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RESEARCH ARTICLE

Control of Movement

Motor imagery helps updating internal models during microgravity exposure

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Abstract

Skilled movements result from a mixture of feedforward and feedback mechanisms conceptualized by internal models. These mechanisms subserve both motor execution and motor imagery. Current research suggests that imagery allows updating feedforward mechanisms, leading to better performance in familiar contexts. Does this still hold in radically new contexts? Here, we test this ability by asking participants to imagine swinging arm movements around shoulder in normal gravity condition and in microgravity in which studies showed that movements slow down. We timed several cycles of actual and imagined arm pendular movements in three groups of subjects during parabolic flight campaign. The first, control, group remained on the ground. The second group was exposed to microgravity but did not imagine movements inflight. The third group was exposed to microgravity and imagined movements inflight. All groups performed and imagined the movements before and after the flight. We predicted that a mere exposure to microgravity would induce changes in imagined movement duration. We found this held true for the group who imagined the movements, suggesting an update of internal representations of gravity. However, we did not find a similar effect in the group exposed to microgravity despite the fact that the participants lived the same gravitational variations as the first group. Overall, these results suggest that motor imagery contributes to update internal representations of the considered movement in unfamiliar environments, while a mere exposure proved to be insufficient.

NEW & NOTEWORTHY Gravity strongly affects the way movements are performed. How internal models process this information to adapt behavior to novel contexts is still unknown. The microgravity environment itself does not provide enough information to optimally adjust the period of natural arm swinging movements to microgravity. However, motor imagery of the task while immersed in microgravity was sufficient to update internal models. These results show that actually executing a task is not necessary to update graviception.

internal models; microgravity; motor imagery; parabolic flight

INTRODUCTION

The execution of the simplest daily life movements, such as grabbing a mug, requires intense computational transformations. These processes depend on body dynamics, object properties, and the nature of the environment. Theories of motor control suggest that these computational steps rely on feedback and feedforward neural mechanisms formalized in internal models. Appropriate motor commands to reach a desired goal are derived through the integration of sensory prediction and recent system states. Forward models implement prediction of sensory consequences of actions by feeding a copy of the motor commands ("efference copy") in a simulator of the dynamics of the action (1–6). Internal models are sensitive to neuroplastic changes that guarantee sensorimotor flexibility and adaptability when the system is exposed to external disturbances and/or new physical constraints (7).

Studies have reported that gravity influences all stages of the chain that lead to an action, from planning to execution (for review, see Ref. 8). Efficient control of any movement is then conditioned by the storage of distributed internal representations of gravity in internal models. When gravity is

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altered, time is necessary to adapt to the new environment, for instance in object manipulation (9–11) or arm reaching movements (12). For example, Augurelle et al. (9) demonstrated that, although the grip force developed on object is much higher than required in an unnatural gravity context, a progressive adaptation of the force exerted by the fingers is possible. This adjustment started as early as the second trial to achieve optimal force coordination after the fifth trial. The gravitational signal is so strong that it seems to set the pace of free rhythmic movements. In a previous study, White et al. (13) showed that the larger (respectively smaller) the gravity, the faster (respectively slower) the cyclic movements. This effect was even observable when the pace of the movement was imposed by a metronome. This behavior was driven by a strategy that minimized energy: participants naturally adopted the pace close to the resonant frequency of the biomechanical system, itself function of gravity. This demonstrates the massive influence of the external environment on movement production and provides a simple and reliable behavioral task to probe the integration of gravity in internal processes.

Motor adaptation is efficient through practice of the motor task. However, it is also possible to learn the task without doing per se. Indeed, kinesthetic motor imagery, defined as the mental simulation of movement based on sensorimotor information (14), relies on internal simulation of actions and hence, on forward models (15). A robust and well-documented property of motor imagery is isochrony: behavioral observations (16, 17) reported a temporal correspondence between motor imagery and execution of the same action, modulated by task constraints (e.g., distance, difficulty, and environmental changes). This property is assumed to reflect a common involvement of motor prediction processes between actual execution and motor imagery. Also, another interesting property of motor imagery is that the motor predictions are not impacted by action-related sensory feedbacks. This is supported by Rousseau et al. (18), who indicated a dual representation of the gravity in the insula. Specifically, the authors found that posterior part of the insular cortex was engaged when action-related sensory feedback was processed, whereas the anterior insula was activated only when mentally simulating the action. The aforementioned properties of motor imagery make the latter a useful tool to probe whether the environment itself (without reinforcement by feedback) updates internal representations. In that way, Papaxanthis et al. (19) tested how internal models were updated following long-term exposure to microgravity during a spaceflight mission. The authors found an isochrone slowdown of actual and imagined movements immediately after spaceflight, suggesting that immersion in microgravity led to an update of internal representations.

Here, we question the nature of the information about the new gravitational environments required to update motor prediction processes. In other words, is motor imagery alone powerful enough to extrapolate the way we would move in a new gravitational environment? If not, then, is it necessary to perform the movement in the new environment to update internal models or, instead, is a mere exposure of the body to the new environment sufficient? If an exposure is sufficient, it would mean that task-specific feedback information are not essential in the adaptation process. To answer this, we asked participants to imagine and execute arm pendular movements before and after short-term exposure to microgravity during parabolic flights. Such rhythmic movement was chosen because of its simplicity and its sensitivity to gravitational variations considering actual (13, 20, 21) and imagined movements (18). Three experimental groups were formed. In the Imagine group, participants were explicitly told to imagine—without doing—a few cycles of arm pendular movements in microgravity. In the Exposed group, participants were immersed in microgravity but did not do the motor imagery task. The third, Control group, did not fly and was free to perform any normal activities during the flight period. These included walking, sitting, and working on a computer. We formulated the following specific hypotheses. *1*) If sensory feedback is necessary for adaptation, then, the Imagine and Exposed groups should not be different from the Control group. Thus, we should observe similar movement duration for both actual and imagined movements after the flight for all groups. *2*) If active mental processes dedicated to the task are necessary, then, only the Imagine group should exhibit a change in imagined movement duration after the flight. *3*) Finally, if being passively immersed in microgravity is powerful enough, such change should be observed for the Exposed group as well.

MATERIALS AND METHODS

Participants and Ethical Considerations

Twenty-three participants (19 men, 26.9 ± 7.1 yr old and 4 women, 27.3 ± 5.3 yr old) without sensory or motor deficits took part in the experiment performed during a parabolic flight campaign funded by the French space agency (Centre National d'Etudes Spatiales). None of the participants had previously been exposed to microgravity. Among the 23 participants, a group of 15 participants took part in one parabolic flight and 8 participants remained on the ground. Flyers were examined by a medical doctor and were qualified for parabolic flights after an in-depth medical examination including rest electrocardiography (ECG). Prior to the flights, participants were invited to take medication (scopolamine) to limit motion sickness. It has been shown that scopolamine does not alter sensorimotor performances (22).

All participants were naïve as to the purpose of the experiment that took place at Novespace-Merignac airport (France). The study was conducted in accordance with the Declaration of Helsinki (1964), and was authorized by the ANSM (French National Agency for Biomedical Security) and received formal ethical approval (Agreement No. 2018-A03379-46). All participants signed an informed consent form stored at the Caen University Hospital.

Parabolic Flight Maneuvers

The experiment was performed during the 142th CNES parabolic flight campaign. Every flight lasted for ∼2.5 h. Each of the 15 flying participants experienced one flight in which they were exposed to 31 parabolas described as follows. From a steady horizontal flight (normogravity, 1 g = 9.81 m·s^{-2}), the aircraft gradually pulled up its nose and started climbing up to an angle of ∼45° for ∼20 s, during which the aircraft experienced an acceleration of around

1.8 *g*. The engine thrust was then reduced to the minimum required to compensate for air drag and the aircraft then followed a close-to free-fall ballistic trajectory (a parabola) lasting an additional 20 s, during which microgravity ($0 \pm 0.02\, g$) was achieved. At the end of this period, the aircraft pulled out of the parabola, which gave rise to another 20 s of 1.8 *g*. Finally, the aircraft returned to normal flight altitude (1 *g*) before the entry into the next parabola within 1 min to 8 min. During the parabolas, the resultant *g* vector was always perpendicular to the floor of the aircraft. Lateral and forward/backward components were in the range $10^{-3}\, g$ and were negligible.

Experimental Procedure

All participants underwent three experimental phases (Pre, Flying time, and Post; Fig. 1). The first phase took place before the flight (Pre; Fig. 1). During that phase, we assessed *1*) the motor imagery vividness with the Kinesthetic and Visual Imagery Questionnaire [KVIQ, short version: kinesthetic items only (23)] and *2*) the duration of actual and imagined arm pendular movements. Participants were seated and had to swing their dominant upper limb around shoulder at comfortable pace and natural amplitude according to three conditions: *1*) actual movements, *2*) imagined movements in 1 *g*, and *3*) imagined movements in 0 *g*. In the last condition, participants had to feel the sensations of the movement as if they imagined themselves evolving in a microgravity environment. Here, we expected that the participants would be unable to extrapolate such information before the flight, and thus to imagine the movement in the same way as in 1 *g*. A slowdown of imagined movement duration after the flight would, in our opinion, reflect a capacity to extrapolate microgravity features in the motor imagery process. Each participant performed four trials per condition. A trial was composed of two contiguous cycles of actual or imagined arm pendular movements. Note that the participants were not instructed to imagine similar movement, because similarity between actual and imagined movements is a well-known, implicit, and expected phenomenon that is assumed to be a hallmark of the involvement of internal models during motor imagery. To normalize, however (and not impose a specific behavior), the task was shown by the same experimenter to every participant. The starting position of the first trial was either in front of or behind the participant and was counterbalanced across participants. Starting positions alternated between trials. The order of the imagined gravitational environment (1 *g* or 0 *g*) was counterbalanced between participants.

In the second phase of the experiment (Flying time; Fig. 1), participants were distributed in three groups. In the first group (Control, $n = 8$), nonflyer participants remained on the ground for the duration of the flight. Participants of the two other groups were considered as flyers. In the second group, participants were exposed to the parabolas while being engaged in various scientific activities, depending on their respective research teams (Exposed, $n = 6$). In the third group (Imagine, $n = 9$), participants were asked to imagine arm pendular movements while physically immersed in 1 *g* or 0 *g*. Each participant of the Imagine group was tested for 10 parabolas. More specifically, during each flight day, one participant was tested either during the first batch of 10 parabolas, the second batch of 10, or the last batch of 10.

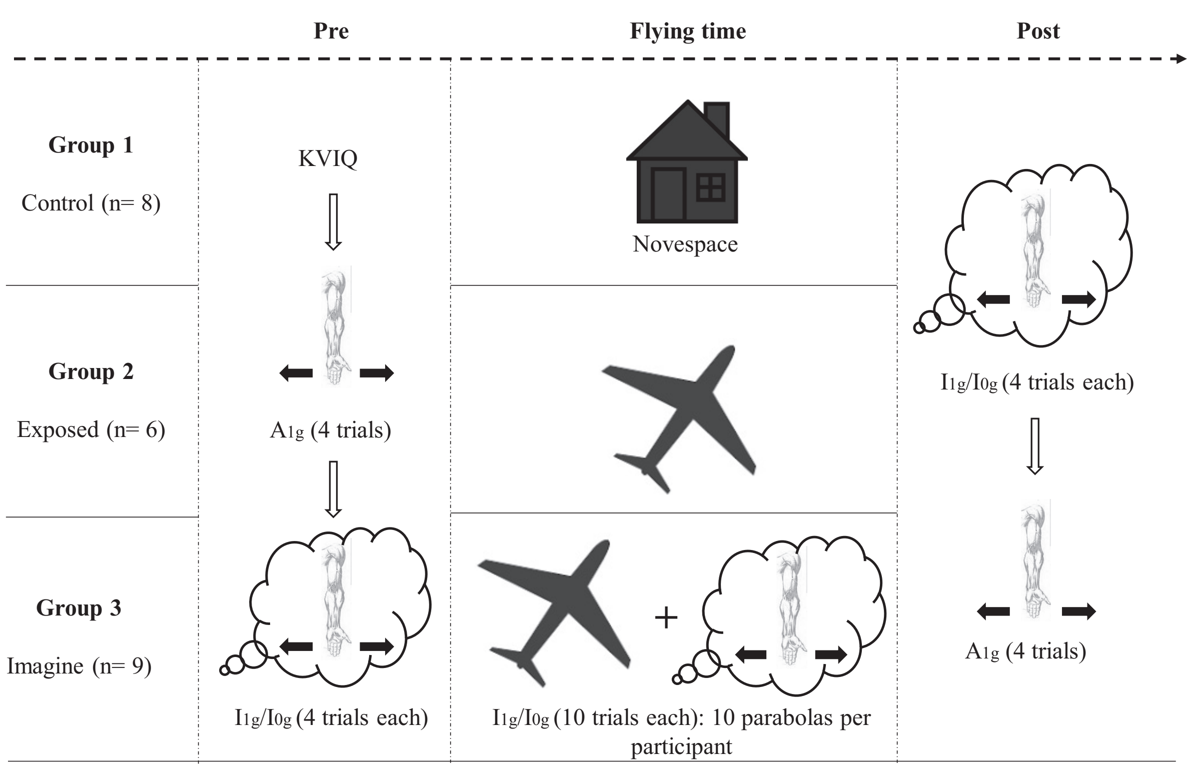

Figure 1. Schematic representation of the experimental procedure. A_{1g}, actual movement in 1 *g*; I_{1g}, imagined movement in 1 *g*; I_{0g}, imagined movement in 0 *g* (during or not during exposure to 0 *g*). KVIQ, Kinesthetic and Visual Imagery Questionnaire.

Participants had to imagine two cycles of pendular movements during the 1 g phase, before entering the parabola, and during the 0 g phase. They started to imagine the motor task as soon as they felt ready after having heard the signal "steady flight" and "injection," announcing 1 g and 0 g phases, respectively. To limit motion sickness and to normalize behavior, participants of the Imagine group were instructed to keep their eyes open during the task while not gazing at anything in particular. When not tested during the flight, participants of the Imagine group were engaged in other scientific activities.

After the flight (Post; Fig. 1), participants repeated exactly the same procedure as the one described in the preflight phase with one notable exception: to avoid a potential resetting of internal representation due to actual execution, participants always first imagined movements under 1 g and 0 g (still counterbalanced) before actually performing the movement. Participants were tested as soon as possible after the flight (between 10 and 30 min depending on their personal priorities).

The duration of actual and imagery movements was recorded with an electronic stopwatch. Participants held the stopwatch in their left hand. They triggered it when they started to move/imagine their right arm and they stopped the device when they had completed the two cycles of pendular movements. Participants never received any information about their actual or imagined movement times to avoid the setting up of implicit strategies.

Data Processing and Statistical Analysis

For each condition and for each group, the mean duration of actual and imagined movements in each condition was calculated. Normality and variance homogeneity assumptions were checked before inferential statistics using visual inspection of residuals Q-Q plots and Bartlett tests. One participant from the Imagine group experienced motion sickness during the flight and has been excluded from further analysis. Presence of outliers has been tested using the median absolute deviation method (24). Since outliers concerns the same participant (too long movement durations for I_{1g} in Pre and A_{1g} in Post), data from this participant (in the Imagine group), were removed from the analysis. The threshold of statistical significance was set to $\alpha = 0.05$.

The first step of the analysis consisted of ensuring that imagery vividness was statistically not different between groups. Therefore, KVIQ results were averaged and compared across groups using a one-way analysis of variance. Then, the temporal correspondence (isochrony) between actual and imagined motions in 1 g was examined before and after the flight. To quantify isochrony between actual and imagined movements in 1 g, we calculated the following index (ISO_{1g}) inspired by Marchesotti et al. (25):

$$ISO_{1g} = 1 - (I_{1g}/A_{1g}),$$

where I_{1g} corresponds to imagined movement times in 1 g and A_{1g} to actual movement times in 1 g. A perfect isochrony would yield an ISO_{1g} equal to 0. In case of mismatch, the ISO_{1g} can be negative (if $I_{1g} > A_{1g}$) or positive (if $I_{1g} < A_{1g}$). To ensure isochrony between A_{1g} and I_{1g}, one-sample t tests against isochrony (0) were conducted for pre- and post-tests ISO_{1g} and for each group separately. Paired-sample t tests were also conducted between pre and post for each group, to check if parabolic maneuvers disturbed the motor prediction process. Each one- and paired-sample t tests conducted on isochrony was completed by an equivalence test (26).

Concerning the Pre-Post effects, a general linear model with Greenhouse–Geisser correction was performed with GROUP (Control, Exposed, and Imagine) as categorical predictor and six-repeated measures factor hierarchized in two levels. The first level is TIME (Pre vs. Post) and the second level is MOVEMENT (actual 1 g, imagined 1 g, and imagined 0 g). Post hoc pairwise comparisons were performed on the GROUP × TIME × MOVEMENT in case of significance and corrected using Bonferroni method. Partial eta-squared (η_p^2) values were reported to provide indication on effect sizes.

Given that a lot of between-subject variability characterizes our data set, the differences of data dispersion between pre- and post-tests led us to an analysis of between-subject variability through the use of coefficients of variation (CV), calculated on averaged pre- and post-test data for each group separately.

Inflight imagined movement durations of the Imagine group were then analyzed. Inflight time measurements were analyzed with one-sided paired-sample t tests, opposing imagined movement in 1 g (I_{1g}) and imagined movement in 0 g (I_{0g}) for each parabola (10 tests). P values were adjusted accordingly using Bonferroni method for multiple testing. Cohen's d values are reported for each test. A percentage of change with respect to 1 g [$\Delta_{0g\ (\%)}$] was calculated for each parabola to provide a complementary descriptive measure of differences between I_{1g} and I_{0g} using the following formula:

$$\Delta_{0g\ (\%)} = (I_{0g} - I_{1g})/I_{1g} \times 100,$$

in which Δ_{0g} can be <0 (if $I_{0g} < I_{1g}$) or >0 (if $I_{0g} > I_{1g}$).

Non-normalized differences between I_{1g} and I_{0g} [$\Delta_{0g\ (s)}$] for each parabola were also presented for the same purpose.

Finally, we used the computational model developed in a recent publication of our team [see Rousseau et al. (18) for an exhaustive presentation of the model]. Briefly, the natural period of a simple compound pendulum depends on the derived moment of inertia of the arm when moving around the shoulder insertion point (J), total mass (m), gravity (g), and position of the center of mass (l) of the equivalent system according to:

$$T = 2\pi\sqrt{\frac{\sum_i J_i}{mlg}}.$$

The model predicts that movements become slower (and have a larger period) as gravity decreases. By assuming one can reliably imagine a movement in 1 g, we used the model to predict what should be the theoretical value of gravity to account for this period change. We calculated the difference between I_{1g} an I_{0g} periods (ΔT) before and after the flight for each participant. We matched m, l, and J to individual participants in the model and solved the following equation for alpha (α), interpreted here as a "gravitational gain":

$$\Delta T = TI_{0g} - TI_{1g} = 2\pi\sqrt{\frac{J}{mlg}} - 2\pi\sqrt{\frac{J}{ml(\alpha g)}}.$$

Algebraic development yields:

$$\alpha = \frac{4\pi 2J}{(2\pi\sqrt{J} + \Delta T\sqrt{mlg})^2}.$$

Then, we used paired-sample t tests to compare α values between the Pre and the Post for the Imagine group. Because arm segments lengths were not recorded for Exposed and Control groups, that analysis has been conducted for the Imagine group only.

Data processing and statistical analysis were done using Statistica (v. 13.3. Stat-Soft). Equivalence testings were done using the TOSTER package (27) on R (R Core Software, 2012).

RESULTS

Participants cyclically moved and imagined pendulum movements of the arm on the ground (1 g) and during gravitational variations induced by parabolic flight maneuvers (1 g and 0 g). The main purpose of the following analysis was to investigate whether the brain can generalize a movement executed in a normal terrestrial context to a microgravity environment.

Vividness

In terms of vividness, participants of the Control group (3.02 ± 0.69), Exposed group (2.68 ± 0.9), and Imagine group (2.94 ± 0.76) are not statistically different [$F(2, 18) < 0.1$, P = 0.72].

Isochrony between Actual and Imagined Movements in 1 *g*

One-sample t tests suggest that the ISO_{1g} score is not statistically different from 0 whatever the group or time (all $P >$ 0.08). ISO_{1g} is not statistically different between Pre and Post for each group either (all $P > 0.15$). ISO_{1g} values are reported in Table 1. Equivalence test are nonsignificant (all $P > 0.25$), suggesting that the present ISO_{1g} values cannot either be considered as equivalent. These results are therefore inconclusive.

Post-Test Effects of Parabolic Maneuvers

Table 2 presents means and standard deviations of movement durations at Pre and Post for the three groups. Figure 2 depicts averaged durations for each type of movement (A_{1g} in blue, I_{1g} in black, and I_{0g} in red) for each group separately (Control, Exposed, or Imagine) and broken down between Pre and Post phases.

There is no significant main effect of GROUP on movement duration [$F(2, 18)$ = 0.72, P = 0.50]. However, main effects are reported for TIME [$F(1, 18)$, = 4.43, P = 0.014, η_p^2 = 0.29] and MOVEMENT [$F(2, 32)$ = 14.41, $P < 0.01$, η_p^2 = 0.44]. The main effect of TIME is explained by longer movement duration, on average, post- than pre-flight (P = 0.015). Regarding the main effect of MOVEMENT, post hoc comparisons reveal differences between I_{0g} and the two other conditions (all $P < 0.01$), since no statistical differences appeared between A_{1g} and I_{1g} (P = 0.68). As can be observed in Fig. 2, the I_{0g} movements durations were indeed longer than those in other conditions, independently of group and time. The study of interactions, summarized in the next paragraph, allows to unravel this effect regarding the influence of GROUP and TIME factors.

Table 1. *Means (±SD) for ISO_{1g} scores in Pre and Post for the three groups*

	Control Means (SD)	Exposed Means (SD)	Imagine Means (SD)
ISO_{1g}			
Pre	−0.03 (0.18)	0.004 (0.16)	−0.11 (0.14)
Post	−0.1 (0.14)	−0.07 (0.17)	−0.09 (0.30)

Table 2. *Means (±SD) for Pre and Post movement durations according to the three experimental groups*

	Pre	Post
	Means (SD)	Means (SD)
Control		
A_{1g} (s)	3.19 (0.57)	3.24 (0.95)
I_{1g} (s)	3.29 (0.79)	3.52 (0.92)
I_{0g} (s)	3.49 (0.69)	3.62 (1.07)
Exposed		
A_{1g} (s)	2.86 (0.42)	2.94 (0.57)
I_{1g} (s)	2.82 (0.46)	3.16 (0.85)
I_{0g} (s)	3.42 (1.37)	3.84 (1.62)
Imagine		
A_{1g} (s)	2.84 (0.23)	3.27 (0.59)
I_{1g} (s)	3.13 (0.22)	3.60 (1.26)
I_{0g} (s)	3.74 (0.62)	5.33 (1.81)

A_{1g}, actual movements in 1 g; I_{1g}, imagined movements in 1 g; I_{0g}: imagined movement in 0 g; s, second.

There is no significant interaction for TIME × GROUP (P = 0.13). Significant interactions are observed for TIME × MOVEMENT [$F(4, 36)$ = 5.39, $P < 0.01$, η_p^2 = 0.23], GROUP × MOVEMENT [$F(4, 36)$ = 2.64, P = 0.049, η_p^2 = 0.23], and GROUP × TIME × MOVEMENT [$F(4, 36)$ = 3.23, P = 0.023, η_p^2 = 0.26]. Post hoc pairwise comparisons reveal that I_{0g} movement times increase in post-test (see Fig. 3) for the Imagine group (5.33 ± 1.81 s) when compared with A_{1g} and I_{1g} in Post, as well as A_{1g}, I_{1g}, and I_{0g} in Pre (all $P < 0.01$), confirming an increase of movement duration of I_{0g} after the flight for this group. That increase would indicate that the update of gravity-related internal representations can persist over time. Pairwise comparisons also revealed a significant difference between A_{1g} and I_{0g} in pretest for the Imagine group ($P < 0.01$).

The coefficients of variation suggest an increase of variability at post-test, more pronounced for the Imagine (CV-Pre = 16.78%, CV-Post = 38.28%) than for the Exposed (CV-Pre = 28.99%, CV-Post = 33.59%) and Control (CV-Pre = 20.23%, CV-Post = 27.57%) groups.

To sum up, the increase of I_{0g} duration at post-test for the Imagine group suggests that motor imagery inflight helped to update internal representations of microgravity, which, in turn, influences motor prediction processes. However, we did not find a similar effect in the Exposed group despite the fact that participants experienced the same gravitational variations as the Imagine group.

Inflight Effects of Parabolic Maneuvers

In this section, we test how gravitational variations, induced by parabolic maneuvers, influenced the duration of

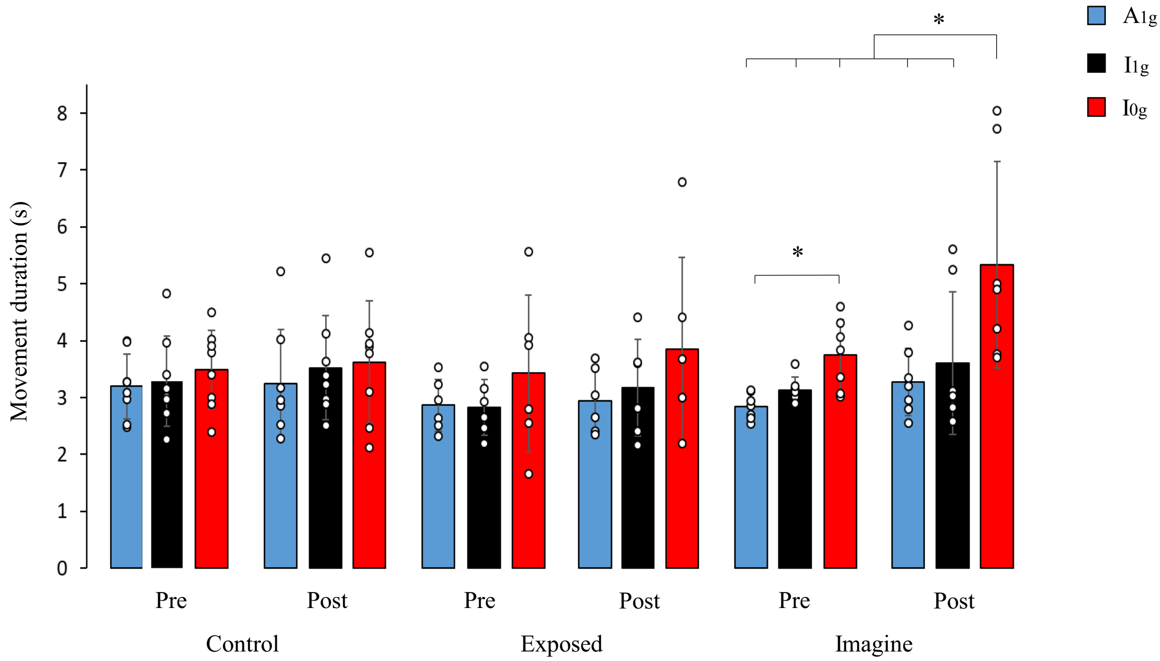

Figure 2. Movement duration for Control, Exposed, and Imagine groups in pre- and post-tests for actual movements in 1 *g* (A_{1g}), imagined movement in 1 *g* (I_{1g}), and 0 *g* (I_{0g}). Vertical bars represent standard deviations. White circles represent individual observations per condition. *$P < 0.05$ (pairwise comparisons).

imagined movements of participants involved in the mental task during the flight (Imagine group).

Descriptive statistics, $\Delta_{0g\ (s)}$ and $\Delta_{0g\ (\%)}$, *t* tests results, adjusted *P* values, and Cohen's *d* are reported in Table 3 and presented in Fig. 3.

The I_{1g} movement durations remain relatively stable during the flight when compared with the average I_{1g} movement durations before the flight for the Imagine group (i.e., 3.13 s). The I_{0g} durations were 0.71 s longer than I_{1g} (i.e., +21.52%) at the beginning of the flight (*parabola 1*), then increased between the beginning and the middle of the flight, reaching a maximal difference of 1.33 s (+41.31%) and 1.27 s (+39.64%) for *parabolas 4* and *5*, respectively. The I_{0g} durations gradually decreased over the second half of the flight

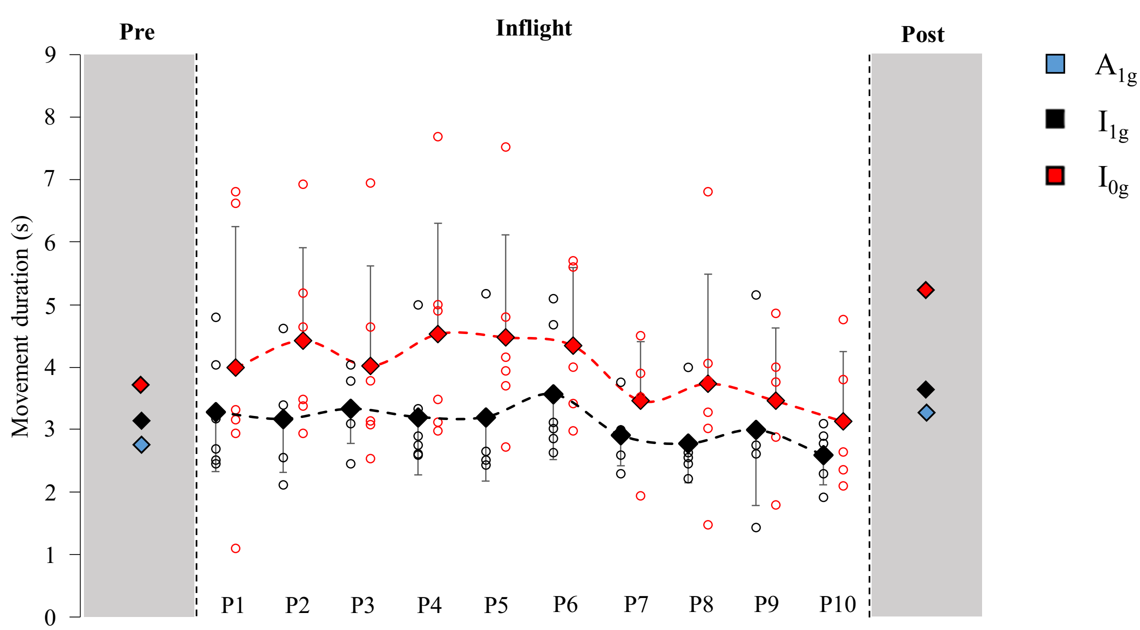

Figure 3. Flying time measurements for the Imagine group. Black and red lozenges represent I_{1g} and I_{0g} averages for each parabola, respectively. Vertical bars represent standard deviations. Black and red circles represent individual observation for I_{1g} and I_{0g}, respectively. Pre and Post movement durations of the Imagine group are depicted in gray zones. I_{1g}, imagined movement in 1 *g*; I_{0g}, imagined movement in 0 *g*. *P1–P10*, *parabola 1–parabola 10*.

Table 3. *Descriptive statistics and paired-samples t tests results for inflight measurements*

	I_{1g} (Means ± SD, in s)	I_{0g} (Means ± SD, in s)	$\Delta_{0g,\ s}$	$\Delta_{0g,\ \%}$	*t*	Adjusted *P* Values	Cohen's *d*
Parabola							
P1	3.28 (0.95)	3.99 (2.25)	0.71	21.52	1.20	1	0.44
P2	3.17 (0.85)	4.42 (1.48)	1.35	39.39	2.72	0.20	1.06
P3	3.34 (0.55)	4.02 (1.60)	0.78	20.47	1.28	1	0.63
P4	3.20 (0.92)	4.53 (1.78)	1.33	41.31	2.79	0.20	0.98
P5	3.20 (1.02)	4.47 (1.64)	1.27	39.64	3.99	0.051	0.95
P6	3.57 (1.04)	4.34 (1.25)	0.77	21.57	1.22	1	0.67
P7	2.91 (0.49)	3.46 (0.94)	0.55	18.90	2.07	0.53	0.77
P8	2.78 (0.63)	3.73 (1.75)	0.95	34.41	1.96	0.52	0.80
P9	3.00 (1.21)	3.46 (1.16)	0.46	15.33	1.54	0.90	0.39
P10	2.60 (0.48)	3.13 (1.14)	0.53	20.46	1.03	1	0.66

I_{1g}, imagined movements in 1 *g*; I_{0g}, imagined movement in 0 *g*; *P1–P10*, *parabola 1–parabola 10*; $\Delta_{0g\ (s)}$, non-normalized differences between I_{1g} and I_{0g}; s: second; $\Delta_{0g\ (\%)}$, percentage of change between I_{1g} and I_{0g}.

and were 0.53 s longer than I_{1g} (+20.46%) at the end of the flight (*parabola 10*). However, considering the adjusted *P* values, I_{0g} was not statistically different from I_{1g} during the flight, despite large effect sizes for certain parabolas (notably *parabolas 2*, *4*, and *5*).

Pendulum Model

The average value for α is 0.74 ± 0.24 before the flight and 0.43 ± 0.15 after the flight, which is closer to zero but clearly not zero. This is not surprising since the model is ill-defined for $g = 0$ (it predicts infinite periods). Furthermore, it was previously shown that the slowdown of cyclic movement periods remains stable between 0 *g* and 0.5 *g* (13), which fits with the current results. Please also note that α values were significantly different when comparing before and after the flight [$t(7) = -3.65$, $P = 0.01$, Cohen's $d = 1.38$], supporting that motor imagery when exposed to microgravity changes the way movement are simulated after it.

DISCUSSION

The purpose of this study was to investigate what information about a novel gravitational environment is required to allow participants to update internal models of gravity and extrapolate their behavior. To this end, we used mental chronometric measurements before, during, and after exposure to microgravity induced by parabolic flights. We found that the duration of movements imagined in microgravity after the flight was longer after the exposure only for the participants engaged in the motor imagery task during the flight (Imagine group), suggesting that the exposure to microgravity and motor imagery helped updating motor representation of gravity. Despite the fact the Exposed and Imagine groups underwent equivalent exposure to altered gravity, the imagined movement duration of the Exposed group showed no variations after the flight. The results of the Exposed group suggest that a mere exposure, nor the execution of movements that are not related to the task, is not sufficient to elicit changes in the internal representation of gravity. With regards to our hypothesis, this suggests that being passively immersed in microgravity is not powerful enough to update these internal representations, at least for short-term exposure.

According to current theories of motor adaptation and learning, sensorimotor adaptation occurs because internal models are updated (28). Most of the time, a parametric change is sufficient, for instance, when switching between objects of different masses. In that case, it was shown that internal models can be additively combined (29). In a number of cases however, structural learning is necessary and becomes much more challenging. For instance, when exposed to new and/or unexperienced constraints (e.g., microgravity), the action is initially disturbed because its characteristics are not reflected in the control policy and therefore in the generated motor command. The generalization of internal models is made possible by a form of learning. One powerful mechanism is error-based learning: exploration induces errors defined as discrepancies between sensorimotor predictions and actual feedback. The difference between predictions and outcomes is a teaching signal for internal models, adapting subsequent motor commands through repetition. Here, participants were confronted to a radically new environment and had then to implement a structural change in the internal models. Such extrapolation of motor plans in completely new environments has been observed recently in a large radius human centrifuge experiment (30). In that study, participants performed a series of three object lifts in hypergravity that varied stair wise between 1 *g* and 3 *g*. The analysis of fine parameters underlying object grasping showed that the task was immediately adjusted during the first trial in the new hypergravity phase. This demonstrated that participants could successfully extrapolate parameters of the internal models to match the requirements of the upcoming gravitoinertial context. In the present study, however, participants did not physically perform the task in microgravity. Nevertheless, we found that isochrony was maintained in the group who was actively engaged in the imagery task. Through inflight kinesthetic motor imagery, participants anticipated the consequences of their imagined movement (sensory prediction) and coupled these simulations with the multimodal sensory inflows induced by altered gravity. In a way, participants closed an internal loop and this learning happened in the absence of relevant feedback. How can we adapt without the sensory prediction error derived from feedback?

Several studies strengthened the view that imagined and executed movement are functionally comparable (albeit not identical) in terms of involved neurocognitive resources (31). Recently, using a somatosensory attenuation paradigm, Kilteni et al. (15) also reported that motor imagery generates sensorimotor predictions comparable with physical execution. As stated by the authors, internal forward models could predict the sensory consequences and the end state of the limbs for imagined movements based on the efference copy and the current system state. Michel et al. (32) showed that motor imagery is likely to induce sensorimotor adaptation using prismatic adaptation tasks. The authors suggested that such update would be driven by the integration of sensory inflow in sensorimotor predictions (33). The teaching signal would here correspond to the gap between the nonupdated motor command and the sensorimotor prediction. Through mental repetition, that teaching signal would be fed back to the controller, correcting the subsequent motor commands via a "self-supervised process" (34).

When immersed in microgravity, the partial integration of the latter during computation of the motor command would result in a gap between the command and the sensorimotor prediction. That information would be sent as input to correct the next motor command, progressively integrating microgravity-related information in motor command computation. We thus suggest that the activation of internal models during motor imagery, combined with the integration of sensory inflow in microgravity, helped update internal models of gravity. In this way, the results of the Imagine group would support that the formation of an adapted internal model of gravity could result from combined motor imagery and sensory integration when exposed to microgravity. This approach is of course quite limitative and not optimal as it prevents using feedback to update internal representation.

That statement could be supported by a recent functional imaging study that pointed toward a redundancy in the internal representation of dynamical constraints for both actual and imagined wrist flexion/extension movements (18). The authors attempted to identify distinct roles within the insula with respect to mechanisms of internal models. The results showed that the posterior part of the insular cortex was engaged when feedback was processed while the anterior insula was activated only in mental simulation of the action. Based on their results, the authors also suggested that the two parts of the insula are unidirectionally connected to allow the update of gravity representation in the anterior insula via its posterior part when sensory feedback is available. The results of the current study could suggest that, when imagining movements while being physically immersed in microgravity, the integration of sensory feedbacks within the posterior insula is conveyed to the anterior insula to update internal representation of gravity that is used during mental simulation.

The proposed interpretation is however to be nuanced when considering the inflight results. Indeed, we expected that I_{0g} movement durations would deviate from I_{1g} as the flight progresses. The emergence of this gap across the parabolas would also have witnessed such update. Although the difference between I_{1g} and I_{0g} seems to increase during the first half of the flight, we reported only a marginally significant difference at the middle of the flight (P = 0.051; 5th parabola). As addressed in further details in the following section, we believe that such absence of significant differences is likely to reflect study own limitations rather than a "true" absence of effects. Also, and surprisingly, I_{0g} movement durations seem to converge toward I_{1g} ones at the second half of the flight. We indeed expected that the difference between I_{1g} and I_{0g} that seem to emerge at the first half of the flight would be maintained during the second half. A tentative explanation could be that, since the imagined movement was never executed when exposed to 0 g, there was no practical needs to adapt it. In the absence of such needs, imagined movement durations in 0 g could have progressively converged to normogravitational values.

As stated earlier, our study has some limitations. During this experiment, we also examined the temporal characteristics of imagined movements during the flight. Surprisingly, the present results showed no statistical differences in the duration of imagined movements when exposed to microgravity (I_{0g}) and to normogravity (I_{1g}). This finding could be explained by methodological limitations, the main one being the weak statistical power inherent to this kind of experimental context. It is worth mentioning that this lack of statistical power could explain the absence of significant equivalence tests regarding vividness, despite extremely close averages for certain tests (27). In addition, participants were tested in succession, each for 10 parabolas. Thus, the cumulative exposure to gravitational variations before the experiment differed between subjects, which could have influenced motor imagery. Although it has been showed that only six parabolas are required to adjust grip force to load force in a rhythmic object manipulation task (9), in our case, however, no action immediately related to the imagined task was performed. Finally, the voluntary mental effort required for motor imagery tasks might have been impacted by vestibular and proprioceptive systems disruption caused by parabolic flight maneuvers (for review, see Ref. 35). It is conceivable that the lack of statistical power and the large variability have masked significant inflight effects, though suggested by some large effect sizes for certain parabolas. Furthermore, there was a lot of variability in the post-test data set in both flyer groups. One could argue that variability increase in post-test was caused by the fact that the imagined movements preceded the execution of actual movements. However, the Control group data remained stable whereas this group received the same order of measurements than Exposed and Imagine groups. Variability increase could instead be understood as resulting from several factors as stress (36, 37), scopolamine injection (38), fatigue induced by parabolic maneuvers (39), and the task-related difficulty of imagining a movement while projecting into different gravitational environments. As participants had to trigger the stopwatch themselves, there could be a potential influence of microgravity on reaction times (40). However, while being a potential confounding factor, the difference observed by Clement (20 ms difference between reaction times in 1 g and 0 g) cannot account for the results reported here. Finally, our results contrast with those of Chabeauti et al. (41), who reported no effects of parabolic maneuvers on the duration of imagined movement. The authors used a sit-to-stand-to-sit task which involved a set of complex and sequential polyarticular movements. Simple pendular arm movements and whole body movement may not be directly comparable. Finally, the absence of actual movements during exposure to microgravity is an important limitation in the current study, because it would have allowed to verify congruency between actual movement inflight and imagined movement post flight.

In conclusion, our results suggest that motor imagery helped update internal models of gravity during short-term exposure to microgravity. Despite the very strong environmental signals, living microgravity in a context unlinked from the task at hand is not sufficient to fine tune the parameters of the internal model engaged in the task.

ETHICS STATEMENT

The protocol was approved by the CPP (2018-A03379-46). This study was carried out in accordance with the recommendations of the ANSM (given on 15th February 2019) with written informed consent from all participants. They gave written informed consent in accordance with the Declaration of Helsinki.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

D.R.M., M.B., F.L., and O.W. conceived and designed research; D.R.M. performed experiments; D.R.M. analyzed data; D.R.M. and O.W. interpreted results of experiments; D.R.M. and M.B. prepared figures; D.R.M., M.B., and O.W. drafted manuscript; D.R.M., M.B., F.L., J.B., G.B., D.N., and O.W. edited and revised manuscript; D.R.M., M.B., F.L., J.B., G.B., D.N., and O.W. approved final version of manuscript.

REFERENCES

1. **Flanagan JR**, **Wing AM.** The role of internal models in motion planning and control: evidence from grip force adjustments during movements of hand-held loads. *J Neurosci* 17: 1519–1528, 1997. doi:10.1523/JNEUROSCI.17-04-01519.1997.
2. **Friston K.** What is optimal about motor control? *Neuron* 72: 488–498, 2011. doi:10.1016/j.neuron.2011.10.018.
3. **Haith AM**, **Krakauer JW.** Model-based and model-free mechanisms of human motor learning. *Adv Exp Med Biol* 782: 1–21, 2013. doi:10.1007/978-1-4614-5465-6_1.
4. **Izawa J**, **Shadmehr R.** Learning from sensory and reward prediction errors during motor adaptation. *PLoS Comput Biol* 7: e1002012, 2011. doi:10.1371/journal.pcbi.1002012.
5. **Kawato M**, **Kuroda T**, **Imamizu H**, **Nakano E**, **Miyauchi S**, **Yoshioka T.** Internal forward models in the cerebellum: FMRI study on grip force and load force coupling. *Prog Brain Res* 142: 171–188, 2003. doi:10.1016/S0079-6123(03)42013-X.
6. **Wolpert D**, **Ghahramani Z**, **Jordan M.** An internal model for sensorimotor integration. *Science* 269: 1880–1882, 1995. doi:10.1126/science.7569931.
7. **Ishikawa T**, **Tomatsu D**, **Izawa J**, **Kakei S.** The cerebro-cerebellum: could it be loci of forward models? *Neurosci Res* 104: 72–79, 2016. doi:10.1016/j.neures.2015.12.003.
8. **White O**, **Gaveau J**, **Bringoux L**, **Crevecoeur F.** The gravitational imprint on sensorimotor planning and control. *J Neurophysiol* 124: 4–19, 2020. doi:10.1152/jn.00381.2019.
9. **Augurelle A**, **Penta M**, **White O**, **Thonnard J-L.** The effects of a change in gravity on the dynamics of prehension. *Exp Brain Res* 148: 533–540, 2003. doi:10.1007/s00221-002-1322-3.
10. **Hermsdörfer J**, **Marquardt C**, **Philipp J**, **Zierdt A**, **Nowak D**, **Glasauer S**, **Mai N.** Grip forces exerted against stationary held objects during gravity changes. *Exp Brain Res* 126: 205–214, 1999. doi:10.1007/s002210050730.
11. **Barbiero M**, **Rousseau C**, **Papaxanthis C**, **White O.** Coherent multimodal sensory information allows switching between gravitoinertial contexts. *Front Physiol* 8: 290, 2017. doi:10.3389/fphys.2017.00290.
12. **Papaxanthis C**, **Pozzo T**, **Popov KE**, **McIntyre J.** Hand trajectories of vertical arm movements in one-G and zero-G environments. *Exp Brain Res* 120: 496–502, 1998. doi:10.1007/s002210050423.
13. **White O**, **Bleyenheuft Y**, **Ronsse R**, **Smith AM**, **Thonnard J-L**, **Lefèvre P.** Altered gravity highlights central pattern generator mechanisms. *J Neurophysiol* 100: 2819–2824, 2008. doi:10.1152/jn.90436.2008.
14. **Jeannerod M.** Mental imagery in the motor context. *Neuropsychologia* 33: 1419–1432, 1995. doi:10.1016/0028-3932(95)00073-c.
15. **Kilteni K**, **Anderson BJ**, **Houborg C**, **Ehrsson HH.** Motor imagery involves predicting the sensory consequences of the imagined movement. *Nat Commun* 9: 1617, 2018. doi:10.1038/s41467-018-03989-0.
16. **Papaxanthis C**, **Pozzo T**, **Skoura X**, **Schieppati M.** Does order and timing in performance of imagined and actual movements affect the motor imagery process? The duration of walking and writing task. *Behav Brain Res* 134: 209–215, 2002. doi:10.1016/S0166-4328(02)00030-X.
17. **Parsons LM.** Temporal and kinematic properties of motor behavior reflected in mentally simulated action. *J Exp Psychol Hum Percept Perform* 20: 709–730, 1994. doi:10.1037//0096-1523.20.4.709.
18. **Rousseau C**, **Barbiero M**, **Pozzo T**, **Papaxanthis C**, **White O.** Actual and imagined movements reveal a dual role of the insular cortex for motor control. *Cereb Cortex* 31: 2586–2594, 2021. doi:10.1093/cercor/bhaa376.
19. **Papaxanthis C**, **Pozzo T**, **Kasprinski R**, **Berthoz A.** Comparison of actual and imagined execution of whole-body movements after a long exposure to microgravity. *Neurosci Lett* 339: 41–44, 2003. doi:10.1016/s0304-3940(02)01472-6.
20. **Mechtcheriakov S**, **Berger M**, **Molokanova E**, **Holzmueller G**, **Wirtenberger W**, **Lechner-Steinleitner S**, **De Col C**, **Kozlovskaya I**, **Gerstenbrand F.** Slowing of human arm movements during weightlessness: the role of vision. *Eur J Appl Physiol* 87: 576–583, 2002. doi:10.1007/s00421-002-0684-3.
21. **Weber T**, **Green DA**, **Attias J**, **Sies W**, **Frechette A**, **Braunstein B**, **Rittweger J.** Hopping in hypogravity—A rationale for a plyometric exercise countermeasure in planetary exploration missions. *PLoS One* 14: e0211263, 2019. doi:10.1371/journal.pone.0211263.
22. **Ritzmann R**, **Freyler K**, **Krause A**, **Gollhofer A.** No neuromuscular side-effects of scopolamine in sensorimotor control and force-generating capacity among parabolic fliers. *Microgravity Sci Technol* 28: 477–490, 2016. doi:10.1007/s12217-016-9504-y.
23. **Malouin F**, **Richards CL**, **Jackson PL**, **Lafleur MF**, **Durand A**, **Doyon J.** The Kinesthetic and Visual Imagery Questionnaire (KVIQ) for assessing motor imagery in persons with physical disabilities: a reliability and construct validity study. *J Neurol Phys Ther* 31: 20–29, 2007. doi:10.1097/01.npt.0000260567.24122.64.

24. **Leys C**, **Delacre M**, **Mora YL**, **Lakens D**, **Ley C.** How to classify, detect, and manage univariate and multivariate outliers, with emphasis on pre-registration. *Int Rev Soc Psychol* 32: 5, 2019. doi:10.5334/irsp.289.
25. **Marchesotti S**, **Bassolino M**, **Serino A**, **Bleuler H**, **Blanke O.** Quantifying the role of motor imagery in brain-machine interfaces. *Sci Rep* 6: 24076, 2016. doi:10.1038/srep24076.
26. **Lakens D**, **Scheel A**, **Isager P.** Equivalence testing for psychological research: a tutorial. *Adv Methods Pract Psychol Sci* 1: 259–269, 2018. doi:10.1177/2515245918770963.
27. **Lakens D.** Equivalence tests: a practical primer for t-tests, correlations, and meta-analyses. *Soc Psychol Personal Sci* 8: 355–362, 2017. doi:10.1177/1948550617697177.
28. **Pierella C**, **Casadio M**, **Mussa-Ivaldi FA**, **Solla SA.** The dynamics of motor learning through the formation of internal models. *PLoS Comput Biol* 15: e1007118, 2019. doi:10.1371/journal.pcbi.1007118.
29. **Davidson PR**, **Wolpert DM.** Internal models underlying grasp can be additively combined. *Exp Brain Res* 155: 334–340, 2004. doi:10.1007/s00221-003-1730-z.
30. **White O**, **Thonnard J-L**, **Lefèvre P**, **Hermsdörfer J.** Grip force adjustments reflect prediction of dynamic consequences in varying gravitoinertial fields. *Front Physiol* 9: 131, 2018. doi:10.3389/fphys.2018.00131.
31. **Hétu S**, **Grégoire M**, **Saimpont A**, **Coll M-P**, **Eugène F**, **Michon P-E**, **Jackson PL.** The neural network of motor imagery: an ALE meta-analysis. *Neurosci Biobehav Rev* 37: 930–949, 2013. doi:10.1016/j.neubiorev.2013.03.017.
32. **Michel C**, **Gaveau J**, **Pozzo T**, **Papaxanthis C.** Prism adaptation by mental practice. *Cortex* 49: 2249–2259, 2013. doi:10.1016/j.cortex.2012.11.008.
33. **Gentili R**, **Papaxanthis C**, **Pozzo T.** Improvement and generalization of arm motor performance through motor imagery practice. *Neuroscience* 137: 761–772, 2006. doi:10.1016/j.neuroscience.2005.10.013.
34. **Gentili R**, **Han CE**, **Schweighofer N**, **Papaxanthis C.** Motor learning without doing: trial-by-trial improvement in motor performance during mental training. *J Neurophysiol* 104: 774–783, 2010. doi:10.1152/jn.00257.2010.
35. **Lacquaniti F**, **Bosco G**, **Indovina I**, **La Scaleia B**, **Maffei V**, **Moscatelli A**, **Zago M.** Visual gravitational motion and the vestibular system in humans. *Front Integr Neurosci* 7: 101, 2013. doi:10.3389/fnint.2013.00101.
36. **Schneider S**, **Brümmer V**, **Göbel S**, **Carnahan H**, **Dubrowski A**, **Strüder HK.** Parabolic flight experience is related to increased release of stress hormones. *Eur J Appl Physiol* 100: 301–308, 2007. doi:10.1007/s00421-007-0433-8.
37. **Steinberg F**, **Kalicinski M**, **Dalecki M**, **Bock O.** Human performance in a realistic instrument-control task during short-term microgravity. *PLoS One* 10: e0128992, 2015. doi:10.1371/journal.pone.0128992.
38. **Bestaven E**, **Kambrun C**, **Guehl D**, **Cazalets J-R**, **Guillaud E.** The influence of scopolamine on motor control and attentional processes. *PeerJ* 4: e2008, 2016. doi:10.7717/peerj.2008.
39. **Collado A**, **Langlet C**, **Tzanova T**, **Hainaut JP**, **Monfort V**, **Bolmont B.** Affective states and adaptation to parabolic flight. *Acta Astronaut* 134: 98–105, 2017. doi:10.1016/j.actaastro.2017.01.043.
40. **Clément G.** Perception of time in microgravity and hypergravity during parabolic flight. *Neuroreport* 29: 247–251, 2018. doi:10.1097/WNR.0000000000000923.
41. **Chabeauti PY**, **Assaiante C**, **Vaugoyeau M.** Extreme short-term environmental constraints do not update internal models of action as assessed from motor imagery in adults. *Neuroscience* 222: 69–74, 2012. doi:10.1016/j.neuroscience.2012.07.002.