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Short Communication

Human movements don’t look the same in a tilted world: Gravitational constraints influence the perception of biological motion.

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Abstract

Here we investigated whether gravitational constraints influence the interaction of visual, proprioceptive and vestibular cues for Biological Motion Perception (BMP). Participants were asked to distinguish between plausible and random point-light movements, while passively placed in either an upright or a tilted body orientation using a human 3D tilting table, leading to different gravitational signals transmitted by the visual, proprioceptive and vestibular systems. Participants were overall faster in distinguishing plausible point-light movements than random movements. Critically response times for biologically plausible point-light movements - but not for random movements - were significantly prolonged in the tilted body orientation. Our results suggest that BMP depends not only on the spatial-temporal cues embedded in a point-light movements dictated by gravity, but also rely on the congruency between current gravitational signals detected by the sensory systems and our previous knowledge of terrestrial gravity.

Statement of Relevance

As mankind is preparing for a new space age, understanding how gravity influences human behavior and cognition has never been more pressing. The direction and magnitude of the Earth's gravitational acceleration has remained constant since the Earth's formation, thus all living organisms have evolved to survive in a terrestrial gravitational field. Although we cannot consciously feel gravity, it has an impact in our life: it affects how we move and interact with the external environment. The signals from the vestibular system in the inner ear are continuously combined with visual and proprioceptive cues to help us in maintaining a stable representation of the world. Here we placed participants in a tilted body orientation and were able to determine that a conflict between prior gravitational knowledge and what was actively sensed significantly affected human biological movement perception. Humans suffer changes in perception under altered-gravity conditions that may potentially compromise performance levels during spaceflight.

Introduction

Gravity is always there: *it is stable, it is permanent, and it is unchanging*. It's hard to imagine a more fundamental and ubiquitous aspect of life on Earth than gravity. That is, gravitational signals influence our behaviour much more pervasively that we have thought. The physical constraints of Earth's gravity are internalized in the human brain (Zago & Lacquaniti, 2005). Humans build a model of terrestrial gravity by integrating visual, vestibular and proprioceptive cues, as well as, semantic knowledge and past-experiences (Lackner & DiZio, 2005; Lacquaniti *et al.*, 2015). We all exploit this internal model of gravity while, for example, intercepting a falling object or while making spatial-temporal judgements (Lacquaniti *et al.*, 2015).

Biological Motion Perception (BMP) involves recognising movements that are originated by a biological human agent (Johansson, 1973). It may be therefore unsurprising that BMP depends on the amplitude and frequency of the moving agent's limbs, which are governed by the physical constraints imposed by terrestrial gravity. Gravity dictates how the body must interact with the ground for successful movements (Jorges & Lopez-Moliner, 2017). Accordingly, reversing the gravitational cues impacts how the local kinematics of bodily movements are perceived (Chang & Troje, 2008). BMP is fastest when the human-like stimulus is upright whereas it is dramatically slower once inverted (Troje & Westhoff, 2006), suggesting a fundamental, yet still unexplored, role played by gravity in BMP.

Here we investigated the contribution of *online* gravitational signals to BMP by asking participants to detect human biological motion vs control stimuli in which no human features were present (Pavlidou *et al.*, 2014b) while passively placed in an upright or in a tilted body orientation. Manipulating the body orientation with respect to the terrestrial gravitational vector reduces the reliability of vestibular cues (Alberts *et al.*, 2016). Although both orientations require the brain to integrate visual, proprioceptive and vestibular signals and compare them with prior knowledge about terrestrial gravity, when the body is tilted vestibular cues are no longer very accurate. This might trigger a conflict between expectations and actual sensory signalling. Here, we investigated whether a conflict between the internalised prior knowledge of terrestrial gravity and the online gravitational sensory information affect BMP. We hypothesised that the online gravitational signals triggered by the tilted body orientation may generate differences in sensory integration ultimately modulating BMP.

Materials and Methods

Participants

Twenty-four healthy participants volunteered to take part in the study (twenty females; mean age 21.9 ± SD, ± 5.4 years). All participants had normal or corrected-to-normal vision and no history of neurological or psychiatric disorders. The sample size was *a priori* decided based on a power analysis with F = 4.3, $\alpha = 0.05$ and power = 0.96, assuming a medium effect size (f=0.40) with moderate correlation between measurements (0.5) (G*Power; (Faul *et al.*, 2007)). The setting specification of the effect size was as in GPower 3.0. Written informed consent was obtained from all participants, and the study was approved by the Royal Holloway University of London Human Research Ethics committee and complies with the tennets of the Declaration of Helsinki.

Point-light-display animations and Procedure

Point-light-display animations were generated by placing sensors attached to the main joints of human actors (head, shoulders, elbows, wrists, hips, knees, and feet) and recording their movements using a motion tracking system (MotionStar; Ascension Technology, Burlington, VT; (Lange & Lappe, 2007)). These joints were represented by 14 small light grey dots (5 x 5 pixels) against a dark grey background. Stimuli were manipulated offline using MATLAB (MathWorks, Natick, MA). Movements were cut into segments representing one cycle of the movement, lasting 1000 ms. The point-light-display animations used in the study depicted six different movements: walking, jumping, skipping forward, skipping side to side, raised legs, and running. All stimuli were viewed from the front, facing the participants' to exclude any non-specific, visual-spatial and attentional effects. Each stimulus was manipulated to create two movement conditions, i.e., plausible and random (example videos are available online as Supplementary Material), while keeping low-level visual information constant (Figure 1A). The plausible movement condition involved movements in their original form as recorded. Their random counterparts, which represent our control stimuli, were created by varying the spatial position of all point-light dots within the field of the original human figure (Grossman *et al.*, 2000; Pavlidou *et al.*, 2014b). This procedure is well-known to destroy the spatial configuration of the human figure while keeping the overall net movement of the dots unchanged.

Each trial started with a light grey fixation cross on a dark grey background for a duration of 500 ms, followed by the presentation of a point-light animation for a duration of 1000 ms (Figure 1A), after which participants had to judge whether the movement observed was plausible or random using a button press. Participants were instructed to respond only after the point-light animation disappeared. The maximum duration of the response window was 1000 ms (maximum time per trial was 2500 ms). Once participants responded a new trial begun. Point-light animations (8.4 x 3.4 cm) were presented via an Oculus Rift CV2 (Oculus VR, California, USA) head mounted display by mirroring the laptop screen with a refresh rate of 60 Hz as a virtual screen using the BigScreen Beta application (Version 0.34.0). For each body orientation the virtual screen was placed in the central region of each participant's visual field. The visual presentation was controlled, and responses were collected, using MATLAB. For the duration of the experiment, participants held the response pad with their right hand and responded using either their left index (plausible movements) or middle (random movements) finger. Participants trained (10 trials) before the start of the actual experiment to familiarize themselves with the experimental procedures.

For the duration of the experiment participants were comfortably placed on a human 3-D inversion table (Teeter Company, Washington, USA) in either a 0° (upright orientation) or a 45° angle (tilted orientation; Figure 1B). In the former condition, the body and vestibular organs are congruent with the direction of terrestrial gravitational acceleration, while in the latter they are not aligned with the perpendicular gravity vector. This manipulation allows to reliably mimic gravitational alterations in controlled lab-settings. For each body orientation, participants completed 84 trials (maximum time 2.91 min) with an equal number of plausible (n = 42) and random (n = 42) trials, presented in a random order. Body orientation was counterbalanced across participants.

Data Analysis

Mean reaction times (RTs) for correct responses and mean number of errors were calculated and presented separately for plausible and random movements for both body orientations (upright and tilted) using scripts written in R (version 3.6.1). Trials where no response was made and trials with RTs less than 200 ms, as well as, trials greater than the mean +2 standard deviation (SD) within each participant for each condition were discarded from further analysis. This resulted in the exclusion of 5.27% of all trials for the upright orientation and 4.96% for the tilted orientation. Statistical analysis for the raw RTs and number of errors was carried out using linear-mixed-effect models in R using the lme4 package (Bates *et al.*, 2015). Movement (plausible and random) and Body Orientation (upright and tilted) and their interaction were added as fixed effects, while a single random intercept parameter estimated for each participant was added as random effects, and used the likelihood ratio test to assess predictor significance.

To account for potential overdispersion induced by the low amount of errors, and therefore of the excess of zero values, we used the Poisson distribution for analysis of the number of errors (Smith & Faddy, 2016).

Results

Data were analysed using linear mixed-models. As expected, a significant effect of Movement ($F_{1,3721} = 26.0$, $p < .0001$; $\eta_p^2 = 0.007$) was observed with participants being overall faster in responding to plausible than random movements, as well as, a main effect of Body Orientation ($F_{1,3721} = 25.0$, $p < .0001$; $\eta_p^2 = 0.007$) with participants responding faster when in an upright versus a tilted orientation. More importantly, a significant interaction between Movement and Body Orientation ($F_{1,3721} = 4.0$, $p < .05$; $\eta_p^2 = 0.001$; Figure 1C) was observed. Post-hoc analysis using Bonferroni tests revealed significantly reduced RTs for plausible compared to random movements selectively for the upright orientation (p=<.0001). In contrast, plausible movements did not differ from random movements in the tilted orientation (p=0.162). Critically, a significant difference was observed for plausible movements (p=<.0001) between the two bodily orientation but not for the random movements (p=.192).

A similar analysis applied to the mean number of errors revealed a significant effect of Body Orientation ($F_{1,92} = 3.81$, $p < .05$; $\eta_p^2 = 0.047$) with participants making on average more errors in the tilted (mean ± SEM; plausible: 0.50 ± 0.24, random: 0.75 ± 0.30) versus the upright orientation (mean ± SEM; plausible: 0.33 ± 0.15, random: 0.33 ± 0.14) for both movements. In contrast, no significant effect of Movement ($F_{1,92} = 1.08$, $p > .05$; $\eta_p^2 = 0.014$) or a significant interaction between factors ($F_{1,92} = 0.40$, $p > .05$; $\eta_p^2 = 0.005$) was observed.

Discussion

We asked participants to evaluate point-light-displays as either biologically plausible or random while manipulating their body orientation with respect to terrestrial gravitational accelerations. Although participants could theoretically base their judgements selectively on the visual information derived from the stimulus, it appears that BMP was strongly affected by participants' current position with respect to gravity. As expected, participants were significantly faster in recognizing plausible versus random movements when in upright orientation (Troje & Westhoff, 2006), while no difference in RT's between plausible and random movements emerged in the tilted orientation. One may speculate that the tilted orientation could have potentially affected the performance on a broader level due to discomfort or disorientation. Critically response times for biologically plausible point-light movements - but not for random movements - were significantly prolonged in the tilted body orientation. Thus, our results suggest that BMP depends not only on the spatial-temporal cues embedded in a point-light movements dictated by gravity, but also rely on current gravitational signals.

Being upright benefits from the comfort of gravity: humans integrate visual, proprioceptive and vestibular signals in order to build an internalised model of gravity which allow us to maintain a stable representation of the external environment (Mergner & Rosemeier, 1998). When placed in a tilted orientation this stable representation is disturbed. Perceptual errors reflect the challenge for the brain to discriminate between prior knowledge of terrestrial gravity and what it is actively sensed by visual, proprioceptive and vestibular sensory modalities (Kheradmand & Winnick, 2017). This is likely to explain alterations in behaviour.

Interestingly, even though both biologically plausible and random stimuli involved biological kinematic cues recorded from actual movements, only plausible movements appeared to be strongly dependent on participants' actual position with respect to gravity. While, previous studies have demonstrated that the shape of the point-light-display plays no role, as long as the display is shown upright and not inverted (Shipley, 2003; Vallortigara & Regolin, 2006; Chang & Troje, 2008) it appears that the internal model of gravity seems to strongly interact with biologically relevant signals.

Neuroimaging evidence indicate that a widespread network of cortical and subcortical areas are involved in the discernment of gravity's influence on visual motion (Indovina *et al.*, 2005), which overlap with areas known to be involved in the observation and execution of movements (Grossman *et al.*, 2000; Rizzolatti & Craighero, 2004; Pavlidou *et al.*, 2014b). Activity in this network is elicited by both biologically plausible and random movements (Pavlidou *et al.*, 2014b), as well as, by biomechanically plausible and implausible movements (Pavlidou *et al.*, 2014a). However, the pattern of activation is stronger when the observed movement conforms to the experiences of the observer (Rizzolatti & Craighero, 2004; Pavlidou *et al.*, 2014b; a). Our ability to understand and infer the actions of other's is accomplished via motor resonance. That is, perceiving other's actions produces a similar brain response to that observed when we ourselves are able to perform the same action (Rizzolatti & Craighero, 2004). This suggests that the more plausible the kinematic cues of the observed movement are, the stronger the motor resonance. Future research may explore this question using biomechanically implausible movements (e.g., the arm or leg bends or extends in an unnatural way (Pavlidou *et al.*, 2014a)). This will clarify how gravity influences BMP when the amplitude and frequency of an agent's limbs goes beyond the physical contraints imposed by terrestrial gravity.

In conclusion, we have showed that gravity contributes to detection of biological movements. Importantly, only plausible human point-light movements are subject to the gravitational constraints imposed when our body does not align with the direction of gravitational acceleration. As mankind is preparing for a new space age understanding how gravity influence our perception of other's actions is essential.

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Competing interest

The authors confirm that they have no conflict of interest.

Author Contributions

A.P. and E.F. developed the concept of the study and designed the experiment; A.P. acquired the data; A.P. analysed data; A.P., J.L., and E.F. interpreted results; A.P. drafted the manuscript; A.P., J.L., and E.F. edited and revised the manuscript; A.P., J.L., and E.F. approved the final version of the manuscript.

Data Accessibility

Please contact the corresponding author for the raw data.

Abbreviations

BMP: Biological Motion Perception; RT’s: Reaction times.

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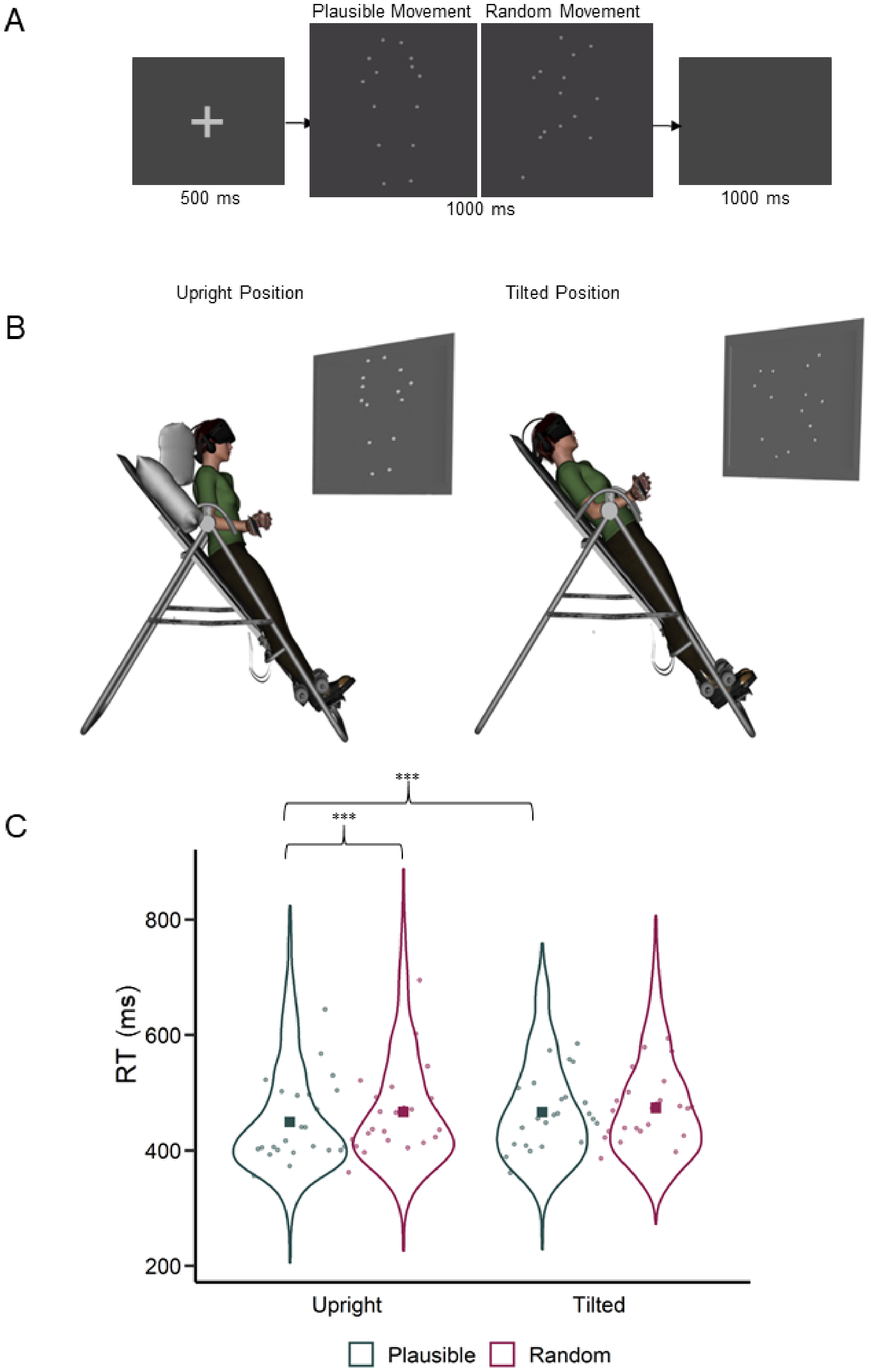
Figure. 1. Experimental setup and results. **(A)** Visual stimuli presented either a plausible or a random point-light-display movement. Each trial started with a fixation cross (500 ms), followed by either a plausible or a random movement (1000 ms), followed by a response window (maximum time 1000 ms) where participants had to indicate with a button press if the observed movement was either plausible (index finger) or random (middle finger). **(B)** Participants were placed on a 3D tilted table in either an upright (0°) or a tilted (45°) body orientation while wearing an Oculus VR headset. Visual stimuli were presented on a virtual screen and placed at the centre of participants' visual field. An upright body orientation with a plausible movement and a tilted body orientation with a random movement is shown here. **(C)** Violin plot represents the data distribution of reaction times in milliseconds for all participants calculated for plausible (dark green) and random (purple) movements for each body orientation (Upright and Tilted). The individual data points represent the mean reaction time of each participant (n=24), while the single square dot represents the mean reaction time for plausible (dark green dots) and random (purple dots) movements for each body orientation. *** denotes a significant difference between movements and body orientations.


A
Plausible Movement
Random Movement
500 ms
1000 ms
1000 ms
B
Upright Position
Tilted Position
C
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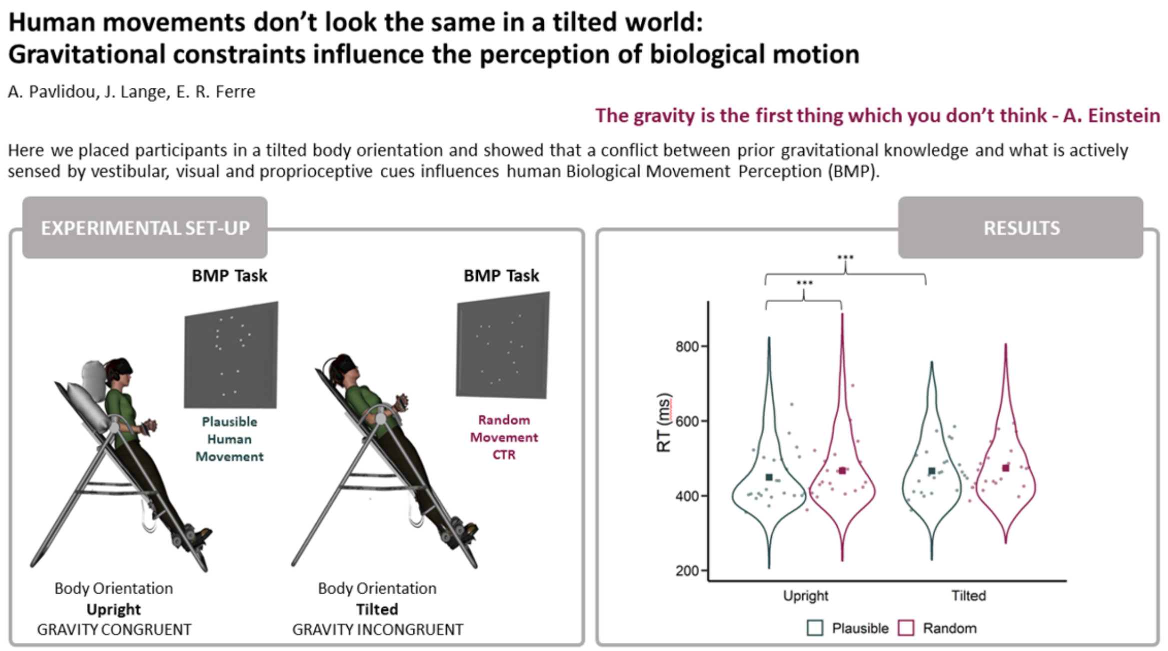
RT (ms)
800
600
400
200
Upright
Tilted
Plausible
Random

Graphical Abstract



Human movements don't look the same in a tilted world: Gravitational constraints influence the perception of biological motion

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The gravity is the first thing which you don't think - A. Einstein

Here we placed participants in a tilted body orientation and showed that a conflict between prior gravitational knowledge and what is actively sensed by vestibular, visual and proprioceptive cues influences human Biological Movement Perception (BMP).