Altered gravity highlights Central Pattern Generator mechanisms

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ABSTRACT

In many non-primate species, rhythmic patterns of activity such as locomotion or respiration are generated by neural networks at the spinal level. These neural networks are called Central Pattern Generators (CPGs). Under normal gravitational conditions, the energy efficiency and the robustness of human rhythmic movements are due to the ability of CPGs to drive the system at a pace close to its resonant frequency. This property can be compared to oscillators running at resonant frequency, for which the energy is optimally exchanged with the environment. However, the ability of the CPG to adapt the frequency of rhythmic movements to new gravitational conditions has never been studied. We show here that the frequency of a rhythmic movement of the upper limb is systematically influenced by the different gravitational conditions created in parabolic flight. The period of the arm movement is shortened with increasing gravity levels. In weightlessness, however, the period is more dependent on instructions given to the participants, suggesting a decreased influence of resonant frequency. Our results are in agreement with a computational model of a CPG coupled to a simple pendulum under the control of gravity. We demonstrate that the innate modulation of rhythmic movements by CPGs is highly flexible across gravitational contexts. This further supports the involvement of CPG mechanisms in the achievement of efficient rhythmic arm movements. Our contribution is of major interest for the study of human rhythmic activities, both in a normal Earth environment and during microgravity conditions in space.

Key words: rhythmic movements, CPG, microgravity, resonance tuning.
INTRODUCTION

The most fundamental central pattern generator (CPG) consists of two groups of neurons with mutual inhibitory connections (Brown 1911). These inhibitory connections generate anti-phase oscillations in the activity of the two groups of neurons that alternately drive a pair of antagonist muscular groups (e.g., flexors-extensors) to induce periodic motion. There is growing evidence for the involvement of CPGs during walking or arm swinging in mammals (Burke 2001), including humans (Marder 2000; Miall 2007), although rhythmic movements in man involve higher brain centres (Marder 2000; Iwasaki and Zheng 2006). Recent insights suggest that the concept of the CPG, as established for human locomotion, applies to the arm as well (Dietz 2002; Zehr et al. 2004).

Some rhythmic activities, like locomotion, are energy-greedy and are sensitive to dynamic constraints induced by the environment. If walking is viewed as a force-driven harmonic oscillator, it requires a periodic forcing actuation to sustain its oscillations against damping forces, which tend to diminish the oscillations. In such systems, a particular frequency - the resonant frequency - is critical: it requires the minimum force to maintain the oscillations and therefore, the minimum muscle activity. When interacting with the environment, the preferred oscillatory movements are not simply dictated by the central nervous system, but are constrained by the dynamics of the system as well (Kugler and Turvey 1987; Hatsopoulos 1996). For instance, a giraffe moves with a much slower pace than small mammals, because giraffes have very long legs. In another context, Neil Armstrong walked on the Moon in 1969 at a much slower velocity than on Earth, because gravitational attraction on the Moon is decreased by a factor of six. From the neuronal control perspective, one functional benefit of modulating the CPG frequency with sensory feedback is that it enables a system to exploit the resonant properties of musculoskeletal dynamics (Hatsopoulos 1996; Hatsopoulos and Warren Jr 1996; Iwasaki and Zheng 2006; Williams and Deweerth 2007).

Activities are calibrated to take into account the existence of gravitational attraction, based on a lifetime of experience in a normal 1 g environment (Papaxanthis et al. 1998). For
instance, our motor control anticipates the fact that more effort is required to move an outstretched limb upward than downward, due to increased gravitational torque. The changes of motor performance in altered gravity (Bock 1998) must somehow be compensated through adaptive control, which is either more or less time-consuming depending on the context (Lackner and DiZio 1996).

In this study, we investigate humans’ ability to sustain rhythmic movements in different gravitational environments. By analogy with a simple pendulum system, the self-generated pace should grow as a function of gravity. However, because the natural period is infinite in 0 g, this simplistic model fails in microgravity. Therefore, we hypothesize that the movements are partly driven by a CPG in a closed-loop with the arm. Since neuronal control systems cooperate with the physical constraints imposed by the dynamics of the body and the environment, we expect that a change of gravity would induce a change of frequency in order to perform efficient rhythmic movements that have adapted to the resonant frequency as a result of gravitational changes. However, in 0 g, since there is no resonant frequency we predict that the pace adopted by the participants will rely mainly on the intrinsic frequency of the neural oscillator.
METHODS

Experimental procedures

Participants

Twelve right-handed volunteers participated in the study. Their health was assessed by their individual National Centres for Aerospace Medicine as meeting the requirement ("Jar Class II") for parabolic flight. No participant reported sensory or motor deficits and they all had normal or corrected to normal vision. All participants gave their informed consent to participate in this study and the procedures were approved by the European Space Agency Safety Committee and by the local ethics committee.

Task

Subjects were successively confronted with periods of normal gravity (1 g), hypergravity (1.8 g) and microgravity (0 g) during parabolic flights (Fig. 1A). They were instructed to perform rhythmic arm movements with a hand-held object (mass 212 g, diameter 82 mm, width 30 mm) around two virtual obstacles situated three meters in front of them, following an “infinity-shaped” trajectory (Fig. 1B). The first group of six participants (Self-paced) were instructed to perform the movement at a self-generated pace. The second group of six volunteers (Metronome-paced) followed the rhythm dictated by a metronome (1 cycle every 1.5 seconds).

Equipment

A video-based device (OptoTrak 3020 system, Northern Digital, Canada) recorded the position of three infrared-light-emitting diodes (IREDs) placed on the hand-held object and on the subject’s head, with a resolution of 0.1 mm. A three-dimensional accelerometer fixed on the floor of the aircraft recorded its acceleration along its fore-aft axis, lateral axis and the axis normal to the floor. The two synchronized acquisition systems (OptoTrak and accelerometers) recorded parameters at a sampling rate of 200 Hz.
**Manipulation of the gravitational context**

The experiments took place in the Airbus A300 ZEROg aircraft on six flights out of Bordeaux (France) spread out over two ESA Campaigns. A total of 180 parabolas were performed (2 campaigns x 3 flight days x 30 parabolas per flight).

Figure 1A illustrates one parabola. From a steady horizontal flight (1 g), the aircraft gradually pulled up its nose and started climbing at an angle of approximately 45 degrees for about 20 seconds, during which the aircraft experiences an acceleration of around 1.8 times g, the gravity level at the surface of the Earth ($g=9.81 \text{ m.s}^{-2}$). The engine thrust was then reduced to the minimum required to compensate for air drag, and the aircraft then followed a free-fall ballistic trajectory (a parabola) lasting an additional 20 seconds, during which weightlessness was achieved. At the end of this period, the aircraft pulled out of the parabolic arc, a manoeuvre which gave rise to another 20 second period of 1.8 g, after which it returned to normal flight attitude (1 g) before the next parabola. During the parabolas, the resultant g vector was always directed to the floor of the aircraft. Lateral and forward/backward components were in the range $10^{-3}$ g and were negligible.

Two participants were tested on each flight during the first and the second blocks of 15 parabolas. The task was carried out continuously across the different gravitational fields, including the 2- to 5-second transition phases separating the stable gravitational phases (Fig. 1A).

**Data analysis**

We calculated the period of the rhythmic movement as the time elapsed between two successive crossings of the centre of the path, as defined by the average horizontal and vertical positions (see red dot on Figure 1B). Since data were not normally distributed, a nonparametric Kruskal-Wallis ANOVA on ranks was used to test the effect of gravity and repetition of parabolas within each group. Significance across gravity conditions was assessed with Dunn’s post hoc comparisons (alpha level was $p<0.05$). Since no effect was found across repetition of parabolas,
we pooled data together in each condition of gravity (0 g [-0.05 g; 0.05 g], 0.5 g [0.05 g; 0.9 g],
1 g [0.9 g; 1.1 g], 1.4 g [1.1 g; 1.65 g], 1.8 g [g > 1.65 g]).

**Computational models**

*The CPG*

The CPG consists of two neurons that are connected with mutually inhibitory synapses, in a
configuration of half-centre oscillator. The dynamics of the CPG were first derived by
Matsuoka (1985). This model describes the firing rate of a real biological neuron with self-
inhibition. The CPG model is presented in Figure 2. The firing rates $x_1(t)$ and $x_2(t)$ are
governed by the following equations:

$$\begin{align*}
\tau_1 \dot{x}_1(t) &= -x_1(t) - \beta v_1(t) - \omega x_2(t) + h[\theta(t)]^+ + c(t) \\
\tau_2 \dot{v}_1(t) &= -v_1(t) + [x_1(t)]^+ \\
\tau_1 \dot{x}_2(t) &= -x_2(t) - \beta v_2(t) - \omega x_1(t) + h[\theta(t)]^+ + c(t) \\
\tau_2 \dot{v}_2(t) &= -v_2(t) + [x_2(t)]^+
\end{align*}$$

(1)

In the above system of nonlinear differential equations, $v_1(t)$ and $v_2(t)$ represent the self-
inhibition of the neurons N1 and N2, modulated by the adaptation constant $\beta$, while strength of
the mutual inhibition is controlled by the parameter $\omega$. The outputs of each neuron $y_1(t)$ and
$y_2(t)$ are taken as the positive part of $x_1(t)$ and $x_2(t)$, respectively:

$$\begin{align*}
y_1(t) &= [x_1(t)]^+ = \max(0, x_1(t)) \\
y_2(t) &= [x_2(t)]^+ = \max(0, x_2(t))
\end{align*}$$

(2)

The output of the whole oscillator $y_{\text{out}}(t)$ results from the subtraction of the two half-centre
outputs:

$$y_{\text{out}}(t) = y_1(t) - y_2(t)$$

(3)

We considered only one proprioceptive input $\theta(t)$ to the CPG. However, any number of inputs
can be applied to the oscillator, which can either be proprioceptive signals or signals from other
neurons. The input is arranged to excite one neuron and inhibit the other, by applying the positive part \( [\theta(t)]^+ \) to N1 and the negative part \( [\theta(t)]^- = \min(0, \theta(t)) \) to N2. The inputs are scaled by the gain \( h \). The tonic excitation \( c \) is self-sufficient to generate the oscillation (i.e., a proprioceptive input is not necessary). The two time constants \( \tau_1 \) and \( \tau_2 \) determine the speed and shape of the oscillator output. For stable oscillations, \( \frac{\tau_1}{\tau_2} \in [0.1;0.5] \) describes when the endogenous - or natural - frequency of the oscillator is proportional to \( \frac{0.112}{\tau_1} \) (Williamson 1998).

**The pendulum subsystem**

The proprioceptive feedback signals \( [h(\theta)]^+ \) and \( [h(\theta)]^- \) are equivalent to the angular displacement \( \theta \) of a damped pendulum under the influence of gravity (Fig. 2). This simplistic model has previously been used to describe a variety of biological movements, and has been shown to sufficiently represent the dynamics of a one-degree-of-freedom system (Obusek et al. 1995). As such, the motion of the mechanical subsystem is governed by:

\[
\ddot{\theta}(t) + \gamma \dot{\theta}(t) + \frac{g}{l} \sin \theta(t) = T_{\text{out}}(t).
\]  
(4)

Equation 4 describes the angular position \( \theta(t) \) of a mass \( m \) attached to a fixed point by a string (length \( l \)). The parameter \( \gamma \) is a constant for the torsional viscous dissipation and \( g \) is gravity. In addition, this pendulum system is driven by a forcing torque \( T_{\text{out}}(t) \), which depends on the CPG output following:

\[
T_{\text{out}}(t) = \frac{K}{ml^2} y_{\text{out}}(t)
\]  
(5)

where \( K \) is gain.
The closed-loop system is then described by three sets of parameters. The first set describes the CPG \((\tau_i, \tau_z, \beta, \omega_c)\), the second set parameterises the pendulum subsystem \((m, l, g, \gamma)\) and the last parameters adjust the coupling between the two systems \((h, K)\).

**Numerical simulations**

The coupled CPG-pendulum model was implemented in MATLAB (The MathWorks, Inc., Natick, MA, USA). For all simulations, we used the Runga–Kutta integration method with a time step of 1 ms, with the initial condition:

\[
\begin{bmatrix}
    x_1(0) & x_2(0) & v_1(0) & v_2(0) & \theta(0) & \dot{\theta}(0)
\end{bmatrix}^T = \begin{bmatrix}
    -0.01 & 0.01 & 0 & 0 & 0 & 0
\end{bmatrix}^T
\]  

(6)
RESULTS

Participants traced rhythmic trajectories following an infinity shape. The elbow of the subjects was in a semi-flexion posture during the task, with an approximate angle of 90 degrees. Most of the movement resulted from motion about the shoulder joint. They were all able to sustain the movement during the complete parabolic profiles. In the Metronome-paced group, participants attempted to synchronize the minimal vertical position of each loop with the emitted tone. Clock signals were emitted twice in a cycle. In the Self-paced group in 1 g, the perimeter of the trajectory was 222±0.9 cm (mean ± SD). The two loops were symmetrical in terms of length (left: 108±12 cm; right: 114±14 cm) and duration (left: 0.61±0.08 s; right: 0.68±0.1 s).

Figure 3 illustrates the average of the period measured in the two groups of volunteers as a function of gravity level. In the Self-paced group (green points), we observed a significant decrease between 1 g to 1.8 g (p<0.001). Gravity during the transition phases (0.5 and 1.4 g) also noticeably scaled the average period. Our data strongly suggest an influence of gravity on the rhythm naturally adopted by the subjects. When compared to the Self-paced group, the period of movement was longer in all gravity fields in the Metronome-paced group (red points), as dictated by the metronome (p<0.001). Despite the fact that the rhythm was imposed in this condition, the period was surprisingly still modulated by the gravitational context (p<0.001) and performance degraded from the instructed 1.5-second pace with increased gravity. However, subjects did not slow down their movement further from 0.5 g to 0 g. Indeed, the periods were similar in the Self-paced group (p>0.05) and slightly smaller in 0 g in the Metronome Paced group (p<0.001).

We tested whether these data would be compatible with our CPG-pendulum model. The two dynamic systems become coupled when the oscillator is connected to this system (Eq. 5). Indeed, the oscillator output drives the torques and the angular position is connected to the oscillator input. The final frequency and amplitude are determined by how they interact. In other words, when a sinusoidal input is applied to the coupled system, the oscillator can entrain the input, locking onto the input frequency.
Considering first the Self-paced group, we ran an iterative procedure to find the best parameters that fit the observed period as a function of gravity (see legend of Figure 3 for details). We found that participants were mainly influenced by the pendulum subsystem in non-zero gravity fields. Indeed, the natural period of a pendulum is inversely related to gravity following:

$$T = 2\pi \sqrt{\frac{l}{g}}$$  \hspace{1cm} (7)

Interestingly, since the natural period of the pendulum reaches infinity in 0 g, the CPG could no longer be entrained by the input. Therefore, the system was attracted by the endogenous frequency of the CPG. This effect is present in the simulation for values of gravity below 0.5 g.

The strength of this model resides in its ability to approach the data of the Metronome-paced group by adjusting only a few parameters. First, the endogenous period of the CPG was set to the instructed period (1.5 s) by tuning $\tau_1$. Second, the coupling factor $h$ that links the pendulum output to the CPG dramatically decreased from 20 to 1, which emphasizes the fact that the entrainment becomes much less influenced by the resonant properties of the coupled system. Third, the length of the pendulum increased by 5 cm. Remarkably, we also found biomechanical evidence that subjects of this group performed the movements further from their body by 5±0.1 cm (mean ± SE, p<0.001). This adaptation allowed participants to follow the imposed rhythm while performing the movement at a pace closer to the resonant frequency of their upper limb.
DISCUSSION

Experimental and theoretical studies suggest that biological rhythmic movements converge to the resonant frequency of a mechanical system through sensory feedback. This property - called resonance tuning -, has been observed in the swimming of jellyfish and scallops (Demont 1990), but also in leg and arm swinging in humans (Holt 1990; Abe and Yamada 2003). Moving at the resonant frequency offers several advantages, including maximization of the movement amplitude and predictability as well as minimization of the degrees of freedom, of the endpoint variability, and of the energy associated with the movement (Holt et al. 1995; Goodman et al. 2000).

Our data strongly suggest a functional and flexible role of the CPG in driving rhythmic arm movements in all gravitational fields, regardless of the instructions to follow. Since human beings live in a normal Earth environment, the endogenous period of the CPG in the Self-paced group was set to the natural frequency adopted by the participants in 1 g (1.25 s). While the effect of gravity on the period of the upper limb in non-zero gravity phases rests on simple mechanics, the same strategy would not have been applied to 0 g. Indeed, in microgravity, the motor system can no longer take advantage of gravity to drive the arm at the resonant frequency. Observations in microgravity suggest a strategy relying more on the intrinsic properties of the CPG. Furthermore, the tight coupling of the oscillator with the actuated system results in quick entrainment and stability to perturbations, despite the fact that subjects were dramatically placed into new environmental conditions such as microgravity. Indeed, participants were stable from the first two cycles of periodic movements. This behaviour is a direct theoretical consequence of the model and is illustrated in Figure 4. The phase plot (Fig. 4A) shows the fast convergence of the motion to a limit cycle, which emphasizes the robustness of the entrainment mechanism. The right panel (Fig. 4B) shows the output of the CPG (solid line) and the input of the pendulum (dotted line) as a function of time. One can observe that after a few cycles, the CPG and the pendulum are locked to a common period, despite the fact that the pendulum could not oscillate in microgravity. The structure of the mechanical
The subsystem (pendulum) is not identified, per se, by the CPG, leading to a computationally efficient collaborative mechanism. Interestingly, our results do not depend critically on the specifics of the model presented here. As in previous works (Sternad et al. 2000; Williams and Deweerth 2007; Williamson 1998), we rested our study on the well-established mathematical formulation of the oscillator by Matsuoka (1985) which provides a simple physiologically plausible model and allows for natural feedback connections. Whereas a more complex CPG model is very likely to converge to the observed behaviour (more degrees of freedom), our conclusions will remain at least qualitatively valid with other very simple oscillators, as we verified with a Van der Pol oscillator (supplementary materials). Furthermore, although the modelling of a biologically plausible double arm pendulum system is out of the scope of the present study, it is worth mentioning that a mass-spring system would also predict similar results. In that simple harmonic oscillator, the resonant frequency is proportional to the square root of the stiffness of the spring. In other words, the larger the stiffness, the shorter the period. Interestingly, a study by Fisk et al. (1993) reported larger stiffness of the upper limb for increasing levels of gravity in reaching movements during parabolic flights. Thus, a mass-spring model with an explicit dependence of stiffness on gravity would predict comparable results. To sum up, our conclusions will remain compatible with changes in the equations describing the CPG or the mechanical subsystem.

Finally, our results show that a given oscillator quickly converges to the most efficient driving frequency without requiring major changes in its pool of parameters. Indeed, in the Metronome-paced group, the same model was able to fit the data as reliably as in the Self-paced group. On the one hand, participants increased the distance from the shoulder joint to the end-effector in order to optimise the movement at the instructed tempo. On the other hand, despite a weak coupling between the CPG and the pendulum, the influence of gravity was still largely present (as subjects reported they could successfully follow the tempo). Consistent with the results reported here, an influence of gravity was also observed in a study investigating grip-
load force coupling in parabolic flights during cyclic vertical arm movements (Augurelle et al. 2003). Participants who never experienced altered gravity failed to synchronize their simple rhythmic movements (1 Hz) with a clock signal. They adopted too fast a tempo in 1.8 g but could match the rhythm in 0 g (Augurelle et al. 2003, see Fig. 4, Frequency, 1.8 g).

Altogether, behaviour in microgravity is different from that in non-zero gravity fields. Indeed, activities in hypergravity can be inferred from normal Earth gravity by applying a gain on calibrated actions in 1 g, whereas microgravity behaviour follows from intrinsically very different rules, since mass and weight become structurally decoupled. However, the same model structure could explain the whole data set by altering the values of a subset of parameters. This process could be responsible for the classically observed slowing of movement in weightlessness (Berger et al. 1997; McIntyre et al. 2001; Mechtcheriakov et al. 2002).

Recently, rhythmic movements have been shown to be performed with better performance than discrete aiming tasks (Miall and Ivry 2004; Smits-Engelsman et al. 2006). Since the human body is a redundant system (Bernstein 1967), the programming of a movement as a whole (i.e., global optimum) should theoretically be more efficient than sequentially optimised sub-movements (i.e., sum of local optima). Furthermore, these global optima are able to adapt to different conditions. By considering together the system and its environment, the central nervous system can estimate another dynamic property – the resonant frequency – which is crucial in performing efficient and robust rhythmic movements (Marder and Goaillard 2006). Earlier experiments showed that the CPG frequency and, consequently, the movement frequency can be altered by sensory feedback from the musculoskeletal system (see e.g. McClellan and Sigvardt 1988) which facilitates resonance tuning. Here, resonance tuning might have been driven by an adjustment of interneurones gains within the CPG. In contrast, the coupling parameter h didn’t change across gravity levels for a given condition (Self-paced vs. Metronome paced) which suggests a control at a higher cortical level. Interestingly, its value decreased between the Self-paced (h=20) group and the Metronome Paced group (h=1),
suggesting that the entrainment relies more on the resonant properties of the coupled system in the free condition (Self-paced group). Large feedback gains ($h=\sim 20$) have been shown to increase the range of resonant frequencies to which the closed loop system can be entrained (Williams and Deweerth, 2007). These flexible mechanisms ensure stable performance despite large fluctuations in the external environment. By allowing for plasticity, the programs implemented by neural control circuits can be parameterised instead of providing single purpose hard-wired circuits, and are thus much more useful to the organism (Katz 1995).

In the context of altered gravity environment, our results provide interesting insights into the role of CPGs in regulating rhythmic arm movements. We show that gravity is an essential parameter that is profoundly integrated in our central nervous system, and is important when tuning the frequency of periodic actions to resonance in order to sustain competitive movements.
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Acknowledgements

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Figure 1. Parabolic flight manoeuvre and typical trajectory performed by the participants.
(A) A single parabolic flight profile generated a sequence of stable episodes of normal (1 g), hyper-(1.8 g) and micro- (0 g) gravity of about 20 seconds each. Gravity level relative to the Earth (g=9.81 ms\(^{-2}\)) is shown on the left Y-axis (green) and flight altitude is reported on the right Y-axis (red), both as a function of time.
(B) One typical cycle trial of a participant in 0 g. The blue dots represent the object position sampled every 50 ms. The arrow marks the path to follow.

Figure 2. Closed-loop neuromechanical system.
Illustration of the connectivity between the neural and mechanical dynamics. The CPG is composed of neurons N1 and N2. Black circles are inhibitory connections and open circles are excitatory connections. The connections parameterized by $\beta$ and $\omega$ correspond to self-inhibition and mutual inhibition, respectively. The two outputs $y_i(t)$ are combined to give the oscillator output $y_{out}(t)$, that in turn applies a torque $T_{out}(t)$ on the pendulum which is parameterized by its length ($l$), mass ($m$) and damping ($\gamma$). The action of gravity ($g$) is symbolized by the downward arrow.

Figure 3. Period as a function of gravity (Earth gravity is 1 g): experimental and simulation data.
The data points are the mean periods adopted by the participants in the Self-paced group (green disks, n=4497) and in the Metronome-paced group (red disks, n=3551) for 0, 0.5, 1, 1.4 and 1.8 g. The lower dotted line indicates the CPG endogenous period (1.25 s). The upper dotted line indicates the instructed rhythm for the Metronome-paced group (1.5 s). Self-paced data were fit by the closed-loop CPG-pendulum model (black lines) with the following CPG, pendulum and
link parameter values, respectively: \( \tau_1 = 0.0997s \), \( \tau_2 = 0.2493s \), \( \beta = 2.5 \), \( \omega = 2.5 \), \( c = 1 \);

\( m = 5kg \), \( l = 1m \), \( g = \alpha g \) (with \( \alpha = 0:0.05:1.9 \)), \( \gamma = 2.1 \) and \( h = 20 \), \( K = 1.25 \). The best fit in the Metronome-paced group was found with the same set of parameters, except for the following: \( \tau_1 = 0.224s \), \( \gamma = 2.15 \), \( l = 1.05 \) and \( h = 1 \). Error bars represent 95% Confidence Interval on both axes.

Figure 4. Robustness and fast entrainment of the input illustrated in 0 g.

The left graph depicts a phase plot of mass motion. This plot shows the velocity against position for a mass actuated by the oscillator under torque feedback. The left graph shows how the oscillator (solid line) gets locked onto the frequency of the input (dotted line). The mass started from \( \theta(0) = 0.1 \) and \( \dot{\theta}(0) = 0 \). The system quickly converges to a limit-cycle behaviour.
Figure 1

A

Gravity (g)

Altitude (km)

Time (s)

B

Vertical position (m)

Horizontal position (m)

Depth (m)
Figure 4

CPG entrainment in 0 g

Phase plot of mass motion