Getting ready for Mars:

How the brain perceives new simulated gravitational environments

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Abstract

On Earth, we are continually exposed to gravity: sensory signals are constantly integrated to form an internal model of gravity. However it is unclear whether this internal model is fixed to Earth gravity or whether it can be applied to a new gravitational environment. Under terrestrial gravity, observers show a “gravitational bias” while judging the speed of falling versus rising objects, as they comply with the physical laws of gravity. We investigated whether this gravitational bias may be present when judging the speed of objects moving upwards or downwards in both Virtual Reality (VR) simulated Earth gravity (9.81 m/s^2) and Mars gravity (3.71 m/s^2). Our results highlighted a gravitational bias in both Earth and Mars VR-simulated gravity: the speed of downwards movement was more precisely detected than the speed of upwards movement. Although the internal model of gravity has been built up under terrestrial gravity, it can quickly expand to novel non-terrestrial gravitational environments.

Introduction

On Earth, gravity provides an absolute reference for perception and action in the surrounding world. Since the beginning of time, humans have evolved under a constant 1g environment. However, mankind is preparing for a *new space age:* space agencies are planning manned missions to the Moon and to Mars, while commercial ventures may open up the prospect for non-astronauts to visit other planets (Macneil, Che, & Khan, 2016; Slezak & Solon, 2017; Wilson, 2017). Significant technological and scientific challenges remain before the colonisation of other planets and manned deep space missions become fact. One such challenge is to understand whether and how the human brain is able to quickly adjust and adapt to altered gravitational environments (Jörges & López-moliner, 2017; Wickman, 2006).

The central nervous system does not have specialised receptors dedicated to gravity. Instead, it integrates online information from different sensory modalities, as well as priors built up from experience (Lackner & DiZio, 2005; Lacquaniti et al., 2014; Mittelstaedt, 1992). The vestibular organs, within the inner ear, sense the pull of gravity via the otolith organs. Otoconia resting atop hair cells are pulled in the direction of gravity when the head moves with respect to the gravitational direction. This change signals the position of the head with respect to gravity (Barra et al., 2010; Green, Shaikh, & Angelaki, 2005; Merfeld, Zupan, & Peterka, 1999; Tarnutzer, Bockisch, Straumann, & Olasagasti, 2009). In addition, visual cues for the direction of ‘up’ and ‘down' are obtained by observing stable gravitational references, such as buildings or trees (Harris, Jenkin, Dyde, & Jenkin, 2011). Finally, proprioceptive signals from the joints, muscles, skin, and viscera provide references for the body's position relative to gravity (Trousselard, Barraud, Nougier, Raphel, & Cian, 2004; Yardley, 1990). All of this sensory information is integrated to form an internal model of the magnitude and direction of gravity (Barra et al., 2010; Lackner & DiZio, 2005; Lacquaniti et al., 2014; Mittelstaedt, 1992).

The internal model of gravity is essential for almost all of our successful behaviours, such as our perceptual judgements of verticality (Barra et al., 2010) and distance (Török et al., 2017), but also our ability to perform skilled actions such as the interception of falling objects

(Jörges & López-moliner, 2017; Zago, McIntyre, Senot, & Lacquaniti, 2009). The influence of gravity on human behaviour is so pervasive that observers typically mis-remember the location of a moving object in space, displacing it downwards as if it were under the influence of gravity (De Sá Teixeira, 2016). Even more impressive, a *gravitational bias* appears to exist, in which people are more precise in their perceptual judgements when observing movements which obey the laws of gravity, versus when they violate them. Moscatelli and Lacquaniti (2011) described that observers were more precise in judging the duration of movement of objects accelerating downwards, i.e. congruent with the laws of gravity, compared to objects accelerating upwards, horizontally, or diagonally, i.e. incongruent with the laws of gravity. Observers therefore incorporated information from their internal model of gravity in making perceptual judgements.

Since gravitational acceleration has been constant throughout the ~4 billion years of biological evolution on Earth, it remains unclear whether the internal model of gravity is fixed to the *terrestrial* gravitational environment, or whether the model can be quickly and flexibly applied to other gravitational contexts. This question is particularly timely given the increased likelihood of exposure to new gravitational contexts as humans push the boundaries of space exploration. Here, we explored whether the internal model of gravity is fixed to the gravitational environment of Earth (9.81m/s^2) or if it could be flexibly adjusted to a Virtual Reality visually-simulated Martian gravity environment (3.71 m/s^2). Participants judged the duration of a ball falling or rising congruent with the gravitational acceleration of Earth or Mars. If participants' adapted their internal model of gravity in the new gravitational environment of Mars, then we would expect the gravitational bias reported by Moscatelli and Lacquaniti (2011) to be present when participants observed the falling object irrespective of gravitational context.

Methods

Ethics

Written informed consent was collected prior to the experiment, and the experimental protocol was approved by the Royal Holloway University of London (RHUL) ethics committee. The study was conducted in line with the Declaration of Helsinki.

Participants

Sixteen participants (8 female, mean age = 25.81, SD = 3.78) were recruited for the experiment from the RHUL participant pool. Participants had normal or corrected-to-normal vision, no history of neurological, psychiatric or vestibular disorders. Participants were right handed according to their Edinburgh Handedness Inventory score, and were naive to the purpose of the experiment. Participants received £5 for taking part in the experiment. The sample size and trial number were determined based on previous studies with similar methodologies (Moscatelli & Lacquaniti, 2011).

Procedure

Verbal and written instructions were given to participants at the beginning of the session. Participants were seated comfortably in a chair with their chin positioned in a chin rest. The virtual environment was rendered in Unity 3D (Unity Technologies, 2018) and was presented on an LCD computer monitor (60 Hz refresh rate). The virtual environment measured 34 x 25.5 cm, with 1024 x 768 resolution. Participants viewed the stimuli from a distance of 40 cm away from the screen. A tube (30 cm diameter) was fitted to the computer monitor such that the virtual environment was presented in an occluded visual field, limiting additional cues from the external environment. The virtual environment was the surface of a planet, with sand dunes and a night sky (Figure 1A). The centre of the environment was marked with a red dot (2 mm diameter, 0.03º visual angle) and participants were instructed to fixate on this point during the experiment. There were two black tubes (diameter = 1.5 cm, 2.15º visual angle, length = 5 cm, 7.13º visual angle) in the scene along the central midline, one placed in the sky and one in the ground. The path length was 15.5 cm, corresponding to 21.18º visual angle.

A black and white football (1.5 cm diameter, 2.15º visual angle) accelerated between the tubes either downwards or upwards in direction. The magnitude of acceleration matched the drag of the Earth gravity ($9.81 m/s^2$) in the Earth condition and Mars gravity ($3.71 m/s^2$) in the Mars condition. This means in the downwards motion conditions the kinematics were congruent with falling under the respective gravitational fields. The initial speed of the football was manipulated between 9.53m/s and 0.05m/s in nine steps resulting in nine different motion durations (0.5 s, 0.65 s, 0.7 s, 0.75 s, 0.80 s, 0.85 s, 0.90 s, 0.95 s, 1.10 s). These durations were selected to help comparison between the results of the current study and previous ones (Moscatelli & Lacquaniti, 2011). The average speed of the ball was 7.24 m/s for Earth gravity and 5.72 m/s for Mars gravity. The average final speed was 9.70 m/s for Earth gravity, and 6.64 m/s for Mars gravity.

Upwards and downwards motion blocks were presented for both Earth and Mars gravity conditions resulting in a total of 4 blocks. The motion direction and planet was counterbalanced across participants. We followed the design of Moscatelli and Lacquaniti (2011), employing the method of single stimuli. Each block started with the presentation of 60 trials of the same reference speed (reference phase). This initial speed was fixed at 3.57m/s. Participants were instructed to memorise the speed. The reference trials were presented with ISI = 1300ms. After the reference phase, a test phase started in which participants had to decide after each trial whether the football was moving faster or slower than the reference trials. The nine motion durations were used during this phase, with the mean corresponding to the reference speed. Thus, the reference speed is implicitly defined by the entire set of trials, rather than having to present a standard stimulus before each test stimulus as in other psychophysical methods. Participants were instructed to press the left cursor button on a keyboard if the ball was moving faster and the right cursor if it was moving slower than the reference trials. Test trials were presented with ISI = 2300ms. Each of the nine levels of stimulus durations were presented 20 times, resulting in 180 test trials. Participants were allowed to have short breaks between blocks. The total duration of the experiment was approximately 45 min.

Data Analysis

Analyses were carried out in R software (R Core Team, 2017) using lme4 (Bates, Mächler, Bolker, & Walker, 2015) and MERpsychophysics (Moscatelli, Mezzetti, & Lacquaniti, 2012).

Before statistical modelling, we removed the outliers. We considered response times shorter than 300 ms and longer than 2 s as outliers and these were removed from further analysis. This step meant the removal of 2.7% of the responses. Trials in which participants did not respond were also not included in the analysis, however in total only 1.5% of the responses were missed. Further, we inspected the response profiles of each participant and decided to exclude participants from further analysis if they showed very poor performance (quantified by the following criterion $\max_P - \min_P < .5$). Two participants were excluded due to not meeting this criterion, leaving 14 participants` data in the analysis.

We followed the analysis strategy implemented by Moscatelli and Lacquaniti (2011). Importantly, spatiotemporal parameters cannot be readily matched between the Earth and Mars conditions (i.e. Earth and Mars gravitational accelerations differ in either the initial speed or the trajectory length). Thus, we did not compare the two conditions directly but performed two separate statistical tests, one on the data from the Earth conditions and one from the Mars conditions.

For each participant and condition, we computed the number of trials in which the test trial was considered slower than the reference. We coded slower as 1 and faster as 0. This data was used to construct psychometric functions. The probit link was chosen based on previously reported results (Moscatelli et al., 2012). Therefore the equation of the psychometric function was given by

$$\Phi^{-1}[P(y = 1)] = \beta_0 + \beta_1 x$$

Precision of the discrimination was given by the β_0 parameter, and the accuracy of the memory for the reference speed expressed by the Point of Subjective Equality (PSE) was derived from the β_0 and β_1 values, using the following equation:

$$PSE = -\frac{\beta_0}{\beta_1}$$

We used the delta method (Casella & Berger, 2002) to estimate the 95% confidence intervals for the PSE for each subject.

We calculated the discrimination threshold ΔT (also commonly referred as Just Noticeable Difference), which represents an alternative measure of (inverse) precision. This is derived from the psychometric function such as

$$\Delta T = \frac{T_{0.75} - T_{0.25}}{2}$$

where $T_{0.25}$ and $T_{0.75}$ are the motion duration values matching the 0.25 and 0.75 probabilities of a "Slower" response. This ΔT can then be used to calculate the Weber fraction

$$\mathrm{WF} = \frac{\Delta \mathrm{T}}{\mathrm{T}_{\mathrm{standard}}}$$

These estimates were fitted with a General Linear Mixed Model (GLMM) to address the effect of motion direction (downwards vs upwards) and motion duration on the population level. The general equation of the GLMM with probit link is the following

$$\Phi^{-1}(\boldsymbol{Y}) = \boldsymbol{\beta X} + \boldsymbol{bZ} + \boldsymbol{\varepsilon}$$

We defined in the random effects *J* levels, i.e. *j* = 1, 2, …, *J,* where J is the number of participants. Based on this, when partitioned, the above formula can be written as:

$$\begin{bmatrix} \boldsymbol{Y}_1 \\ \boldsymbol{Y}_2 \\ \vdots \\ \boldsymbol{Y}_{J-1} \\ \boldsymbol{Y}_J \end{bmatrix} = \begin{bmatrix} \boldsymbol{X}_1 & \boldsymbol{Z}_1 & 0 & 0 & 0 \\ \boldsymbol{X}_2 & 0 & \boldsymbol{Z}_2 & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ \boldsymbol{X}_{J-1} & 0 & 0 & \boldsymbol{Z}_{J-1} & 0 \\ \boldsymbol{X}_J & 0 & 0 & 0 & \boldsymbol{Z}_J \end{bmatrix} \begin{bmatrix} \boldsymbol{\beta} \\ \boldsymbol{b}_1 \\ \boldsymbol{b}_2 \\ \vdots \\ \boldsymbol{b}_{J-1} \\ \boldsymbol{b}_J \end{bmatrix} + \begin{bmatrix} \boldsymbol{\varepsilon}_1 \\ \boldsymbol{\varepsilon}_2 \\ \vdots \\ \boldsymbol{\varepsilon}_{J-1} \\ \boldsymbol{\varepsilon}_J \end{bmatrix}$$

Where $\boldsymbol{Y}_j$ is a n_j X 1 matrix containing the observations of level j, $\boldsymbol{X}_j$ and $\boldsymbol{Z}_j$ are n_j X 4 design matrices and $\boldsymbol{\varepsilon}_j$ is the residual matrix of size n_j X 1. Writing them in explicit form, we have:

$$\boldsymbol{Y}_J = \begin{bmatrix} y_{1j} \\ y_{2j} \\ \vdots \\ y_{n_j-1j} \\ y_{n_jj} \end{bmatrix},$$

$$\boldsymbol{X}_J = \boldsymbol{Z}_J = \begin{bmatrix} 1 & v_{1j} & w_{1j} & vw_{1j} \\ 1 & v_{2j} & w_{2j} & vw_{2j} \\ \vdots & \vdots & \vdots & \vdots \\ 1 & v_{n_j-1j} & w_{n_j-1j} & vw_{n_j-1j} \\ 1 & v_{n_jj} & w_{n_jj} & vw_{n_jj} \end{bmatrix},$$

$$\boldsymbol{\varepsilon}_J = \begin{bmatrix} \varepsilon_{1j} \\ \varepsilon_{2j} \\ \vdots \\ \varepsilon_{n_j-1j} \\ \varepsilon_{n_jj} \end{bmatrix}, \qquad \varepsilon_{n_jj} \sim N(0, \sigma^2)$$

Where y_{n_jj} is the response of the participant *j* in trial n_j, v_{n_jj} is the motion duration of the object, w_{n_jj} is the direction of motion in one-hot vector form in the n_jth row of level *j*. Given this, the coefficients in the model can be written also in matrix form:

$$\boldsymbol{\beta} = \begin{bmatrix} \beta_0 \\ \beta_1 \\ \beta_2 \\ \beta_3 \end{bmatrix}, \boldsymbol{b}_j = \begin{bmatrix} u_{0j} \\ u_{1j} \\ u_{2j} \\ u_{3j} \end{bmatrix},$$

We estimated correlated random slopes and intercepts. For each parameter, we computed Wald statistics using the following equation:

$$\mathrm{z} = \frac{\beta}{\mathrm{SE}}$$

where β is the estimated parameter value and SE is the respective standard error. We checked whether the mixed effects approach is justified by testing whether the standard deviation of the random intercept is different from zero. The results showed that our approach was justified, consistently with earlier studies (Moscatelli & Lacquaniti, 2011). Following the data analysis of Moscatelli and Lacquaniti (2011), we normalized the slope parameters to the downwards motion's slope.

*** Please add Figure 1 Here ***

Results

Figure 1B shows the psychometric curves fitted to the pooled responses over all 14 participants. As visual inspection suggests, slopes are generally higher for downward motion.

Thus, motion duration discrimination is more precise for the gravity congruent direction (Moscatelli & Lacquaniti, 2011).

To evaluate the numerical effects, we fitted psychometric functions on the single subject level. The Just Noticeable Difference (JND) and Point of Subjective Equality (PSE) were calculated from the functions for each participant in each condition. The gravitational bias was found in 10/14 participants both under Earth and Mars conditions. We also used these estimates to test for any potential effect of block order and found none (*p* = .14). Statistical comparison was done using linear mixed effect modelling in R (R Core Team, 2017) and lme4 (Bates et al., 2015).

The slope was steeper for downwards compared to upwards motion in both Earth and Mars conditions (Wald χ^2_{Earth}= 4.1483, p = .042; Wald χ^2_{Mars}= 9.1881, p = .002) (Figure 1C). On average the JND values were 116.05±8.38 ms (*M* ± *SE*) (*WF* = 0.15±0.010) for Earth upwards motion, 93.68±9.08 ms (*WF* = 0.12±0.011) for Earth downwards motion, 86.44±6.52 ms (*WF* = 0.11±0.008) for Mars upwards motion, and 66.21±7.39 ms (*WF* = 0.08±0.009) for Mars downwards motion. A qualitative comparison of these values suggests that the gravitational bias was robust present under both Terrestrial and Martian gravity conditions.

PSE estimates showed no difference between Motion directions in either gravitational condition (Wald χ^2_{Earth}= 0.4077, p = .523; Wald χ^2_{Mars}= 1.0641, p = .302) (Figure 1D). On average, the PSE values were 814.05 ± 20.62 ms (*M* ± *SE*) for Earth downwards motion, 820.52 ± 18.69 ms for Earth upwards motion, 776.60 ± 20.68 ms for Mars downwards motion, and 792.28 ± 16.98 ms for Mars upwards motion. Overall, these values appear similar to the reference duration of 800 ms, suggesting participants had a good memory of the reference trials.

Taken together, our results indicated that that the perceptual gravitational bias described by Moscatelli and Lacquaniti (2011) is also present over simulated Martian gravity conditions, suggesting that the human perceptual system underlying gravity perception is robust but dynamic enough to quickly adapt to altered gravity.

Discussion

Previous research has established that humans exhibit a gravitational bias in their perceptual experiences (Lacquaniti et al., 2013; Moscatelli & Lacquaniti, 2011). When judging the duration of motion, observers rely on an internal model of gravity and are therefore much more precise if the objects fall downwards, congruent with the gravitational acceleration of Earth's gravity, compared to upwards acceleration, violating gravitational constraints (Barra et al., 2010; Jörges & López-moliner, 2017; Moscatelli & Lacquaniti, 2011). Here we explored whether the internal model of gravity could adapt to a new virtual visually-simulated gravitational environment. Observers were asked to judge the duration of falling or rising objects which accelerated congruent with the gravity of Earth or Mars. Participants displayed the well-known gravitational bias for falling objects (Moscatelli & Lacquaniti, 2011), both under Terrestrial and Martian simulated gravity. We thus believe that the internal model of gravity has the potential to rapidly and flexibly adapt to the new gravitational environment, and is not rigidly fixed to Earth's gravity.

Perception of gravitational motion involves a diverse range of brain regions, particularly those also implicated in vestibular processing (Miller et al., 2008; Indovina et al., 2005; Zu Eulenberg et al., 2012). For example, Indovina et al. (2005) found activation in the posterior thalamus, putamen, insular cortex, temporoparietal junction, supplementary motor area, middle cingulate cortex and postcentral gyrus in response to both caloric vestibular stimulation and gravitational visual motion. Moreover, Miller et al. (2008) described activations in posterior vermis and left superior nucleus specifically for gravitational motion embedded in a pictorial context. However, to our knowledge, no studies have yet investigated whether these regions are also be implicated in processing of gravitational motion which differs from Earth gravity.

Here we modified the gravitational acceleration of objects rising and falling within the virtual environment, leading to different kinematics between gravity conditions. As such, a direct comparison between Earth and Mars gravity conditions is not possible, potentially limiting the findings of our study. Future research could consider whether the gravitational bias would be present under Earth and Mars gravity if the spatiotemporal parameters were directly matched. Moreover, it is important to note that other terrestrial factors may cause objects to move with different speeds, such as air resistance. As such we cannot exclude the possibility that the participants interpreted differences between conditions on the basis of these terrestrial (i.e., air resistance) versus gravitational factors. However, we believe that such a strategy is unlikely, as no cues within the virtual environment nor task instructions indicated differences in such terrestrial features. Thus, the only difference between the environments was the altered gravitational acceleration.

Visual information from the external environment is essential in graviception. For example, Moscatelli and Lacquaniti (2011) found a reduction in the gravitational bias when a blank scene was presented to participants – while downwards motion was more precisely perceived over upwards motion, it was no longer superior to horizontal motion. However, when observers were presented with a detailed scene which was tilted relative to physical gravity, a gravitational bias was still present, with greater precision for downwards motion according to scene gravity. Moreover, Miller et al. (2008) found that observers anticipated Earth gravity during interception only when targets were embedded in a pictorial scene: when a blank scene was presented, interception performance was similar under normal and reversed gravity. We found that participants had a gravitational bias for both Earth and Mars gravity when these accelerations were embedded within a visual scene. In particular, we used a pictorial context which contained cues for verticality (e.g. the tubes between which the football travelled, the background hills, and the horizon) and was overall deliberately ambiguous as to the gravitational environment. For example, the scene could be interpreted by participants as either a desert scene on Earth, or the surface of another planet, however no explicit explanation was given about these factors. Future research could consider whether the gravitational bias under Mars gravity persists in a virtual environment which is clearly Earth-based (for example, a room or indoor scene), or whether performance is similar for both Earth and Mars accelerations embedded in a blank context.

Our results demonstrate a very rapid adaptation to an altered visually simulated environment. This might be in contrast with previous findings showing that individuals tend to rely on the Earth-based internal model of gravity for perceptual judgements, even when physically exposed to discrepant gravitational contexts. For example, Mcintyre, Zago, Berthoz, and Lacquaniti (2001) reported that astronauts timed the interception of constantly accelerating objects according to Earth gravity while in weightlessness, and only adjusted to the weightless environment after days. On Earth, participants who are shown objects accelerating constantly, i.e. as in a weightless environment, mis-time the interception, in anticipation of natural gravity (Zago & Lacquaniti, 2005). Moreover, Zago et al. (2005) found that performance on simulated 0g trials rapidly improved by the fourth repetition, however while performance improves with practice, it never reaches the performance level for objects accelerating according to Earth gravity. Similarly, de Rugy et al. (2012) found that participants' performance in interception of constantly-accelerating objects was significantly worse than the interception of objects which accelerated according to natural gravitational and motion laws. Interestingly, however, performance in a 'reversed gravity' condition was similar to performance under the natural gravity condition. These findings suggested that while object interception relied on natural laws, these laws did not have to occur under an ecologically valid setting.

Taken together, the previous literature suggests that individuals rely on an internal model of gravity based on a 1g environment. Crucially, there are clear differences between previously reported and the present study. First, exposure to altered gravity is much more invasive affecting the entire body physiology. Second, participants in the present study provided pure perceptual judgements, rather than motor efferent outcomes. Importantly, many interception studies allowed participants to have feedback on their performance, i.e., successfully catching the ball. Participants' performance in the present study was unknown to them. Thus, adaptation to the altered Mars gravitational environment occurred in the absence of any additional motor, learning or performance feedback. Third, while de Rugy et al. (2012) showed that adaptation to a reversed, and therefore unusual, gravitational environment was possible, this adaptation occurred within a sparse environment, which did not by itself provide cues for gravity. By contrast, here we found poorer performance in the upwards conditions, however the virtual environment contained cues for the expected direction of gravity, possibly explaining the divergence in findings. Moreover, we were specifically interested in whether participants could adapt to a gravitational environment where gravity was present, but differed from Earth gravity, contrasting with previous research which has used either 1g, -1g, or constant acceleration (0g) trials. Overall, therefore, we believe that our findings provide novel evidence for fast adaptation to simulated altered gravitational environments.

As human space exploration is no longer a far distant future, understanding whether we can adapt to new gravitational contexts is crucial. Our findings suggest that, contrary to previous results, people might adapt to novel gravity environments. Critically, this occurred rapidly after only a few minutes of habituation to the new gravity. Thus, the human brain can adjust to gravitational environments other than Earth alone.

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Conflict of interest

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Author Contributions

M.G. and C.L. performed experiments; M.G. and A.T. analysed data; E.R.F., M.G. and A.T. conception and design of research; E.R.F., M.G. and A.T. interpreted results of experiments; E.R.F., M.G. and A.T. edited and revised manuscript; all authors approved final version of manuscript.

Figure Caption

Figure 1. Experimental conditions and results.

A: Participants saw a virtual environment depicting the surface of a planet and two tubes through which a ball moved downwards (gravity congruent) or upwards (gravity incongruent). B: Psychometric functions fitted across all participant data. C: Slope Ratios for each experimental condition. D: Point of Subjective Equality (PSE) values for each experimental condition.