

Adiabatic invariants drive rhythmic human motion in variable gravityN. Boulanger^{1,*}, F. Buisseret^{2,3,†}, V. Dehouck^{1,4,‡}, F. Dierick^{2,5,6,§} and O. White^{4,||}¹*Service de Physique de l'Univers, Champs et Gravitation, Université de Mons, UMONS Research Institute for Complex Systems, Place du Parc 20, 7000 Mons, Belgium*²*CeREF, Chaussée de Binche 159, 7000 Mons, Belgium*³*Service de Physique Nucléaire et Subnucléaire, Université de Mons, UMONS Research Institute for Complex Systems, 20 Place du Parc, 7000 Mons, Belgium*⁴*Université de Bourgogne INSERM-U1093 Cognition, Action, and Sensorimotor Plasticity, Campus Universitaire, BP 27877, 21078 Dijon, France*⁵*Faculté des Sciences de la Motricité, Université Catholique de Louvain, 1 Place Pierre de Coubertin, 1348 Louvain-la-Neuve, Belgium*⁶*Centre National de Rééducation Fonctionnelle et de Réadaptation – Rehazenter, Laboratoire d'Analyse du Mouvement et de la Posture (LAMP), Luxembourg, Grand Duchy of Luxembourg*

(Received 21 June 2019; accepted 10 November 2020; published 1 December 2020)

Voluntary human movements are stereotyped. When modeled in the framework of classical mechanics they are expected to minimize cost functions that may include energy, a natural candidate from a physiological point of view also. In time-changing environments, however, energy is no longer conserved—regardless of frictional energy dissipation—and it is therefore not the preferred candidate for any cost function able to describe the subsequent changes in motor strategies. Adiabatic invariants are known to be relevant observables in such systems, although they still need to be investigated in human motor control. We fill this gap and show that the theory of adiabatic invariants provides an accurate description of how human participants modify a voluntary, rhythmic, one-dimensional motion of the forearm in response to variable gravity (from 1 to 3g). Our findings suggest that adiabatic invariants may reveal generic hidden constraints ruling human motion in time-changing gravity.

DOI: [10.1103/PhysRevE.102.062403](https://doi.org/10.1103/PhysRevE.102.062403)**I. INTRODUCTION**

All living organisms experience a constant terrestrial gravitational acceleration, denoted as $1g$ (9.81 m/s^2). Gravity, “the first thing which you don’t think” (A. Einstein), is the most persistent sensory signal in the brain. However, the sensory experiences it generates lack the clear phenomenology of an identifiable stimulus event that characterizes sound, sight, and even taste. Critically, gravity influences human behavior more pervasively than any other sensory signal. Exposure to Earth-discrepant gravity—as during spaceflight—leads to dramatic structural and functional changes in the human physiology, including alterations in the cardiovascular [1], neural [2], and musculoskeletal systems [3]. Nowadays the cerebellum appears to be a major structure in gravity perception [4,5]. From experiments done on rhesus monkeys, the latter reference reports on results showing the relevance of the cerebellum in the detection of the gravitational field and inertial motions. This includes the neural network analyses sensed by the otolith organs in the inner ear (see Ref. [5] and references therein).

Recent neurocomputational approaches explain behavior by a mixture of feedback and feedforward mechanisms, conceptualized by internal models [6]: The brain plans an action using available sensory information and makes predictions about the consequences of that action in the environment. Any mismatch between this prediction and the information conveyed by feedback will yield a prediction error used to improve other actions. This mechanism drives motor adaptation. On Earth, gravity is immutable and plays a primary role in minimizing prediction errors by providing a strong prior reference.

What is the best way to fundamentally address the role of gravity in motor control? One approach consists in challenging the brain by changing a feature of the environment that is never supposed to change: gravity itself. Our original approach is to assess the impact of time-changing gravity on rhythmic biological motion from a purely mechanical vantage point, thereby providing further insights into the fundamental representation of gravity that shapes motor actions. In mechanics, the more robust way to track the adaptation of a dynamical system to a slow change in the external conditions is through the study of adiabatic invariants and their related action-angle variables describing the system (see, e.g., Ref. [7] and Sec. II).

Obviously, living organisms are extraordinarily more complex than a simple point-particle body. It is not at all clear *a priori* that the actions of a minded human being can be

*nicolas.boulanger@umons.ac.be

†buisseretf@helha.be

‡Victor.DEHOUCk@alumni.umons.ac.be

§frederic.dierick@gmail.com

||olivier.white@u-bourgogne.fr

reduced to a standard, simple Lagrangian. Let us give an everyday example: Lifting a glass of water off a table requires estimating its weight to adjust the grasping force accordingly. Drinking half of its content with a straw while the glass rests on the table does not, however, allow the brain to program a smaller grasping force, more adapted to the lighter glass [8]. Explicit knowledge of the simplest change in object dynamics is not sufficient to update internal models, and one can hardly hope to model such behaviors by a standard Lagrangian or Hamiltonian. Nevertheless our working hypothesis is that some human actions, one of them being presented in Sec. III, comply with the behavior of a simple mechanical system, even if subject to a slowly changing environment, such as a slowly varying gravitational field.

II. ADIABATIC INVARIANTS AND HUMAN MOTION

An adiabatic invariant determines a property of a system that stays approximately constant when external changes occur slowly. Despite their power in revealing constraints on complex dynamical systems, adiabatic invariants have been poorly investigated in biomechanics. For instance, in arm rhythmic motion, the changes in frequency (df) occurring during a one-dimensional periodic motion are correlated with changes in energy (dE) [9] such that the action variable

$$I = \frac{1}{2\pi} \frac{dE}{df} \quad (1)$$

is constant. Action-angle coordinates are usually adopted when the Hamiltonian does not depend explicitly on time. The present work goes beyond previous approaches by immersing participants in a time-dependent gravitational environment where the action variables are not necessarily constant unless the changes in time are adiabatic.

The action-angle variables appeared in the context of classical mechanics in order to study the integrability of dynamical systems with finitely many degrees of freedom. Such systems are said to be *integrable* if the Hamilton-Jacobi equation describing them is completely separable. In the early 1960s, the famous Kolmogorov-Arnold-Moser theorem—see Ref. [10] for a very interesting book telling the history behind this theorem—brought back the action-angle variables on the scene of classical mechanics in order to characterize chaotic Hamiltonian systems. Since then and with the seminal works of Nekhoroshev [11,12] their importance has never faded out. When a Hamiltonian $H(P_\alpha, Q^\alpha)$, $\alpha = 1, \dots, n$, is integrable and leads to bounded trajectories in phase space, action variables may be defined as follows, in terms of a set of phase-space coordinates that separates the Hamiltonian,

$$I_\alpha = \frac{1}{2\pi} \oint_{\Gamma_\alpha} P_\alpha dQ^\alpha, \quad (2)$$

where Γ_α is the projection of the bounded trajectory in the plane (P_α, Q^α) for fixed α . Once the Hamilton-Jacobi equation is separated in the variables (Q^α, P_α) , on the solution of Hamilton's canonical equations each momentum variable P_α will depend only on its canonically conjugate variable Q^α and on the initial conditions. The action variables give all the conserved quantities of the dynamical system under

study, as certified by the Bour-Liouville theorem. They can be geometrically interpreted as the area enclosed by Γ_α .

If the Hamiltonian is time dependent and slowly varying in comparison with the typical period of a cycle, then the action variables are slowly varying too. They are called adiabatic invariants [7,13,14] and may be used in a wide range of applications such as in electromagnetism [15], plasma physics [16], and cosmology [17]. Previous works in biomechanics showed the invariance of the action variable when experimental conditions are time independent [9,18–20]. We apply this concept to human motion in time-varying environments. Our approach can reveal the important and otherwise hidden quantities on which the brain relies to plan actions. Advances in this field can potentially not be reached with other, more classical, methods that rest on energy conservation [21]. We therefore designed an experimental setup in which the external factors are time dependent. It is described in the next section, together with its mechanical model.

III. EXPERIMENT

A. Setup

Six right-handed male participants (40.1 ± 7.2 years old) took part in two centrifugation sessions at QinetiQ's Flight Physiological Centre in Linköping, Sweden. The centrifuge was controlled to deliver specific $g(t)$ profiles. The real-time control of the orientation of the gondola ensured alignment of local gravity with the long body axis (Fig. 1, inset). One session of centrifugation consisted in a ramp-up followed by a ramp-down $g(t)$ profile for 180 s. There were two equivalent sessions separated by a 5-min break bringing the centrifuge back to an idle position. The initial 1g phases (idle) lasted for 27.4 s. Then, the system generated 1.5g, 2g, 2.5g, 3g, 2.5g, 2g, 1.5g, and 1g. Each phase lasted 18.4 s and transitions lasted 1.6 s (average rate of 0.31g/s), except for the first and last ones. We label a given transition by T_n^\pm where it is meant that $g(t)$ goes from the value $(n+1)g/2$ to the value $(n+1+\eta)g/2$, with $\eta = \pm 1$. The increasing (decreasing) gravitational transitions correspond to $\eta = +1$ (-1). In both cases, $n \in \{1, 2, 3, 4\}$. The first decreasing- g series is T_4^- while the last one is T_1^- (Fig. 1). A medical flight doctor assessed the participant's health status before the experiment. The clinical examination consisted in the recording of an electrocardiogram and the measurement of arterial pressure in addition to a health questionnaire that aimed at estimating lifestyle (smoker, sport activities, etc). 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. A similar protocol was used in a previous study where the human centrifuge is described in detail [22].

Participants were asked to perform upper arm rhythmic movements about the elbow at a free, comfortable pace and amplitude only during the transitions between gravitational environments, to limit fatigue. The elbow was first in contact with the support. When prompted by a GO signal, the

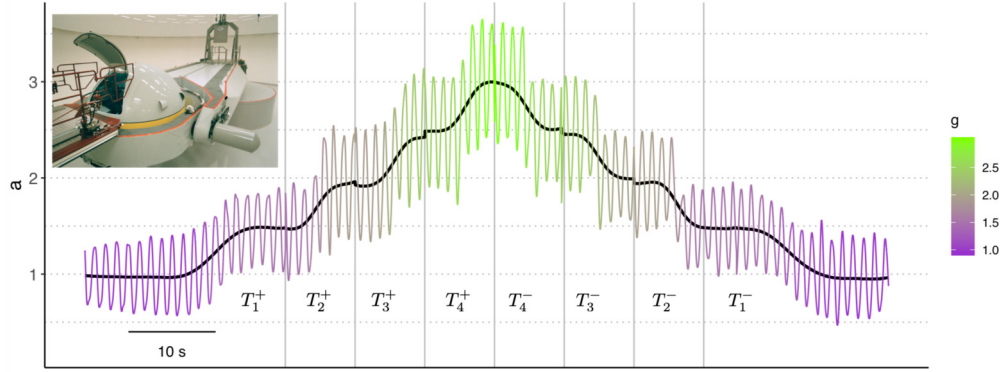


FIG. 1. Typical plot of raw data recorded by the accelerometer (colored line) during a single session of centrifugation (inset). The black line depicts local gravity. All measured accelerations are expressed in units of $g = 9.81 \text{ m/s}^2$. The plateau phases are shown for the first and last transitions. For the other transitions, plateau phases and rest periods are not displayed for the sake of clarity but are replaced by vertical lines.

participant started to perform the movement while holding a test object. This wireless test object (mass of 0.13 kg) embedded an accelerometer that measured combined gravitational and kinematic accelerations along the object's long axis (AIS326DQ, range 30 m/s^2 , accuracy $\pm 0.2 \text{ m/s}^2$). The acceleration signal was sampled at a frequency of 120 Hz. The upper arm produced movements of about 30° with the horizontal. When the operator announced the STOP signal, the participant gently let the object touch the support again while still securing it with his hand. A schematic representation of raw data (acceleration versus time) of one session for one subject is displayed in Fig. 1. We refer the interested reader to Ref. [22] for more detail and pictures about the experimental setup.

B. Harmonic oscillator and participant's motion

Accelerations $a(t)$ were numerically integrated and linearly detrended after subtraction of $g(t)$ to yield the object's speed and position $x(t)$. The link

$$a = -\omega^2 x \quad (3)$$

is observed for all participants within a given transition (96 time series): The averaged Pearson's correlation coefficient between a and x is indeed equal to -0.82 ± 0.1 . A typical plot is shown in Fig. 2; the behavior observed for all the participants is similar. On average, $\omega = 6.3 \text{ Hz}$ leading to a typical period of $T = 0.99 \text{ s}$. Hence, we are on safe ground to assume that the effective dynamics of the test object along the body axis is compatible with that of a harmonic oscillator, i.e., with a Hamiltonian of the form

$$H = \frac{P^2}{2} + \frac{1}{2}\omega(t)^2 Q^2, \quad \text{with } P = \dot{Q} \text{ and } Q = x. \quad (4)$$

The parameter of model (4) is the function $\omega(t)$. Careful inspection of the experimental data let us conclude that $\omega(t)$ vs $g(t)$ is compatible with a weakly increasing linear shape (see Fig. 2, inset). Hence we assume

$$\omega(t) = \varpi \left(1 + \frac{\epsilon}{g} g(t) \right), \quad (5)$$

and we will perform computations up to first order in ϵ throughout the rest of the paper. Equation (5) has the following physiological interpretation: Muscle stiffness increases with gravitational acceleration to account for the larger motor commands required to perform the same movement. This leads to a modified frequency and to $\epsilon > 0$.

Figure 3 depicts a typical phase space of a complete centrifugation session. Elliptic cycles are clearly visible and are the consequence of the harmonic-oscillator dynamics. The area of these ellipses is slowly changing with g as expected from adiabatic invariant's theory [7] that we now use to model the experiment described above.

C. Model

Let us now focus on a given transition T_n^\pm . Equation (5) can be adapted to the peculiar shape of $g(t)$ imposed during

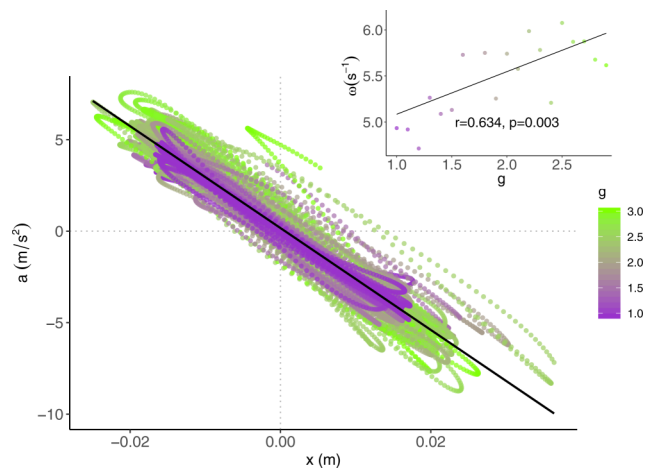


FIG. 2. Typical plot of acceleration vs position for the test object during one centrifugation session, with the same participant as Fig. 1 (colored points). A global linear regression is shown (solid line). The inset quantifies the significant linear relationship between ω and g . Dots result from a fit of the form (3) by bins of 0.1g.

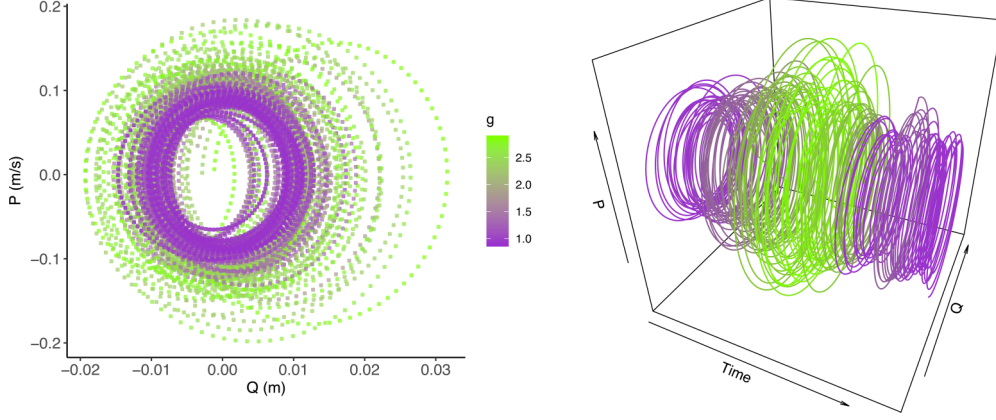


FIG. 3. Left panel: Typical phase-space plot of the test object trajectory during one centrifugation session, with the same participant as Fig. 1. Right panel: Same data but the consecutive cycles are now unfolded along the time dimension.

the centrifugation, compatible with

$$\begin{aligned} \omega_n(t) &= \varpi_n [1 + \epsilon s(t)], \quad \varpi_n = \omega_0 \left[1 + \frac{\epsilon}{2} \left(n - \frac{1}{2} \right) \right], \\ s(t) &= \frac{\eta}{4} \sin(\Omega t), \quad \eta = \pm 1, \quad \text{with } t \in \left[-\frac{\pi}{2\Omega}, \frac{\pi}{2\Omega} \right]. \end{aligned} \quad (6)$$

Action-angle coordinates (I, ϕ) may be defined from (4) through the standard definition [7]

$$Q = \sqrt{\frac{2I}{\omega}} \sin \phi, \quad P = \sqrt{2I\omega} \cos \phi, \quad (7)$$

and their equations of motion read

$$\dot{I} = -\frac{\dot{\omega}}{\omega} I \cos 2\phi, \quad \dot{\phi} = \omega + \frac{\dot{\omega}}{2\omega} \sin 2\phi. \quad (8)$$

We have shown in Ref. [23] that $I(t)$ and $\phi(t)$ can be analytically computed at order ϵ from Eq. (8) when $g(t)$ is of trigonometric form. This gives

$$\begin{aligned} I(t) &= \bar{I} \left[1 - \epsilon \eta \frac{\Omega}{16} \left(\frac{1}{\omega^+} \sin[2(\omega^+ t + \alpha)] + (+ \leftrightarrow -) \right) \right], \\ \phi(t) &= \alpha + \varpi_n t - \epsilon \eta \frac{\omega_0}{4\Omega} \cos(\Omega t) \\ &\quad - \epsilon \eta \frac{\Omega}{32} \left(\frac{1}{\omega^+} \cos[2(\omega^+ t + \alpha)] + (+ \leftrightarrow -) \right), \end{aligned} \quad (9)$$

with $\omega^\pm = \omega_0 \pm \frac{\Omega}{2}$ and $\omega_0 > \Omega$.

The action variable takes a simpler form when $P = 0$, i.e., for t_k such that

$$\phi(t_k) = (2k + 1)\pi/2 =: \phi_k, \quad k \in \mathbb{Z} \quad (10)$$

[see Eq. (7)]. The analytical shape of the times t_k such that $\phi(t_k) = \phi_k$ may be complicated but since our goal is the computation of $I(t_k)$, it is sufficient to work with the lowest-order solution $t_k = \frac{\phi_k - \alpha}{\omega_0}$, leading to

$$I(t_k) = \bar{I} \left(1 - \epsilon \frac{\Omega^2}{4\omega_0^2 - \Omega^2} s(t_k) \right). \quad (11)$$

For a given transition T_n^\pm , $g(t)/g = \frac{n+6}{2} + s(t)$. Hence, $I(t_k) = A_{n,\eta} + B g(t_k)$, where $A_{n,\eta}$ and B are real constants,

and where $B = dI/dg$ does not depend on n and η . It allows us to append the transitions and get an affine relation between $I(t_k)$ and $g(t_k)$ during the whole centrifugation session,

$$I(t_k) =: I_0 + I_1 g(t_k), \quad (12)$$

with $I_0 \in \mathbb{R}^+$ and $I_1 \in \mathbb{R}$. The shift in $I(t)$ predicted by Eqs. (9) and (12) extends previous results obtained in Ref. [24] where an analytical shape is obtained for $I(t)$ with arbitrary $\omega(t)$ provided that the latter is not C^∞ . Equation (12) defines a model that can be compared to experimental data.

IV. RESULTS

We have computed phase-space trajectories of all participants in both centrifugation sessions. It is therefore possible to compute the action variable as a function of time. Indeed, Eq. (2) can be rewritten as $I(t) = \int_t^{t^*} \dot{Q}^2 dt$ from (4), with t^* the end of the phase-space cycle starting at t . The instant $t^* > t$ is such that the distance between the points $(Q(t), P(t))$ and $(Q(t^*), P(t^*))$ in phase space is minimal and the difference $t^* - t$ is numerically as close as possible to T . Once the action variables $I(t)$ are known, the times t_k such that $P(t_k) = 0$ are computed as well as the action variables $I(t_k)$. Continuous values $I(t_k)$ of all participants and all trials are finally discretized into 0.1g bins ranging from 1 to 3g. Each bin contains between 14 and 23 data points. Average values and standard deviations (SD) of I normalized to the 1g value (I_{norm}) are finally displayed in Fig. 4.

The adiabatic invariant exhibits a strong and significant positive ($I_1 > 0$) linear relationship with gravity both in the increasing and decreasing phases (Fig. 4). According to Eq. (1), it shows an expected higher energetic cost in high gravity for a given change in frequency, which is expected since raising the test object by a height Δh has a potential energetic cost of order $mg\Delta h$.

Despite this overall coherent dependence of I over g , we observed asymmetries in the slopes I_1 [Eq. (12)] between ascending and descending phases. To quantify this effect, we ran a two-way repeated measures analysis of variance (ANOVA) with the factors session (1 or 2) and phase (increasing or decreasing). This analysis shows that the slope I_1 is significantly larger in the increasing phase than in the

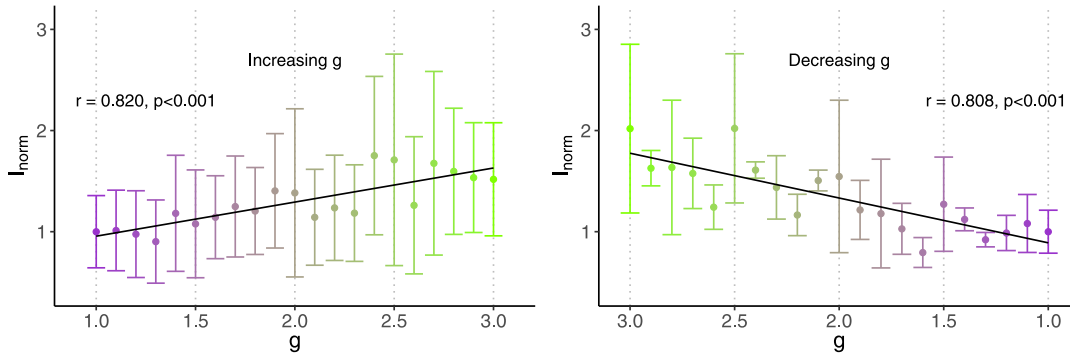


FIG. 4. Mean values (and 1 SD error bars) of the adiabatic invariant I_{norm} per bin, normalized to the $1g$ value, vs $g(t)$. Significant linear regressions of the experimental data are depicted as a solid black line together with their Pearson’s correlation coefficients and p values. The left panel presents data in the ascending $g(t)$ phase and the right panel presents data in the descending $g(t)$ phase. Note that in the descending phase, the horizontal axis is decreasing in order to provide a continuous and chronological reading of the evolution of I_{norm} .

decreasing phase ($I_1 = 0.296 \pm 0.306 > 0.523 \pm 0.219$, $p = 0.037$). This asymmetry was not influenced by session ($p = 0.130$). Behavioral asymmetries with respect to gravity have already been reported in other tasks such as collisions between an object and a target [25] and in grip-load force modulation in rhythmic movements executed in ascending and descending hypergravity phases [22]. The stronger reliance of the adiabatic invariant on g may reflect a more salient cognitive strategy in situations when mechanical constraints become more challenging due to the increase of gravity.

It may be conjectured that the adiabatic invariant is eventually modulated by vestibular and/or proprioceptive gains and readjustments of central pattern generators (CPGs) during that phase. At a spinal cord level, indeed, rhythmic movements in mammals are organized by a network of interneurons and motor neurons called CPGs [26,27]. The observation of rapid adaptation of rhythmic forearm movements may suggest that vestibular and proprioceptive feedbacks are the major source of information used by CPGs to ensure adjustments to altered gravity, especially when it increases and becomes more demanding for the control of the task.

The variability of I_{norm} at a given g is globally lower in the decreasing than in the increasing- g phase as can be seen from the error bars in Fig. 4. It suggests habituation takes place because the decreasing- g phase always followed the increasing- g one. The higher variability during the increasing phase is consistent with the realization of a movement in a new situation. During the decreasing phase, motor learning achieved in the previous phase made it possible to induce a gradual reduction of variability in order to optimize the movement patterns that are compatible with a simple harmonic oscillator. Of course, anharmonic corrections are expected at higher orders in ϵ . Still, it is remarkable that such a simple textbook model of harmonic oscillator with time-dependent frequency can capture the essential features of human motor control when facing variable gravity.

V. CONCLUSION

In summary, participants show a spontaneous adaptation of their motion that is compatible with the expectation of

a simple harmonic oscillator with weakly gravity-dependent frequency. Previous analyses using the same centrifuge data did not involve the computation of the action variable and focused instead on other physical quantities, such as the grip force [22]. Here, the participant’s adaptation is assessed by the computation of adiabatic invariants, whose experimental behavior versus g complies with our model’s prediction. Adiabatic invariants may thus be a relevant model of the choices made by spinal and supraspinal nervous structures among an infinite number of possible solutions to a given problem, i.e., the motion of our test object in the present case. It is worth noting that, according to our model, $I \sim T \bar{E}_c$, with T one cycle’s period and \bar{E}_c the average kinetic energy on this period. The behavior of I vs g reveals a “hidden” constraint in the participants’ movements: They may show variability in the cycle durations and speed profiles, but still they will be such that the product $T \bar{E}_c$ will be that imposed by the adiabatic invariant theory. This simple mechanical constraint is revealed behind the complexity of the human actions involved in the forearm motion.

Future works might go beyond the harmonic oscillator description of the effective dynamics but still in a phase-space-based formalism. As shown in Ref. [23], adiabatic invariants can be computed in the case of higher-derivative Hamiltonians of Pais-Uhlenbeck type. Such Hamiltonians could describe rhythmic motions with several frequencies and discrete movements through, e.g., minimal jerk models [28]. We are currently investigating how our model can be generalized by analyzing complex trajectories performed during parabolic flight, therefore also including the very particular case of an absence of gravity [29,30].

ACKNOWLEDGMENTS

This research was supported by the European Space Agency (ESA) in the framework of the Delta-G Topical Team (e), the Institut National de la Santé et de la Recherche Médicale (INSERM) and the Conseil Général de Bourgogne (France), and by the Centre National d’Etudes Spatiales Grant No. 4800000665 (CNES).

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