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1 2 3 **Gravity Prior in Human Behaviour:** 4 a Perceptual or Semantic Phenomenon? 5 6 Maria Gallagher^{1,2}, Agoston Torok³, Johanna Klaas¹ & Elisa Raffaella Ferrè¹ 7 8 9 ¹ Department of Psychology, Royal Holloway University of London, Egham, UK 10 ² School of Psychology, Cardiff University, Cardiff, UK ³ Brain Imaging Centre RCNS, Magyar tudosok krt 2, Budapest, 1111, Hungary 11 12 13 14 15 16 17 Corresponding Author: 18 Elisa Raffaella Ferrè 19 Department of Psychology 20 Royal Holloway University of London 21 Egham 22 Surrey 23 TW200EX 24 UK 25 e.ferre@rhul.ac.uk 26

1 Abstract

Humans show a gravitational advantage in perception: we are more precise at judging
the speed of downwards-moving than upwards-moving objects, indicating that gravitational
acceleration is an internalised prior. However, it is unclear whether this gravity prior is based
on purely perceptual cues or whether it can incorporate semantic knowledge. Previous
research has used only objects which are known to comply with gravity, possibly confounding
semantic and perceptual cues. Here we have addressed this question by asking participants
to judge the speed of objects typically moving coherently with gravity (ball) or against it
(rocket). Our results showed a perceptual advantage for falling stimuli, irrespective of object
identity, suggesting the gravity prior is based on perceptual cues.

11

2 Keywords

13 Graviception, gravity prior, perception, visual motion.

1 Introduction

2 Since the beginning of time, all living organisms have evolved under a constant terrestrial gravitational field of approximately 9.81 m/s², known as 1g. On Earth, gravity is 3 always there; it is therefore not surprising that the physical constraints of Earth's gravity are internalised in the human brain to shape our perception and action (Indovina et al., 2005). For 5 instance, random accelerations are hardly perceived at all (Werkhoven et al., 1992), falling objects are expected to accelerate even when their velocity is constant (Zago et al., 2004), and observers misremember the location of moving objects in space (De Sá Teixeira, 2016). In addition, gravity can influence eye movements, with improved smooth pursuit of objects which move according to 1g versus objects which move according to weightlessness (0g), 10 reversed gravity (-1g) or hypergravity (2g) (Delle Monache, Lacquaniti and Bosco, 2015; 11 Jörges and López-Moliner, 2019). We are so exceptionally adapted to terrestrial gravity, that 12 a gravitational advantage appears in perceptual judgements: observers are more precise in 13 judging the speed of objects accelerating downwards compared to upwards (Bosco, Carrozzo 14 and Lacquaniti, 2008; Moscatelli and Lacquaniti, 2011; Torok et al., 2019). The neural 15 correlates of this gravitational advantage have been identified in a widespread brain network 16 including the insular cortex, temporoparietal junction, premotor and supplementary motor 17 areas, middle cingulate cortex, postcentral gyrus, thalamus and putamen (Indovina et al., 18 2005; Maffei et al., 2015). 19

The visual context seems to play a role in the gravitational advantage. For instance, while observers tend to anticipate the effects of gravity when intercepting objects, this is only the case when targets are embedded in a realistic visual scene (Miller *et al.*, 2008). Accordingly, interception performance is similar under reversed and natural gravity conditions when targets are presented in a blank scene (Miller *et al.*, 2008). Delle Monache, Lacquaniti and Bosco (2015) reported a key role of gravitational acceleration in guiding smooth pursuit and saccadic eye movements when target motion was embedded in a realistic context compared to a neutral background. Moreover, the gravitational advantage may depend on the

- 1 gravity within the visual scene: when the environment is tilted relative to physical gravity,
- 2 participants demonstrate an advantage for stimuli which move downwards according to the
- 3 direction of the scene (Moscatelli and Lacquaniti, 2011).

4 The gravitational advantage can be considered a proxy for the internalised gravity prior. Previous research has assumed that this prior is built from sensory experience of Earth 5 gravity throughout the lifespan (Jörges and López-moliner, 2017). However, it is not yet clear 6 whether the gravity prior is purely made of constant exposure to online multimodal – vestibular, visual, proprioceptive, and visceral – gravitational signals, or whether it may also be built on semantic knowledge about physical gravitational constraints. Critically, in all previous studies (e.g. Moscatelli & Lacquaniti, 2011; Torok et al., 2019; Zago et al., 2004), observers have 10 been presented with objects which are most often seen to comply with the laws of gravity in 11 12 the real world, such as a ball. Thus, it could be possible that the gravitational advantage was influenced by implicit semantic knowledge and expectations that a ball is normally falling down. 13 14 rather than accelerating upwards.

Here we investigated whether participants would show the gravitational advantage when observing objects which move congruently with gravity and objects which can move against gravity. Participants judged the duration of motion for a ball or rocket moving downwards with or upwards against the terrestrial gravity vector in a virtual environment. A perceptual-based gravity prior predicts that the gravitational advantage would be present for both gravity-congruent and gravity-incongruent objects. However, a semantic-based gravity prior instead predicts that participants would show the gravitational advantage only for the ball, while performance would be similar in upwards and downwards conditions when viewing the rocket.

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1 Methods

2 Participants

Twenty-four participants (four male, mean age = 20.25, SD = 1.67) were recruited from
the Royal Holloway University subject pool. Seven participants were left-handed, while the
remaining 17 participants were right-handed according to their Edinburgh Handedness
Questionnaire (Oldfield, 1971) results. Participants had no history of neurological, psychiatric,
or vestibular disorders, and all had normal or corrected-to-normal vision. Written informed
consent was obtained before commencing the experiment. The study received ethical
approval from Royal Holloway University of London and was conducted in line with the
Declaration of Helsinki.

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2 Stimuli and Procedure

Before the experiment, participants received detailed instructions. Participants viewed
a virtual environment on a liquid crystal display (LCD) computer monitor (LG Flatron, 17 inch,
60Hz refresh rate) while seated with a chin rest 40cm away from the screen. A cone was fitted
to the screen to occlude additional cues from the external environment. The cone measured
30cm in diameter at the participant end, and approximately 25cm at the screen end. The
centre of the cone was aligned vertically and horizontally to the centre of the screen.

19 The virtual environment was rendered in Unity 3D (2017.3.0f3, Unity Technologies, 2018) and consisted of the surface of a planet with sand dunes and a night sky (Figure 1A). 20 The virtual environment measured 34x25.5cm with 1024x768 resolution. Accordingly, 21 participants saw approximately 56.62% of the virtual environment through the cone. A red dot 22 23 (2mm diameter) marked the centre of the environment and participants were asked to fixate 24 on this point during the task. Two black tubes (1.5cm diameter, 5cm length) were placed in the sky and ground along the central midline, creating a path length of 15.5cm. A rugby ball 25 or rocket (both approx. 1.5cm in length) accelerated upwards or downwards between the two 26

1 black tubes (Figure 1A). The magnitude of acceleration matched the drag of Earth gravity 2 (9.81m/s²).

3 We used a factorial design combining Motion Direction (Upward and Downward) and Object Type (Rocket and Ball) in four different blocks (i.e., Rocket moving Upwards; Rocket moving Downwards; Ball moving Upwards; Ball moving Downwards). Blocks were presented 5 in a counterbalanced order across participants. Each block started with a learning phase in which participants were asked to memorise a reference speed of 3.57m/s (duration = 800ms; 60 reference trials per block, inter-stimulus interval (ISI) = 1300ms). During the test phase, participants had to judge after each trial whether the object was moving faster or slower than 10 the reference trials. Participants were instructed to press the left arrow on a keyboard if the object was moving faster and the right arrow if it was moving slower than the reference trials. 11 12 The initial speed of the object during test trials was manipulated between 9.53m/s and 0.05m/s in nine steps resulting in nine different motion durations (0.5s, 0.65s, 0.7s, 0.75s, 0.80s, 0.85s, 13 14 0.90s, 0.95s, 1.10s) as in previous studies (Moscatelli & Lacquaniti, 2011; Torok et al., 2019). Each motion duration was presented 20 times, resulting in 180 test trials per block with ISI = 15 2300ms. Thus, we used 2 Motion Directions * 2 Object Types * 9 Motion Durations * 20 16 Repetitions for a total of 720 test trials across the whole experiment. 17

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19 Data Analysis

Analyses were carried out in R software (R Core Team, 2017) using Ime4 (Bates *et al.*, 2015) and MERpyschophysics (Moscatelli *et al.*, 2012). Four participants were excluded from analysis as they showed poor performance (quantified by $max_p - min_p < .5$, where *p* is the proportion of "slower" responses at the fastest (max) and slowest (min) test stimuli speeds). For each participant and condition, we computed the number of trials in which the test trial was considered slower than the reference, with slower coded as 1 and faster as 0.

- 1 Missed responses, where the participant responded faster than 300ms or slower than 2s, were
- 2 not included in the analysis (total = 3.21%).
- The probability of a 'slower' response was calculated for each motion duration.
- 4 Psychometric functions with probit link were constructed, based on previous studies
- 5 (Moscatelli & Lacquaniti, 2011; Torok et al., 2019):

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

7 Precision was given by the β_0 parameter, while the point of subjective equality (PSE)

8 was determined as:

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

The delta method (Casella and Berger, 2002) was used to estimate the 95%

11 confidence intervals for the point of subjective equality (PSE) for each subject. Discrimination

12 thresholds, ΔT , or just-noticeable differences (JND) were determined by:

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

14 where $T_{0.25}$ and $T_{0.75}$ are the motion duration values matching the 0.25 and 0.75 probabilities

15 of a "Slower" response. This ΔT was then used to calculate the Weber fraction:

$$WF = \frac{\Delta T}{T_{standard}}$$

Both PSE and ΔT (JND) were fitted with General Linear Mixed Models (GLMM) to

18 address the effect of motion direction (Downwards vs Upwards) and object type (Rocket vs

19 Ball) on the population level. The GLMM included a single random intercept parameter, which

20 was estimated for each subject and parameters for the fixed effects for the two object types,

21 the two motion directions, the nine motion durations, and their interactions. For each

22 parameter, we computed Wald statistics:

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

- where is the estimated parameter and SE is respective standard error. the Slope
- 3 parameters were normalised to the downwards motion's slope.
- 4 We also estimated the Bayes Factor (BF) from the Bayesian information criterion (BIC)
- 5 of the null model and GLMM as:

$$BF = exp[ii](\frac{BIC_{null} - BIC_{GLMM}}{2})$$

7 Conventional interpretations of the Bayes Factor were used, with values < 0.3

8 indicating moderate evidence for the null hypothesis, and values > 3 moderate evidence for

9 the alternative hypothesis (Lee & Wagenmakers, 2013).

1 Results

Figure 1B shows the average psychometric function pooled across participants.

Slopes for downwards motion are generally steeper than those for upwards motion across

4 both object types, as predicted by the gravitational advantage (Moscatelli & Lacquaniti, 2011).

JNDs were significantly lower in downwards versus upwards motion conditions (Wald $\chi^2 = 9.62$, p < .01) (Table 1). No significant difference in JND between object types (Wald $\chi^2 = 0.15$, p = .70), and no interaction (Wald $\chi^2 = 0.68$, p = .41) were found. The Bayes' Factor was 0.05 (moderate evidence for the null hypothesis). These results suggest that object identity is not incorporated into the internal model of gravity.

Table 1. JND values (ms). Mean (SE)

Object Type	Motion Direction	
	Upwards	Downwards
Ball	120.16 (6.27)	104.36 (5.00)
Rocket	115.52 (5.96)	106.67 (5.18)

PSEs were significantly different between downwards and upwards motion conditions (Wald χ^2 = 32.34, p < .001), with lower PSEs for downwards vs upwards motion (Table 2). A significant difference was also found between object types (Wald χ^2 = 34.19, p < .001), with lower PSEs for the ball versus rocket. A significant interaction between motion direction and object type was also found (Wald χ^2 = 18.14, p < .001), with the lowest PSE for the rugby ball in the downwards motion condition.

Table 2. PSE values (ms). Mean (SE)

Object Type	Motion Direction	
	Upwards	Downwards
Ball	796.48 (12.47)	766.14 (10.29)
Rocket	795.92 (12.04)	798.48 (11.21)

1 Discussion

2 Gravity is a ubiquitous cue implicated in a range of human behaviours, such as object interception, verticality and motion perception (Zago et al., 2004; de Rugy et al., 2012; 3 Lacquaniti et al., 2015). A gravitational advantage has been reported, whereby individuals are more precise at judging the motion duration of objects which fall congruently with gravity 5 (Moscatelli & Lacquaniti, 2011; Torok et al., 2019). These findings suggest that observers use an internalised gravity prior when forming perceptual judgements. However, it is unclear whether the internalised gravity prior is based on purely perceptual information, or whether it also incorporates semantic knowledge regarding a particular object's usual interaction with gravity. Here we investigated whether participants would exhibit the gravitational advantage 10 for objects which typically comply with gravitational laws and those which move against 11 The gravitational advantage was present for downwards motion conditions 12 gravity. independently from object types. Thus, the gravity prior does not seem to be built on semantic 13 knowledge about the physical constraints of gravity. 14

15 Our results suggest that the gravity prior is predominantly based on perceptual cues, rather than semantic knowledge regarding objects. A perceptual-based prior may incorporate knowledge that the gravity vector is typically aligned with the body axis, as the head is usually 17 18 upright (Lacquaniti et al., 2015; Mittelstaedt, 1983). For instance, individuals in a weightless environment where a physical gravitational reference is absent therefore revert to basing their 19 perception of verticality on the location of the body axis (de Winkel et al., 2012). Importantly, 20 cues from the context also seem crucial for anticipating the effects of gravity (Miller et al., 21 22 2008; Moscatelli and Lacquaniti, 2011; Delle Monache, Lacquaniti and Bosco, 2015). Accordingly, visual cues for the direction of verticality, such as the orientation of objects or the 23 location of the sky and ground, may also play a key role in the gravity prior.

Here we found that the gravitational advantage was similar for both objects which can move against gravity and those which typically move with gravity, suggesting no influence of object identity, or semantics in general, on the precision of speed judgements. Curiously

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however, we found a significant interaction between object type and movement direction on the point of subjective equality, with participants perceiving the downwards moving ball as faster than the other conditions. These findings may contrast with previously-reported results 3 suggesting that upwards-moving stimuli may be perceived as faster than downwards-moving 5 ones, particularly at higher speeds (Thompson and Stone, 1997). However, differences between the stimuli and methods may account for this discrepancy: specifically, here we displayed objects moving within a scene, while previous studies have used simple gratings. 8 Thus, the additional context provided by the virtual environment may have influenced participants' speed judgements beyond what may be predicted by simply low-level visual features. Recently, Moscatelli et al. (2019) suggested that biases in perceived speed may be 10 influenced by priors for motion dynamics within a scene, which may depend on factors such 11 as gravity and the scene medium (i.e. water or air). Accordingly, downwards moving targets 12 13 with high luminance contrast were perceived as faster than upwards moving and lower contrast targets (Moscatelli et al., 2019). Similarly, semantics concerning the object may also 14 have influenced the expected motion dynamics of the scene, affecting speed biases 15 independently from the gravitational advantage. Thus, the precision of speed judgements 16 17 depends solely on a prior for gravity, resulting in a similar gravitational advantage for both gravity-congruent and incongruent objects. By contrast, biases in speed judgements may arise 18 from broader scene dynamics, and may subsequently be affected by object identity. 19 Consequently, a downwards moving ball is perceived as faster than an upwards moving one, 20 while knowledge that rockets can be propelled upwards results in similar speed judgements 21 in both upwards and downwards conditions. 22

To avoid discrepancies in visual saliency and to closely match previous studies (Moscatelli and Lacquaniti, 2011; Torok *et al.*, 2019), we presented both the rugby ball and rocket at the same size and scale within the virtual environment. It may be possible that the rocket condition was significantly less realistic than the rugby ball condition, considering that a real rocket would be many times larger than we presented here. A rocket was chosen to

emphasize semantic differences. While this may have resulted in less realism for the rocket condition, people have clear semantic knowledge concerning the usual movement trajectories of a rocket compared to a ball. However, an open question remains whether differences in gravitational bias are present when objects are presented with greater realism (i.e., correct scaling within the virtual environment). It is also important to note that while rockets can move against gravity, they do not move at gravitational acceleration. Here, we ensured that the acceleration of the objects was identical in both upwards and downwards conditions to closely match previous studies of the gravitational advantage (Moscatelli and Lacquaniti, 2011; Torok et al., 2019). Future studies might focus on whether the gravitational advantage would be modulated if the rocket was presented with a more realistic upwards acceleration profile.

Evidence for the role of the gravity prior in perception is growing. Investigating which factors influence gravity-related perceptual judgements is therefore an expanding area of research. While previous studies have found that perception and action is more precise for objects obeying the laws of gravity, the role of object-related information has largely been neglected. Here we found that participants exhibited the same gravitational bias whether observing objects which typically obey gravitational laws or those which typically violate them. Thus, our findings suggest that the gravity prior is largely based on perceptual information, rather than semantic knowledge of the effect of gravity on objects.

1 References

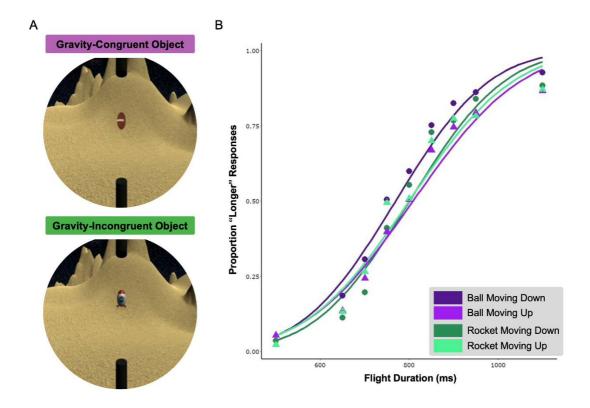
- 2 Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015) Fitting Linear Mixed-Effects Models
- 3 Using Ime4. J. Stat. Softw., **67**, 1–48.
- 4 Bosco, G., Carrozzo, M., & Lacquaniti, F. (2008) Contributions of the human temporoparietal
- 5 junction and MT/V5+ to the timing of interception revealed by transcranial magnetic
- 6 stimulation. *J. Neurosci.*, **28**, 12071–12084
- 7 de Rugy, A., Marinovic, W., & Wallis, G. (2012) Neural prediction of complex accelerations
- 8 for object interception. *J. Neurophysiol.*, **107**, 766–771.
- 9 De Sá Teixeira, N.A. (2016) The visual representations of motion and of gravity are
- 10 functionally independent: Evidence of a differential effect of smooth pursuit eye
- 11 movements. *Exp. Brain Res.*, **234**, 2491–2504.
- 12 de Winkel, K.N., Clément, G., Groen, E.L., Werkhoven, P.J. (2012) The perception of
- verticality in lunar and Martian gravity conditions. *Neurosci. Lett.*, **529**, 7–11.
- 14 Delle Monache, S., Lacquaniti, F., & Bosco, G. (2015) Eye movements and manual
- 15 interception of ballistic trajectories: effects of law of motion perturbations and
- occlusions. *Exp. Brain Res.*, **233**, 359–374.
- 17 Indovina, I., Maffei, V., Bosco, G., Zago, M., Macaluso, E., & Lacquaniti, F. (2005)
- 18 Representation of visual gravitational motion in the human vestibular cortex. Science,
- **308**, 416–419.
- 20 Jörges, B. & López-moliner, J. (2017) Gravity as a Strong Prior: Implications for Perception
- and Action. Front. Hum. Neurosci., 11, 1–16.
- 22 Jörges, B. & López-Moliner, J. (2019) Earth-Gravity Congruent Motion Facilitates Ocular
- 23 Control for Pursuit of Parabolic Trajectories. Sci. Rep., 9, 1–13.
- 24 Lacquaniti, F., Bosco, G., Gravano, S., Indovina, I., La Scaleia, B., Maffei, V., & Zago, M.

- 1 (2015) Gravity in the Brain as a Reference for Space and Time Perception. *Multisens*.
- 2 Res., 28, 397–426.
- 3 Lee, M.D. & Wagenmakers, E.J. (2013) Bayesian Cognitive Modeling: A Practical Course.
- 4 Maffei, V., Indovina, I., Macaluso, E., Ivanenko, Y.P., Orban, G.A., & Lacquaniti, F. (2015)
- 5 Visual gravity cues in the interpretation of biological movements: Neural correlates in
- 6 humans. *Neuroimage*, **104**, 221–230.
- 7 Miller, W.L., Maffei, V., Bosco, G., Iosa, M., Zago, M., Macaluso, E., & Lacquaniti, F. (2008)
- 8 Vestibular Nuclei and Cerebellum Put Visual Gravitational Motion in Context. J.
- 9 *Neurophysiol.*, **99**, 1969–1982.
- 10 Mittelstaedt, H. (1983) A new solution to the problem of the subjective vertical.
- 11 *Naturwissenschaften*, **70**, 272–281.
- 12 Moscatelli, A. & Lacquaniti, F. (2011) The weight of time: Gravitational force enhances
- discrimination of visual motion duration. *J. Vis.*, **11**, 1–17.
- 14 Moscatelli, A., Mezzetti, M., & Lacquaniti, F. (2012) Modeling psychophysical data at the
- population-level: The generalized linear mixed model. J. Vis., **12**, 26–26.
- 16 Moscatelli, A., La Scaleia, B., Zago, M., & Lacquaniti, F. (2019) Motion direction, luminance
- 17 contrast, and speed perception: An unexpected meeting. J. Vis., 19, 1–13.
- 18 Oldfield, R.C. (1971) The assessment and analysis of handedness: The Edinburgh
- inventory. *Neuropsychologia*, **9**, 97–113.
- 20 R Core Team (2017) R: A language and environment for statistical computing.
- 21 Thompson, P. & Stone, L.S. (1997) Up-Down Asymmetries in Speed Perception. *Perception*,
- **26**, 6–6.
- 23 Torok, A., Gallagher, M., Lasbareilles, C., & Ferrè, E.R. (2019) Getting ready for Mars: How
- the brain perceives new simulated gravitational environments. Q. J. Exp. Psychol., 72,

- 1 174702181983996.
- 2 Unity 3D [Computer Software] (2018). Retrieved from https://unity.com/
- 3 Werkhoven, P., Snippe, H.P., & Toet, A. (1992) Visual Processing of Optic Acceleration.
- 4 *Vision Res.*, **32**, 2313–2329.
- 5 Zago, M., Bosco, G., Maffei, V., Iosa, M., Ivanenko, Y.P., & Lacquaniti, F. (2004) Internal
- 6 Models of Target Motion: Expected Dynamics Overrides Measured Kinematics in
- Timing Manual Interceptions. *J. Neurophysiol.*, **91**, 1620–1634.

1 Figure Caption

2



4 Figure 1.

5 A) Participants viewed a virtual environment depicting a planet. A rugby ball (top) or rocket

(bottom) moved upwards against or downwards with gravity. B) Average psychometric

7 function for each object type and motion direction pooled across participants.

8

1 Declarations

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6

7 Conflict of interest

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

10

11 Availability of data and material

12 All data and material are available from the authors on request.

13

14 Code availability

15 All analysis and stimulus presentation codes are available from the authors on request.

16

17 Author contributions

- 18 M.G. and J. K. performed experiments; M.G. and A.T. analysed data; E.R.F., M.G. and A.T.
- 19 conceived and designed the research; E.R.F., M.G. and A.T. interpreted the results of the
- 20 experiments; E.R.F., M.G. and A.T. edited and revised the manuscript; all authors approved
- 21 the final version of the manuscript.

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