Where is my hand in space?

The Internal Model of Gravity Influences Proprioception

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Abstract

Knowing where our limbs are in space is crucial for a successful interaction with the external world. Joint Position Sense (JPS) relies on both cues from muscle spindles and joint mechanoreceptors, as well as the effort required to move. However, JPS may also rely on the perceived external force on the limb, such as the gravitational field. It is well-known that the internal model of gravity plays a large role in perception and behaviour. Thus, we have explored whether direct vestibular-gravitational cues could influence JPS. Participants passively estimated the position of the hand while they were upright and therefore aligned with terrestrial gravity, or pitch-tilted 45° backwards from gravity. Overall participants overestimated the position of the hand in both upright and tilted postures, however the proprioceptive bias was significantly reduced when participants were tilted. Our findings therefore suggest that the internal model of gravity may influence and update JPS in order to allow the organism to interact with the environment.

Keywords: Vestibular system, proprioception, Joint Position Sense, gravity.

1. Introduction

Knowing the position of the limbs in space is crucial for successful interactions with the external world. Joint Position Sense (JPS) is primarily driven by proprioceptors, such as muscle spindles, indicating to the brain the orientation and position of the limbs and contributing to the execution of movements (1,2). In addition, external forces on the limb must be accounted for when performing particular movements: moving the arm upwards or lifting a heavy object, such as when you drink a cup of tea, requires additional effort to overcome terrestrial gravity (3,4). Our brain might integrate cues regarding these external forces to generate and update coherent JPS.

On Earth, gravity is a constant downwards acceleration of approximately $9.81 m/s^2$. All terrestrial organisms have evolved under this force, and most will be subject to gravitational acceleration throughout their entire lifespan. It’s hard to imagine a more fundamental and ubiquitous aspect of life on Earth than gravity. The vestibular otoliths – sophisticated receptors inside the inner ear – constantly detect the magnitude and direction of gravitational acceleration. When the head moves with respect to gravity, the vestibular otoliths shift with the direction of gravitational acceleration, moving hair cell receptors and signalling to the brain actual gravity. Vestibular signals are integrated with sensory inputs from vision, proprioception, and viscera to form an *internal model of gravity* (5–7).

Gravity is probably the most persistent cue for the brain, and its internal representation is one of the most pervasive signals for successful interactions with the environment. It might not be surprising therefore that gravity plays a substantial role in shaping our perception and behaviour. A gravitational advantage has been identified in human vision, whereby the perception of motion duration is more precise for objects falling according to gravity, versus objects moving against gravity (8–10). Eye movements are also more precise when tracking objects moving with normal gravity (1g), versus objects that move according to Weightlessness or Hypergravity (11,12). Finally, interception of objects is more precise when objects obey natural gravity, with performance under Weightlessness showing significant impairments (13,14). Together, these findings imply that gravitational acceleration is taken into account when interacting with the world, potentially in the form of a strong sensory *prior*, according to recent Bayesian frameworks (15–17).

We constantly interact with a terrestrial gravity environment and it might be possible that the internal model of gravity influences JPS. Studies indicate that changes in gravitational torque at the limb may bias JPS (18,19). Ettinger and Ostrander (19) reported an overshoot of approximately 2° when participants attempted to match a target angle when seated upright normally and when a small weight was applied to the arm. An undershoot was reported when participants were submerged in water, reducing the effect of gravitational torque on the arm. Similarly, participants experiencing Hypergravity during a parabolic flight consistently overshot reproduction of a target arm angle relative to terrestrial gravity, but undershot the target during Weightlessness (18). However, adding additional torque to the arm during Weightlessness returned performance to that of the terrestrial gravity condition (18). Importantly, the effort required to move the limb has been shown to contribute to JPS (20). Altering gravitational torque on the limb may therefore change the amount of effort required to move against gravity, resulting in overshoots, or an *upwards bias*, with increased gravity and undershoots with reduced gravity (18,19). Although there is general agreement that effort depends on the effect of gravitational torque on muscle spindles, whether an internal gravity representation influences JPS is still unclear.

Here we investigated whether the upwards bias in proprioception would be modulated when the head and body were passively tilted away from the gravitational vertical. In this posture, the reliability of vestibular otoliths signalling the position of the head with respect to gravity is reduced (21,22), modulating the internal model of gravity. Crucially, gravitational torque and joint angles at the wrist were identical between the upright and tilted conditions.

2. Material and Methods

(a) Participants

Eighteen participants (1 male, mean age=18.56, SD=0.89) completed the study. All participants were right-handed, assessed through their Edinburgh Handedness Inventory scores (23). Exclusion criteria were any history of neurological, psychiatric, or vestibular conditions. Participants were recruited from the Royal Holloway Psychology Subject Pool and received course credit for their participation.

(b) Procedure

Participants' posture was controlled using a human tilting table. Participants rested comfortably against the tilting table, with their legs secured using a brace (Figure 1A). In the Upright condition, the participants were upright in alignment with the gravitational vertical. In the Tilted condition, the participants were pitch-tilted 45° backwards from vertical. Body postures were passively set prior to commencing each condition, and the table remained stationary throughout the block. A within-subjects design was used, with the order of body posture counterbalanced across participants.

Hand position was controlled by a custom 3D-printed platform. Participants rested their left hand on the platform, with forearm and elbow supported by the tilting table armrest. The hand was secured to the platform with Velcro to prevent movements. The platform was mounted on a hinge, which enabled the experimenter to passively move the participants' hand at the wrist ±50° from horizontal in 10° steps. The right arm remained stationary on the tilting table armrest throughout the experiment.

Before each trial, the participant's hand was placed in a neutral horizontal position. At the start of the trial, the experimenter moved the participant's hand to a randomised position within 2s. An Oculus Rift CV1 was used to show a visual reference for their hand position, with random letters corresponding to each potential hand angle. The participant indicated the letter which corresponded to the sensed position of their hand. The hand was then returned to a neutral position and the next trial commenced. Each of the 10 potential postures was repeated three times, resulting in a total of 30 trials per condition.

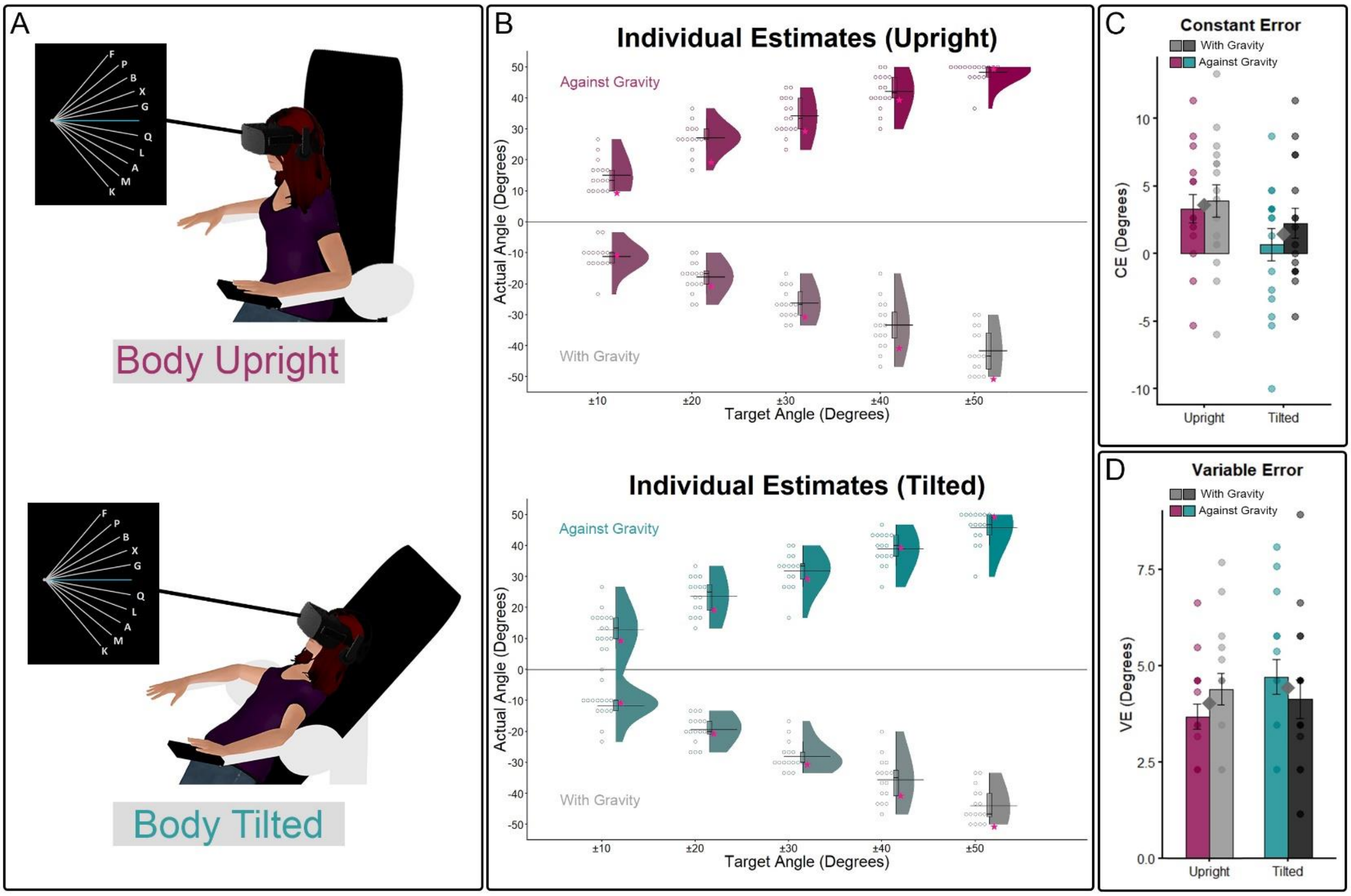

Figure 1. A) Setup and body postures. A 3D-printed platform supported the hand. An Oculus Rift CV1 showed references for hand location. B) Raincloud plot (24) indicating each participants' CE at each target angle in Upright (top) and Tilted (bottom) body postures. Target angles Against Gravity are shown above the horizontal line, while targets With Gravity are shown below the line. Long horizontal lines in each target angle indicate means, while pink stars indicate the actual target angle. C) CEs in Upright (pink and light grey) and Tilted (teal and dark grey) body postures. Coloured bars indicate target angles Against Gravity, while grey bars indicate target angles With Gravity. Points indicate individual estimates, while error bars reflect standard error. Diamonds indicate the overall means in each posture across all target angles. D) VEs in Upright and Tilted body postures. Colours and legend as Figure 1C.

(c) Data Analysis

For each trial, a difference value was calculated by subtracting the target angle from the response angle. Thus, negative values corresponded to an underestimate of hand position, or a *downwards bias*, while positive values corresponded to an overshoot, or *upwards bias*. For each target angle, Constant Error (CE) and Variable Error (VE) were calculated. CE was identified as the mean of the difference values, while VE was the standard deviation. “Against Gravity” CEs and VEs were calculated by taking the mean of target angles above 0°, while “With Gravity” CEs and VEs were the mean of target angles below 0°. Overall CEs and VEs were calculated by taking the mean across all target angles. Individual estimates for each hand angle in each Body Posture are shown in Figure 1B.

Two participants were excluded from analysis as their data were more than 2.5 standard deviations from the mean in at least one condition, resulting in a total sample size of 16 participants for analysis. Shapiro-Wilk normality tests revealed no significant deviations from normality assumptions once outliers were removed (all $p > .05$).

First, one-sample *t*-tests between the Overall CE and 0 were used to test for the presence of the upwards bias in Upright and Tilted postures. Next, repeated measures ANOVAs with factors Target Angle (Against Gravity vs With Gravity) and Body Posture (Upright vs Tilted) were used to investigate the effect of gravity and hand position on both CE and VE values (Figure 1C, 1D). Data were analysed in JASP version 0.11.1, figures were generated with R. Data are available as online supplementary materials.

3. Results

(a) Constant Error

As expected, the one-sample *t*-tests revealed significant upwards biases in both Upright ($t(15) = 5.84$, $p < .001$, Cohen’s $d = 1.46$ (95% CI [0.74, 2.16])) and Tilted ($t(15) = 2.67$, $p < .05$, Cohen’s $d = 0.67$ (95% CI [0.12, 1.20])) body postures.

A 2x2 repeated measures ANOVA was performed to investigate the effect of gravity and hand position on CEs. This analysis revealed no significant main effect of Target Angle on CEs ($F(1, 15) = 0.35$, $p = .56$, $\eta_p^2 = .02$). A significant main effect of Body Posture was found ($F(1, 15) = 32.71$, $p < .001$, $\eta_p^2 = .69$), with a lower CE in the Tilted (mean = 1.46, SD = 2.18) vs Upright (mean = 3.63, SD = 2.49) body posture (Figure 1C). No significant interaction was found ($F(1, 15) = 0.48$, $p = .50$, $\eta_p^2 = .03$).

(b) Variable Error

A 2x2 repeated measures ANOVA was performed to investigate the effect of gravity and hand position on VEs. This analysis revealed no significant main effect of Target Angle ($F(1, 15) = 0.03$, $p = .87$, $\eta_p^2 = .02$) or Body Posture ($F(1,15) = 0.88$, $p = .36$, $\eta_p^2 = .06$) on VEs (Figure 1D). No significant interaction was found ($F(1, 15) = 3.12$, $p = .10$, $\eta_p^2 = .17$).

4. Discussion

Gravity is accounted for when estimating the location of the limbs (4,18,19). Here we found a significant reduction in upwards bias when participants were tilted away from the gravitational vertical, manipulating vestibular-gravitational cues while maintaining the same gravitational torque at the limb itself. In addition, we found no change in variable errors, implying that gravitational cues may relate to JPS biases specifically. These findings suggest that the internal model of gravity can also impact JPS.

To estimate JPS, the brain may use a range of cues both from the joint itself, such as muscle spindles indicating muscle length and joint mechanoreceptors signalling the limits of joint position (2), as well as central signals, such as efferent motor commands and a sense of effort (20,26). Here we suggest that the internal model of gravity may also contribute to JPS in the absence of changes in gravitational torque at the limb. The internal model of gravity is formed of priors, such the knowledge that the body is usually upright (15), and online multimodal cues from vision, proprioception, viscera, and the vestibular system (5,22). Modulating these inputs to the internal model, for example through altered visual cues, or natural or artificial vestibular stimulation, may result in changes to gravity-related perception and action, such as object interception, estimates of verticality and motion duration (8,22,27). Crucially, our findings suggest similar impacts of gravity on proprioception and JPS.

Participants showed an upwards bias in JPS, which was reduced in the tilted compared to the upright posture. Previous studies have shown an upwards bias with increased gravity load at the limb (18,19), suggesting a link between the upwards bias and the sense of effort required to compensate for gravity. Accordingly, when tilted, the internal model of gravity is altered by noisier vestibular cues, resulting in a change in the estimated effort needed to lift the limb which may reduce the upwards bias.

The internal model of gravity is represented by a diverse network of cortical and subcortical regions, including insular cortex, temporoparietal junction, supplementary motor area, primary somatosensory and motor cortex, posterior thalamus, putamen, middle cingulate cortex, cerebellar vermis and vestibular nuclei (16,28–30). These regions show increased activity when viewing targets falling according to terrestrial gravity versus viewing objects accelerating according to reversed gravity (16,28,29). The core of this gravity network is centred on regions associated with vestibular processing, including the insula and regions in the parietal cortex (16,28,29,31), and also incorporates key regions encoding proprioceptive information, including somatosensory cortex and parietal operculum (16,30,32). The vestibular system is highly interlinked with the proprioceptive system, with a large number of thalamic neurons responding to both vestibular and proprioceptive inputs from the neck, arms, and trunk (33,34). The change in upwards bias may be driven by a modulation of activity in integrated proprioceptive and vestibular cortico-thalamic neurons, however direct evidence is necessary.

Previous studies have found direct influences of vestibular stimulation on JPS. Artificial vestibular stimulation induced biases in horizontal arm JPS (35). Similarly, Knox, Coppieters and Hodges (2006) reported increased constant errors in elbow JPS away from the illusory head tilt during artificial vestibular stimulation (36). Although vestibular cues are important for JPS, somatosensory and proprioceptive signals also play a vital role. For example, adding additional torque at the limb during active arm movements in Weightlessness resulted in kinematics near-identical to those found under terrestrial gravity conditions, despite significant differences in Weightlessness and Hypergravity when no additional torque was applied (18). In addition, vertical arm movements differ when the arm is under normal gravitational torque versus when the arm is supported before the onset of the movement, indicating an essential role of proprioceptive information to overcome gravity (37). While otolith cues are a principal signal for locating the body with respect to gravity (21,22), clinical reports from a somatosensory deafferented patient also suggested an important contribution of somatosensation in detection of small, slow-velocity body tilts (38); the patient was unable to detect body tilts of up to 18°, despite an unimpaired vestibular signalling. As we used a whole-body tilt, we cannot rule out a contribution of somatosensory and proprioceptive cues on JPS. Overall, however, it is likely that each of these sensory inputs to the internal model of gravity influences JPS to varying degrees.

Tilting participants away from the direction of gravity is purported to result in greater vestibular noise (21,22), and therefore reduced vestibular precision. Previous studies have suggested that being subjectively aware of body tilt may have different effects on perception (39). Awareness of body tilt resulted in greater variability, but similar bias, in verticality perception relative to upright, while not being aware of body tilt resulted in increased bias with no change in variability (39). In our study, participants were aware of the tilt away from upright, however, we found that tilting away from gravity resulted in changes in bias with no change in variability, in contrast to previous findings on the subjective vertical.

In sum, we report changes in JPS when participants are tilted away from the gravitational vertical. Specifically, constant error is reduced in a tilted versus upright posture. Importantly, these findings occurred during a passive task in the absence of any change in torque or joint angle at the wrist, suggesting that they are not simply due to actual physical motion against gravity, but rather result from modulations to an internal model of gravity.

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