

BIROn - Birkbeck Institutional Research Online

Kao, C.-L. and Török, Á. and Ferrè, Elisa Raffaella and Kokkinara, E. and Csépe, V. and Swapp, D. and Haggard, P. (2017) Up, down, near, far: an online vestibular contribution to distance judgement. PLoS One 12 (1), e0169990. ISSN 1932-6203.

Downloaded from: <https://eprints.bbk.ac.uk/id/eprint/45552/>

Usage Guidelines:

Please refer to usage guidelines at <https://eprints.bbk.ac.uk/policies.html>

or alternatively

contact lib-eprints@bbk.ac.uk.

Running title: Vestibular contributions to distance judgement

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42

Up, down, near, far:

an online vestibular contribution to distance judgement

Ágoston Török^{1,*}, Elisa Raffaella Ferrè^{2,3,*}, Elena Kokkinara⁴,

Valéria Csépe¹, David Swapp⁵, Patrick Haggard²

¹ Brain Imaging Centre, Research Centre for Natural Sciences, Hungarian Academy of Sciences, Budapest, Hungary

² Institute of Cognitive Neuroscience, University College London, London, UK

³ Department of Psychology, Royal Holloway University of London, Egham, UK

⁴ Department of Personality, Assessment and Psychological Treatments, University of Barcelona, Barcelona, Spain

⁵ Department of Computer Science, University College London, London, UK

* Co-first authors

Corresponding Author:

Patrick Haggard

Institute of Cognitive Neuroscience

17 Queen Square

London WC1N 3AR, UK

Telephone: 00 44 (0)20 7679 1153

Email: p.haggard@ucl.ac.uk

Keywords:

Vestibular system, Multisensory interaction, Distance perception, Gravity, Virtual Reality.

43 **Abstract**

44 Whether a visual stimulus seems near or far away depends partly on its vertical elevation.
45 Contrasting theories suggest either that perception of distance could vary with elevation, because of
46 memory of previous upwards efforts in climbing to overcome gravity, or because of fear of falling
47 associated with the downwards direction. The vestibular system provides a fundamental signal for
48 the downward direction of gravity, but the relation between this signal and depth perception remains
49 unexplored. Here we report an experiment on vestibular contributions to depth perception, using
50 Virtual Reality. We asked participants to judge the absolute distance of an object presented on a
51 plane at different elevations during brief artificial vestibular inputs. **Relative to distance estimates**
52 **collected with the object at the level of horizon, participants tended to overestimate distances when**
53 **the object was presented above the level of horizon and the head was tilted upward and underestimate**
54 **them when the object was presented below the level of horizon.** Interestingly, adding artificial
55 vestibular inputs strengthened these distance biases, showing that online multisensory signals, and
56 not only stored information, contribute to such **distance** illusions. Our results support the gravity
57 theory of depth perception, and show that vestibular signals make an on-line contribution to the
58 perception of effort, and thus of distance.

59

60 **1. Introduction**

61 Perceiving how far away an object is from one's own body is essential for interacting with the
62 environment. Distance can be inferred directly from visual information, using accommodation (1)
63 and binocular cues such as vergence (2) and disparity (3). However, distance perception is
64 dramatically biased if the target objects are presented above or below the level of horizon. For
65 example, a mountain refuge seems farther or closer depending on whether we look up at it from below
66 or down at it from above (4). Hence, purely visual information about distance may be affected by
67 non-visual factors (5,6), such as fear of heights (4) or perceived effort of access (7).

68 Contrasting explanations have been proposed for non-visual *distance biases*. On the one hand,
69 the *gravity theory* claims that distance perception is based on the estimated motor effort of navigating
70 to the perceived object (7,8). Accordingly upward distances are overestimated (9). On the other
71 hand, the *evolved navigation* theory posits an evolutionary advantage in overestimating the risk of
72 falling (10,11). On this view, contrary to gravity theory, downward distances are overestimated. Both
73 theories assume that current **head and gaze elevations** are combined with internally-stored
74 information in order to compute distance. Gravity theories require stored information about previous
75 motor efforts (8), while evolved navigation theories require internal information about potential risks
76 of falling (12). Critically, removing the fear of falling by experimenting in low detail Virtual Reality
77 (13) or reducing the expected effort of access by e.g. not wearing any heavy backpacks (9) reportedly
78 diminishes these **elevation** distance biases.

79 In principle, the influence of **upward/downward head inclination** on distance perception could
80 be based on *online* information, rather than stored information. In particular, under terrestrial
81 conditions, the vestibular system constantly provides signals relating current head orientation to the
82 direction of gravity. Combining a vestibular signal with an eye position signal specifies whether a
83 visual object is located above or below the eye. Although vestibular signals do not directly code the
84 spatial location of external objects, the interaction between vestibular and visual information is
85 essential in providing the organism with space representation (14–16). For instance, vestibular

86 peripheral organs detect the motion of the head, producing experiences of self-motion in three-
87 dimensional space. Cortical vestibular pathways integrate information from other sensory modalities
88 to generate appropriate and accurate responses to self-motion, such as the stabilization of gaze,
89 balance and postural motor commands (17), and the perception of the subjective visual vertical (18).
90 Microgravity experiments showed that visual perception of horizontal depth is influenced by altered
91 vestibular signals (19). For example, perceived distances were underestimated during either short-
92 term exposure to microgravity using parabolic flight (20) or long term exposure on the International
93 Space Station (21) leading to perceptual distortions of three dimensional space. However, the
94 vestibular contribution to elevation biases in visual depth perception remains under-investigated.

95 Recent studies indicated that reaching an object can be affected by the posture of the body (6).
96 Tilting the body forward caused errors in the reaching movement, because participants
97 underestimated the distance between their own body and the virtual object. These results seem to
98 support the gravity based model. Similarly, Harris and Mander (5) reported that tilting the body
99 backward caused overestimation of the perceived length of a rod, and hence, the wall seemed
100 presumably closer. However, these studies do not specify under which circumstances one expects
101 underestimation vs. overestimation, and why.

102 Here we asked participants to judge the distance of an object presented at different distances on
103 an inclined plane, leading to different head and gaze elevations. We developed a novel Virtual Reality
104 environment in which neither risks of falling (22), nor navigational effort were actually present (23).
105 This minimised confounds such as familiarity, and memory for previous efforts, that could affect
106 previous field-based experiments. The participants' head inclination was systematically varied by
107 asking them to tilt both the head and gaze upwards or downwards to fixate a target object. We could
108 thus directly compare predictions of gravity and evolved navigation theories. Further, we applied
109 event-related galvanic vestibular stimulation (GVS) during each judgement, to investigate whether
110 online vestibular signals indeed affected the distance perception biases. Importantly, GVS is a non-
111 invasive method that directly stimulates the vestibular receptors (24), producing complex oculomotor,

112 perceptual and postural responses. In the traditional bilateral bipolar GVS configuration, an anode
113 and cathode are placed on the left and right mastoid, or vice versa. Perilymphatic cathodal currents
114 are thought to depolarize the trigger site and lead to excitation, whereas anodal currents hyperpolarize
115 it resulting in inhibition (25). This is considered to enhance the vestibular activity by mimicking a
116 natural movement of the head, which elicits a virtual sensation of roll tilt.

117

118 **2. Methods**

119 **2.1. Ethics Statement**

120 The experimental protocol was approved by the local ethics committee (University College
121 London) and the study was conducted in line with the Declaration of Helsinki. Participants gave
122 written informed consent to participate in the experiment before inclusion in the experiment.

123

124 **2.2. Participants**

125 Sixteen healthy participants volunteered for the study. Data from two participants was
126 discarded because they proved unable to follow the instruction of the experiment (see below). Thus,
127 fourteen participants (5 females, mean age \pm standard deviation: 26.64 ± 6.64 years) completed the
128 experiment. All participants were right-handed according to their Edinburgh handedness inventory
129 scores. The sample size was decided *a priori* based on similar experiments (5,6).

130

131 **2.3. Galvanic Vestibular Stimulation**

132 **Bipolar galvanic vestibular stimulation (GVS)** was applied using a commercial stimulator
133 (Good Vibrations Engineering Ltd., Nobleton, Ontario, Canada) delivering a boxcar pulse of 1mA
134 for 3s. This low intensity was used to minimise non-specific cueing effects, such as arousal from

135 cutaneous sensations or vertigo. Importantly, several studies confirm that this level of GVS activates
136 the vestibular organs. For instance, both postural (24) and behavioural changes have been reported
137 with such low intensities GVS (26–30). GVS is known to increase the firing rate in vestibular
138 afferents on the cathodal side and to decrease the firing rate on the anodal side (25), enhancing the
139 ongoing natural vestibular responses and evoking virtual sensations of roll tilt. These effects do not
140 outlast the stimulation (31). Carbon rubber electrodes (area 10 cm²) coated with electrode gel were
141 placed binaurally over the mastoid processes and fixed in place with adhesive tape. The area of
142 application was first cleaned, and electrode gel was applied to reduce the impedance. Left anodal
143 and right cathodal configuration is named ‘L-GVS’ (Figure 1b). The inverse polarity, namely right
144 anodal and left cathodal configuration, is named ‘R-GVS’. We also applied a sham stimulation using
145 electrodes placed on the left and right side of the neck, about 5cm below the GVS electrodes (32,33)
146 with left anodal and right cathodal configuration. This sham stimulation evoked similar tingling skin
147 sensations to GVS but not modulation of vestibular afferents. It thus provided a control for non-
148 specific alerting effects and for the knowledge that an unusual stimulation is occurring.

149

150 **2.4. Virtual Reality Environment**

151 The experiment was carried out in the Immersive Virtual Reality Laboratory at University
152 College London, using a CAVE facility (34). This system consists of four stereo-projected surfaces:
153 three back-projected vertical walls, each 3m wide x 2.2m high, and the floor (3m x 3m) form a
154 continuous projection surface. The Virtual Reality environment was created using Unity3D game
155 engine (www.unity3d.com), rendered using a K5000 graphics card to drive 4 Christie Mirage DLP
156 projectors, each of which projected to one of the 4 screens at 96Hz. The participant wore shutter
157 glasses synchronized with the projectors creating active stereo-projection in each eye at 48Hz. The
158 glasses provided a field of view per eye of approx. 90-100° horizontally and 60-70° vertically (the
159 precise field of view depends to some extent on how closely the glasses fitted to the participant’s
160 eyes). The position of the glasses was tracked by an InterSense™ IS-900 system with high accuracy.

161 The system was calibrated to the participant's own eye height at the beginning of every experiment,
162 and this data was used to accurately compute object distances for the upward, downward, and level
163 inclinations. This calibration was performed to account for small changes in eye-to-ground distance
164 among participants. A geometrical model accounting for the pitch of the ground plane and the eye-
165 height of the participant ensured that the distance from the participant's eye to the near-top edge of
166 the target object was identical for both upward and downward pitched objects (as well as among
167 participants with different eye-heights). The virtual scene was a green grass-like plane with blue
168 skies and no visible landmarks. The experimental object was a 2m X 2m gift box with purple ribbon
169 (see Figure 1a). The object rested on the ground and the same proportion of object and environment
170 was visible at all inclinations. The unusual size of the target object was chosen to be appropriate for
171 the range of distances presented in the experiment and the consequent visual angle subtended by the
172 target object at these distances. As the distance was varied between 5m and 25m, and the object had
173 2m sides, the visual angle subtended varied between 23° and 4.6°.

174

175 **2.5. Experimental procedure**

176 Verbal and written instructions about the task were given to participants prior to the
177 experiment. Participants were seated in the centre of the CAVE, 1.5m from the front screen. A visual
178 scene was presented on vertical screens and on the floor in order to create a seamless, wide field-of-
179 view immersive display. Participants made absolute judgements about the distance between their
180 own body and an object (a gift box) that appeared in front of them (29, see Figure 1a). At the
181 beginning of the task, the target object was displayed for few minutes to allow participants to
182 familiarise with its size. Then object positions slightly under (1.5m) and slightly over (30m) the
183 experimental range were presented, and the experimenter informed the participant about the actual
184 distance in metres.

185 Participants were encouraged to use these as anchor points to calibrate distance judgements
186 in experimental trials. The positions of the present box were distributed logarithmically between 5m

187 and 25m; thus, the possible distances were 5, 6.9, 9.52, 13.3, 18.2, 25m. These distances were chosen
188 to produce a wide range of perceived distances. Our predictions did not focus on the effects of object
189 distance itself but rather on the effects of two other experimental factors: head inclination and
190 vestibular stimulation. Participants were instructed to look horizontally relative to the head and visual
191 ground plane, but the angle of the head was manipulated across experimental conditions. The object
192 appeared on a smooth plane that was inclining (+20°), flat (0°), or declining (-20°), and participants
193 were asked to tilt their head accordingly (backwards, natural and downwards). The experiment was
194 divided into blocks; head inclination (+20°, 0°, -20°) and vestibular stimulation (L-GVS, R-GVS,
195 Sham) changed only between blocks. Each block consisted of 18 trials; there were three repetitions
196 of the same distance in each block. Distances were presented in random order. Block order followed
197 a Latin square design. Each trial started with the presentation of the grass-like plane in the actual
198 inclination and the blue sky. Participants adjusted their head pitch angle to fixate the object and,
199 therefore, the horizon, while a 6 degrees head tracking system monitored their posture. This
200 procedure ensured that participants saw the same proportion of grass and sky at all head inclinations.
201 The head tracking system measured the inclination of the head and a sound signalled when the
202 participant's head reached the correct vertical angle. Thus, the head position in space was decoded
203 by our custom-built software for presenting stimuli, which started each trial if and only if participants'
204 head was in the correct inclination. Participants were told to keep their head at the same position for
205 the duration of the block. Then GVS/Sham started and lasted for 3s. 1s after GVS onset, the gift box
206 became visible for 1s and then disappeared. This delay was used to ensure that vestibular cortical
207 projections would be activated when visual stimulus was present: Fitzpatrick and Day (24) reported
208 that 1s of 1mA GVS produced clear postural adjustments in standing participants, implying successful
209 activation of the vestibular system. The image was then blurred, and the GVS/Sham pulse ended.
210 Participants made absolute verbal judgements (in metres) of the distance of the object after the screen
211 was blurred. The response was recorded, and the next trial started. This method of reporting distance
212 percepts has high face validity, and allows many estimates to be acquired rapidly. It was thus

213 preferred to the method of limits and method of constant stimuli favoured in classical psychophysical
214 studies. Very importantly, any imprecision or bias resulting from this method of measurement should
215 affect all GVS conditions equally. We did not aim to quantify the limits of visual distance perception,
216 but only to compare estimates of perceived visual distance between GVS conditions. We wanted to
217 sample a range of environmental distances to minimise the number of GVS stimulations (GVS can
218 cause mildly unpleasant sensations) and to minimise duration of the CAVE immersion. Absolute
219 judgements might be criticised because different participants may use different subjective standards.
220 However, our experimental design was based only on within-participant comparisons; therefore,
221 differences between individuals in reported values do not affect our inferences.

222

223

*** Insert Figure 1 Here ***

224

225 **Figure 1. Experimental set up and results.** (a) Participants were seated in the centre of the cave.
226 During the experiment, participants made absolute judgements of the distance between their own
227 body and an object (a gift box) appearing in front of them. The positions of the gift box were
228 distributed logarithmically between 5m and 25m. The same distances were presented with the three
229 head inclinations -20° , 0° , and $+20^\circ$. **The gaze was aligned with head inclinations.** (b) Left anodal
230 and right cathodal configuration is named 'L-GVS'. The inverse polarity, namely right anodal and
231 left cathodal configuration, is named 'R-GVS'. A sham stimulation was also applied placing the
232 electrodes to the left and right side of the neck about 5cm below the GVS electrodes. GVS and sham
233 stimulation were applied delivering a boxcar pulse of 1ma for 3s. (c) Distance errors have been
234 calculated by subtracting the actual distance from the judged distance. **Estimation bias in 0° head
235 inclination condition was used as baseline, and all values were corrected by this baseline. Thus,
236 negative values on the ordinate indicate underestimation compared to the horizontal, zero-inclination
237 baseline condition, whereas positive values indicate overestimations. Distance perception varied
238 significantly according head inclination. Specifically, downward distances were underestimated,
239 while upward distances were overestimated, relative to baseline.** This pattern of distance illusions is
240 in line with the predictions of the gravity theories. Note that GVS enhances this pattern. (d)
241 Predictions based on linear mixed-effects model. **The model containing both fixed and random terms
242 fits well to the actual data.**

243

244

245 3. Results

246 Trials containing either recording errors or multiple responses were eliminated before the
247 analysis. Less than one percent of all participants' data was removed according to this criterion. **We**

248 calculated the *distance judgement errors* by subtracting the simulated distance from the judged
249 distance. We inspected the distribution of errors expressed both in metres, and as a percentage of the
250 actual distance. The former distribution was normal, whereas the latter was left-skewed. We
251 therefore preferred to express errors in physical units (m). The distance bias in the 0° head inclination
252 condition, corresponding to horizontal gaze, was been considered as baseline, which allowed us to
253 define underestimation (negative values) and overestimation (positive values) relative to it.

254

255 First, distance judgement errors for each participant were averaged for each combination of
256 head inclination and vestibular stimulation conditions and analysed using factorial repeated measures
257 ANOVA and planned contrasts. Our theoretical predictions focused on the interaction between **head**
258 **inclination** and vestibular stimulation factors. These analyses therefore pooled across the different
259 distances judged. Distance perception varied significantly across **head inclinations** ($F(2,26) = 23.694$;
260 $p < .001$; $\eta_p^2 = 0.65$) (Figure 1c). Overall estimations showed a slight underestimation trend, but only
261 estimations in the -20° head inclination condition were significantly underestimated compared to
262 actual distances ($t(13) = -2.75$, $p = .02$, *Cohen's d* = -1.52, all other $p > .3$). Downward distances were
263 underestimated by 1.65m ($SD = 3.50$), while upward distances were overestimated by 1.19m ($SD =$
264 3.90), compared to ground level. This pattern of results fits the predictions of gravity theories but
265 opposes the predictions of evolved navigation theories. A planned linear trend contrast confined to
266 the sham condition also showed a trend in the direction predicted by gravity theories (**down vs. up**
267 **head inclination** $t(1,13) = 1.670$; $p = .059$, *Cohen's d* = 0.45, one-tailed, numerical effect present in
268 10/14 participants). The corresponding planned contrast for evolved navigation was not supported
269 (**flat vs down head inclination**: $t(1,13) = -1.274$, n.s.). The main effect of **vestibular stimulation** was
270 not significant ($F(2,26) = 0.196$; $p = .823$). However, and more importantly, we found an interaction
271 between vestibular stimulation condition and **head inclination** ($F(4,52) = 3.318$; $p = .017$; $\eta_p^2 = 0.20$).
272 This interaction occurred because the linear trend predicted by gravity theories was amplified by both
273 polarities of GVS (down vs. up **head inclination** L-GVS $t(1,13) = 4.891$, $p < .001$, *Cohen's d* = 1.31;

274 R-GVS $t(1,13) = 6.585, p < .001, \text{Cohen's } d = 1.76$, numerical effect averaged across GVS polarities
275 present in 14/14 participants). This pattern of results is consistent with an inclination effect generated
276 online by a vestibular signal that is boosted by artificial vestibular stimulation.

277

278 Second, we fitted a mixed effects model to investigate intersubject variability, following Barr
279 et al (36). In this mixed effects approach, we entered head inclination ($-20^\circ, 0^\circ, 20^\circ$) and object
280 position as scalar variables (37), while vestibular stimulation (L-GVS, R-GVS, Sham) was handled
281 as factorial. Mixed effects modelling was performed in R (38) using lme4 (37); ggplot2 was adopted
282 for visualisation (39).

283 We inspected how distance judgement errors varied as a function of object position for each
284 participant (Figure 2). We observed a strong correlation between object distance and judgement error
285 within most participants, together with strong differences between participants in the strength and
286 even the sign of these correlations. This pattern of variation justifies the explicit modelling of both
287 fixed and random effects provided by the mixed model approach (36). We included both fixed (i.e.
288 population general) and random (i.e. subject specific) effects of head inclination, object position and
289 vestibular stimulation (37,40). We aimed to keep maximal random effect structure in the model (36),
290 therefore random intercepts were estimated for individual subjects, individual subject and vestibular
291 stimulation combinations, individual subject and inclination combinations, and individual subject,
292 vestibular stimulation and inclination combinations. Random slope is only estimated for the object
293 position, but separate random slopes (correlated with their respective intercepts) were estimated for
294 different random intercept terms. For this model the restricted maximum likelihood (RMEL)
295 estimation reached convergence. This model appeared to fit our data well according to the Akaike
296 Information Criteria (AIC) of 3243.747 ($df = 31$, baseline model containing no fixed effects, and only
297 the subjects as random effects resulted in AIC 5211.152). The fixed effect significances were tested
298 using F tests, where p values were based on the Kenward-Roger approximation of the degrees of
299 freedom (42). We found a significant main effect of head inclination ($F(2, 26.17) = 23.70, p < .001$,

Running title: Vestibular contributions to distance judgement

300 $\eta_p^2 = 0.64$) and a main effect of object position ($F(1, 19.87) = 41.75, p < .001, \eta_p^2 = 0.68$). Critically,
301 the interaction between head inclination and vestibular stimulation was significant ($F(4, 52.92) =$
302 $3.68, p = .010, \eta_p^2 = 0.22$). The pattern of interaction was consistent with an involvement of vestibular
303 gravitational signals in distance estimates, with the effects of actual distance on reported distance
304 being greater with GVS than in Sham. Least square means post hoc contrasts revealed significant
305 differences between -20° and 20° head inclination conditions in the Sham ($p = .035$). Finally, the
306 three way interaction between head inclination, vestibular stimulation, and object position was also
307 significant ($F(4, 67.56) = 39.10, p < .001, \eta_p^2 = 0.70$), primarily due to changes in slopes estimated
308 for some head inclination and vestibular stimulation combinations. The overall model explained
309 more than 80 % of total variance in the data (*Conditional* $R^2 = 0.82$) with a compelling contribution
310 of the fixed effects (*Marginal* $R^2 = 0.23$) (Figure 1d). The difference between conditional and
311 marginal R^2 indicates how much variance is present on the subject level and captured by the random
312 effects in our model. This suggests that our mixed effects model fitted well with the observed data,
313 and validated hierarchical modelling of the experimental variable.

314
315 To summarise, the ANOVA and the mixed effects model showed converging results.
316 Downward distances were underestimated, whereas upward distances were overestimated compared
317 to estimations made on flat surface. Furthermore, GVS enhanced these biases.

318
319 *** Insert Figure 2 Here ***

320
321 **Figure 2. Relation between object position and judgement error in individual participants. See**
322 **text for explanation. Note that the size and even direction of the relation differs between participants.**
323

324
325 **4. Discussion**

326 Participants overestimated visual distances when their head was tilted upward and
327 underestimated them when their head was tilted downward, compared to judgements made in a zero-
328 degree, horizontal baseline condition. The observed effect is in the direction predicted by gravity
329 theories, but opposite to the predictions of evolved navigation theories. More strikingly, the distance
330 biases increased strongly with event-related GVS. Our results suggest that the gravitational
331 modulation of visual distance perception depends on on-line vestibular signals. This elevation
332 distance bias is, therefore, not merely a product of learned contextual associations but rather reflects
333 a specific multisensory integration mechanism.

334 Gravitational signals are coded by vestibular receptors in the inner ear, whose signal depends
335 on the position of the head relative to gravitational vertical (43,44). The precise mode of action of
336 GVS remains debated, but recent evidence confirms activation of both otolithic fibres and
337 semicircular canals (45). In the bilateral bipolar GVS configuration, perilymphatic cathodal currents
338 are thought to depolarize the trigger site and lead to excitation, whereas anodal currents hyperpolarize
339 it resulting in inhibition (25). Neuroimaging studies using GVS have revealed widespread vestibular
340 projections reaching many areas of the cerebral cortex, such as the retroinsular cortex, the superior
341 temporal gyrus, the temporo-parietal cortex, the basal ganglia and the anterior cingulate (46,47).
342 Critically, recent studies suggested that otolithic gravitational inputs in the vestibular system have a
343 direct influence on cognitive tasks involving three-dimensional perception (5,6,14,15). In particular,
344 perception of depth was altered in microgravity and in peripheral vestibular disorders (15,48).
345 However, these results were attributed to changes in visual linear perspective and visual size
346 perception, which should be specific to visual horizontal stimuli. Our data suggest an alternative
347 mechanism for these effects. We found that artificial activation of vestibular projections in the brain
348 by GVS modulated distance illusions. The pattern of modulation suggests that GVS amplified the
349 neural signals generated by head and gaze elevation changes required to fixate targets above or below
350 the ground plane (49,50). Our results therefore suggest that vestibular inputs contribute to an on-line
351 representation of head movement and position which is used in estimation of visual distance.

352 Gaze position and the perceived orientation of the ground plane are already known to
353 contribute to perceived depth (50,51). Critically, these factors both depend on head position,
354 suggesting a fundamental interaction between visual, vestibular and proprioceptive signals in
355 computing distance estimates. Combining traditional visual cues to depth, such as accommodation
356 and vergence, with vestibular signals about current head position relative to gravity provides
357 sufficient information to compute a possible motion path to a visual object (17), as suggested by
358 navigation theories. **In our study, participants overestimated distances when their head was tilted
359 upward and underestimated them when their head was tilted downward compared to estimates in the
360 horizontal plane.** This distance perceptual bias was enhanced with event-related GVS. Interestingly,
361 GVS did not interfere with distance perception when head inclination was zero. Presumably, when
362 the head is level and not inclined, the brain computes distances to visual targets with respect to an
363 assumed level ground. This represents an intermediate, neutral situation where there is neither cost
364 nor benefit of gravity (cf (7,8,52)). In this special case, the online vestibular-gravitational signal
365 generated by GVS does not need to be integrated.

366 **Importantly, although the current results supported the predictions of the gravity theory, we
367 do not suggest a globally linear relation between head inclination and distance error.** In fact, not all
368 possible angles are equally experienced in real environments (9,53). Our experience of inclines
369 typically involves either slight elevations (e.g. road gradients are usually under 20 degrees) or risky,
370 non-navigable surfaces (e.g. the sheer drop from a balcony). One might expect the biases of evolved
371 navigation theory to be most apparent for dramatic elevation angles associated with dangerous
372 environments.

373 Verbal reporting of absolute distance judgements was used in the present study. This does
374 not figure among the classical psychophysical methods. However, it has been used earlier (54,55).
375 The results of those studies were broadly similar to others that used other measures to assess distance
376 estimation (56–58). The verbal method has the advantage of being extremely rapid. This is important
377 in environments such as VR, where long exposure is uncomfortable and impractical. **Although**

378 absolute response accuracy may be low, this need not obscure the difference between our
379 experimental conditions (59–62). Thus, it seems very unlikely that the particular features of this
380 psychophysical judgement can explain our results, unless additional and unwarranted ad hoc
381 assumptions are made.

382 We cannot exclude that the difference between estimated distances and actual distances might
383 have been influenced by some parameters used in our study. For instance, visual distance perception
384 seems to rely on the familiar size of the to-be-estimated object (63). We adopted an unusual large
385 box to account for the visual angles subtended by the object at far distances. A large object is
386 therefore required to avoid further uncertainty in the distance judgments, especially at greater
387 distances. The size of our box might have affected distance perception *in general*, but not specifically
388 at some head inclinations or vestibular stimulation conditions.

389 Previous accounts of visual distance perception identified a gravitational bias. Some views
390 treat these as top-down, cognitive biases, which may therefore be post-perceptual. For example, the
391 perceived effort to climb to overcome gravity may lead to the summit of a slope seeming far away
392 (53). In our experiment these cognitive factors were minimized: in VR there is no actual effort of
393 movement, nor any fear of falling. Our results suggest that upward slope visual distances are
394 overestimated compared to ground level, and we provide novel, causal evidence of why this might be
395 so. We show that gravitational modulation of visual distance perception depends on *on-line* vestibular
396 signals. Previous accounts emphasised memory of past experiences of efforts to overcome gravity,
397 or potential effects of gravity in falling. That is, those accounts treated vertical biases in distance
398 perception as results of prior learning, or as predictions, rather than as on-line modulations of
399 perception. Since concurrent, event-related artificial vestibular inputs boosted visual distance
400 illusions, these illusions may not simply be products of learned and internally-stored contextual
401 associations. Rather, such illusions may owe more to multisensory perceptual integration than has
402 been previously thought.

403

404 **Acknowledgments**

405 The datasets supporting this article have been uploaded as part of the Supplementary Material.

406 A.T. and E.K. were supported by European Community's Research Infrastructure Action -
407 VISIONAIR 262044 - under the Seventh Framework Programme (FP7/2007-2013). A.T. was
408 additionally supported by a Young Researcher Fellowship from the Hungarian Academy of Sciences.
409 E.R.F. and P.H. were supported by European Union Seventh Framework Programme (EU FP7)
410 project VERE WP1 and by a BIAL foundation bursary (269/14). P.H. was additionally supported by
411 a Professorial Fellowship from ESRC and by ERC Advanced Grant HUMVOL.

412 The authors declare no competing interests.

413

414 **References**

- 415 1. Mon-Williams M, Tresilian JR. Some recent studies on the extraretinal contribution to distance
416 perception. *Perception*. 1999;28(2):167–81.
- 417 2. Mon-Williams M, Tresilian JR, Roberts a. Vergence provides veridical depth perception from
418 horizontal retinal image disparities. *Exp Brain Res* [Internet]. 2000;133(3):407–13. Available
419 from: <http://www.ncbi.nlm.nih.gov/pubmed/10958531>
- 420 3. Mayhew JE, Longuet-Higgins HC. A computational model of binocular depth perception.
421 *Nature* [Internet]. 1982;297(5865):376–8. Available from:
422 [http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation](http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=7078648)
423 [&list_uids=7078648](http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=7078648)
- 424 4. Jackson RE, Cormack LK. Evolved navigation theory and the descent illusion. *Percept*
425 *Psychophys* [Internet]. 2007 Apr [cited 2015 Feb 21];69(3):353–62. Available from:
426 <http://www.ncbi.nlm.nih.gov/pubmed/17672423>
- 427 5. Harris LR, Mander C. Perceived distance depends on the orientation of both the body and the
428 visual environment. *J Vis* [Internet]. The Association for Research in Vision and
429 Ophthalmology; 2014 Jan 1 [cited 2016 Jan 4];14(12):17. Available from:
430 <http://jov.arvojournals.org/article.aspx?articleid=2193904>
- 431 6. Scotto Di Cesare C, Sarlegna FR, Bourdin C, Mestre DR, Bringoux L. Combined influence of
432 visual scene and body tilt on arm pointing movements: gravity matters! *PLoS One*. Public
433 Library of Science; 2014;9(6):e99866.
- 434 7. Proffitt DR, Stefanucci J, Banton T, Epstein W. The role of effort in perceiving distance.
435 *Psychol Sci* [Internet]. 2003 Mar 1 [cited 2015 Jan 8];14(2):106–12. Available from:
436 <http://pss.sagepub.com/content/14/2/106.short>
- 437 8. Howard IP, Templeton WB. *Human Spatial Orientation* [Internet]. John Wiley & Sons Ltd;
438 1966 [cited 2013 Jan 7]. 533 p. Available from: [http://www.amazon.com/Human-Spatial-](http://www.amazon.com/Human-Spatial-Orientation-Ian-Howard/dp/0471416622)
439 [Orientation-Ian-Howard/dp/0471416622](http://www.amazon.com/Human-Spatial-Orientation-Ian-Howard/dp/0471416622)

- 440 9. Bhalla M, Proffitt DR. Visual-motor recalibration in geographical slant perception. *J Exp*
441 *Psychol Hum Percept Perform* [Internet]. 1999 Aug [cited 2015 Feb 21];25(4):1076–96.
442 Available from: <http://www.ncbi.nlm.nih.gov/pubmed/10464946>
- 443 10. Jackson RE, Cormack LK. Evolved navigation theory and the descent illusion. *Percept*
444 *Psychophys* [Internet]. 2007 Apr [cited 2015 Feb 21];69(3):353–62. Available from:
445 <http://www.ncbi.nlm.nih.gov/pubmed/17672423>
- 446 11. Willey CR, Jackson RE. Visual field dependence as a navigational strategy. *Atten Percept*
447 *Psychophys* [Internet]. 2014 May [cited 2015 Aug 17];76(4):1036–44. Available from:
448 [http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=4429127&tool=pmcentrez&rend](http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=4429127&tool=pmcentrez&rendertype=abstract)
449 [ertype=abstract](http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=4429127&tool=pmcentrez&rendertype=abstract)
- 450 12. Gibson EJ, Walk RD. The“ visual cliff.” WH Freeman Company; 1960.
- 451 13. Jackson RE, Cormack LK. Reducing the presence of navigation risk eliminates strong
452 environmental illusions. *J Vis* [Internet]. 2010 Jan [cited 2015 Feb 21];10(5):9. Available
453 from: <http://www.ncbi.nlm.nih.gov/pubmed/20616118>
- 454 14. Villard E, Garcia-Moreno FT, Peter N, Clément G. Geometric visual illusions in microgravity
455 during parabolic flight. *Neuroreport* [Internet]. 2005;16(12):1395–8. Available from:
456 <http://www.ncbi.nlm.nih.gov/pubmed/16418941>
- 457 15. Clément G, Fraysse M-J, Deguine O. Mental representation of space in vestibular patients with
458 otolithic or rotatory vertigo. *Neuroreport*. 2009;20:457–61.
- 459 16. Clément G, Skinner A, Richard G, Lathan C. Geometric illusions in astronauts during long-
460 duration spaceflight. *Neuroreport* [Internet]. 2012;23(15):894–9. Available from:
461 <http://www.ncbi.nlm.nih.gov/pubmed/22955144>
- 462 17. Cullen KE. The vestibular system: Multimodal integration and encoding of self-motion for
463 motor control. *Trends Neurosci* [Internet]. 2012;35(3):185–96. Available from:
464 <http://dx.doi.org/10.1016/j.tins.2011.12.001>
- 465 18. Bömmer A, Mast F. Assessing otolith function by the subjective visual vertical. *Ann N Y Acad*

- 466 Sci. 1999;871:221–31.
- 467 19. Clément G, Reschke MF. Neuroscience in space. Springer Science & Business Media; 2010.
- 468 20. Clément G, Lathan C, Lockerd A. Perception of depth in microgravity during parabolic flight.
469 Acta Astronaut. 2008;63(7–10):828–32.
- 470 21. Clément G, Skinner A, Lathan C. Distance and Size Perception in Astronauts during Long-
471 Duration Spaceflight. Life [Internet]. 2013;3(4):524–37. Available from:
472 <http://www.mdpi.com/2075-1729/3/4/524/>
- 473 22. Jackson RE, Cormack LK. Reducing the presence of navigation risk eliminates strong
474 environmental illusions. J Vis [Internet]. 2010 Jan [cited 2015 Feb 21];10(5):9. Available
475 from: <http://www.ncbi.nlm.nih.gov/pubmed/20616118>
- 476 23. Bhalla M, Proffitt DR. Visual-motor recalibration in geographical slant perception. J Exp
477 Psychol Hum Percept Perform [Internet]. 1999 Aug [cited 2015 Feb 21];25(4):1076–96.
478 Available from: <http://www.ncbi.nlm.nih.gov/pubmed/10464946>
- 479 24. Fitzpatrick RC, Day BL. Probing the human vestibular system with galvanic stimulation. J
480 Appl Physiol. 2004;96(6):2301–16.
- 481 25. Goldberg JM, Smith CE, Fernández C. Relation between discharge regularity and responses to
482 externally applied galvanic currents in vestibular nerve afferents of the squirrel monkey. J
483 Neurophysiol. 1984;51(6):1236–56.
- 484 26. Wilkinson D, Zubko O, Degutis J, Milberg W, Potter J. Improvement of a figure copying
485 deficit during subsensory galvanic vestibular stimulation. J Neuropsychol [Internet]. 2010;4(Pt
486 1):107–18. Available from: <http://www.ncbi.nlm.nih.gov/pubmed/19706224>
- 487 27. Kerkhoff G, Hildebrandt H, Reinhart S, Kardinal M, Dimova V, Utz KS. A long-lasting
488 improvement of tactile extinction after galvanic vestibular stimulation: Two Sham-stimulation
489 controlled case studies. Neuropsychologia. 2011;49(2):186–95.
- 490 28. Schmidt L, Utz KS, Depper L, Adams M, Schaadt A-K, Reinhart S, et al. Now You Feel both:
491 Galvanic Vestibular Stimulation Induces Lasting Improvements in the Rehabilitation of

- 492 Chronic Tactile Extinction. *Front Hum Neurosci* [Internet]. 2013;7(March):90. Available
493 from:
494 [http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3602932&tool=pmcentrez&rend](http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3602932&tool=pmcentrez&rendertype=abstract)
495 [ertype=abstract](http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3602932&tool=pmcentrez&rendertype=abstract)
- 496 29. Ferrè ER, Day BL, Bottini G, Haggard P. How the vestibular system interacts with
497 somatosensory perception: A sham-controlled study with galvanic vestibular stimulation.
498 *Neurosci Lett*. 2013;550:35–40.
- 499 30. Ferrè ER, Vagnoni E, Haggard P. Vestibular contributions to bodily awareness.
500 *Neuropsychologia*. 2013;51(8):1445–52.
- 501 31. Fitzpatrick RC, Day BL. Probing the human vestibular system with galvanic stimulation. *J*
502 *Appl Physiol. Am Physiological Soc*; 2004;96(6):2301–16.
- 503 32. Ferrè ER, Vagnoni E, Haggard P. Vestibular contributions to bodily awareness.
504 *Neuropsychologia*. Elsevier; 2013;51(8):1445–52.
- 505 33. Lopez C, Lenggenhager B, Blanke O. How vestibular stimulation interacts with illusory hand
506 ownership. *Conscious Cogn. Elsevier*; 2010;19(1):33–47.
- 507 34. Cruz-Neira C, Sandin DJ, DeFanti TA. Surround-screen projection-based virtual reality: the
508 design and implementation of the CAVE. In: *Proceedings of the 20th annual conference on*
509 *Computer graphics and interactive techniques*. ACM; 1993. p. 135–42.
- 510 35. Klein E, Swan JE, Schmidt GS, Livingston M, Stadt OG. Measurement protocols for medium-
511 field distance perception in large-screen immersive displays. In: *Virtual Reality Conference,*
512 *2009 VR 2009 IEEE*. IEEE; 2009. p. 107–13.
- 513 36. Barr DJ, Levy R, Scheepers C, Tily HJ. Random effects structure for confirmatory hypothesis
514 testing: Keep it maximal. *J Mem Lang*. Elsevier; 2013;68(3):255–78.
- 515 37. Bates DM. Fitting Mixed-Effects Models Using the lme4 Package in R. In: *International*
516 *Meeting of the Psychometric Society* [Internet]. 2008. Available from:
517 <http://pages.stat.wisc.edu/~bates/IMPS2008/lme4D.pdf>

- 518 38. Team RC. R: A language and environment for statistical computing. R Foundation for
519 Statistical Computing, Vienna, Austria, 2012. ISBN 3-900051-07-0; 2014.
- 520 39. Wickham H. ggplot2: an Implementation of the Grammar of Graphics. R package version 0.7.
521 ... 07, URL <http://CRAN.R-project.org/package=ggplot2> [Internet]. 2008; Available from:
522 <http://scholar.google.de/scholar?hl=de&q=ggplot2&btnG=&lr=#1>
523 <http://scholar.google.de/scholar?hl=de&q=ggplot2&btnG=&lr=#2>
- 524 40. Quene, Hugo Bergh H Van Den. Memory and Language Examples of mixed-effects modeling
525 with crossed random effects and with binomial data. *J Mem Lang*. 2008;59:413–25.
- 526 41. Bates DM. lme4: Mixed-effects modeling with R. URL <http://lme4.r-forge.r-project.org/>.
527 2010;
- 528 42. Kenward MG, Roger JH. Small sample inference for fixed effects from restricted maximum
529 likelihood. *Biometrics*. JSTOR; 1997;983–97.
- 530 43. Barany R. Untersuchungen über den vom Vestibularapparat des Ohres reflektorisch
531 ausgelösten rhythmischen Nystagmus und seine Begleiterscheinungen. Oscar Coblentz; 1906.
- 532 44. Guldin WO, Grüsser OJ. Is there a vestibular cortex? *Trends Neurosci*. Elsevier;
533 1998;21(6):254–9.
- 534 45. Curthoys IS, MacDougall HG. What galvanic vestibular stimulation actually activates. *Front*
535 *Neurol*. 2012;JUL(July):1–5.
- 536 46. Bense S, Stephan T, Yousry TA, Brandt T, Dieterich M. Multisensory cortical signal increases
537 and decreases during vestibular galvanic stimulation (fMRI). *J Neurophysiol* [Internet].
538 2001;85(2):886–99. Available from: <http://www.ncbi.nlm.nih.gov/pubmed/11160520>
- 539 47. Bucher SF, Dieterich M, Wiesmann M, Weiss A, Zink R, Yousry TA, et al. Cerebral functional
540 magnetic resonance imaging of vestibular, auditory, and nociceptive areas during galvanic
541 stimulation. *Ann Neurol*. 1998;44(1):120–5.
- 542 48. Villard E, Garcia-Moreno FT, Peter N, Clément G. Geometric visual illusions in microgravity
543 during parabolic flight. *Neuroreport*. 2005;16(12):1395–8.

- 544 49. Ooi TL, Wu B, He ZJ. Distance determined by the angular declination below the horizon.
545 Nature [Internet]. 2001;414(6860):197–200. Available from:
546 <http://www.nature.com/doi/10.1038/35102562>
- 547 50. Jr BG, Agents FB, Wu B, Ooi TL, He ZJ. Perceiving distance accurately by a directional
548 process of integrating ground information. *Nature*. 2004;428(6978):73–7.
- 549 51. Gajewski D a, Wallin CP, Philbeck JW. Gaze behavior and the perception of egocentric
550 distance. *J Vis*. 2014;14(1):1–19.
- 551 52. Willey CR, Jackson RE. Visual field dependence as a navigational strategy. *Atten Percept*
552 *Psychophys* [Internet]. 2014 May [cited 2015 Aug 17];76(4):1036–44. Available from:
553 [http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=4429127&tool=pmcentrez&rend](http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=4429127&tool=pmcentrez&rendertype=abstract)
554 [ertype=abstract](http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=4429127&tool=pmcentrez&rendertype=abstract)
- 555 53. Proffitt DR, Bhalla M, Gossweiler R, Midgett J. Perceiving geographical slant. *Psychon Bull*
556 *Rev*. Springer-Verlag; 1995;2(4):409–28.
- 557 54. Leyrer M, Linkenauger SA, Bühlhoff HH, Kloos U, Mohler B. The influence of eye height and
558 avatars on egocentric distance estimates in immersive virtual environments. In: *Proceedings*
559 *of the ACM SIGGRAPH Symposium on Applied Perception in Graphics and Visualization*.
560 ACM; 2011. p. 67–74.
- 561 55. van der Hoort B, Guterstam A, Ehrsson HH. Being barbie: The size of one’s own body
562 determines the perceived size of the world. *PLoS One* [Internet]. 2011 Jan 25 [cited 2015 Jan
563 9];6(5):e20195. Available from:
564 <http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0020195>
- 565 56. Servos P. Distance estimation in the visual and visuomotor systems. *Exp Brain Res*.
566 2000;130(1):35–47.
- 567 57. Sun H, Campos JL, Young M, Chan GSW, Ellard CG. The contributions of static visual cues,
568 nonvisual cues, and optic flow in distance estimation. *Perception*. 2004;33(1):49–65.
- 569 58. Andre J, Rogers S. Using verbal and blind-walking distance estimates to investigate the two

- 570 visual systems hypothesis. *Percept Psychophys*. 2006;68(3):353–61.
- 571 59. Alexandrova I V, Teneva PT, de la Rosa S, Kloos U, Bühlhoff HH, Mohler BJ. Egocentric
572 distance judgments in a large screen display immersive virtual environment. In: *Proceedings*
573 *of the 7th Symposium on Applied Perception in Graphics and Visualization*. ACM; 2010. p.
574 57–60.
- 575 60. Proffitt DR, Stefanucci JK, Banton T, Epstein W. The role of effort in perceiving distance.
576 *Psychol Sci* [Internet]. 2003 Mar 1 [cited 2015 Jan 8];14(2):106–12. Available from:
577 <http://pss.sagepub.com/content/14/2/106.short>
- 578 61. Sugovic M, Witt JK. An older view on distance perception: Older adults perceive walkable
579 extents as farther. *Exp Brain Res*. 2013;226(3):383–91.
- 580 62. Loomis J, Knapp J. Visual perception of egocentric distance in real and virtual environments.
581 *Virtual Adapt Environ* [Internet]. 2003;(11):21–46. Available from:
582 <http://psycnet.apa.org/psycinfo/2003-06908-002>
- 583 63. Nakamizo S, Imamura M. Verification of Emmert’s law in actual and virtual environments. *J*
584 *Physiol Anthropol Appl Human Sci*. 2004;23(6):325–9.
- 585

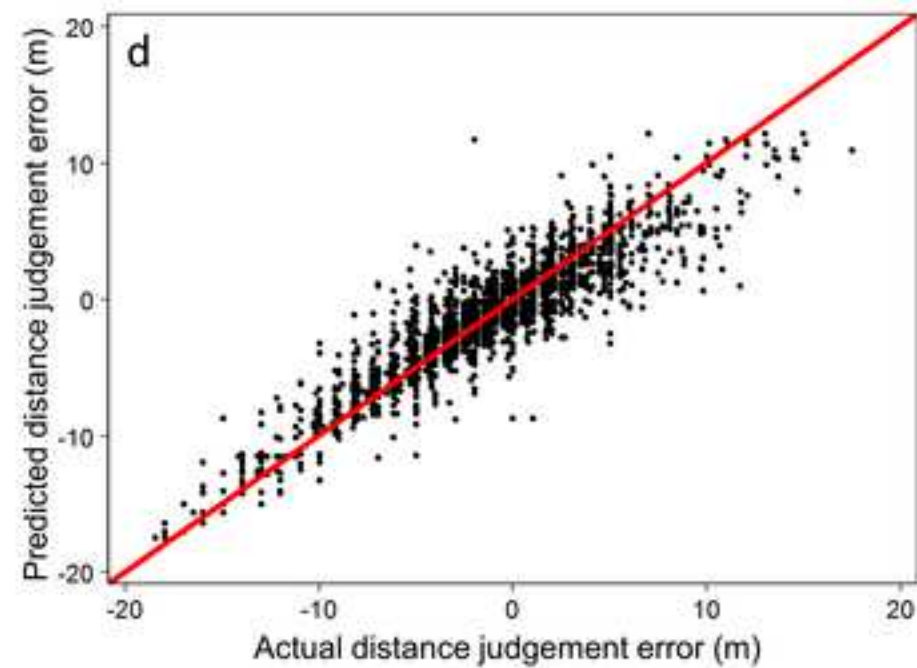
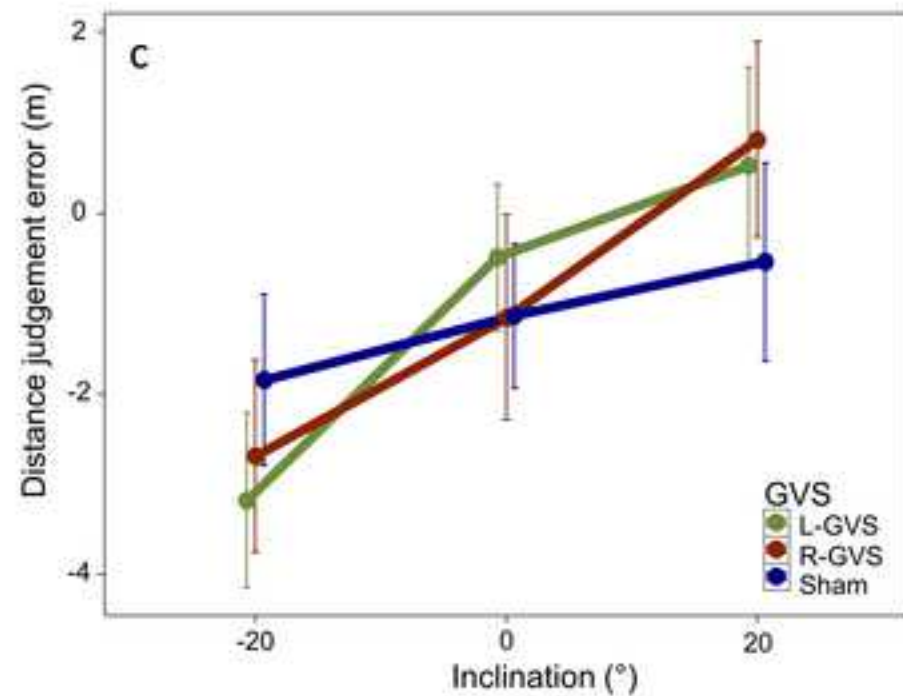
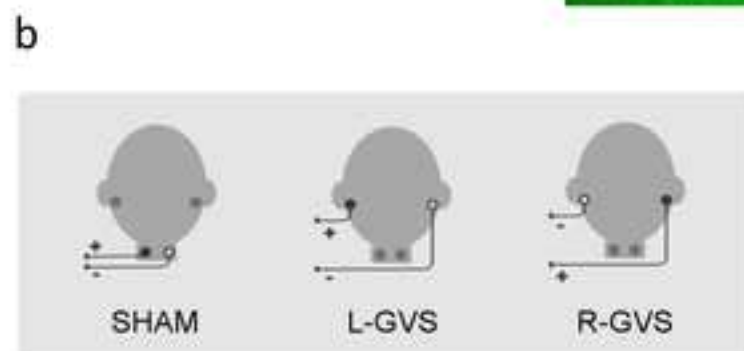
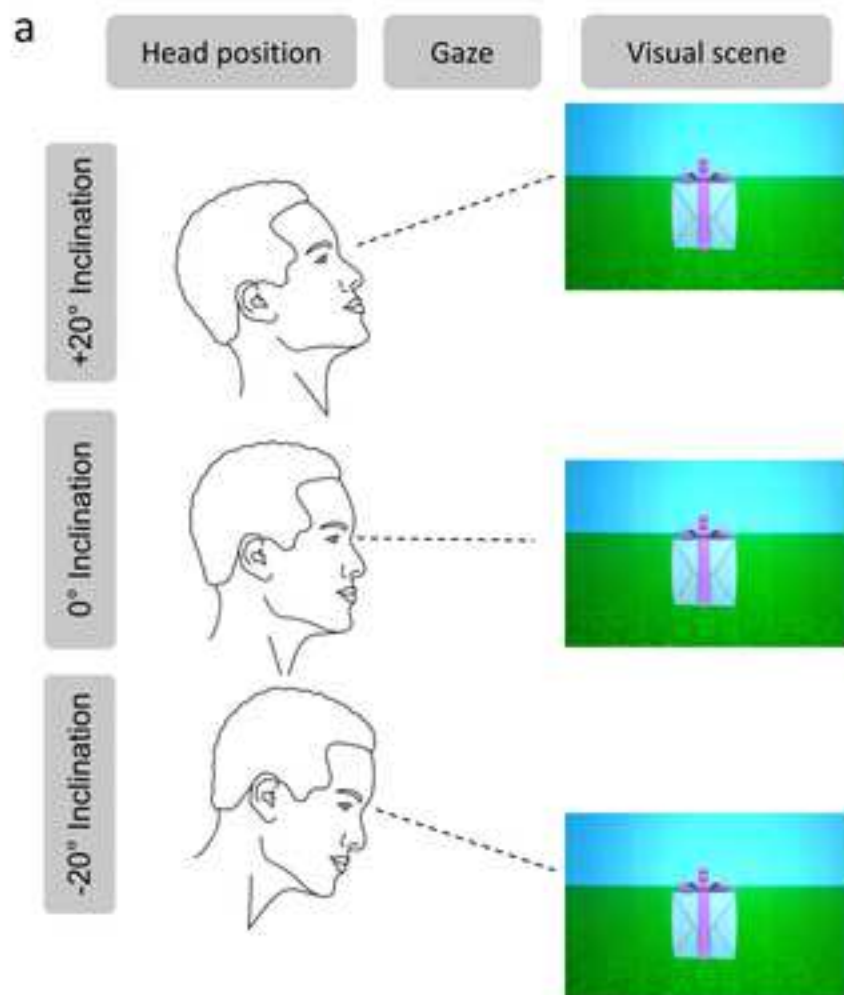


Figure 2

