

This is an Open Access document downloaded from ORCA, Cardiff University's institutional repository:<https://orca.cardiff.ac.uk/id/eprint/141714/>

This is the author's version of a work that was submitted to / accepted for publication.

Citation for final published version:

Gallagher, Maria, Kearney, Breanne and Ferrè, Elisa Raffaella 2021. Where is my hand in space? The internal model of gravity influences proprioception. *Biology Letters* 17 (6) , 20210115. 10.1098/rsbl.2021.0115

Publishers page: <http://dx.doi.org/10.1098/rsbl.2021.0115>

Please note:

Changes made as a result of publishing processes such as copy-editing, formatting and page numbers may not be reflected in this version. For the definitive version of this publication, please refer to the published source. You are advised to consult the publisher's version if you wish to cite this paper.

This version is being made available in accordance with publisher policies. See <http://orca.cf.ac.uk/policies.html> for usage policies. Copyright and moral rights for publications made available in ORCA are retained by the copyright holders.



Where is my hand in space?

The Internal Model of Gravity Influences Proprioception

Maria Gallagher^{1,2}, Breanne Kearney¹, Elisa Raffaella Ferrè¹

¹ Department of Psychology, Royal Holloway, University of London

² School of Psychology, Cardiff University

Corresponding Author:

Elisa Raffaella Ferre
Department of Psychology
Royal Holloway, University of London
Egham
Surrey
TW200EX
e.ferre@rhul.ac.uk

Abstract

1
2 Knowing where our limbs are in space is crucial for a successful interaction with the external
3 world. Joint Position Sense (JPS) relies on both cues from muscle spindles and joint
4 mechanoreceptors, as well as the effort required to move. However, JPS may also rely on the
5 perceived external force on the limb, such as the gravitational field. It is well-known that the
6 internal model of gravity plays a large role in perception and behaviour. Thus, we have
7 explored whether direct vestibular-gravitational cues could influence JPS. Participants
8 passively estimated the position of the hand while they were upright and therefore aligned with
9 terrestrial gravity, or pitch-tilted 45° backwards from gravity. Overall participants overestimated
10 the position of the hand in both upright and tilted postures, however the proprioceptive bias
11 was significantly reduced when participants were tilted. Our findings therefore suggest that
12 the internal model of gravity may influence and update JPS in order to allow the organism to
13 interact with the environment.

14

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

16

17 **1. Introduction**

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

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

35 Gravity is probably the most persistent cue for the brain, and its internal representation
36 is one of the most pervasive signals for successful interactions with the environment. It might
37 not be surprising therefore that gravity plays a substantial role in shaping our perception and
38 behaviour. A gravitational advantage has been identified in human vision, whereby the
39 perception of motion duration is more precise for objects falling according to gravity, versus
40 objects moving against gravity (8–10). Eye movements are also more precise when tracking
41 objects moving with normal gravity (1g), versus objects that move according to
42 Weightlessness or Hypergravity (11,12). Finally, interception of objects is more precise when
43 objects obey natural gravity, with performance under Weightlessness showing significant

44 impairments (13,14). Together, these findings imply that gravitational acceleration is taken into
45 account when interacting with the world, potentially in the form of a strong sensory *prior*,
46 according to recent Bayesian frameworks (15–17).

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

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

68

69 **2. Material and Methods**

70 (a) Participants

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

76

77 (b) Procedure

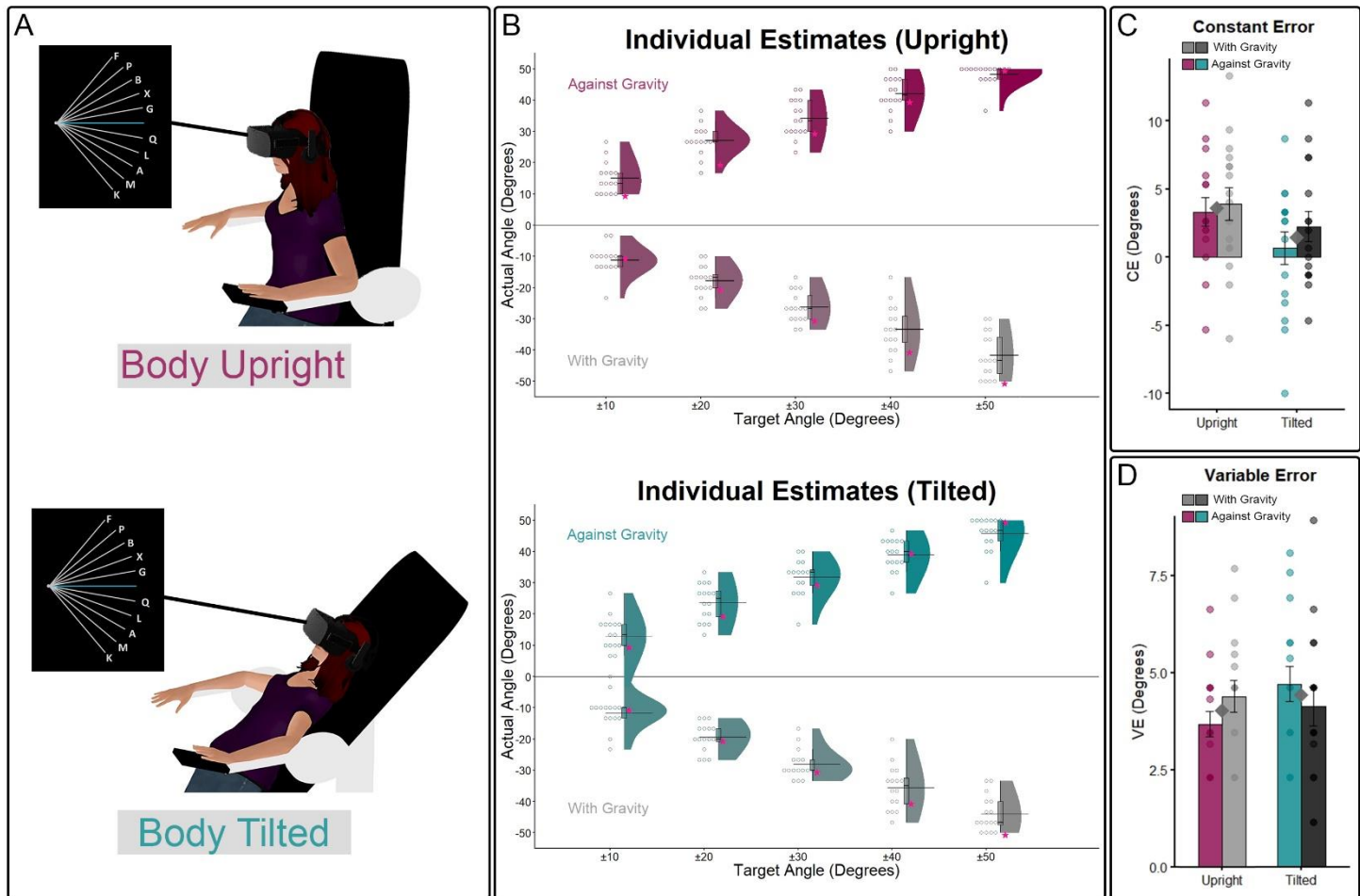
78 Participants' posture was controlled using a human tilting table. Participants rested
79 comfortably against the tilting table, with their legs secured using a brace (Figure 1A). In the
80 Upright condition, the participants were upright in alignment with the gravitational vertical. In
81 the Tilted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

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

91 Before each trial, the participant's hand was placed in a neutral horizontal position. At
92 the start of the trial, the experimenter moved the participant's hand to a randomised position
93 within 2s. An Oculus Rift CV1 was used to show a visual reference for their hand position, with
94 random letters corresponding to each potential hand angle. The participant indicated the letter

95 which corresponded to the sensed position of their hand. The hand was then returned to a
 96 neutral position and the next trial commenced. Each of the 10 potential postures was repeated
 97 three times, resulting in a total of 30 trials per condition.

98



99

100

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

112 (c) Data Analysis

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

122 Two participants were excluded from analysis as their data were more than 2.5
123 standard deviations from the mean in at least one condition, resulting in a total sample size of
124 16 participants for analysis. Shapiro-Wilk normality tests revealed no significant deviations
125 from normality assumptions once outliers were removed (all $p > .05$).

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

132

133 **3. Results**

134 (a) Constant Error

135 As expected, the one-sample t -tests revealed significant upwards biases in both
136 Upright ($t(15) = 5.84, p < .001$, Cohen’s $d = 1.46$ (95% CI [0.74, 2.16])) and Tilted ($t(15) = 2.67$,
137 $p < .05$, Cohen’s $d = 0.67$ (95% CI [0.12, 1.20])) body postures.

138 A 2x2 repeated measures ANOVA was performed to investigate the effect of gravity
139 and hand position on CEs. This analysis revealed no significant main effect of Target Angle
140 on CEs ($F(1, 15) = 0.35, p = .56, \eta_p^2 = .02$). A significant main effect of Body Posture was
141 found ($F(1, 15) = 32.71, p < .001, \eta_p^2 = .69$), with a lower CE in the Tilted (mean = 1.46, SD =
142 2.18) vs Upright (mean = 3.63, SD = 2.49) body posture (Figure 1C). No significant interaction
143 was found ($F(1, 15) = 0.48, p = .50, \eta_p^2 = .03$).

144

145 (b) Variable Error

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

150

151 4. Discussion

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

158 To estimate JPS, the brain may use a range of cues both from the joint itself, such as
159 muscle spindles indicating muscle length and joint mechanoreceptors signalling the limits of
160 joint position (2), as well as central signals, such as efferent motor commands and a sense of
161 effort (20,26). Here we suggest that the internal model of gravity may also contribute to JPS
162 in the absence of changes in gravitational torque at the limb. The internal model of gravity is

163 formed of priors, such the knowledge that the body is usually upright (15), and online
164 multimodal cues from vision, proprioception, viscera, and the vestibular system (5,22).
165 Modulating these inputs to the internal model, for example through altered visual cues, or
166 natural or artificial vestibular stimulation, may result in changes to gravity-related perception
167 and action, such as object interception, estimates of verticality and motion duration (8,22,27).
168 Crucially, our findings suggest similar impacts of gravity on proprioception and JPS.

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

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

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

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

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

References

- 220 1. Taylor JL. Proprioception. *Encycl Neurosci*. 2009;1143–9.
- 221 2. Tuthill JC, Azim E. Proprioception. *Curr Biol*. 2018;28(5):R194–203.
- 222 3. Papaxanthis C, Pozzo T, Schieppati M. Trajectories of arm pointing movements on the
223 sagittal plane vary with both direction and speed. *Exp Brain Res*. 2003;148(4):498–503.
- 224 4. Gentili R, Cahouet V, Papaxanthis C. Motor planning of arm movements is direction-
225 dependent in the gravity field. *Neuroscience*. 2007;145(1):20–32.
- 226 5. Harris LR, Jenkin M, Dyde RT, Jenkin H. Enhancing visual cues to orientation:
227 Suggestions for space travelers and the elderly. *Prog Brain Res*. 2011;191:133–42.
- 228 6. Trousselard M, Barraud PA, Nougier V, Raphel C, Cian C. Contribution of tactile and
229 interoceptive cues to the perception of the direction of gravity. *Cogn Brain Res*.
230 2004;20(3):355–62.
- 231 7. Lacquaniti F, Bosco G, Gravano S, Indovina I, La Scaleia B, Maffei V, et al. Multisensory
232 integration and internal models for sensing gravity effects in primates. *Biomed Res Int*.
233 2014;1–11.
- 234 8. Moscatelli A, Lacquaniti F. The weight of time: Gravitational force enhances
235 discrimination of visual motion duration. *J Vis*. 2011 Apr 8;11(4):1–17.
- 236 9. Torok A, Gallagher M, Lasbarelles C, Ferrè ER. Getting ready for Mars: How the brain
237 perceives new simulated gravitational environments. *Q J Exp Psychol*. 2019 Sep
238 5;72(9):2342-2349.
- 239 10. Gallagher M, Torok A, Klaas J, Ferrè ER. Gravity prior in human behaviour: a
240 perceptual or semantic phenomenon? *Exp Brain Res*. 2020; 238(9):1957-1962
- 241 11. Delle Monache S, Lacquaniti F, Bosco G. Ocular tracking of occluded ballistic
242 trajectories: Effects of visual context and of target law of motion. *J Vis*. 2019;19(4):1–

- 243 21.
- 244 12. Delle Monache S, Lacquaniti F, Bosco G. Differential contributions to the interception
245 of occluded ballistic trajectories by the temporoparietal junction, area hMT/V5+, and the
246 intraparietal cortex. *J Neurophysiol.* 2017 Sep;118(3):1809–23.
- 247 13. Zago M, Bosco G, Maffei V, Iosa M, Ivanenko YP, Lacquaniti F. Fast adaptation of the
248 internal model of gravity for manual interceptions: evidence for event-dependent
249 learning. *J Neurophysiol.* 2005;93:1055–68.
- 250 14. La Scaleia B, Zago M, Lacquaniti F. Hand interception of occluded motion in humans:
251 a test of model-based vs. on-line control. *J Neurophysiol.* 2015 Sep;114(3):1577–92.
- 252 15. Lacquaniti F, Bosco G, Gravano S, Indovina I, La Scaleia B, Maffei V, et al. Gravity in
253 the Brain as a Reference for Space and Time Perception. *Multisens Res.* 2015;28(5–
254 6):397–426.
- 255 16. Indovina I, Maffei V, Bosco G, Zago M, Macaluso E, Lacquaniti F. Representation of
256 visual gravitational motion in the human vestibular cortex. *Science.*
257 2005;308(5720):416–9.
- 258 17. Jörges B, López-moliner J. Gravity as a Strong Prior : Implications for Perception and
259 Action. *Front Hum Neurosci.* 2017; 28;11:203.
- 260 18. Bringoux L, Blouin J-S, Coyle T, Ruget H, Mouchnino L. Effect of gravity-like torque on
261 goal-directed arm movements in microgravity. *J Neurophysiol.* 2012;107(9):2541–8.
- 262 19. Ettinger L, Ostrander T. Gravitational torque partially accounts for proprioceptive acuity.
263 *Hum Mov Sci.* 2018;62:41–7.
- 264 20. Gandevia SC, Smith JL, Crawford M, Proske U, Taylor JL. Motor commands contribute
265 to human position sense. *J Physiol.* 2006;571(3):703–10.
- 266 21. Vimal VP, DiZio P, Lackner JR. Learning dynamic balancing in the roll plane with and

- 267 without gravitational cues. *Exp Brain Res.* 2017;235(11):3495–503.
- 268 22. Albers BBGT, Selen LPJ, Bertolini G, Straumann D, Medendorp WP, Tarnutzer XAA,
269 et al. Dissociating Vestibular and Somatosensory Contributions to Spatial Orientation.
270 *J Neurophysiol.* 2016;116(1):30-40.
- 271 23. Oldfield RC. The assessment and analysis of handedness: The Edinburgh inventory.
272 *Neuropsychologia.* 1971;9(1):97–113.
- 273 24. Allen M, Poggiali D, Whitaker K, Marshall TR, van Langen J, Kievit RA. Raincloud plots:
274 a multi-platform tool for robust data visualization. *Wellcome Open Res.* 2021;4:63.
- 275 25. Klein J, Whitsell B, Artemiadis PK, Buneo CA. Perception of Arm Position in Three-
276 Dimensional Space. *Front Hum Neurosci.* 2018;12:1–11.
- 277 26. Winter JA, Allen TJ, Proske U. Muscle spindle signals combine with the sense of effort
278 to indicate limb position. *J Physiol.* 2005;568(3):1035–46.
- 279 27. De Sá Teixeira NA, Hecht H, Artiles AD, Seyedmadani K, Sherwood DP, Young LR, et
280 al. Vestibular stimulation interferes with the dynamics of an internal representation of
281 gravity. *Q J Exp Psychol.* 2016;218:1–16.
- 282 28. Miller WL, Maffei V, Bosco G, Iosa M, Zago M, Macaluso E, et al. Vestibular Nuclei and
283 Cerebellum Put Visual Gravitational Motion in Context. *J Neurophysiol.*
284 2008;99(4):1969–82.
- 285 29. Maffei V, Mazzarella E, Piras F, Spalletta G, Caltagirone C, Lacquaniti F, et al.
286 Processing of visual gravitational motion in the peri-sylvian cortex: Evidence from brain-
287 damaged patients. *Cortex.* 2016;78:55–69.
- 288 30. Lacquaniti F, Bosco G, Indovina I, La Scaleia B, Maffei V, Moscatelli A, et al. Visual
289 gravitational motion and the vestibular system in humans. *Front Integr Neurosci.* 2013;
290 26;7:101.

- 291 31. Zu Eulenburg P, Caspers S, Roski C, Eickhoff SB. Meta-analytical definition and
292 functional connectivity of the human vestibular cortex. *Neuroimage*. 2012;60(1):162–9.
- 293 32. Bretas R V., Taoka M, Suzuki H, Iriki A. Secondary somatosensory cortex of primates:
294 beyond body maps, toward conscious self-in-the-world maps. *Exp Brain Res*.
295 2020;238(2):259–72.
- 296 33. Deecke L, Schwarz DWF, Fredrickson JM. Vestibular Responses in the Rhesus
297 Monkey Ventroposterior Thalamus. II. Vestibulo-Proprioceptive Convergence at
298 Thalamic Neurons. *Exp Brain Res*. 1977;30:219–32.
- 299 34. Schwarz DWF, Deecke L, Fredrickson JM. Cortical projection of group I muscle
300 afferents to areas 2, 3a, and the vestibular field in the rhesus monkey. *Exp Brain Res*.
301 1973 Jul;17(5):516–26.
- 302 35. Schmidt L, Artinger F, Stumpf O, Kerkhoff G. Differential effects of galvanic vestibular
303 stimulation on arm position sense in right- vs. left-handers. *Neuropsychologia*.
304 2013;51(5):893–9.
- 305 36. Knox JJ, Coppieters MW, Hodges PW. Do you know where your arm is if you think your
306 head has moved? *Exp Brain Res*. 2006;173(1):94–101.
- 307 37. Rousseau C, Papaxanthis C, Gaveau J, Pozzo T, White O. Initial information prior to
308 movement onset influences kinematics of upward arm pointing movements. *J*
309 *Neurophysiol*. 2016;116(4):1673–83.
- 310 38. Bringoux L, Di Cesare CS, Borel L, Macaluso T, Sarlegna FR. Do visual and vestibular
311 inputs compensate for somatosensory loss in the perception of spatial orientation?
312 Insights from a deafferented patient. *Front Hum Neurosci*. 2016 Apr 28;10:181.
- 313 39. Barra J, Pérennou D, Thilo K V., Gresty MA, Bronstein AM. The awareness of body
314 orientation modulates the perception of visual vertical. *Neuropsychologia*. 2012.
315 50(10):2492-8