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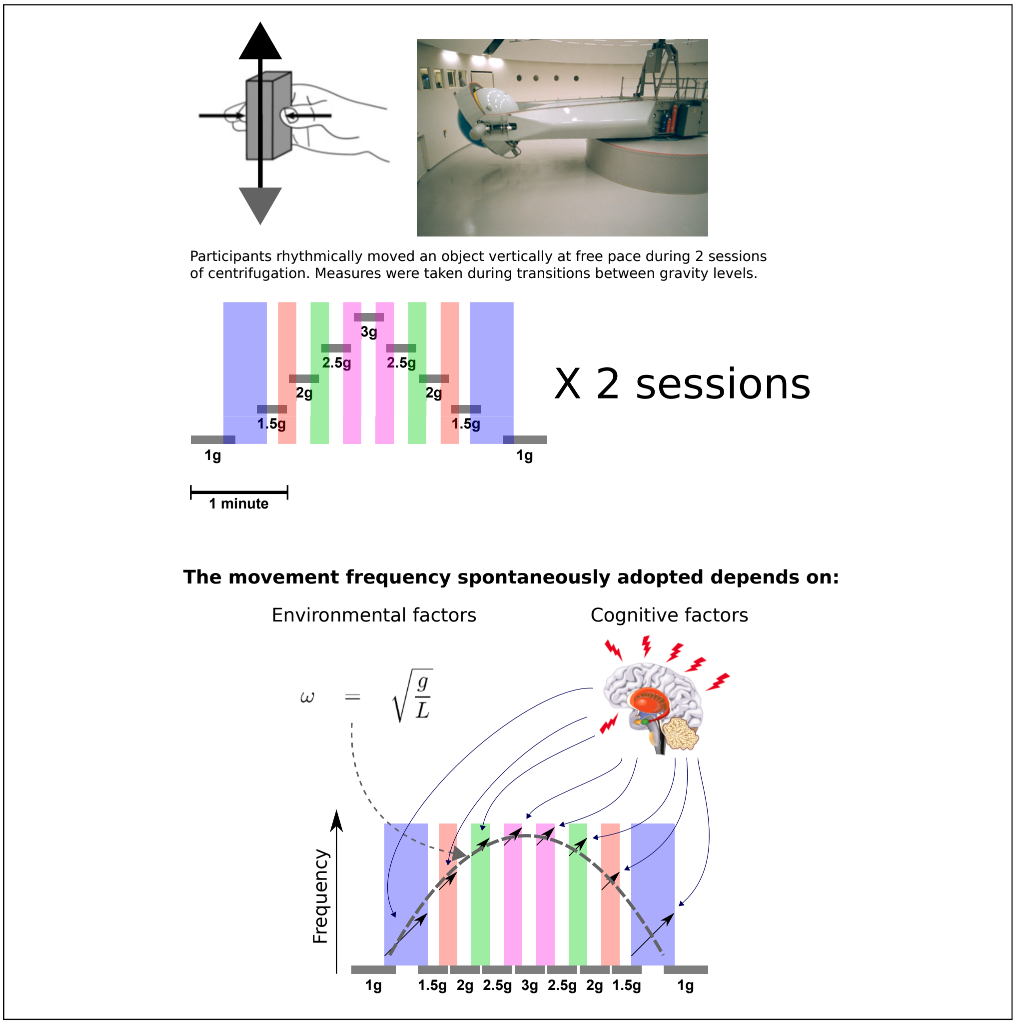

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Highlights

Natural rhythm is influenced by environment and cognitive factors

Environment modulates pace over long timescales following principles of physics

Cognition accelerates tempo during gravitational transitions at short timescales

The free-energy principle can explain this interaction

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Article

Resonance tuning of rhythmic movements is disrupted at short time scales: A centrifuge study

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SUMMARY

The human body exploits its neural mechanisms to optimize actions. Rhythmic movements are optimal when their frequency is close to the natural frequency of the system. In a pendulum, gravity modulates this spontaneous frequency. Participants unconsciously adjust their natural pace when cyclically moving the arm in altered gravity. However, the timescale of this adaptation is unexplored. Participants performed cyclic movements before, during, and after fast transitions between hypergravity levels (1g–3g and 3g–1g) induced by a human centrifuge. Movement periods were modulated with the average value of gravity during transitions. However, while participants increased movement pace on a cycle basis when gravity increased (1g–3g), they did not decrease pace when gravity decreased (3g–1g). We highlight asymmetric effects in the spontaneous adjustment of movement dynamics on short timescales, suggesting the involvement of cognitive factors, beyond standard dynamical models.

INTRODUCTION

Have you ever tried to drive a swing faster or slower than your spontaneous pace? Probably not, unless there is a good reason to do so. Why? Because it would require much more effort either way than leaving the system behave with minimal intervention. Frequency tuning allows humans to optimally control rhythmic movements from energetic, controllable, and predictable points of view[1] by involving a minimal number of active degrees of freedom and minimizing noise.[2] A system that oscillates at its natural frequency optimizes the exchange of energy between itself and its environment. Energy losses in this process are therefore minimal.[3]

Gravity acts as a key player in this phenomenon. A simple compound pendulum, that is a toy although realistic model for many rhythmic activities, has a natural frequency that is governed by basic physical properties such as inertia, length, mass … and the gravitational acceleration, denoted by g (9.81 ms^{-2}). Previous work has shown that living beings adopt a pace that is largely defined by these properties. For instance, tall people swing their leg with a longer period than small people, heavy animals walk more slowly than light animals, and the Apollo mission astronauts walked on the Moon with longer periods of step intervals.

In a parabolic flight experiment where gravitational acceleration varied in the range 0g–1.8g, participants even modulated the rhythm of free arm movements in close to real time gravitational changes.[4] That is, periods of movements increased in hypogravity [0g; 1g], and decreased in hypergravity [1g; 1.8g], consistently with model predictions. Remarkably, this was even observed when participants were instructed to follow a constant pace prompted by a metronome. That result shows that the effects of gravity transcend more cognitive processes such as complying with instructions. Today, space exploration missions move from low orbit to distant destinations, including the Moon and Mars. These will inevitably face new challenges that will include not only neurobehavioural[5] but also more psychological aspects.[6]

With a few notable exceptions, these effects were only addressed macroscopically, in different but constant environments. Here, we focus on fast transitions between levels of hypergravity separated by ± 0.5g to investigate the mechanism of this adaptation of the brain to the

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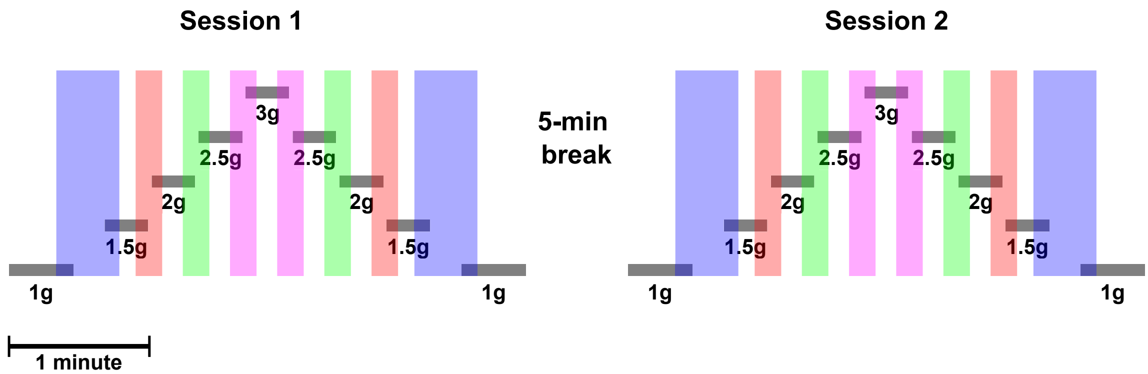

Figure 1. Time scaled and chronological illustration of the Gz profiles programmed in the centrifuge

Horizontal rectangles represent the stable Gz phases. Colored rectangles highlight the transitions between stable gravity levels. Note the longer transition times from and to 1g (13.4 s) compared to the other transitions (1.6 s).

environment. Participants rhythmically moved the forearm during transitions to a larger (1g → 1.5g, 1.5g → 2g, 2g → 2.5g, and 2.5g → 3g) or a lower hypergravity level (3g → 2.5g, 2.5g → 2g, 2g → 1.5g, and 1.5g → 1g) in two sessions of centrifugation. We continuously recorded accelerometry of the hand and analyzed cycle frequency—cycle by cycle and not by computing average trends—across gravitational conditions at two different timescales: between transitions and sessions and within transitions.

RESULTS

The present study investigates the phenomenon of resonance tuning of rhythmic arm movements at different timescales during two sessions of human centrifugation. Participants were exposed first to increasing and then to decreasing levels of hypergravity between 1g and 3g. In the following, we first analyze the spontaneously adopted frequency during whole transitions between constant gravito-inertial environments and between sessions (macroscopic, long timescale effects). In the second section, we consider the dynamics of resonance tuning within transitions (microscopic, short timescale). We report results in terms of periods (inverse to frequency).

Macroscopic effects of gravity on resonance tuning

Figure 2 shows the period as a function of gravity averaged during transitions (x axis) and separated by session (circles for session 1 and squares for session 2). The ANOVA revealed a main effect of SESSION ($F_{1,1424} = 9.6$, $p = 0.002$, $\eta^2 = 0.03$) on period. A post hoc test reports that movements were faster (i.e., shorter periods) in the second session. Furthermore, we also found a main effect of GRAVITY ($F_{3,1424} = 10.4$, $p < 0.001$, $\eta^2 = 0.02$). There was, however, neither an effect of RAMP ($F_{3,1424} = 3.2$, $p = 0.072$) nor an interaction between any of the factors (all $F < 0.5$, all $p > 0.724$).

Altogether, we replicate a previous solid finding in that frequency tuning holds on a long timescale. In addition, we also show that thee movement pace increased between sessions 1 and 2. Finally, there was no asymmetry between ramps (+0.5g vs. −0.5g).

Microscopic effects of gravity on resonance tuning

The previous section showed that participants modulate the spontaneous period of their arm movements according to the average value of gravito-inertial transitions. We now zoom into positive and negative ramps and analyze how the period varies on a cycle basis.

Figure 3 (upper panel) depicts mean values of the gravito-inertial field over time. Each dot corresponds to gravito-inertial values averaged over a single movement cycle. Sessions 1 and 2 are collapsed as they were equivalent ($F_{1,80} = 0.26$, $p = 0.61$). The ascending and descending phases are clearly visible and were not different statistically either ($F_{1,80} = 0.22$, $p = 0.881$). Mean gravito-inertial values were, obviously, highly different ($F_{3,80} = 2438$, $p < 0.001$, $\eta^2 = 0.99$). Gravity levels were highly different across TRIAL ($F_{29,227} = 21.3$, $p < 0.001$, $\eta^2 = 0.63$) and there was a very strong interaction between TRIAL and SESSION ($F_{29,227} = 5.6$, $p < 0.001$, $\eta^2 = 0.17$).

A closer look, however, reveals a very different story when we consider a shorter timescale. Figure 3 (lower panel) displays cycle periods over time, following the same logic as in the upper panel. A quick look at that panel again highlights the macroscopic frequency tuning effect. We can indeed notice small vertical shifts of dots corresponding to the same average gravito-inertial condition. The smaller the gravito-inertial field, the longer the periods. On the one hand, we observe a decrease in the periods over trials in the ascending phase, which is compatible with the hypothesis of a frequency tuning. Very surprisingly, however, we observe the opposite effect in the descending phase: the gravito-inertial field decreases over time but we still observe a very consistent decrease in periods, on a cycle basis. While we expected a mirror symmetric effect of the variation of period over time between UP and DOWN ramps, we observed replications of these time series ($F_{3,40} = 0.28$, $p = 0.84$), which is also reflected by a lack of interaction between TRIALS and RAMP ($F_{29,227} = 0.17$, $p = 0.99$). Furthermore, the amplitude of variation of periods spans a very large 300-ms interval compared to the effects observed for the macroscopic effect (ca 140-ms interval).

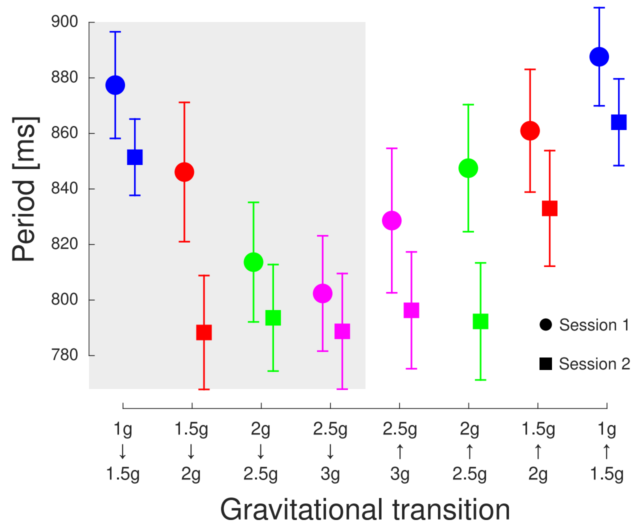

Figure 2. Mean periods as a function of transitions

Each color corresponds to a different transition. Colors correspond to the code depicted in Figure 1. The first four pairs of points (light gray area) correspond to increasing gravito-inertial transitions (UP) and the last four pairs of points correspond to decreasing transition (DOWN). Filled circles and squares correspond to the first and second sessions, respectively. Error bars correspond to standard deviations.

Figure 4 magnifies this asymmetry. Each panel corresponds to a transition between two gravito-inertial levels and follows the same logic. For instance, in Figure 4 (left panel), periods decrease during RAMP UP transitions, between 1g and 1.5g (dark blue upper triangles). It also shows that periods decrease as well (movement accelerates) from 1.5g to 1g (light blue lower triangles).

Beside the effect of gravity on the natural period of a compound pendulum, stiffness also influences this property. The larger the stiffness, the smaller the period (or the faster the frequency). Participants held the test object using an isometric grasping configuration. In that case, stiffness is proportional to grip force. Might stiffness explain why periods increased on a trial basis whatever the ramp condition? If so, grip force should then have increased also during RAMP DOWN trials. To test this, we correlated the mean grip force measured during one cycle with the mean of the gravito-inertial field experienced during the same period. We found significant and positive correlations between grip force and the gravito-inertial environment during RAMP UP but also during RAMP DOWN trials (Table 1). Put differently, participants exerted grip forces proportional to the level of the instantaneous gravito-inertial environments, irrespective of whether the phase was increasing or decreasing. This result therefore rules out the fact that participants would have regulated stiffness through grip force asymmetrically in both ramps.

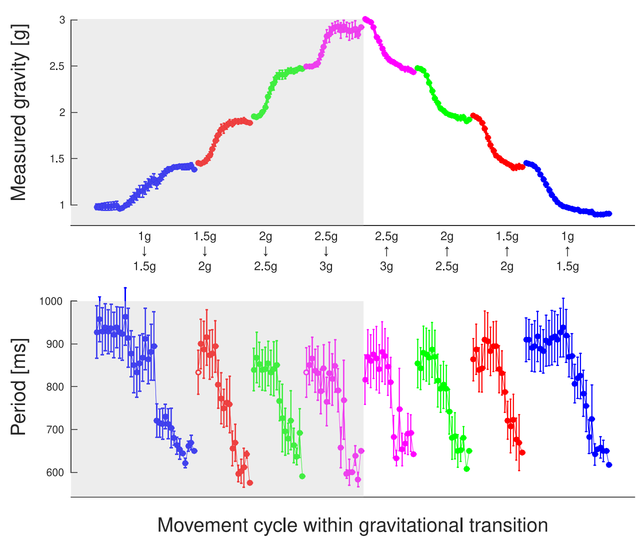

Figure 3. Gravito-inertial fields (upper panel) and period (lower panel) in function of movement cycle

Data are averaged across participants and sessions. Each color corresponds to a different transition. Error bars correspond to standard deviations.

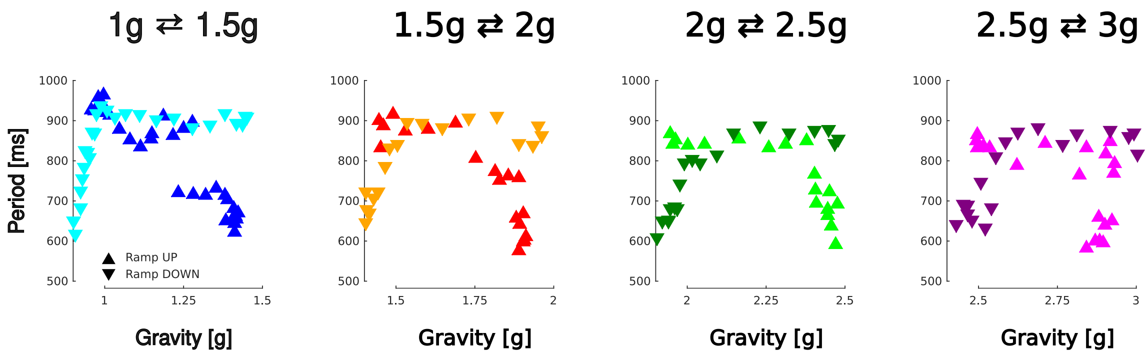

Figure 4. Mean cycle period in function of gravito-inertial field during transitions

Each panel depicts a transition. Upper triangles correspond to RAMP UP and lower triangles correspond to RAMP DOWN transitions.

DISCUSSION

Frequency or resonance tuning is the tendency of mechanical systems to oscillate at their preferred frequency. This property of passive systems is observable with zero or close to zero lag. The musculoskeletal system makes no exception: the central nervous system exploits resonance tuning to optimize voluntary actions. While these effects appear after 10–20 s, it is unknown how volitional control interacts with frequency tuning immediately after a change in the environment. In this study, we explored two timescales for frequency tuning during transitions between different gravito-inertial contexts. On long timescales, the period changes agree with basic tuning principles: the movement, which is akin to a simple pendulum motion, speeds up in larger gravito-inertial force fields and slows down in lower gravito-inertial environments. Surprisingly, this is not the case for short timescales. While the period decreases during RAMP UP, it also decreases during RAMP DOWN, in contrast to what we expected.

Adaptation can occur either explicitly or implicitly. Through the first mechanism, one can use cognitive strategies to analyze the context and adjust the action plan accordingly. In other words, behavior is conscious and driven by explicit rules. In contrast, implicit learning is defined as a non-intentional and automatic process.[7] In that case, people are not aware of its hidden action on their musculoskeletal system. It can even be so strong that people cannot act against it. In presence of explicit errors, participants tend to cancel them out through error-based learning, even if they are explicitly told not to adapt. A similar phenomenon has been observed in rhythmic movements in altered gravity during parabolic flights. Participants were unable to follow the constant pace of a metronome even though they were instructed to do so.[4,8] Frequency tuning is a form of implicit learning, as also demonstrated in this report. However, it holds at long timescales but seems to fail at shorter time scales.

The control policy picks a strategy that minimizes a cost function through optimal control.[9,10] In this process, many simultaneous constraints influence a composite cost function that includes not only physical parameters, such as gravity, but also more subjective variables like muscle fatigue.[11] Indeed, as gravity changes so do the basic musculoskeletal constraints: torques, load forces, weight, etc. During the transitions, the central nervous system, whose most basic function is prediction, also tries to make sense of the change in environment and therefore constrains motion.

It seems that two types of constraints are interfering here. Indeed, purely musculoskeletal changes should appear immediately as the acceleration changes and decrease (increase) the period in RAMP UP (DOWN). This is not the case as is clearly seen in Figure 3 (bottom panel) and Figure 4; it seems that mainly cognitive processes govern the first phase of the transition, most likely because the internal model issued a prediction of arm movement based on the current gravito-inertial condition. Because of the speed of the transition, which is quite swift,

Table 1. Correlation between mean grip force and level of gravito-inertial environment during each transition (rows) and separately for each RAMP (columns)

		RAMP UP	RAMP DOWN
1g ⇄ 1.5g	Slope	2.7	3.1
	R	0.15	0.39
1.5g ⇄ 2g	Slope	2.6	4.2
	R	0.04	0.35
2g ⇄ 2.5g	Slope	4.5	4.9
	R	0.36	0.41
2.5g ⇄ 3g	Slope	7.9	7.0
	R	0.42	0.36

Values report the coefficient of correlation (R) and the slope of the linear regression (slope).

around 1.6 s or 0.31 g/s, the central nervous system might not be able to process such a drastic change of environment that quickly locks itself in this predicted steady, albeit now non-optimal, state. During the second phase of the transition when a new stable; higher, gravito-inertial environment is reached, the internal model slowly incorporates feedback regarding the new acceleration, sensory prediction error, and lets the musculoskeletal constraints adjust, therefore decreasing the period in RAMP UP.

Strangely, this is also the case for RAMP DOWN. While there is still a plateau during the first phase, suggesting once again that the cognitive processes trump musculoskeletal ones, the period also decreases in the second phase. This could be because the participant and its internal model, coming out of a complex and stressful new environment, does not actually have time to reach an optimal state i.e., it does not have the time to come close to its resonant frequency again or because the participant remains very conscious of the cognitive aspect of the motion. It is no longer automatic but very much conscious. Indeed, participants held the test object; it was not merely strapped to the hand. Holding and moving an object in changing gravito-inertial contexts also involve cognitive processes that might have interfered or been in competition with the general production of forearm movement in that same context. Physical interactions with complex objects pose control challenges not present in unconstrained movements. This slightly different control can also be explained by the fact participants adopted a constant motor command (in terms of muscle torque) during RAMP DOWN transitions. Consequently, the pace of the musculoskeletal system naturally accelerated at the end of the transition. Actually, it was shown that participants do not always try to minimize interaction force, which may seem to run counter to many studies on unconstrained movements that have shown that humans favor energy- or effort-efficient strategies.[12,13] Increasing the impedance through coactivation of antagonist muscles, which results in higher muscular effort, also increases predictability of the object dynamics. Indeed, these strategies, which involve higher exerted force and lower object smoothness, are also associated with higher predictability of interaction dynamics.[14] Predictability can, therefore, afford a way to minimize the overall muscular effort. Interestingly, stiffness is a parameter that also describes the natural period of a compound pendulum. Larger stiffness leads to higher frequencies. Nevertheless, stiffness, as assessed by grip force proxy, does not account for the observed decrease in periods across all trial conditions. This finding dismisses the possibility that periods are asymmetrical because stiffness control is symmetrical in both ramps.

Still, the question remains. What other factors could explain the persistence of participants to accelerate across trials during transitions between gravito-inertial environments? Optimal control theory delineates the manner in which humans execute actions from one state to another, employing an *explicit* strategy characterized by the definition and minimization of a cost function dependent on state and control variables. This necessitates the specification of physical parameters, such as mass, inertia, length, or gravity, within the model. However, human movements diverge from robotic precision, introducing the crucial consideration of environmental uncertainties.

The brain Bayesian framework addresses these stochastic processes, proposing a conceptual *implicit* approach wherein the brain functions as a Bayesian inference system.[15] In essence, the brain continually updates its beliefs and predictions through the integration of new sensory information and prior knowledge. This Bayesian probability theory-based framework underlines the brain's capacity to probabilistically infer the causes of sensory input, optimizing perception and decision-making in an unpredictable environment. This Bayesian framework is particularly pertinent to addressing attention[16] and graviception, a distributed process.[17,18] Gravity estimation involves the integration of multimodal information, including vestibular, visual, proprioceptive, visceral, and previous experiences. The Bayesian framework guides this integration by assigning weights proportional to the inverse of the reliability of each modality.

Considering intangible variables such as attention, anxiety, or stress in the context of human behaviors introduces additional complexity. Some studies report an effect of the internal state, such as mental stress, on the spontaneous movement tempo values.[19] These results indicate that the spontaneous tempo is not robust and that intra-individual variability exists.[20] The free-energy principle, initially proposed by Friston, emerges as a more encompassing framework from which optimal control theory and Bayesian approaches naturally derive.[21] This principle posits that the brain minimizes surprise or uncertainty by generating predictions based on internal models and refining them using sensory input. Stress, in this context, can be interpreted as surprise.

Here, we speculate that an explicit strategy and an implicit strategy compete. In certain and stable environments—like in the example of the introduction section—, explicit information carries greater weight, as illustrated by a larger weight (W_e) in Figure 5 (red area). Conversely, in novel or unpredictable situations, implicit information is deemed more reliable to avert action failure, indicated by a larger weight (W_i) in Figure 5 (blue area). The time course of these processes is different, very much like use-dependent learning and error-based learning operate at long and short timescales, respectively.[22] Here, explicit information provides general trends along long timescales, governed by physical laws and the dynamics of the environment (red area). These trends are modulated by high W_i because the context is stressful. The discomfort associated with transitioning from one stressful environment to another emphasizes the role of exploration through reinforcement learning to gather information about newly reached states. One way to collect information about these newly reached states is exploration through reinforcement learning. This allows us to find a policy that maps states of the uncertain world to actions performed by the agent through a process of exploration/exploitation. This exploration translates into more movements. Participants exhibit increased movements during RAMP UP and RAMP DOWN transitions, approaching the new stable yet mentally stressful state in the centrifuge. This framework explains why participants adopt asymmetrical strategies regarding spontaneous tempo. This has also been observed in a very similar experiment in the asymmetry between grip force adjustment between RAMP UP and RAMP DOWN conditions.[23]

Performing movements is not just a matter of activating muscles. As deep space exploration missions are envisaged, the crews will face a different set of challenges, including psychological ones.[6] Our findings advocate for the adoption of more general frameworks that accommodate various information types for decision-making, perception, and action. Moreover, the suggestion to probe short timescale resonance tuning with slow transitions, mitigating central nervous system strain and controlling psychological biases like stress, offers a refined avenue for future investigation.

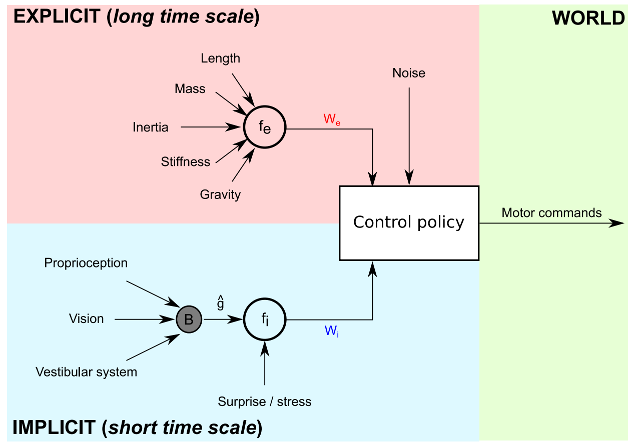

Figure 5. Conceptual sketch illustrating the competition between explicit and implicit information to allow the control policy to calculate the motor command

Explicit information that describe the environment (red area) and implicit information that are used to derive internal states such as a representation of gravity $\hat{g}$ or stress (blue area) are weighted by gains noted We and Wi, respectively. The functions fe and fi integrate these flows following a Bayesian approach. The concept is multi-layered: $\hat{g}$ is itself estimated from multimodal information.

STAR★METHODS

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

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AUTHOR CONTRIBUTIONS

O.W. and J.B. designed the experiment and conducted the experiment. O.W., V.D., and F.B. analyzed the data. O.W. prepared figures. O.W. and V.D. wrote the manuscript. All authors provided feedback on the manuscript and approved its current version. OW is the lead and corresponding author.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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REFERENCES

1. Hatsopoulos, N.G., and Warren, W.H. (1996). Resonance tuning in rhythmic arm movements. J. Mot. Behav. *28*, 3–14. https://doi.org/10.1080/00222895.1996.9941728.
2. Goodman, L., Riley, M.A., Mitra, S., and Turvey, M.T. (2000). Advantages of rhythmic movements at resonance: minimal active degrees of freedom, minimal noise, and maximal predictability. J. Mot. Behav. *32*, 3–8. https://doi.org/10.1080/00222890009601354.
3. Rizal, G., Sharma, P., Thinley, S., Subba, B., Chilaka, V., and Islam, K. (2022). Energy Analysis and the Determination of the Resonant Frequency of a Custom-Designed Scientific Oscillating Body. J. Adv. Res. Appl. Sci. Eng. Technol. *28*, 39–48. https://doi.org/10.37934/araset.28.3.3948.
4. White, O., Bleyenheuft, Y., Ronsse, R., Smith, A.M., Thonnard, J.L., and Lefèvre, P. (2008). Altered gravity highlights central pattern generator mechanisms. J. Neurophysiol. *100*, 2819–2824. https://doi.org/10.1152/jn.90436.2008.
5. Stahn, A.C., Bucher, D., zu Eulenburg, P., Denise, P., Smith, N., Pagnini, F., and White, O. (2023). Paving the way to better understand the effects of prolonged spaceflight on operational performance and its neural bases. Npj Microgravity *9*, 59. https://doi.org/10.1038/s41526-023-00295-y.
6. Pagnini, F., Manzey, D., Rosnet, E., Ferravante, D., White, O., and Smith, N. (2023). Human behavior and performance in deep space exploration: next challenges and research gaps. Npj Microgravity *9*, 27. https://doi.org/10.1038/s41526-023-00270-7.
7. Mazzoni, P., and Krakauer, J.W. (2006). An implicit plan overrides an explicit strategy during visuomotor adaptation. J. Neurosci. *26*, 3642–3645. https://doi.org/10.1523/JNEUROSCI.5317-05.2006.
8. Augurelle, A.S., Penta, M., White, O., and Thonnard, J.L. (2003). The effects of a change in gravity on the dynamics of prehension. Exp. Brain Res. *148*, 533–540. https://doi.org/10.1007/s00221-002-1322-3.
9. Liu, D., and Todorov, E. (2007). Evidence for the flexible sensorimotor strategies predicted by optimal feedback control. J. Neurosci. *27*, 9354–9368. https://doi.org/10.1523/JNEUROSCI.1110-06.2007.
10. Todorov, E., and Jordan, M.I. (2002). Optimal feedback control as a theory of motor coordination. Nat. Neurosci. *5*, 1226–1235. https://doi.org/10.1038/nn963.
11. Berret, B., Chiovetto, E., Nori, F., and Pozzo, T. (2011). Evidence for composite cost functions in arm movement planning: An inverse optimal control approach. PLoS Comput. Biol. *7*, e1002183. https://doi.org/10.1371/journal.pcbi.1002183.
12. Alexander, R.M. (2000). Energy-minimizing choices of muscles and patterns of movement. Mot. Control *4*, 45–116. https://doi.org/10.1123/mcj.4.1.45.
13. Prilutsky, B.I., and Zatsiorsky, V.M. (2002). Optimization-based models of muscle coordination. Exerc. Sport Sci. Rev. *30*, 32–38. https://doi.org/10.1097/00003677-200201000-00007.
14. Nasseroleslami, B., Hasson, C.J., and Sternad, D. (2014). Rhythmic Manipulation of Objects with Complex Dynamics: Predictability over Chaos. PLoS Comput. Biol. *10*, e1003900. https://doi.org/10.1371/journal.pcbi.1003900.
15. Knill, D.C., and Pouget, A. (2004). The Bayesian brain: the role of uncertainty in neural coding and computation. Trends Neurosci. *27*, 712–719. https://doi.org/10.1016/j.tins.2004.10.007.
16. Pagnini, F., Barbiani, D., Cavalera, C., Volpato, E., Grosso, F., Minazzi, G.A., Vailati Riboni, F., Graziano, F., Di Tella, S., Manzoni, G.M., et al. (2023). Placebo and Nocebo Effects as Bayesian-Brain Phenomena: The Overlooked Role of Likelihood and Attention. Perspect. Psychol. Sci. *18*, 1217–1229. https://doi.org/10.1177/17456916221141383.
17. Jörges, B., and López-Moliner, J. (2017). Gravity as a Strong Prior: Implications for Perception and Action. Front. Hum. Neurosci. *11*, 203. https://doi.org/10.3389/fnhum.2017.00203.
18. White, O., Gaveau, J., Bringoux, L., and Crevecoeur, F. (2020). The gravitational imprint on sensorimotor planning and control. J. Neurophysiol. *124*, 4–19. https://doi.org/10.1152/jn.00381.2019.
19. Murata, J., Matsukawa, K., Shimizu, J., Matsumoto, M., Wada, T., and Ninomiya, I. (1999). Effects of mental stress on cardiac and motor rhythms. J. Auton. Nerv. Syst. *75*, 32–37. https://doi.org/10.1016/s0165-1838(98)00171-4.
20. Desbernats, A., Martin, E., and Tallet, J. (2023). Which factors modulate spontaneous motor tempo? A systematic review of the literature. Front. Psychol. *14*, 1161052.
21. Friston, K. (2010). The free-energy principle: a unified brain theory? Nat. Rev. Neurosci. *11*, 127–138. https://doi.org/10.1038/nrn2787.
22. Diedrichsen, J., White, O., Newman, D., and Lally, N. (2010). Use-dependent and error-based learning of motor behaviors. J. Neurosci. *30*, 5159–5166. https://doi.org/10.1523/JNEUROSCI.5406-09.2010.
23. White, O., Thonnard, J.L., Lefèvre, P., and Hermsdörfer, J. (2018). Grip force adjustments reflect prediction of dynamic consequences in varying gravitoinertial fields. Front. Physiol. *9*, 131. https://doi.org/10.3389/fphys.2018.00131.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Raw and analyzed data	This paper	
Software and algorithms		
MATLAB R2015a	MathWorks	https://nl.mathworks.com/
Other		
Human large radius centrifuge	QinetiQ's Flight Physiological Centre, Linköping, Sweden	https://www.qinetiq.com/en/what-we-do/services-and-products/flight-physiological-centre

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Olivier White (olivier.white@u-bourgogne.fr).

Materials availability

This study did not generate new unique reagents or other materials.

Data and code availability

Data and code are available upon simple request to the Lead Author.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Participants

Six right-handed male participants (40.1 years old, SD=7.2 years) took part in this experiment. A medical flight doctor checked their health status before the experiment. The protocol was reviewed and approved by the Facility Engineer from the Swedish Defence Material Administration (FMV) and an independent medical officer. The experiment was overseen by a qualified medical officer. The study was conducted in accordance with the Declaration of Helsinki (1964). All participants gave informed and written consent prior to the study.

METHOD DETAILS

Centrifuge facility and instrumented object

A similar protocol was used in a previous study where the human centrifuge is described in detail.[23] Centrifugation took place at QinetiQ's Flight Physiological Centre in Linköping, Sweden. Gravito-inertial profiles along the body axis (Gz) could be programmed, and real time control of the gondola ensured that gravitoinertial force was always aligned with the body axis. Participants were strapped while seated and cushioning was provided for comfort. Their electrocardiogram was continuously monitored during the entire centrifuge runs for safety. One-way video and two-way audio contacts with the control room were available at all time. To minimize nauseogenic tumbling sensations during acceleration and deceleration, participants were instructed to avoid head movements. Furthermore, Gz-transitions between stable phases were operated below 0.31 g/s until the desired level was reached.

The wireless test object had a mass of 0.13 kg. An accelerometer that measured combined gravitational and kinematic accelerations along the object's long axis was mounted inside the test object (AIS326DQ, range ± 30 m/s^2, accuracy ± 0.2 m/s^2). The acceleration signal was A/D-converted and sampled at a frequency of 120 Hz. Once digitized, it was transmitted to a Palm device through a Bluetooth connection. Data were downloaded after the recordings to a standard PC for analysis.

Procedure: Rhythmic arm movements during centrifugation

A centrifugation session consisted in a ramp up followed by a ramp down Gz-profile for 180 s (Figure 1). There were two equivalent sessions separated by a five-minute break during which the centrifuge was brought back to idle position. The initial 1g phases (idle) lasted for 27.4 s. Then, the system was controlled to generate 1.5g, 2g, 2.5g, 3g, 2.5g, 2g and 1.5g. Each phase lasted 18.4 s and transitions lasted 1.6 s

(0.31g/s). After a final prolonged transition, the system reached its last 1g phase and the recording stopped after another 27.4 s. Note that the transitions between 1 and 1.5g were longer (13.4 s, 0.04g/s), as they were more likely to induce motion sickness.

The operator received feedback on the real-time gravity and was able to interact with the participant if needed. Participants maintained contact with the object that rested on a foam support through a natural grasp configuration. At each GO signal ("START!"), the participant started to perform free-pace rhythmic upper arm movements about the elbow joint. The elbow remained in contact with the support and the upper arm made movements of about 30 degrees with the horizontal. When the operator announced the STOP signal ("STOP!"), the participant gently let the object touch the support again while still securing it with his/her hand. The operator announced the START signal 2 seconds before the Gz-transition and the STOP signal 2 seconds after the Gz-transition. This task was highly demanding. We had to make compromises between data collection and accumulation of fatigue to ensure natural movements were performed. We therefore decided to focus only on transitions and allowed the participant to rest during stable phases. Furthermore, we restricted movements to the upper arm only since preliminary testing aboard the centrifuge demonstrated a significant accumulation of fatigue when participants moved both the upper and lower arms. All participants could easily execute natural rhythmic movements during all transitions, and for the two centrifugation sessions. Table below reports the average number of cycles recorded during transitions and between the two sessions. As it can be observed in below table, the average number of cycles in transitions was significantly higher in the second session (paired t-test, t_7=2.5, p=0.042, η^2=0.42).

Average (SD) number of cycles in each transition (rows) and between sessions (columns)

	Number of cycles (SD)	
Transition (g)	Session 1	Session 2
1.0 → 1.5	13.0 (8.5)	14.8 (8.9)
1.5 → 2.0	6.9 (4.5)	7.6 (4.5)
2.0 → 2.5	7.4 (4.4)	7.5 (4.5)
2.5 → 3.0	7.6 (4.5)	8.1 (4.9)
3.0 → 2.5	7.4 (4.5)	7.5 (4.4)
2.5 → 2.0	6.9 (4.0)	7.7 (4.6)
2.0 → 1.5	7.2 (4.2)	7.3 (4.5)
1.5 → 1.0	11.5 (6.8)	11.6 (6.9)

Note the higher number of cycles in the first (1–1.5g) and last transitions (1.5–1g).

QUANTIFICATION AND DATA ANALYSIS

Data analysis

Object acceleration along the vertical axis was low-pass filtered at 20Hz with a zero-phase lag autoregressive filter. We identified every cycle of movement with the minmax function (Matlab R2015a, The Mathworks, Chicago, IL) and recorded their duration.

Quantile-quantile plots were used to assess normality of the data. Repeated-measure ANOVAs were performed on the above variables to test for the effects of gravity (factor GRAVITY=1g ↔ 1.5g, 1.5g ↔ 2g, 2g ↔ 2.5g, and 2.5g ↔ 3g), session (factor SESSION=1 or 2) and ramp direction (factor RAMP=UP or DOWN). When needed, we also considered the effect of individual cycle trials (factor TRIAL). Participants were only faced once to the 3g-phase. Therefore, it was not included in the ANOVA when factor RAMP was considered. Post hoc Scheffé tests were used for multiple comparisons and paired t-test of individual subject means were used to investigate differences between conditions. Alpha level was set at 0.05. Because the sample size is small (n=6 participants), partial eta-squared are reported for significant results to provide indication on effect sizes. The dataset was visually inspected to ensure these parameters were accurately extracted by custom routines developed in Matlab (The Mathworks, Chicago, IL).