findings and conclusions.

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Reviewer #3 (Public review):

Summary:

The authors describe an interesting study of arm movements carried out in weightlessness after a prolonged exposure to the so-called microgravity conditions of orbital spaceflight. Subjects performed radial point-to-point motions of the fingertip on a touch pad. The authors note a reduction in movement speed in weightlessness, which they hypothesize could be due to either an overall strategy of lowering movement speed to better accommodate the instability of the body in weightlessness or an underestimation of body mass. They conclude for the latter, mainly based on two effects. One, slowing in weightlessness is greater for movement directions with higher effective mass at the end effector of the arm. Two, they present evidence for increased number of corrective submovements in weightlessness. They contend that this provides conclusive evidence to accept the hypothesis of an underestimation of body mass.

Strengths:

In my opinion, the study provides a valuable contribution, the theoretical aspects are well presented through simulations, the statistical analyses are meticulous, the applicable literature is comprehensively considered and cited and the manuscript is well written.

Weaknesses:

I nevertheless am of the opinion that the interpretation of the observations leaves room for other possible explanations of the observed phenomenon, thus weakening the strength of the arguments.

To strengthen the conclusions, I feel that the following points would need to be addressed:

(1) The authors model the movement control through equations that derive the input control variable in terms of the force acting on the hand and treating the arm as a second-order low pass filter (Eq. 13). Underestimation of the mass in the computation of a feedforward command would lead to a lower-than-expected displacement to that command. But it is not clear if and how the authors account for a potential modification of the time constants of the 2nd order system. The CNS does not effectuate movements with pure torque generators. Muscles have elastic properties that depend on their tonic excitation level, reflex feedback and other parameters. Indeed, Fisk et al.* showed variations of movement characteristics consistent with lower muscle tone, lower bandwidth and lower damping ratio in 0g compared to 1g. Could the variations in the response to the initial feedforward command be explained by a misrepresentation of the limbs damping and natural frequency, leading to greater uncertainty to the consequences of the initial command. This would still be an argument for un-adapted feedforward control of the movement, leading to the need for more corrective movements. But it would not necessarily reflect an underestimation of body mass.

*Fisk, J. O. H. N., Lackner, J. R., & DiZio, P. A. U. L. (1993). Gravitoinertial force level influences arm movement control. Journal of neurophysiology, 69(2), 504-511.

While the authors attempt to differentiate their study from previous studies where limb neuromechanical impedance was shown to be modified in weightlessness by emphasizing that in the current study the movements were rapid and the initial movement is "feedforward". But this incorrectly implies that the limb's mechanical response to the motor command is determined only by active feedback mechanisms. In fact:

(a) All commands to the muscle pass through the motor neurons. These neurons receive descending activations related not only to the volitional movement, but also to the dynamic state of the body and the influence of other sensory inputs, including the vestibular system. A decrease in descending influences from the vestibular organs will lower the background sensitivity to all other neural influences on the motor neuron. Thus, the motor neuron may be less sensitive to the other volitional and reflexive synaptic inputs that it may receive.

(b) Muscle tone plays a significant role in determining the force and the time course of the muscle contraction. In a weightless environment, where tonic muscle activity is likely to be reduced, there is the distinct possibility that muscles will react more slowly and with lower amplitude to an otherwise equivalent descending motor command, particularly in the initial moments before spinal reflexes come into play. These, and other neuronal mechanisms could lead to the "under-actuation" effect observed in the current study, without necessarily being reflective of an underestimation of mass per se.

(2) The subject's body in weightless is much more sensitive to reaction forces in interactions with the environment in the absence of the anchoring effect of gravity pushing the body into the floor and in the absence of anticipatory postural adjustments that typically accompany upper-limb motions in Earth gravity in order to maintain an upright posture. The authors dismiss this possibility because the taikonauts were asked to stabilize their bodies with the contralateral hand. But the authors present no evidence that this was sufficient to maintain the shoulder and trunk at a strictly constant position, as is supposed by the simplified biomechanical model used in their optimal control framework. Indeed, a small backward motion of the shoulder would result in a smaller acceleration of the fingertip and a smaller extent of the initial ballistic motion of the hand with respect to the measurement device (the tablet), consistent with the observations reported in the study. Note that stability of the base might explain why 45º movements were apparently less affected in weightlessness, according to many of the reported analyses, including those related to corrective movements (Fig. 5 B, C, F; Fig. 6D), than the other two directions. If the trunk is being stabilized by the left arm, the same reaction forces on the trunk due to the acceleration of the hand will result in less effective torque on the trunk, given that the reaction forces act with a much smaller moment arm with respect to the left shoulder (the hand movement axis passes approximately through the left shoulder for the 45º target) compared to either the forward or rightward motions of the hand.

(3) The above is exacerbated by potential changes in the frictional forces between the fingertip and the tablet. The movements were measured by having the subjects slide their finger on the surface of a touch screen. In weightlessness, the implications of this contact can be expected to be quite different than on the ground. While these forces may be low on Earth, the fact is that we do not know what forces the taikonauts used on orbit. In weightlessness, the taikonauts would need to actively press downward to maintain contact with the screen, while on Earth gravity will do the work. The tangential forces that resist movement due to friction might therefore be different in 0g. . Indeed, given the increased instability of the body and the increased uncertainty of movement direction of the hand, taikonauts may have been induced to apply greater forces against the tablet in order to maintain contact in weightlessness, which would in turn slow the motion of the finger on the table and increase the reaction forces acting on the trunk. This could be particularly relevant given that the effect of friction would interact with the limb in a direction-dependent fashion, given the anisotropy of the equivalent mass at the fingertip evoked by the authors

I feel that the authors have done an admirable job of exploring the how to explain the modifications to movement kinematics that they observed on orbit within the constraints of the optimal control theory applied to a simplified model of the human motor system. While I fully appreciate the value of such models to provide insights into question of human sensorimotor behaviour, to draw firm conclusions on what humans are actually experiencing based only on manipulations of the computational model, without testing the model's implicit assumptions and without considering the actual neurophysiological and biomechanical mechanisms, can be misleading. One way to do this could be to examine these questions through extensions to the model used in the simulations (changing activation dynamics of the torque generators, allowing for potential motion backward motion of the shoulder and trunk, etc.). A better solution would be to emulate the physiological and biomechanical conditions on Earth (supporting the arm against gravity to reduce muscle tone, placing the subject on a moveable base that requires that the body be stabilized with the other hand) in order to distinguish the hypothesis of an underestimation of mass vs. other potential sources of under-actuation and other potential effects of weightlessness on the body.

In sum, my opinion is that the authors are relying too much on a theoretical model as a ground truth and thus overstate their conclusions. But to provide a convincing argument that humans truly underestimate mass in weightlessness, they should consider more judiciously the neurophysiology and biomechanics that fall outside the purview of the simplified model that they have chosen. If a more thorough assessment of this nature is not possible, then I would argue that a more measured conclusion of the paper should be 1) that the authors observed modifications to movement kinematics in weightlessness consistent with an under-actuation for the intended motion, 2) that a simplified model of human physiology and biomechanics that incorporates principles of optimal control suggest that the source of this under-actuation might be an underestimation of mass in the computation of an appropriate feedforward motor command, and 3) that other potential neurophysiological or biomechanical effects cannot be excluded due to limitations of the computational model.

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Author response:

The following is the authors' response to the original reviews

> ***eLife Assessment***
>
> *This paper undertakes an important investigation to determine whether movement slowing in microgravity is due to a strategic conservative approach or rather due to an underestimation of the mass of the arm. While the experimental dataset is unique and the coupled experimental and computational analyses comprehensive, the authors present incomplete results to support the claim that movement slowing is due to mass underestimation. Further analysis is needed to rule out alternative explanations.*

We thank the editor and reviewers for the thoughtful and constructive comments, which helped us substantially improve the manuscript. In this revised version, we have made the following key changes:

- Directly presented the differential effect of microgravity in different movement directions, showing its quantitative match with model predictions.

- Showed that changing cost function with the idea of conservative strategy is not a viable alternative.

- Showed our model predictions remain largely the same after adding Coriolis and centripetal torques.

- Discussed alternative explanations including neuromuscular deconditioning, friction, body stability, etc.

- Detailed the model description and moved it to the main text, as suggested.

Our point-to-point response is numbered to facilitate cross-referencing.

We believe the revisions and the responses adequately addresses the reviewers' concerns, and new analysis results strengthened our conclusion that mass underestimation is the major contributor to movement slowing in microgravity.

> ***Reviewer #1 (Public review):***
>
> *Summary:*
>
> *This article investigates the origin of movement slowdown in weightlessness by testing two possible hypotheses: the first is based on a strategic and conservative slowdown, presented as a scaling of the motion kinematics without altering its profile, while the second is based on the hypothesis of a misestimation of effective mass by the brain due*

> *to an alteration of gravity-dependent sensory inputs, which alters the kinematics following a controller parameterization error.*
>
> *Strengths:*
>
> *The article convincingly demonstrates that trajectories are affected in 0g conditions, as in previous work. It is interesting, and the results appear robust. However, I have two major reservations about the current version of the manuscript that prevent me from endorsing the conclusion in its current form.*
>
> *Weaknesses:*
>
> *(1) First, the hypothesis of a strategic and conservative slow down implicitly assumes a similar cost function, which cannot be guaranteed, tested, or verified. For example, previous work has suggested that changing the ratio between the state and control weight matrices produced an alteration in movement kinematics similar to that presented here, without changing the estimated mass parameter (Crevecoeur et al., 2010, J Neurophysiol, 104 (3), 1301-1313). Thus, the hypothesis of conservative slowing cannot be rejected. Such a strategy could vary with effective mass (thus showing a statistical effect), but the possibility that the data reflect a combination of both mechanisms (strategic slowing and mass misestimation) remains open.*

Response (1): Thank you for raising this point. The basic premise of this concern is that changing the cost function for implementing strategic slowing can reproduce our empirical findings, thus the alternative hypothesis that we aimed to refute in the paper remain possible. At least, it could co-exist with our hypothesis of mass underestimation. In the revision, we show that changing the cost function only, as suggested here, cannot produce the behavioral patterns observed in microgravity.

As suggested, we modified the relative weighting of the state and control cost matrices (i.e., Q and R in the cost function Eq 15) without considering mass underestimation. While this cost function scaling can decrease peak velocity – a hallmark of strategic slowing – it also inevitably leads to later peak timings. This is opposite to our robust findings: the taikonauts consistently “advanced” their peak velocity and peak acceleration in time. Note, these model simulation patterns have also been shown in Crevecoeur et al. (2010), the paper mentioned by the reviewer (see their Figure 7B).

We systematically changed the ratio between the state and control weight matrices in the simulation, as suggested. We divided Q and multiplied R by the same factor α, the cost function scaling parameter α as defined in Crevecoeur et al. (2010). This adjustment models a shift in movement strategy in microgravity, and we tested a wide range of α to examine reasonable parameter space. Simulation results for α = 3 and α = 0.3 are shown in Figure 1—figure supplement 2 and Figure 1—figure supplement 3 respectively. As expected, with α = 3 (higher control effort penalty), peak velocities and accelerations are reduced, but their timing is delayed. Conversely, with α = 0.3, both peak amplitude and timing increase. Hence, changing the cost function to implement a conservative strategy cannot produce the kinematic pattern observed in microgravity, which is a combination of movement slowing and peak timing advance.

Therefore, we conclude that a change in optimal control strategy alone is insufficient to explain our empirical findings. Logically speaking, we cannot refute the possibility of strategic slowing, which can still exist on top of the mass underestimation we proposed here. However, our data does not support its role in explaining the slowing of goal-directed hand reaching in microgravity. We have added these analyses to the Supplementary Materials and expanded the Discussion to address this point.

> *(2) The main strength of the article is the presence of directional effects expected under the hypothesis of mass estimation error. However, the article lacks a clear demonstration of such an effect: indeed, although there appears to be a significant effect of direction, I was not sure that this effect matched the model's predictions. A directional effect is not sufficient because the model makes clear quantitative predictions about how this effect should vary across directions. In the absence of a quantitative match between the model and the data, the authors' claims regarding the role of misestimating the effective mass remain unsupported.*

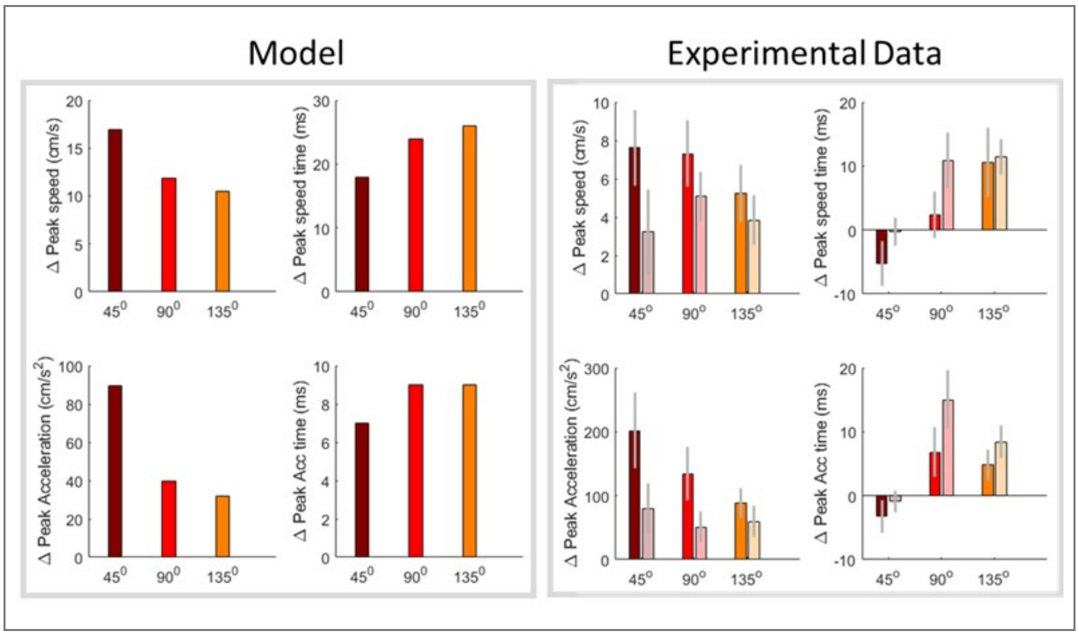
Response (2): First, we have to clarify that our study does not aim to quantitatively fit observed hand trajectory. The two-link arm model simulates an ideal case of moving a point mass (effective mass) on a horizontal plane without friction (Todorov, 2004; 2005). In contrast, in the experiment, participants moved their hand on a tabletop without vertical arm support, so the movement was not strictly planar and was affected by friction. Thus, this kind of model can only illustrate qualitative differences between conditions, as in the majorities of similar modeling studies (e.g., Shadmehr et al., 2016). In our study, qualitative simulation means the model is intended to reproduce the directional differences between conditions—not exact numeric values—in key kinematic measures. Specifically, it should capture how the peak velocity and acceleration amplitudes and their timings differ between normal gravity and microgravity (particularly under the mass-underestimation assumption).

Second, the reviewer rightfully pointed out that the directional effect is essential for our theorization of the importance of mass underestimation. However, the directional effect has two aspects, which were not clearly presented in our original manuscript. We now clarify both here and in the revision. The first aspect is that key kinematic variables (peak velocity/acceleration and their timing) are affected by movement direction, even before any potential microgravity effect. This is shown by the ranking order of directions for these variables (Figure 1C-H). The direction-dependent ranking, confirmed by pre-flight data, indicates that effective mass is a determining factor for reaching kinematics, which motivated us to study its role in eliciting movement slowing in space. This was what our original manuscript emphasized and clearly presented.

The second aspect is that the hypothetical mass underestimation might also differentially affect movements in different directions. This was not clearly presented in the original manuscript. However, we would not expect a quantitative match between model predictions and empirical data, for the reasons mentioned above. We now show this directional ranking in microgravity-elicited kinematic changes in both model simulations and empirical data. The overall trend is that the microgravity effect indeed differs between directions, and the model predictions and the data showed a reasonable qualitative match (Author response image 1 below).

Shown in Author response image 1, we found that for amplitude changes (Δ peak speed, Δ peak acceleration) both the model and the mean of empirical data show the same directional ordering (45° > 90° > 135°) in pre-in and post-in comparisons. For timing (Δ peak-speed time, Δ peak-acceleration time), which we consider the most diagnostic, the same directional ranking was observed. We only found one deviation, i.e., the predicted sign (earlier peaks) was confirmed at 90° and 135°, but not at 45°. As discussed in Response (6), the absence of timing advance at 45° may reflect limitations of our simplified model, which did not consider that the 45° direction is essentially a single-joint reach. Taken together, the directional pattern is largely consistent with the model predictions based on mass underestimation. The model successfully reproduces the directional ordering of amplitude measures -- peak velocity and peak acceleration. It also captures the sign of the timing changes in two out of the three directions. We added these new analysis results in the revision and expanded Discussion accordingly.

The details of our analysis on directional effects: We compared the model predictions (Author response image 1, left) with the experimental data (Author response image 1, right) across the three tested directions (45°, 90°, 135°). In the experimental data panels, both Δ(pre-in) (solid bars) and Δ(post-in) (semi-transparent bars) with standard error are shown. The directional trends are remarkably similar between model prediction and actual data. The post-in comparison is less aligned with model prediction; we postulate that the incomplete after-flight recovery (i.e., post data had not returned to pre-flight baselines) might obscure the microgravity effect. Incomplete recovery has also been shown in our original manuscript: peak speed and peak acceleration did not fully recover in post-flight sessions when compared to pre-flight sessions. To further quantify the correspondence between model and data, we performed repeated-measures correlation (rm-corr) analyses. We found significant within-subject correlations for three of the four metrics. For pre–in, Δ peak speed time (r_{rm} = 0.627, t(23) = 3.858, p < 0.001), Δ peak acceleration time (r_{rm} = 0.591, t(23) = 3.513, p = 0.002), and Δ peak acceleration (r_{rm} = 0.573, t(23) = 3.351, p = 0.003) were significant, whereas Δ peak speed was not (r_{rm} = 0.334, t(23) = 1.696, p = 0.103). These results thus show that the directional effect, as predicted our model, is observed both before spaceflight and in spaceflight (the pre-in comparison).



Author response image 1. Directional comparison between model predictions and experimental data across the three reach directions (45°, 90°, 135°). Left: model outputs. Right: experimental data shown as Δ relative to the in-flight session; solid bars = Δ(in − pre) and semi-transparent bars = Δ(in − post). Colors encode direction consistently across panels (e.g., 45° = darker hue, 90° = medium, 135° = lighter/orange). Panels (clockwise from top-left): Δ peak speed (cm/s), Δ peak speed time (ms), Δ peak acceleration time (ms), and Δ peak acceleration (cm/s²). Bars are group means; error bars denote standard error across participants.

Citations:

Todorov, E. (2004). Optimality principles in sensorimotor control. Nature Neuroscience, 7(9), 907.

Todorov, E. (2005). Stochastic optimal control and estimation methods adapted to the noise characteristics of the sensorimotor system. Neural Computation, 17(5), 1084–1108.

Shadmehr, R., Huang, H. J., & Ahmed, A. A. (2016). A Representation of Effort in Decision-Making and Motor Control. *Current Biology: CB*, *26*(14), 1929–1934.

> *In general, both the hypotheses of slowing motion (out of caution) and misestimating mass have been put forward in the past, and the added value of this article lies in demonstrating that the effect depended on direction. However, (1) a conservative strategy with a different cost function can also explain the data, and (2) the quantitative match between the directional effect and the model's predictions has not been established.*

We agree that both hypotheses have been put forward before, however they are competing hypotheses that have not been resolved. Furthermore, the mass underestimation hypothesis is a conjecture without any solid evidence; previous reports on mass underestimation of object cannot directly translate to underestimation of body. As detailed in our responses above, we have shown that a conservative strategy implemented via a different cost function cannot reproduce the key findings in our dataset, thereby supporting the alternative hypothesis of mass underestimation. Moreover, we found qualitative agreement between the model predictions and the experimental data in terms of directional effects, which further strengthens our interpretation.

> *Specific points:*
>
> *(1) I noted a lack of presentation of raw kinematic traces, which would be necessary to convince me that the directional effect was related to effective mass as stated.*

Response (3): We are happy to include exemplary speed and acceleration trajectories. Kinematic profiles from one example participant are shown in Figure 2—figure supplement 6.

> *(2) The presentation and justification of the model require substantial improvement; the reason for their presence in the supplementary material is unclear, as there is space to present the modelling work in detail in the main text. Regarding the model, some choices require justification: for example, why did the authors ignore the nonlinear Coriolis and centripetal terms?*

Response (4): Great suggestion. In the revision, we have moved the model into the main text and added further justification for using this simple model.

We initially omitted the nonlinear Coriolis and centripetal terms in order to start with a minimal model. Importantly, excluding these terms does not affect the model's main conclusions. In the revision we added simulations that explicitly include these terms. The full explanation and simulations are provided in the Supplementary Notes 2 (this time we have to put it into the Supplementary to reduce the texts devoted to the model). More explanations can also be found in our response to Reviewer 2 (response (6)). The results indicate that, although these velocity-dependent forces show some directional anisotropy, their contribution is substantially smaller relative to that of the included inertial component; specifically, they have only a negligible impact on the predicted peak amplitudes and peak times.

> *(3) The increase in the proportion of trials with subcomponents is interesting, but the explanatory power of this observation is limited, as the initial percentage was already quite high (from 60-70% during the initial study to 70-85% in flight). This suggests that the potential effect of effective mass only explains a small increase in a trend already present in the initial study. A more critical assessment of this result is warranted.*

Response (5): Thank you for your thoughtful comment. You are correct that the increase in the percentage of trials with submovements is modest, but a more critical change was observed in the timing between submovement peaks—specifically, the inter-peak interval (IPI). These intervals became longer during flight. Taken together with the percentage increase, the submovement changes significantly predicted the increase in movement duration, as shown by our linear mixed-effects model, which indicated that IPI increased.

> ***Reviewer #2 (Public review):***
>
> *This study explores the underlying causes of the generalized movement slowness observed in astronauts in weightlessness compared to their performance on Earth. The authors argue that this movement slowness stems from an underestimation of mass rather than a deliberate reduction in speed for enhanced stability and safety.*
>
> *Overall, this is a fascinating and well-written work. The kinematic analysis is thorough and comprehensive. The design of the study is solid, the collected dataset is rare, and the model tends to add confidence to the proposed conclusions. That being said, I have several comments that could be addressed to consolidate interpretations and improve clarity.*
>
> *Main comments:*
>
> *(1) Mass underestimation*
>
> *a) While this interpretation is supported by data and analyses, it is not clear whether this gives a complete picture of the underlying phenomena. The two hypotheses (i.e., mass underestimation vs deliberate speed reduction) can only be distinguished in terms of velocity/acceleration patterns, which should display specific changes during the flight with a mass underestimation. The experimental data generally shows the expected changes but for the 45° condition, no changes are observed during flight compared to the pre- and post-phases (Figure 4). In Figure 5E, only a change in the primary submovement peak velocity is observed for 45°, but this finding relies on a more involved decomposition procedure. It suggests that there is something specific about 45° (beyond its low effective mass). In such planar movements, 45° often corresponds to a movement which is close to single-joint, whereas 90° and 135° involve multi-joint movements. If so, the increased proportion of submovements in 90° and 135° could indicate that participants had more difficulties in coordinating multi-joint movements during flight. Besides inertia, Coriolis and centripetal effects may be non-negligible in such fast planar reaching (Hollerbach & Flash, Biol Cyber, 1982) and, interestingly, they would also be affected by a mass underestimation (thus, this is not necessarily incompatible with the author's view; yet predicting the effects of a mass underestimation on Coriolis/centripetal torques would require a two-link arm model). Overall, I found the discrepancy between the 45° direction and the other directions under-exploited in the current version of the article. In sum, could the corrective submovements be due to a misestimation of Coriolis/centripetal torques in the multi-joint dynamics (caused specifically -or not- by a mass underestimation)?*

Response (6): Thank you for raising these important questions. We unpacked the whole paragraph into two concerns: 1) the possibility that misestimation of Coriolis and centripetal torques might lead to corrective submovements, and 2) the weak effect in the 45° direction unexploited. These two concerns are valid but addressable, and they did not change our general conclusions based on our empirical findings (see Supplementary note 2. Coriolis and centripetal torques have minimal impact).

Possible explanation for the 45° discrepancy

We agree with the reviewer that the 45° direction likely involves more single-joint (elbow-dominant) movement, whereas the 90° and 135° directions require greater multi-joint (elbow + shoulder) coordination. This is particularly relevant when the workspace is near body midline (e.g., Haggard & Richardson, 1995), as the case in our experimental setup. To demonstrate this, we examined the curvature of the hand trajectories across directions. Using cumulative curvature (positive = counterclockwise), we obtained average values of 6.484° ± 0.841°, 1.539° ± 0.462°, and 2.819° ± 0.538° for the 45°, 90°, and 135° directions, respectively. The significantly larger curvature in the 45° condition suggests that these movements deviate more from a straight-line path, a hallmark of more elbow-dominant movements.

Importantly, this curvature pattern was present in both the pre-flight and in-flight phases, indicating that it is a general movement characteristic rather than a microgravity-induced effect. Thus, the 45° reaches are less suitable for modeling with a simplified two-link arm model compared to the other two directions. We believe this is the main reason why the model predictions based on effective mass become less consistent with the empirical data for the 45° direction.

We have now incorporated this new analysis in the Results and discussed it in the revised Discussion.

Citation: Haggard, P., Hutchinson, K., & Stein, J. (1995). Patterns of coordinated multi-joint movement. Experimental Brain Research, 107(2), 254-266.

> *b) Additionally, since the taikonauts are tested after 2 or 3 weeks in flight, one could also assume that neuromuscular deconditioning explains (at least in part) the general decrease in movement speed. Can the authors explain how to rule out this alternative interpretation? For instance, weaker muscles could account for slower movements within a classical time-effort trade-off (as more neural effort would be needed to generate a similar amount of muscle force, thereby suggesting a purposive slowing down of movement). Therefore, could the observed results (slowing down + more submovements) be explained by some neuromuscular deconditioning combined with a difficulty in coordinating multi-joint movements in weightlessness (due to a misestimation or Coriolis/centripetal torques) provide an alternative explanation for the results?*

Response (7): Neuromuscular deconditioning is indeed a space effect; thanks for bringing this up as we omitted the discussion of this confounds in our original manuscript. Prolonged stay in microgravity can lead to a reduction of muscle strength, but this is mostly limited to lower limb. For example, a recent well-designed large-sample study have shown that while lower leg muscle showed significant strength reductions, no changes in mean upper body strength was found (Scott et al., 2023), consistent with previous propositions that muscle weakness is less for upper-limb muscles than for postural and lower-limb muscles (Tesch et al., 2005). Furthermore, the muscle weakness is unlikely to play a major role here since our reaching task involves small movements (~12cm) with joint torques of a magnitude of ~2N·m. Of course, we cannot completely rule out the contribution of muscle weakness; we can only postulate, based on the task itself (12 cm reaching) and systematic microgravity effect (the increase in submovements, the increase in the inter-submovements intervals, and their significant prediction on movement slowing), that muscle weakness is an unlikely major contributor for the movement slowing.

The reviewer suggests that poor coordination in microgravity might contribute to slowing down + more submovements. This is also a possibility, but we did not find evidence to support it. First, there is no clear evidence or reports about poor coordination for simple upper-limb movements like reaching investigated here. Note that reaching or aiming movement is one of the most studied tasks among astronauts. Second, we further analyzed our reaching trajectories and found no sign of curvature increase, a hallmark of poor coordination of Coriolis/centripetal torques, in our large collection of reaching movements. We probably have the largest dataset of reaching movements collected in microgravity thus far, given that we had 12 taikonauts and each of them performed about 480 to 840 reaching trials during their spaceflight. We believe the probability of Type II error is quite low here.

Citation: Tesch, P. A., Berg, H. E., Bring, D., Evans, H. J., & LeBlanc, A. D. (2005). Effects of 17-day spaceflight on knee extensor muscle function and size. European journal of applied physiology, 93(4), 463-468.

Scott J, Feiveson A, English K, et al. Effects of exercise countermeasures on multisystem

function in long duration spaceflight astronauts. npj Microgravity. 2023;9(11).

> *(2) Modelling*
>
> *a) The model description should be improved as it is currently a mix of discrete time and continuous time formulations. Moreover, an infinite-horizon cost function is used, but I thought the authors used a finite-horizon formulation with the prefixed duration provided by the movement utility maximization framework of Shadmehr et al. (Curr Biol, 2016). Furthermore, was the mass underestimation reflected both in the utility model and the optimal control model? If so, did the authors really compute the feedback control gain with the underestimated mass but simulate the system with the real mass? This is important because the mass appears both in the utility framework and in the LQ framework. Given the current interpretations, the feedforward command is assumed to be erroneous, and the feedback command would allow for motor corrections. Therefore, it could be clarified whether the feedback command also misestimates the mass or not, which may affect its efficiency. For instance, if both feedforward and feedback motor commands are based on wrong internal models (e.g., due to the mass underestimation), one may wonder how the astronauts would execute accurate goal-directed movements.*
>
> *b) The model seems to be deterministic in its current form (no motor and sensory noise). Since the framework developed by Todorov (2005) is used, sensorimotor noise could have been readily considered. One could also assume that motor and sensory noise increase in microgravity, and the model could inform on how microgravity affects the number of submovements or endpoint variance due to sensorimotor noise changes, for instance.*
>
> *c) Finally, how does the model distinguish the feedforward and feedback components of the motor command that are discussed in the paper, given that the model only yields a feedback control law? Does 'feedforward' refer to the motor plan here (i.e., the prefixed duration and arguably the precomputed feedback gain)?*

Response (8): We thank the reviewer for raising these important and technically insightful points regarding our modeling framework. We first clarify the structure of the model and key assumptions, and then address the specific questions in points (a)–(c) below.

We used Todorov's (2005) stochastic optimal control method to compute a finite-horizon LQG policy under sensory noise and signal-dependent motor noise (state noise set to zero). The cost function is: $J = \sum_t (x_t^T Q x_t + u_t^T R u_t)$ (see details in updated Methods). The resulting time-varying gains $\{L_k, K_k\}$ correspond to the feedforward mapping and the feedback correction gain, respectively. The control law can be expressed as:

$$u_k = u_k^{ff} + u_k^{fb} = -L_k x_k^{nom} - K_k(\hat{x}_k - x_k^{nom}),$$

where u_k is the control input, x_k^{nom} is the nominal planned state, x_k^{nom} is the estimated state, L_k is the feedforward (nominal) control associated with the planned trajectory, and K_k is the time-varying feedback gain that corrects deviations from the plan.

To define the motor plan for comparison with behavior, we simulate the deterministic open-loop

trajectory by turning off noise and disabling feedback corrections, i.e., $u_k = u_k^{ff} = -L_k x_k^{nom}$. In this framework, "feedforward" refers to this nominal motor plan. Thus, sensory and signal-dependent noise influence the computed policy (via the gains), but are not injected when generating the nominal trajectory. This mirrors the minimum-jerk practice used to obtain nominal kinematics in prior utility-based work (Shadmehr, 2016), while optimal control provides a more physiologically grounded nominal plan. In the revision, we have updated the equations, provided more modeling details, and moved the model description to the main text to reduce possible confusions.

In the implementation of the "mass underestimation" condition, the mass used to compute the policy is the underestimated mass ($\hat{m}$), whereas the actual mass is used when simulating the feedforward trajectories. Corrective submovements are analyzed separately and are not required for the planning-deficit findings reported here.

Answers of the three specific questions:

a) We mistakenly wrote a continuous-time infinite-horizon cost function in our original manuscript, whereas our controller is actually implemented as a discrete-time finite-horizon LQG with a terminal cost, over a horizon set by the utility-based optimal movement duration T_{opt}. The underestimated mass is used in both the utility model (to determine T_{opt}) and in the control computation (i.e., internal model), while the true mass is used when simulating the movement. This mismatch captures the central idea of feedforward planning based on an incorrect internal model.

b) As described, our model includes signal-dependent motor noise and sensory noise, following Todorov (2005). We also evaluated whether increased noise levels in microgravity could account for the observed behavioral changes. Simulation results showed that increasing either source of noise did not alter the main conclusions or reverse the trends in our key metrics. Moreover, our experimental data showed no significant increase in endpoint variability in microgravity (see analyses and results in Figure 2—figure supplement 3 & 4), making it unlikely that increased sensorimotor noise alone accounts for the observed slowing and submovement changes.

c) In our framework, the time-varying gains $\{L_K, K_K\}$define the feedforward and feedback components of the control policy. While both gains are computed based on a stochastic optimal control formulation (including noise), for comparison with behavior we simulate only the nominal feedforward plan, by turning off both noise and feedback:
$u_k = u_k^{ff} = -L_k x_k^{nom}$. This defines a deterministic open-loop trajectory, which we use to capture planning-level effects such as peak timing shifts under mass underestimation. Feedback corrections via gains exist in the full model but are not involved in these specific analyses. We clarified this modeling choice and its behavioral relevance in the revised text.

We have updated the equations and moved the model description into the main text in the revised manuscript to avoid confusion.

> *(3) Brevity of movements and speed-accuracy trade-off*
>
> *The tested movements are much faster (average duration approx. 350 ms) than similar self-paced movements that have been studied in other works (e.g., Wang et al., J Neurophysiology, 2016; Berret et al., PLOS Comp Biol, 2021, where movements can last about 900-1000 ms). This is consistent with the instructions to reach quickly and accurately, in line with a speed-accuracy trade-off. Was this instruction given to highlight the inertial effects related to the arm's anisotropy? One may however, wonder if the same*

results would hold for slower self-paced movements (are they also with reduced speed compared to Earth performance?). Moreover, a few other important questions might need to be addressed for completeness: how to ensure that astronauts did remember this instruction during the flight? (could the control group move faster because they better remembered the instruction?). Did the taikonauts perform the experiment on their own during the flight, or did one taikonaut assume the role of the experimenter?

Response (9): Thanks for highlighting the brevity of movements in our experiment. Our intention in emphasizing fast movements is to rigorously test whether movement is indeed slowed down in microgravity. The observed prolonged movement duration clearly shows that microgravity affects people's movement duration, even when they are pushed to move fast. The second reason for using fast movement is to highlight that feedforward control is affected in microgravity. Mass underestimation specifically affects feedforward control in the first place, shown by the microgravity-related changes in peak velocity/acceleration. Slow movement would inevitably have online corrections that might obscure the effect of mass underestimation. Note that movement slowing is not only observed in our speed-emphasized reaching task, but also in whole-arm pointing in other astronauts' studies (Berger, 1997; Sangals, 1999), which have been quoted in our paper. We thus believe these findings are generalizable.

Regarding the consistency of instructions: all our experiments conducted in the Tiangong space station were monitored in real time by experimenters in the control center located in Beijing. The task instructions were presented on the initial display of the data acquisition application and ample reading time was allowed. All the pre-, in-, and post-flight test sessions were administered by the same group of personnel with the same instruction. It is common that astronauts serve both as participants and experimenters at the same time. And, they were well trained for this type of role on the ground. Note that we had multiple pre-flight test sessions to familiarize them with the task. All these rigorous measures were in place to obtain high-quality data. In the revision, we included these experimental details for readers that are not familiar with space studies, and provided the rationales for emphasizing fast movements.

Citations:

Berger, M., Mescheriakov, S., Molokanova, E., Lechner-Steinleitner, S., Seguer, N., & Kozlovskaya, I. (1997). Pointing arm movements in short- and long-term spaceflights. Aviation, Space, and Environmental Medicine, 68(9), 781–787.

Sangals, J., Heuer, H., Manzey, D., & Lorenz, B. (1999). Changed visuomotor transformations during and after prolonged microgravity. Experimental Brain Research. Experimentelle Hirnforschung. Experimentation Cerebrale, 129(3), 378–390.

(4) No learning effect

This is a surprising effect, as mentioned by the authors. Other studies conducted in microgravity have indeed revealed an optimal adaptation of motor patterns in a few dozen trials (e.g., Gaveau et al., eLife, 2016). Perhaps the difference is again related to single-joint versus multi-joint movements. This should be better discussed given the impact of this claim. Typically, why would a "sensory bias of bodily property" persist in microgravity and be a "fundamental constraint of the sensorimotor system"?

Response (10): We believe that the presence or absence of adaptation between our study and Gaveau et al.'s study cannot be simply attributed to single-joint versus multi-joint movements. Their adaptation concerned incorporating microgravity into movement control to minimize effort, whereas ours concerned accurately perceiving body mass. Gaveau et al.'s task involved large-amplitude vertical reaching, a scenario in which gravity strongly affects joint torques and movement execution. Thus, adaptation to microgravity can lead to better execution, providing a strong incentive for learning. By contrast, our task consisted of small-amplitude horizontal movements, where the gravitational influence on biomechanics is minimal.

More importantly, we believe the lack of adaptation for mass underestimation is not totally surprising. When an inertial change is perceived (such as an extra weight attached to the forearm, as in previous motor adaptation studies), people can adapt their reaching within tens of trials. In that case, sensory cues are veridical, as they correctly signal the inertial perturbation. However, in microgravity, reduced gravitational pull and proprioceptive inputs constantly inform the controller that the body mass is less than its actual magnitude. In other words, sensory cues in space are misleading for estimating body mass. The resulting sensory bias prevents the sensorimotor system from adapting. Our initial explanation on this matter was too brief; we expanded it in the revised Discussion.

> ***Reviewer #3 (Public review):***
>
> *Summary:*
>
> *The authors describe an interesting study of arm movements carried out in weightlessness after a prolonged exposure to the so-called microgravity conditions of orbital spaceflight. Subjects performed radial point-to-point motions of the fingertip on a touch pad. The authors note a reduction in movement speed in weightlessness, which they hypothesize could be due to either an overall strategy of lowering movement speed to better accommodate the instability of the body in weightlessness or an underestimation of body mass. They conclude for the latter, mainly based on two effects. One, slowing in weightlessness is greater for movement directions with higher effective mass at the end effector of the arm. Two, they present evidence for an increased number of corrective submovements in weightlessness. They contend that this provides conclusive evidence to accept the hypothesis of an underestimation of body mass.*
>
> *Strengths:*
>
> *In my opinion, the study provides a valuable contribution, the theoretical aspects are well presented through simulations, the statistical analyses are meticulous, the applicable literature is comprehensively considered and cited, and the manuscript is well written.*
>
> *Weaknesses:*
>
> *Nevertheless, I am of the opinion that the interpretation of the observations leaves room for other possible explanations of the observed phenomenon, thus weakening the strength of the arguments.*
>
> *First, I would like to point out an apparent (at least to me) divergence between the predictions and the observed data. Figures 1 and S1 show that the difference between predicted values for the 3 movement directions is almost linear, with predictions for 90º midway between predictions for 45º and 135º. The effective mass at 90º appears to be much closer to that of 45º than to that of 135º (Figure S1A). But the data shown in Figure 2 and Figure 3 indicate that movements at 90º and 135º are grouped together in terms of reaction time, movement duration, and peak acceleration, while both differ significantly from those values for movements at 45º.*
>
> *Furthermore, in Figure 4, the change in peak acceleration time and relative time to peak acceleration between 1g and 0g appears to be greater for 90º than for 135º, which appears to me to be at least superficially in contradiction with the predictions from Figure S1. If the effective mass is the key parameter, wouldn't one expect as much difference between 90º and 135º as between 90º and 45º? It is true that peak speed (Figure 3B) and peak speed time (Figure 4B) appear to follow the ordering according to*

> *effective mass, but is there a mathematical explanation as to why the ordering is respected for velocity but not acceleration? These inconsistencies weaken the author's conclusions and should be addressed.*

Response (11): Indeed, the model predicts an almost equal separation between 45° and 90° and between 90° and 135°, while the data indicate that the spacing between 45° and 90° is much smaller than between 90° and 135°. We do not regard the divergence as evidence undermining our main conclusion since 1) the model is a simplification of the actual situation. For example, the model simulates an ideal case of moving a point mass (effective mass) without friction and without considering Coriolis and centripetal torques. 2) Our study does not make quantitative predictions of all the key kinematic measures; that will require model fitting, parameter estimation, and posture-constrained reaching experiments; instead, our study uses well-established (though simplified) models to qualitatively predict the overall behavioral pattern we would observe. For this purpose, our results are well in line with our expectations: though we did not find equal spacing between direction conditions, we do confirm that the key kinematic measures (Figure 2 and Figure 3 as questioned) show consistent directional trends between model predictions and empirical data. We added new analysis results on this matter: the directional effect we observed (how the key measures changed in microgravity across direction condition) is significantly correlated with our model predictions in most cases. Please check our detailed response (2) above. These results are also added in the revision.

We also highlight in the revision that our modeling is not to quantitatively predict reaching behaviors in space, but to qualitatively prescribe that how mass underestimation, but not the conservative control strategy, can lead to divergent predictions about key kinematic measures of fast reaching.

> *Then, to strengthen the conclusions, I feel that the following points would need to be addressed:*
>
> *(1) The authors model the movement control through equations that derive the input control variable in terms of the force acting on the hand and treat the arm as a second-order low-pass filter (Equation 13). Underestimation of the mass in the computation of a feedforward command would lead to a lower-than-expected displacement to that command. But it is not clear if and how the authors account for a potential modification of the time constants of the 2nd order system. The CNS does not effectuate movements with pure torque generators. Muscles have elastic properties that depend on their tonic excitation level, reflex feedback, and other parameters. Indeed, Fisk et al. showed variations of movement characteristics consistent with lower muscle tone, lower bandwidth, and lower damping ratio in 0g compared to 1g. Could the variations in the response to the initial feedforward command be explained by a misrepresentation of the limbs' damping and natural frequency, leading to greater uncertainty about the consequences of the initial command? This would still be an argument for unadapted feedforward control of the movement, leading to the need for more corrective movements. But it would not necessarily reflect an underestimation of body mass.*
>
> *Fisk, J. O. H. N., Lackner, J. R., & DiZio, P. A. U. L. (1993). Gravitoinertial force level influences arm movement control. Journal of neurophysiology, 69(2), 504-511.*

Response (12): We agree that muscle properties, tonic excitation level, proprioception-mediated reflexes all contribute to reaching control. Fisk et al. (1993) study indeed showed that arm movement kinematics change, possibly owing to lower muscle tone and/or damping. However, reduced muscle damping and reduced spindle activity are more likely to affect feedback-based movements. Like in Fisk et al.'s study, people performed continuous arm movements with eyes closed; thus their movements largely relied on proprioceptive control. Our major findings are about the feedforward control, i.e., the reduced and "advanced" peak velocity/acceleration in discrete and ballistic reaching movements. Note that the peak acceleration happens as early as approximately 90-100ms into the movements, clearly showing that feedforward control is affected -- a different effect from Fisk et al's findings. It is unlikely that people "advanced" their peak velocity/acceleration because they feel the need for more later corrective movements. Thus, underestimation of body mass remains the most plausible explanation.

> *(2) The movements were measured by having the subjects slide their finger on the surface of a touch screen. In weightlessness, the implications of this contact are expected to be quite different than those on the ground. In weightlessness, the taikonauts would need to actively press downward to maintain contact with the screen, while on Earth, gravity will do the work. The tangential forces that resist movement due to friction might therefore be different in 0g. This could be particularly relevant given that the effect of friction would interact with the limb in a direction-dependent fashion, given the anisotropy of the equivalent mass at the fingertip evoked by the authors. Is there some way to discount or control for these potential effects?*

Response (13): We agree that friction might play a role here, but normal interaction with a touch screen typically involves friction between 0.1N and 0.5N (e.g., Ayyildiz et al., 2018). We believe that the directional variation of the friction is even smaller than 0.1N. It is very small compared to the force used to accelerate the arm for the reaching movement (10N-15N). Thus, friction anisotropy is unlikely to explain our data. Indeed, our readers might have the same concern, we thus added some discussion about possible effect of friction.

Citation: Ayyildiz M, Scaraggi M, Sirin O, Basdogan C, Persson BNJ. Contact mechanics between the human finger and a touchscreen under electroadhesion. Proc Natl Acad Sci U S A. 2018 Dec 11;115(50):12668-12673.

> *(3) The carefully crafted modelling of the limb neglects, nevertheless, the potential instability of the base of the arm. While the taikonauts were able to use their left arm to stabilize their bodies, it is not clear to what extent active stabilization with the contralateral limb can reproduce the stability of the human body seated in a chair in Earth gravity. Unintended motion of the shoulder could account for a smaller-than-expected displacement of the hand in response to the initial feedforward command and/or greater propensity for errors (with a greater need for corrective submovements) in 0g. The direction of movement with respect to the anchoring point could lead to the dependence of the observed effects on movement direction. Could this be tested in some way, e.g., by testing subjects on the ground while standing on an unstable base of support or sitting on a swing, with the same requirement to stabilize the torso using the contralateral arm?*

Response (14): Body stabilization is always a challenge for human movement studies in space. We minimized its potential confounding effects by using left-hand grasping and foot straps for postural support throughout the experiment. We think shoulder stability is an unlikely explanation because unexpected shoulder instability should not affect the feedforward (early) part of the ballistic reaching movement: the reduced peak acceleration and its early peak were observed at about 90-100ms after movement initiation. This effect is too early to be explained by an expected stability issue. This argument is now mentioned in the revised Discussion.

The arguments for an underestimation of body mass would be strengthened if the authors could address these points in some way.

> ***Recommendations for the authors:***
>
> ***Reviewing Editor Comments:***

> *General recommendation*
>
> *Overall, the reviewers agreed this is an interesting study with an original and strong approach. Nonetheless, there were significant weaknesses identified. The main criticism is that there is insufficient evidence for the claim that the movement slowing is due to mass underestimation, rather than other explanations for the increased feedback corrections. To bolster this claim, the reviewers have requested a deeper quantitative analysis of the directional effect and comparison to model predictions. They have also suggested that a 2-dof arm model could be used to predict how mass underestimation would influence multi-joint kinematics, and this should be compared to the data. Alternatively, or additionally, a control experiment could be performed (described in the reviews). We do realize that some of these options may not be feasible or practical. Ultimately, we leave it to you to determine how best to strengthen and solidify the argument for mass underestimation, rather than other causes.*
>
> *As an alternative approach, you could consider tempering the claim regarding mass underestimation and focus more on the result that slower movements in microgravity are not simply a feedforward, rescaling of the movement trajectories, but rather, have greater feedback corrections. In this case, the reviewers feel it would still be critical to explain and discuss potential reasons for the corrections beyond mass underestimation.*
>
> *We hope that these points are addressable, either with new analyses, experiments, or with a tempering of the claims. Addressing these points would help improve the eLife assessment.*
>
> ***Reviewer #1 (Recommendations for the authors):***
>
> *(1) Move model descriptions to the main text to present modelling choices in more detail*

Response (15): Thank you for the suggestion. We have moved the model descriptions to the main text to present the modeling choices in more detail and to allow readers to better cross-reference the analyses.

> *(2) Perform quantitative comparisons of the directional effect with the model's predictions, and add raw kinematic traces to illustrate the effect in more detail.*

Response (16): Thanks for the suggestion, we have added the raw kinematics figure from a representative participant and please refer to Response (2) above for the comparisons of directional effect.

> *(3) Explore the effect of varying cost parameters in addition to mass estimation error to estimate the proportion of data explained by the underestimation hypothesis.*

Response (17): Thank you for the suggestion. This has already been done—please see Response (1) above.

> ***Reviewer #2 (Recommendations for the authors):***
>
> *Minor comments:*
>
> *(1) It must be justified early on why reaction times are being analyzed in this work. I understood later that it is to rule out any global slowing down of behavioral responses in microgravity.*

Response (18): Exactly, RT results are informative about the absence of a global slowing down. Contrary to the conservative-strategy hypothesis, taikonauts did not show generalized slowing; they actually had faster reaction times during spaceflight, incompatible with a generalized slowing strategy. Thanks for point out; we justified that early in the text.

> *(2) Since the results are presented before the methods, I suggest stressing from the beginning that the reaching task is performed on a tablet and mentioning the instructions given to the participants, to improve the reading experience. The "beep" and "no beep" conditions also arise without obvious justification while reading the paper.*

Response (19): Great suggestions. We now give out some experimental details and rationales at the beginning of Results.

> *(3) Figure 1C: The vel profiles are not returning to 0 at the end, why? Is it because the feedback gain is computed based on the underestimated mass or because a feedforward controller is applied here? Is it compatible with the experimental velocity traces?*

Response (20): Figure. 1C shows the forward simulation under the optimal control policy. In our LQG formulation the terminal velocity is softly penalized (finite weight) rather than hard-constrained to zero; with a fixed horizon° the optimal solution can therefore end with a small residual velocity.

In the behavioral data, the hand does come to rest: this is achieved by corrective submovements during the homing phase.

> *(4) Left-skewed -> I believe this is right-skewed since the peak velocity is earlier.*

Response (21): Yes, it should be right-skewed, thanks for point that out.

> *(5) What was the acquisition frequency of the positional data points? (on the tablet).*

Response (22): The sampling frequency is 100 Hz. Thanks for pointing that out; we've added this information to the Methods.

> *(6) Figure S1. The planned duration seems to be longer than in the experiment (it is more around 500 ms for the 135-degree direction in simulation versus less than 400 ms in the experiment). Why?*

Response (23): We apologize for a coding error that inadvertently multiplied the body-mass parameter by an extra factor, making the simulated mass too high. We have corrected the code, rerun the simulations, and updated Figures 1 and S1; all qualitative trends remain unchanged, and the revised movement durations (≈300–400 ms) are closer to the experimental values.

> *(7) After Equation 13: "The control law is given by". This is not the control law, which should have a feedback form u=K*x in the LQ framework. This is just the dynamic equations for the auxiliary state and the force. Please double-check the model description.*

Response (24): Thank you for point this out. We have updated and refined all model equations and descriptions, and moved the model description from the Supplementary Materials to the main text; please see the revised manuscript.

> ***Reviewer #3 (Recommendations for the authors):***
>
> *(1) I have a concern about the interpretation of the anisotropic "equivalent mass". From my understanding, the equivalent mass would be what an external actor would feel as an equivalent inertia if pushing on the end effector from the outside. But the CNS does not push on the arm with a pure force generator acting at the hand to effectuate movement. It applies torque around the joints by applying forces across joints with muscles, causing the links of the arm to rotate around the joints. If the analysis is carried out in joint space, is the effective rotational inertia of the arm also anisotropic with respect to the direction of the movement of the hand? In other words, can the authors reassure me that*

> *the simulations are equivalent to an underestimation of the rotational inertia of the links when applied to the joints of the limb? It could be that these are mathematically the same; I have not delved into the mathematics to convince myself either way. But I would appreciate it if the authors could reassure me on this point.*

Response (25): Thank you for raising this point. In our work, “equivalent mass” denotes the operational-space inertia projected along the hand-movement direction u, computed as:

$\tau = J^T F.$

This formulation describes the effective mass perceived at the end effector along a given direction, and is standard in operational-space control.

Although the motor command can be coded as either torque/force in the CNS, the actual executions are equivalent no matter whether it is specified as endpoint forces or joint torques, since force and torque are related by . For small excursions as investigated here, this makes the directional anisotropy in endpoint inertia consistent with the anisotropy of the effective joint-space inertia required to produce the same endpoint motion. Conceptually, therefore, our “mass underestimation” manipulation in operational space corresponds to underestimating the required joint-space inertia mapped through the Jacobian. Since our behavioral data are hand positions, using the operational-space representation is the most direct and appropriate way for modeling.

> *(2) I would also like to suggest one more level of analysis to test their hypothesis. The authors decomposed the movements into submovements and measured the prevalence of corrective submovements in weightlessness vs. normal gravity. The increase in corrective submovements is consistent with the hypothesis of a misestimation of limb mass, leading to an unexpectedly smaller displacement due to the initial feedforward command, leading to the need for corrections, leading to an increased overall movement duration. According to this hypothesis, however, the initial submovement, while resulting in a smaller than expected displacement, should have the same duration as the analogous movements performed on Earth. The authors could check this by analyzing the duration of the extracted initial submovements.*

Response (26): We appreciate the reviewer’s suggestion regarding the analysis of the initial submovement duration. In our decomposition framework, each submovement is modeled as a symmetric log-normal (bell-shaped) component, such that the time to peak speed is always half of the component duration. Thus, the initial submovement duration is directly reflected in the initial submovement peak-speed time already reported in our original manuscript (Figure. 5F).

However, we respectfully disagree with the assumption that mass underestimation would necessarily yield the same submovement duration as on Earth. Under mass underestimation, the movement is effectively under-actuated, and the initial submovement can terminate prematurely, leading to a shorter duration. This is indeed what we observed in the data. Therefore, our reported metrics already address the reviewer’s proposal and support the conclusion that mass underestimation reduces the initial submovement duration in microgravity. Per your suggestion, we now added one more sentence to explain to the reader that initial submovement peak-speed time reflect the duration of the initial submovement.

> *Some additional minor suggestions:*
>
> *(1) I believe that it is important to include the data from the control subjects, in some form, in the main article. Perhaps shading behind the main data from the taikonauts to show similarities or differences between groups. It is inconvenient to have to go to the supplementary material to compare the two groups, which is the main test of the experiment.*

Response (27): Thank you for the suggestion. For all the core performance variables, the control group showed flat patterns, with no changes across test sessions at all. Thus, including these figures (together with null statistical results) in the main text would obscure our central message, especially given the expanded length of the revised manuscript (we added model details and new analysis results). Instead, following eLife's format, we have reorganized the Supplementary Material so that each experimental figure has a corresponding supplementary figure showing the control data. This way, readers can quickly locate the control results and directly compare them with the experimental data, while keeping the main text focused.

> *(2) "Importantly, sensory estimate of bodily property in microgravity is biased but evaded from sensorimotor adaptation, calling for an extension of existing theories of motor learning." Perhaps "immune from" would be a better choice of words.*

Response (28): Thanks for the suggestion, we edited our text accordingly.

> *(3) "First, typical reaching movement exhibits a symmetrical bell-shaped speed profile, which minimizes energy expenditure while maximizing accuracy according to optimal control principles (Todorov, 2004)." While Todorov's analysis is interesting and well accepted, it might be worthwhile citing the original source on the phenomenon of bell-shaped velocity profiles that minimize jerk (derivative of acceleration) and therefore, in some sense, maximize smoothness. Flash and Hogan, 1985.*

Response (29): Thanks for the suggestion, we added the citation of minimum jerk.

> *(4) "Post-hoc analyses revealed slower reaction times for the 45° direction compared to both 90° ($p < 0.001$, $d = 0.293$) and 135° ($p = 0.003$, $d = 0.284$). Notably, reactions were faster during the in-flight phase compared to pre-flight ($p = 0.037$, $d = 0.333$), with no significant difference between in-flight and post-flight phases ($p = 0.127$)." What can one conclude from this?*

Response (30): Although these decreases reached statistical significance, their magnitudes were small. The parallel pattern across groups suggests the effect is not driven by microgravity, but is more plausibly a mild learning/practice effect. We now mentioned this in the Discussion.

> *(5) "In line with predictions, peak acceleration appeared significantly earlier in the 45° direction than other directions (45° vs. 90°, $p < 0.001$, $d = 0.304$; 45° vs. 135°, $p < 0.001$, $d = 0.271$)." Which predictions? Because the effective mass is greater at 45°? Could you clarify the prediction?*

Response (31): We should be more specific here; thank you for raising this. The predictions are the ones about peak acceleration timing (shown in Fig. 1H). We now modified this sentence as:

"In line with model predictions (Figure 1H), ...".

> *(6) Figure 2: Why do 45° movements have longer reaction times but shorter movement durations?*

Response (32): Appreciate your careful reading of the results. We believe this is possibly due to flexible motor control across conditions and trials, i.e., people tend to move faster when people react slower with longer reaction time. This has been reflected in across-direction comparisons (as spotted by the reviewer here), and it has also been shown within participant and across participants: For both groups, we found a significant negative correlation between movement duration (MD) and reaction time (RT), both across and within individuals (Figure 2—figure supplement 5). This finding indicates that participants moved faster when their RT was slower, and vice versa. This flexible motor adjustment, likely due to the task requirement for rapid movements, remained consistent during spaceflight.

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