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Title Page

Title

A singular theory of sensorimotor coordination: On targeted motions in space.

Abbreviated title

A singular theory of sensorimotor coordination

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The authors declare no competing financial interests.

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1 Abstract

2 Gravity has long been purported to serve a unique role in sensorimotor coordination,
3 but the specific mechanisms underlying gravity-based visuomotor realignment remain
4 elusive. In this study, astronauts (9 males, 2 females) performed targeted hand
5 movements with eyes open or closed, both on the ground and in weightlessness.
6 Measurements revealed systematic drift in hand-path orientation seen only when eyes
7 were closed and only in very specific conditions with respect to gravity. In
8 weightlessness, drift in path orientation was observed in two postures (seated, supine)
9 for two different movement axes (longitudinal, sagittal); on Earth, such drift was only
10 observed during longitudinal (horizontal) movements performed in the supine posture.

11 In addition to providing clear evidence that gravitational cues play a fundamental role in
12 sensorimotor coordination, these unique observations lead us to propose an “inverted
13 pendulum” hypothesis to explain the saliency of the gravity vector for eye-hand
14 coordination – and why eye-hand coordination is altered during body tilt or in
15 weightlessness.

16 **Significance statement**

17 In an experiment performed with astronauts, we made an unexpected observation that
18 bears upon the fundamental question of gravity’s role in aligning visuomotor reference
19 frames. Measurements of targeted motions performed on the ground and in
20 weightlessness revealed systematic drift in path orientation seen only in very specific
21 conditions. These unique observations lead us to propose an “inverted pendulum”
22 hypothesis to explain the saliency of the gravity vector for sensorimotor coordination.

23 **Introduction**

24 Since the pioneering work of J. Paillard (1971) describing the theoretical and empirical
25 bases of sensorimotor behavior, the direction of gravity has been assigned a primary
26 role in the encoding of spatial relationships within the nervous system. Paraphrasing
27 Paillard, maintaining the body upright creates a critical reference position specific to
28 states of vigilance and alertness, the true basis of any sensorimotor intervention in the
29 surrounding environment. The ubiquitous and constant presence of gravity is proposed
30 to provide a reliable cue for calibrating visual, vestibular, and proprioceptive
31 representations of the so-called “body scheme” with respect to the environment
32 (Gurfinkel et al., 1988; Paillard, 1991; Berthoz and Pozzo, 1994; Tagliabue and
33 McIntyre, 2014).

34 Indeed, gravity represents a common signal that can be detected across sensory
35 modalities. While it is generally accepted that the vestibular system can signal the
36 orientation of the head with respect to gravity (Angelaki et al., 2004; Angelaki and
37 Laurens, 2020), gravity can also be sensed through proprioceptive cues (the weight of
38 an outstretched arm pulling it downward (Worringham and Stelmach, 1985)) and tactile
39 signals (pressure on the soles of the feet (Carriot et al., 2004), direction of the forces
40 on fingers holding an object (Birznieks et al., 2001; Delhayé et al., 2021)). One can
41 even “see” gravity by the constraints that it imposes on objects and motions (Asch and
42 Witkin, 1948; Sciutti et al., 2012; Scotto Di Cesare et al., 2014): walls are typically
43 vertical so as not to topple over, objects fall downward toward the center of the Earth.
44 The cross-modal nature of gravity perception makes this signal a prime candidate for
45 aligning the reference frames that the CNS employs to perform coordinated actions
46 (Soechting and Flanders, 1989; Buneo et al., 2002; Cohen and Andersen, 2002;
47 McGuire and Sabes, 2009).

48 Numerous studies have illustrated the saliency of the gravity vector for spatial
49 perception and sensorimotor coordination. The perception of the vertical axis is most
50 accurate and most precise when the test subject is upright (Aubert, 1861; Bauermeister
51 et al., 1964; Mittelstaedt, 1983). So-called “oblique” effects (Appelle, 1972) – wherein
52 the alignment of visual lines, hand postures or haptically explored objects are
53 significantly more precise for stimuli aligned with the vertical – are attenuated when the
54 observer is tilted with respect to gravity (McIntyre and Lipshits, 2008). During eye-hand
55 coordination, visuomotor alignments are more precise when the head is aligned with
56 gravity (Tani et al., 2018; Bernard-Espina et al., 2022), while eye-hand coordination is
57 perturbed in weightlessness (Bock et al., 1992; Young et al., 1993).

58 Gravity also plays an intrinsic role in the dynamics of limb movements. Subtle
59 variations in hand trajectories for upward vs. downward motions (Atkeson and
60 Hollerbach, 1985; Papaxanthis et al., 1998) indicate that the CNS takes advantage of
61 gravity to optimize movement dynamics (Berret et al., 2008; Crevecoeur et al., 2009;
62 Gaveau et al., 2016). The fact that these direction-dependent optimizations depend on
63 the availability of visual information on Earth (Le Seac'h and McIntyre, 2007) and
64 persist (at least temporarily) in weightlessness (Papaxanthis et al., 2005; Gaveau et al.,
65 2016), indicate that the CNS *anticipates* the effects of gravity based on a multisensory
66 perception of *up* and *down*, even if changes in sensorimotor performance in the
67 absence of gravity have not yet been fully explained (Weber and Proske, 2022).

68 To better understand how visual, gravitational, and proprioceptive cues interact during
69 sensorimotor coordination, we studied targeted arm movements performed in various
70 body postures, on the ground or in weightlessness, and with eyes open or closed.
71 Analyses of hand paths revealed an unexpected, and indeed surprising, phenomenon
72 that highlights gravity's role in aligning multimodal visuomotor information. During
73 motions with eyes closed, hand-path orientation drifted when gravitational cues were
74 absent as well as in one very specific condition on Earth (horizontal movements while
75 lying supine). We propose a new hypothesis, based on the biomechanical singularities
76 brought about by gravity, to explain how gravitational cues improve sensorimotor
77 coordination.

78 **Materials and Methods**

79 ***Participants***

80 Thirteen astronauts were recruited to participate in the experiment. Two of them were
81 obliged to drop out after their first preflight session due to operational constraints and
82 were thus excluded from the analyses, leaving a sample of 11 astronauts (aged 33-51
83 at the time of their first preflight session; 9 males, 2 females; all right-handed). They
84 were tested onboard the International Space Station (ISS). Seven had never before
85 experienced long-term exposure to microgravity, whereas the other 4 had previously
86 participated to one mission to the ISS. All astronauts stayed at least 5 months on the
87 ISS (min: 157 days, max: 272). The experimental protocol was approved by the
88 Medical Board of the European Space Agency, the Institutional Review Board of the
89 National Aeronautics and Space Administration and the Human Research Multilateral
90 Review Board. All astronauts provided written informed consent prior to testing.

91 ***Task***

92 The astronauts performed sequences of repeated point-to-point movements of the right
93 hand to visually presented targets (LED's), while holding a 400-g instrumented object
94 (the so-called manipulandum, see below) using a precision grip between the thumb
95 and index finger (Fig 1). The movements were performed in different conditions
96 determined by 4 factors: 1) eyes open or closed, 2) seated upright (Fig 1A) or lying
97 supine (Fig 1B), 3) targets aligned with the subject's longitudinal or sagittal axis, 4) in
98 normal Earth gravity or during orbital spaceflight.

99 Each sequence consisted of 19 point-to-point movements, 10 in one direction and 9 in
100 the other, and lasted around 30s. In the eyes-open condition, the participant moved the
101 manipulandum between two targets with both hand and target visible at all times. In the
102 eyes-closed condition, the hand movements were performed to the remembered
103 location of the two targets, with the eyes kept closed during the whole movement
104 sequence. At the beginning of each sequence, the participant was instructed to grip the
105 manipulandum at its center, to place it to the right of the start target (the lowest of the

106 two targets for longitudinal movements and the closest of the two targets for sagittal
107 movements) and to align the center of the object with the position of the target. Once
108 the manipulandum was positioned correctly, the other target turned on. The participant
109 was then instructed to either keep their eyes open or to close them until the end of the
110 sequence, depending on the defined vision condition. Each movement was then
111 triggered by an audible signal, with the time delay between go signals varying randomly
112 between 1.0, 1.3, 1.6 and 1.9 seconds. The participant was instructed to move the
113 manipulandum quickly and accurately to the target after each go signal, to mark a full
114 stop at the target and to wait for the next go signal to perform the next movement in the
115 opposite direction.

116 The location of the targets was adapted to each subject to allow comfortable
117 movements, but once chosen was kept the same for all sessions. Two targets were
118 placed 40 cm apart on an axis parallel to the subject's longitudinal axis, in front and
119 slightly to the right of the participant, at a distance that allowed comfortable reaching
120 movements in the head-to-toe or toe-to-head directions without complete extension of
121 the arm. Two other targets were placed 30 cm apart on an axis parallel to the sagittal
122 (anteroposterior) axis, in front and slightly to the right of the participant, at a distance
123 that allowed comfortable forward and backward reaching movements, also without
124 complete extension of the arm. On Earth, the longitudinal and sagittal axes were
125 aligned with the gravitational vertical and horizontal, respectively, in the seated
126 condition, and vice versa when supine. In weightlessness, where gravity no longer
127 provides a perceptible direction, the longitudinal and sagittal axes were respectively
128 aligned with the implicit vertical (deck-ceiling) and horizontal (port-starboard) axes
129 defined by the visual environment in the space station module, in the seated posture,
130 and vice-versa in the supine posture. On orbit, subjects were restrained by belts to
131 maintain the desired seated and supine postures despite the lack of gravity's stabilizing
132 effect on the body. On Earth, a pillow was placed under the participant's head in the
133 supine posture for comfort. Legs were fully extended in the supine posture, with no
134 contact on the soles of the feet.

135 **Session design**

136 Each participant performed a total of 10 sessions, each organized in a similar fashion.
137 In each session, the participant first completed eight sequences of movements in the
138 seated posture. Sequences 1-4 were performed along the longitudinal axis and
139 sequences 5-8 along the sagittal axis. Odd sequences were performed with eyes open
140 and even sequences were performed with eyes closed. These eight sequences were
141 then repeated in the supine posture after a delay of 30min to 3 days. In exceptional
142 cases (3 out of 98) the supine condition preceded the seated condition, on separate
143 days, due to scheduling constraints or technical issues. Only one subject performed the
144 supine condition outside the 4-day window after the seated condition (50 days after) in
145 their Late inflight session (see below).

146 After learning to execute the required targeted motions in a separate training session,
147 the astronauts completed two preflight sessions, three inflight sessions and five
148 postflight sessions. One preflight session was performed 65 to 274 days prior to
149 launch, the other 43 to 173 days prior to launch, with a minimum of 27 days between
150 the first and second sessions. The Early inflight session was performed between flight
151 day (FD) 4 and 12; the Middle inflight session between FD 70 and 91; and the Late
152 inflight session between FD 132 and 146 (except for the supine condition of one
153 participant, which was performed on FD 196, as noted above). Three Early postflight
154 sessions were conducted, the day after the return to the ground (R+1) as well as on

155 R+5 (± 2) and on R+11 (± 3). Finally, two Late postflight sessions were performed
156 between R+46 and R+152 and between R+63 and R+410, respectively, to check for
157 return to the preflight baseline. Due to time and safety constraints, only the seated
158 posture was tested on R+1. One participant did not perform the last Late postflight
159 session due to time constraints.

160 ***Complementary experiment***

161 Based on our results from the main experiment, we asked whether observed drift was
162 related to a cumulative effect of movement repetition, or a temporal drift related to the
163 time elapsed since the eyes were closed. A group of 18 additional participants (aged
164 21-65, median age 27; 7 males, 11 females; 17 right-handed) performed the same
165 Seated Longitudinal and Supine Longitudinal conditions as the astronauts but varied
166 the number of discrete movements performed in blocks of fixed duration by varying the
167 delay between consecutive movements (dictated by an audible signal). In the Short-
168 Delay condition, the delay between movements was equal to 2s on average (chosen
169 pseudo-randomly between 1.5, 1.7, 1.9, 2.1, 2.3, and 2.5s from trial to trial) such that
170 24 movements (12 in each direction) were performed over the 48s that lasted each
171 block. In the Long-Delay condition, the delay was equal to 8s on average (chosen
172 pseudo-randomly between 6.0, 6.8, 7.6, 8.4, 9.2, and 10.0s from trial to trial), such that
173 only 6 movements (3 in each direction) were performed in these blocks (which also
174 lasted 48s). After a short training, during which the participants were familiarized with
175 the task and the two delay conditions, the participants performed 4 blocks in each
176 combination of posture (Seated or Supine) and delay (Short- or Long-Delay). As in the
177 main experiment, blocks 1 and 3 were always performed with eyes open, while blocks
178 2 and 4 were always performed with eyes closed. The order of the posture and delay
179 conditions, however, was counterbalanced across participants.

180 ***Data collection and post-processing***

181 Three experimental sets of hardware were used for the main experiment, all essentially
182 identical. In addition to the equipment used onboard the ISS, one setup was located at
183 the European Astronaut Center in Cologne and another at the Johnson Space Center
184 in Houston for preflight and postflight testing.

185 The manipulandum was an instrumented object of dimensions 102 x 50 x 62 mm, mass
186 400g, and grip aperture 40mm. It was covered with 8 infrared markers. Two motion-
187 tracking units (Codamotion CX-1 units adapted for spaceflight requirements;
188 Codamotion Ltd, UK) were used to track the position of these markers in 3D, at 200 Hz.
189 The manipulandum was additionally equipped with an accelerometer and a gyroscope
190 to measure linear acceleration and angular velocity of the object in 3D, at 1000 Hz,
191 allowing continuous recording of the trajectory despite occasional occlusions of the
192 infrared markers. The position of the center of mass of the manipulandum was
193 reconstructed using the measured position of the 8 infrared markers combined with the
194 accelerometer and gyroscope signals using custom routines. The accelerometer and
195 gyroscope signals were low-pass filtered using a Butterworth filter of order four with a
196 cut-off frequency of 50 Hz. After reconstruction, the position of the center of mass was
197 low-pass filtered using a Butterworth filter of order four with a cut-off frequency of 7 Hz,
198 then differentiated numerically to compute object velocity.

199 For the complementary experiment, the position of the participant's hand was recorded
200 with a motion-tracking system (two CX-1 unit, Codamotion) tracking the 3-D position of
201 an infrared marker attached to the nail of the participant's index finger. As in the main
202 experiment, the participants held a small mass (125g, 8.5 x 2 x 3cm) between the

203 thumb and index finger of the right hand and had a pillow under their head in the
204 supine posture for comfort, as was used by astronauts during testing on ground.

205 All data postprocessing and analyses were performed with Matlab R2022a (The
206 MathWorks, USA), with filter parameters computed and applied using the butter and
207 filtfilt functions, respectively.

208 **Data analysis**

209 The first trial of each sequence of the main experiment was not included in the
210 analyses, because its kinematics often differed significantly from the subsequent trials.
211 Indeed, the first trial was often performed hastily, and sometimes with eyes open
212 instead of closed, because the participants were startled by the first go cue. Thus, 18
213 trials per sequence were kept for the analyses.

214 We used velocity thresholds to define the start and end time points of each discrete
215 movement. Movement start was defined as the first time at which hand velocity along
216 the target axis exceeded 5% of maximum velocity for at least 50 ms; similarly,
217 movement end was defined as the first time at which hand velocity fell below 5% of
218 maximum velocity for at least 50ms. Within each trial, we measured the orientation of
219 the path of the hand+object as the orientation of the line connecting the start and end
220 points in the parasagittal plane. The 0° orientation was defined in world coordinates,
221 parallel to the vertical axis (longitudinal axis in the seated posture, sagittal axis in the
222 supine posture), and the 90° orientation was parallel to the horizontal axis (sagittal axis
223 in the seated posture, longitudinal axis in the supine posture), as illustrated in Figure 1.
224 We computed the drift in path orientation within each sequence of trials as the slope of
225 a linear regression fitted (in the least-square sense) between path orientation and trial
226 number (°/trial).

227 To further investigate if the determinant independent variable was indeed trial number
228 or if it was rather the time elapsed since closing the eyes, for the complementary
229 experiment we computed the drift in path orientation with respect to movement
230 repetition (°/trial) as above, and with respect to time (°/s) by computing the slope of a
231 linear regression between path orientation and elapsed time. In both cases, a positive
232 (negative) slope indicates that the path rotated clockwise (counterclockwise) in the
233 parasagittal plane when looking towards the participant's right side.

234 **Statistical analyses**

235 To test for possible practice effects on the ground, effects of gradual adaption to
236 microgravity, and effects of readaptation to Earth's gravity, we performed 8 one-way
237 repeated-measures ANOVAs testing the effect of session on path-orientation drift for
238 each combination of posture (Seated or Supine), motion axis (Longitudinal or Sagittal)
239 and gravity (1g or 0g) condition performed with eyes closed. When a significant effect
240 of session was observed, we performed t-tests with Holm corrections for multiple
241 comparisons to compare sessions pairwise. Results on these initial tests showed no
242 functionally significant differences between the different ground sessions or between
243 the different in-flight sessions (see Results). As our primary hypothesis concerned the
244 effect of gravity on path characteristics, we collapsed the data and performed
245 subsequent analyses on the average of all Ground measurements versus the average
246 of all 3 Inflight measurements for each combination of vision, posture and movement
247 axis.

248 For the main experiment we performed a 3-way repeated-measures ANOVA to test the
249 effect of gravity (Ground vs. Spaceflight), vision (Eyes open vs closed), and posture-

250 axis condition (Seated Longitudinal, Seated Sagittal, Supine Longitudinal, Supine
251 Sagittal) on path-orientation drift. To break the interactions, we tested the effect of
252 vision on the drift in each posture-axis and gravity condition separately using two-sided
253 paired t-tests. In addition, we used two-sided paired t-tests to test the effect of gravity
254 on the drift with eyes closed in each movement condition separately. Finally, we used
255 two-sided t-tests to test the null hypothesis of zero drift. For the complementary
256 experiment, we performed a 3-way repeated-measures ANOVA to test the effects of
257 vision, posture and delay conditions on path-orientation drift and checked that we
258 replicated the findings of the main experiment. We then used two-sided paired t-test to
259 test the specific hypothesis of whether or not there was a significant difference in drift,
260 measured either in %/s or %/trial, between the Short-Delay and Long-Delay conditions
261 during movements performed in supine posture with eyes closed.

262 Statistical tests were performed in Rstudio with the functions *ezANOVA*, *t.test*, *lillie.test*,
263 and *pairwise.t.test*. A significance level of 0.05 was chosen for all tests. Effects sizes
264 were reported using η^2 and Cohen's *d* parameters. We verified data normality using
265 Kolmogorov-Smirnov test with Lilliefors adjustment. Mauchly's test was used to check
266 sphericity, and Greenhouse–Geisser corrections were applied when necessary.

267 Results

268 The main result of the experiment is presented in Figure 2, which shows hand paths of
269 a typical subject as well as the evolution of hand-path orientation across trials for all
270 subjects, during the first pre-flight session and the first inflight session in all conditions.
271 In many cases we observed parallel shifts of the hand paths in the absence of visual
272 feedback (see example traces in Fig 2A, 2B), in agreement with previous studies
273 (Brown et al., 2003; Smeets et al., 2006; Patterson et al., 2017). Much more interesting
274 and consistent across subjects was the observation of drift in hand-path *orientation*, but
275 only under certain conditions (see black stars in Fig 2B,C,D). On Earth, such drift was
276 observed only for longitudinal movements performed in the supine posture (i.e.,
277 horizontal movements with respect to gravity, Fig 2B). On orbit, however, drift in path
278 orientation was observed for both target axes in both postures when the eyes were
279 closed (Fig 2C-D). When drift occurred, it was almost always in the same direction:
280 path orientation rotated progressively clockwise in the sagittal plane when looking
281 toward the subject's right side. These data highlight a clear effect of gravity on the
282 stability of hand-path orientation for trials performed with eyes closed.

283 To quantify the drift, we computed for each movement sequence the slope of the linear
284 regression that best fitted the path orientation as a function of trial number. This slope
285 gives an approximation of the rate at which path orientation changed, in degrees per
286 trial. Based on previous work revealing asymmetries in the characteristics of
287 movements performed with or against gravity (Atkeson and Hollerbach, 1985;
288 Papaxanthis et al., 2005; Le Seac'h and McIntyre, 2007; Gaveau et al., 2016) we
289 compared drift as a function of movement direction (forward/backward) within each
290 posture-axis condition and found no significant differences ($p > 0.05$). We therefore
291 pooled all trials of a given sequence together independent of movement direction. We
292 found no significant changes in drift over pre- and postflight ground sessions in the
293 Eyes-Closed condition ($p > .05$ in all conditions), justifying our decision to average
294 across all ground sessions for subsequent statistical analyses. We did find a significant
295 change between inflight sessions, but only in the Seated Longitudinal condition with
296 eyes closed ($F(2,20)=4.17$, $p=0.03$). As shown in Figure 3, the drift was slightly larger
297 during the Early session than during the other sessions in that condition, but the effect

298 was small and did not survive the post-hoc Holm corrections applied when comparing
299 the three inflight sessions pairwise. In subsequent analyses, we therefore pooled
300 results from all preflight and postflight sessions and pooled data from the three inflight
301 sessions for each of the vision/posture/axis combinations.

302 Figure 4 shows the average of the path-orientation drift in each condition after
303 collapsing the different sessions. The omnibus statistical test used to test the effect of
304 the different conditions on the drift revealed strong interaction effects between vision,
305 posture-axis, and gravity. More specifically, we found significant interaction effects
306 between gravity and vision ($F(1,10)=15.2$, $p<.005$, $\eta^2=0.13$), between posture-axis and
307 vision ($F(3,30)=19.9$, $p<.001$, $\eta^2 = 0.20$), and between gravity and posture-axis
308 ($F(3,30)=20.2$, $p<.001$, $\eta^2 = 0.12$) on the drift. There was also a marginal second-order
309 interaction effect between these three factors ($F(3,30)=2.7$, $p=0.06$, $\eta^2 = 0.02$). These
310 interaction effects reflect the fact that path orientation drifted only in specific conditions,
311 as detailed below.

312 On the ground, a significant effect of vision on the drift in path orientation was found
313 only in the Supine Longitudinal condition ($t(10)=6.7$, $p<.001$, $d=2.02$). In that condition,
314 the drift was significantly greater than zero when the eyes were closed ($t(10)=6.24$,
315 $p<.001$, $d=1.88$). In all other conditions on the ground, the drift was not significantly
316 different from zero, whether the eyes were open or closed. During spaceflight, closing
317 the eyes caused a significant increase in path-orientation drift in the four posture-axis
318 conditions, compared to eyes open (Seated Longitudinal: $t(10)=4.6$, $p<.005$, $d=1.37$;
319 Seated Sagittal: $t(10)=4.0$, $p<.005$, $d=1.21$; Supine Longitudinal: $t(10)=4.8$, $p<.001$,
320 $d=1.43$; Supine Sagittal: $t(10)=3.2$, $p<.01$, $d=0.96$). With eyes closed, the drift was
321 significantly greater than zero in all four conditions (Seated Longitudinal: $t(10)=4.11$,
322 $p<.005$, $d=1.24$; Seated Sagittal: $t(10)=6.1$, $p<.001$, $d=1.84$; Supine Longitudinal:
323 $t(10)=4.3$, $p<.005$, $d=1.30$; Supine Sagittal: $t(10)=5.1$, $p<.001$, $d=1.55$). Furthermore,
324 the drift was significantly larger than on the ground in the Seated Longitudinal
325 ($t(10)=4.36$, $p<.005$, $d=1.31$; Fig 4A), Seated Sagittal ($t(10)=5.9$, $p<.001$, $d=1.77$; Fig
326 4C) and Supine Sagittal ($t(10)=2.8$, $p<.05$, $d=0.83$; Fig 4D) conditions. No significant
327 difference between Ground and Spaceflight was found in the Supine Longitudinal
328 condition, since in that case the drift was high in both gravity conditions ($t(10)=0.33$,
329 $p=0.74$, $d=0.10$; Fig 4B).

330 We next looked at whether drift observed in distinct movement conditions was
331 correlated across participants and found that it usually was (Figure 5). During
332 spaceflight, we found moderate to strong correlations in drift between seated and
333 supine (Fig 5A) and between longitudinal and sagittal movements (Fig 5B). In 0g,
334 astronauts that showed large drift in one condition were therefore likely to show large
335 drift in another. We also found a moderate but non-significant correlation between the
336 drift measured on Earth in the Supine Longitudinal condition, and the drift measured
337 during spaceflight in the same condition (Fig 5C). We further considered whether
338 previous experience in weightlessness might affect the presence or absence of path-
339 orientation drift. Consistent with the lack of consistent evolution across inflight
340 sessions, subjects who had flown to the ISS on a previous mission (empty circles in Fig
341 5C) showed similar drift in path orientation as subjects who had no previous experience
342 with long-term weightlessness exposure (filled circles), even during the Early
343 spaceflight session.

344 Finally, the complementary experiment was used to test whether observed drift was
345 related to a cumulative effect of movement repetition, or a temporal drift related to the

346 time elapsed since the eyes were closed. A group of non-astronaut subjects performed
347 a greater or lesser number of discrete movements within a given time window, i.e. with
348 a larger or smaller average inter-movement time delay. We first confirmed that the
349 effects of visual feedback (eyes open vs. closed) and posture (seated vs. supine) on
350 path-orientation drift were consistent with results obtained on the ground in our main
351 experiment with astronauts: there was a significant main effect of Vision ($F(1,17)=18.1$,
352 $p<.001$, $\eta^2=0.17$) and Posture ($F(1,17)=18.5$, $p<.001$, $\eta^2=0.11$) on the drift measured in
353 $^\circ/s$, as well as a significant interaction effect between these two factors ($F(1,17)=14.3$,
354 $p<.005$, $\eta^2=0.14$) reflecting the fact that path orientation drifted in the supine posture,
355 but not in the seated posture, as was the case with the astronauts on Earth. Regarding
356 the effect of movement repetitions, we found that the delay condition (Short Delay vs.
357 Long Delay) did not significantly affect drift when the drift was expressed relative to
358 time (main Delay effect: $F(1,17)=0.84$, $p=0.37$; $p>.05$ for all interaction effects involving
359 the Delay factor). Fig 6A shows the evolution of path orientation over time in the two
360 delay conditions in the Supine posture with eyes closed: path orientation drifted over
361 time at a similar rate ($t(17)=-0.94$, $p=0.36$; Fig 6B) whether participants performed 6 or
362 24 movements in the same time interval. In contrast, when expressing the drift as the
363 amount of change in path orientation per trial (instead of per second), a highly
364 significant effect of Delay appeared ($t=-4.98$, $p<.001$, $d=-1.5$; Fig 6C), as more time
365 elapsed between two consecutive movements in the Long-Delay compared with the
366 Short-Delay condition. Thus, we have shown that path orientation drifts as a function of
367 time, not as a function of movement repetition.

368 To summarize, the orientation of hand paths for targeted, point-to-point movements
369 drifted in weightlessness whenever the astronauts moved between remembered visual
370 targets with eyes closed. We also observed drift on Earth with eyes closed, but only in
371 a supine posture for motion perpendicular to gravity. Expressed in another way, drift
372 was suppressed whenever vision was available or when either the head or the motion
373 of the hand was aligned with gravity.

374 **Discussion**

375 Our results show that in the absence of gravitational and visual cues, humans fail to
376 reproduce constant path orientations during repeated point-to-point hand motions. But
377 if gravity is a key anchoring cue in the absence of vision, why did it not suppress drift
378 for all postures and movement directions on Earth? Here we propose a new
379 hypothesis, based on the singularity of an unstable, inverted pendulum, to explain the
380 saliency of the gravity vector for maintaining proprioceptive alignment with the external
381 world.

382 ***Singular hypothesis***

383 A standing human body or an upright head can be modeled in their simplest form as
384 inverted pendulums (Stoffregen and Riccio, 1988). When perfectly aligned with gravity
385 a pendulum is at an unstable singular point (Fig 7A). No torque at the pivot is needed
386 to resist gravity, but any small misalignment from the vertical will generate gravitational
387 torque that, if not opposed, will cause it to tumble. Heightened vigilance is needed due
388 to the unpredictable direction of the fall from this singular position. At the same time,
389 the sensorimotor system should be most sensitive to deviations from this posture,
390 where change in gravitational torque per change in tilt is maximal, allowing fine
391 discrimination of nearby orientations (Butts and Goldman, 2006). According to Weber's
392 law (Ekman, 1959), the perceptual system will be more sensitive to deviations when
393 the underlying signal is small. We postulate that on Earth, the singular configuration of

394 the head on shoulders provides an unambiguous indicator as to when the head is
395 upright, reducing errors in sensorimotor transformations (Paillard, 1991; Burns and
396 Blohm, 2010; Tagliabue et al., 2013; Bernard-Espina et al., 2022).

397 When lying supine with the head supported, the singularity of an unstable head
398 disappears, and the estimation of head orientation becomes much more uncertain.
399 However, displacing a mass against gravity gives rise to effects analogous to that of
400 the inverted pendulum. For any given joint torque, small variations in joint angles will
401 cause changes in the direction of the force applied by the hand (Fig 7B). This purely
402 biomechanical effect results in a divergent force field surrounding the object (Mussa-
403 Ivaldi et al., 1985; McIntyre et al., 1996) in the plane perpendicular to gravity. Any
404 deviation off the vertical path will produce proprioceptive and cutaneous signals at the
405 finger-object interface that are uniquely conspicuous because the driving forces
406 perpendicular to the line of motion should otherwise be zero. Not so for any other
407 movement axis, where gravity is constantly pushing the object off the desired line of
408 motion. The heightened vigilance needed to keep the hand on a vertical path, and the
409 heightened sensitivity to forces perpendicular to it, increase the saliency of this path
410 orientation. We believe that this is why directional drift did not occur for vertical hand
411 motions when lying supine on Earth.

412 The unstable nature of holding the head upright or pushing directly against gravity
413 requires, therefore, heightened vigilance in the form of muscle co-contraction (Hogan,
414 1984; Burdet et al., 2001; Berret and Jean, 2020), augmented reflex activity (Damm
415 and McIntyre, 2008), grip force adjustments (Johansson and Westling, 1984; Hadjiosif
416 and Smith, 2015) or increased visual attention. At the same time, deviations of head
417 orientation or hand displacement from the singular direction determined by gravity are
418 the easiest for the CNS to detect. We posit, therefore, that the singularities created by
419 a constant gravitational field induce a *pop-out* effect (Treisman and Gelade, 1980),
420 such that unstable postures and movements brought on by gravity serve as critical
421 markers for multisensory alignment. Absent gravity and vision, hand-path orientation
422 will drift regardless of posture or target axis, as we observed.

423 Our hypothesis can explain why the accuracy and precision of head-orientation
424 perception is highest close to the upright posture. This phenomenon has often been
425 attributed to hypothetical tilt-dependent noise of the otoliths (De Vrijer et al., 2008;
426 Tarnutzer et al., 2009; Vingerhoets et al., 2009). Mathematical models show that
427 maintaining the head near upright is critical for disentangling tilt from linear
428 acceleration in vestibular signals (Farkhatdinov et al., 2019). Our hypothesis, also
429 based on mathematical principles, is more general. It can be applied to the vestibular
430 system (the hair cells of the utricle behave like tiny, inverted pendulums), to the head-
431 neck proprioceptive system (the head leaves the singular posture when tilted or
432 supported), and to the kinesthetic system of the upper limb. Our hypothesis might also
433 explain why closing the eyes influences the kinematics of horizontal movements, but
434 not vertical movements, when lying down (Le Seac'h and McIntyre, 2007) and why
435 near-vertical arm movements can ameliorate verticality perception (Tani et al., 2021).

436 **Potential causes of drift**

437 While our theory explains how biomechanical singularities engendered by gravity can
438 suppress drift in movement path orientation, it provides no explanation as to why these
439 paths go adrift when this anchor disappears. One might postulate that in
440 weightlessness, or in the infrequent supine posture, the CNS incorrectly computes
441 gravity-tuned motor commands habitually used to achieve the desired hand
442 displacement, with a subsequent accumulation of errors in the absence of visual

443 feedback (Bock et al., 1992). But in our complementary experiment path orientation
444 drifted at a consistent rate with respect to the time elapsed since closing the eyes,
445 irrespective of the number of movement repetitions and irrespective of the direction of
446 movement along the path (forward or backward). Furthermore, occurrence of drift
447 persisted over several months spent on orbit, despite ample opportunities in the
448 astronauts' daily lives to learn the unfamiliar force fields of weightlessness through
449 visually-guided movement (Ohashi et al., 2019). We conclude that drift does not stem
450 from an accumulation of errors in the motor command used to follow the path.

451 Instead, we believe that the drift arises in the mapping from remembered target
452 locations to intended hand paths. Subjects show systematic bias when visually (Aubert,
453 1861; Mittelstaedt, 1983) or haptically (Bauermeister et al., 1964) reporting their
454 perception of vertical and misreport the orientation of their body axis when tilted with
455 respect to gravity (Bauermeister, 1964; McIntyre and Lipshits, 2008) or when faced
456 with vestibular disorders (Saj et al., 2013). Biases in the perceived vertical are
457 purported to arise from prior assumptions in the absence of salient orientating cues (De
458 Vrijer et al., 2008; Sinnott et al., 2023) or from unbalanced vestibular signals
459 (Mittelstaedt, 1983; Glasauer and Mittelstaedt, 1998), while visual and proprioceptive
460 reference frames appear to rely on different estimates of gravity (Fraser et al., 2015). In
461 addition, remembered arm postures in a gravitational field can be biased towards the
462 resting state of the limb (Han et al., 2024). Under these effects, vision and
463 proprioception may fall out of register. According to Bayesian models of multisensory
464 integration, the rotation of the hand paths that we observed could stem from a gradual
465 shift in weighting between misaligned visual and proprioceptive representations of the
466 targeted motion as the visual representation degrades in memory; a concept that has
467 been used to explain translational drift in hand path when vision of the hand is removed
468 (Smeets et al., 2006). Visual-vestibular reweighting might also explain why the
469 subjective vertical deviates gradually over ~20 s when a biasing visual stimulus is
470 removed (Gibson, 1937; Dichgans et al., 1972). Alternatively, the mapping from an
471 allocentric representation of the targets in memory to egocentric representation of the
472 required motion might change gradually due to drift in the estimation of body orientation
473 with respect to the world. Indeed, when human participants are tilted in the dark,
474 perception of the visual vertical rotates progressively, with time constants on the order
475 of several minutes (Wade, 1970; Tarnutzer et al., 2013). Computational models that
476 include the effects of biased signal from the semi-circular canals would predict such
477 drift in the estimation of head/body orientation (Laurens and Angelaki, 2011) in the
478 absence of the anchoring cues provided by gravity.

479 **Open questions**

480 Our hypothesis about the saliency of gravity as an anchoring cue explains, therefore,
481 how the CNS avoids the drift that we observed, but does not explain the drift *per se*.
482 For instance, why does the drift almost always occur in the same direction? And does it
483 depend on the amount of body tilt or the mass of the hand-held object? Other
484 questions remain as well. For instance, it is still not clear whether neck proprioceptors,
485 otolith signals or both provide the key anchoring cue (Pettorossi and Schieppati, 2014),
486 as the inverse pendulum analogy applies to each one. Similarly, is tactile interaction
487 with a hand-held object critical, or does alignment of the movement with gravity pop out
488 from proprioception alone? Our experimental paradigm does, however, suggest
489 avenues for exploring these and other open questions, e.g. by further studying hand-
490 path drift on the ground in the supine position.

491 **Conclusions**

492 The results reported here provide irrefutable evidence that gravity plays a prominent
493 role in sensorimotor integration and eye-hand coordination, affording insight into how
494 pathologies affecting eye-hand coordination might be addressed. Furthermore, the
495 testable hypothesis presented here, based on singularities provoked by the
496 gravitational field, gives rise to the intriguing notion that postural *instability* subserves
497 behavioral *stability* in sensorimotor coordination.

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671

672 **Figure legends**

673 **Figure 1:** Participant's posture in the Seated (A) and Supine (B) conditions. The
674 colored disks depict the position of the targets in the Longitudinal and Sagittal
675 conditions. The dashed lines illustrate the convention used for path orientation.

676 **Figure 2:** Hand-path orientation across individual trials as a function of body posture
677 (seated or supine), visual feedback (eyes open or closed), target movement axis
678 (longitudinal or sagittal) and gravitational context (ground or spaceflight). A: seated
679 posture on the ground (first preflight session). B: Supine posture on the ground (first
680 preflight session). C: Seated posture in flight (Early session). D: Supine posture in flight
681 (Early session). Empty (eyes open) and filled (eyes closed) disks show the mean
682 across participants and error bars show the standard error of the mean (N=11). Light
683 traces show data from individual participants (average of the two sequences of trials
684 performed in each condition). Trials were aggregated into bins containing two
685 consecutive trials (performed in opposite directions). Trial-by-trial hand trajectories
686 performed with eyes closed by a representative subject are shown on the right of each
687 panel, with color intensity indicating trial number from lightest (first trial) to darkest (last
688 trial). The stars show the conditions in which a significant effect of vision on the drift in
689 path orientation (slope of path orientation vs. trial number) was detected at the 0.01
690 significance level.

691 **Figure 3.** Drift of hand-path orientation in the Eyes-closed condition over preflight,
692 inflight, and postflight sessions for the Seated Longitudinal (A), Supine Longitudinal (B),
693 Seated Sagittal (C) and Supine Sagittal (D) posture-axis conditions. Thick dark traces
694 show the mean across subjects, with error bars showing the 95% confidence interval of
695 the mean (N=11). Fine light traces show data from individual subjects.

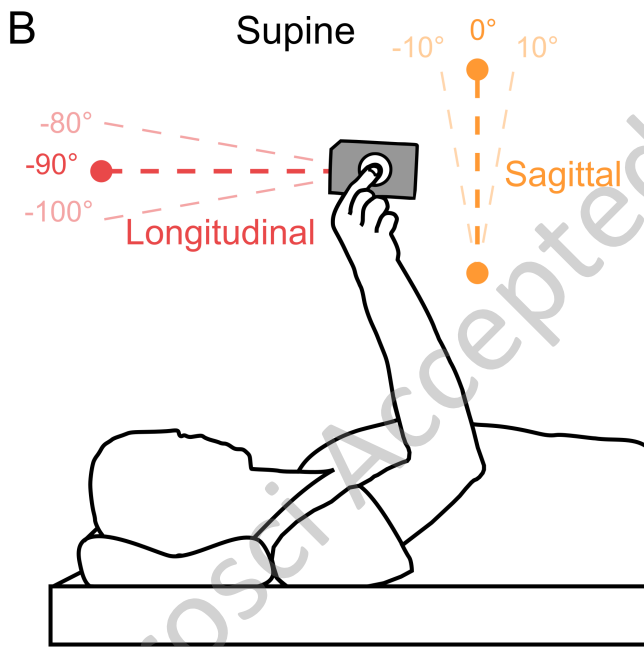
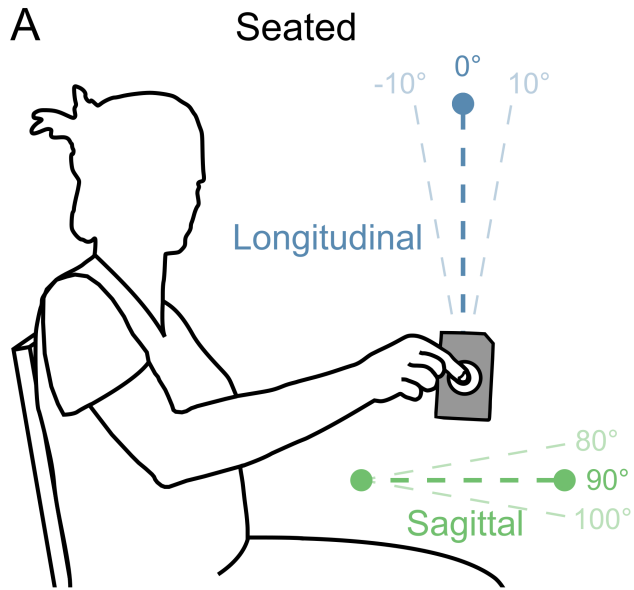
696 **Figure 4:** Path orientation drift in the Seated Longitudinal (A), Supine Longitudinal (B),
697 Seated Sagittal (C) and Supine Sagittal (D) posture-axis conditions. Disks (open: eyes
698 open; filled: eyes closed) and error bars show the mean and 95% confidence interval of
699 the mean across participants (N=11). Thin light lines show the eyes-closed data of
700 individual participants. Stars emphasize significant differences between 0g and 1g or
701 between Eyes Open and Eyes Closed (paired t-tests: * $p < .05$; ** $p < .01$; *** $p < .001$).

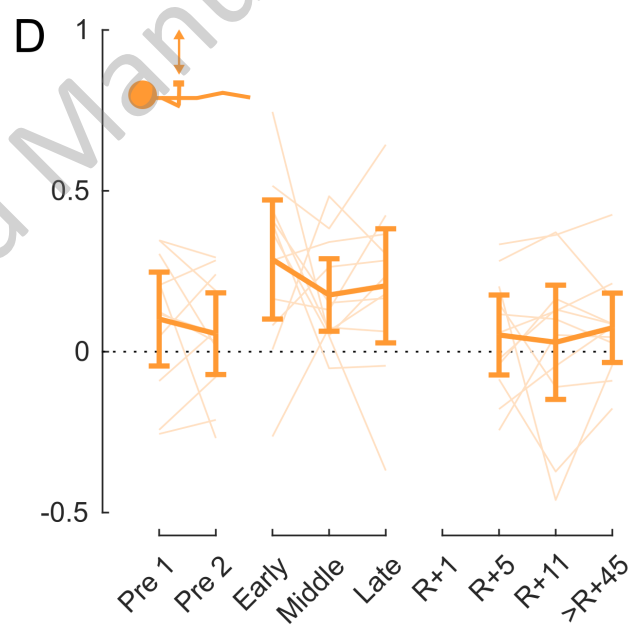
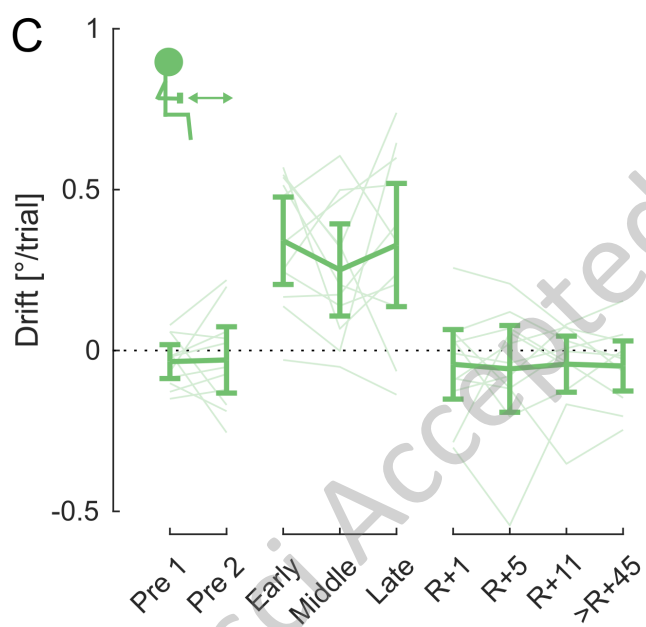
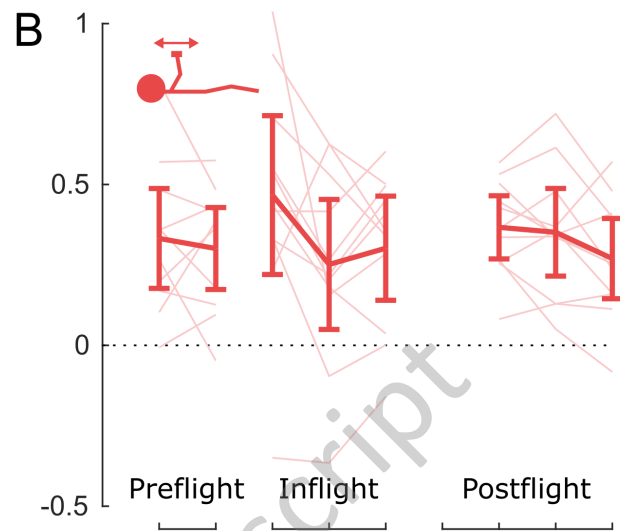
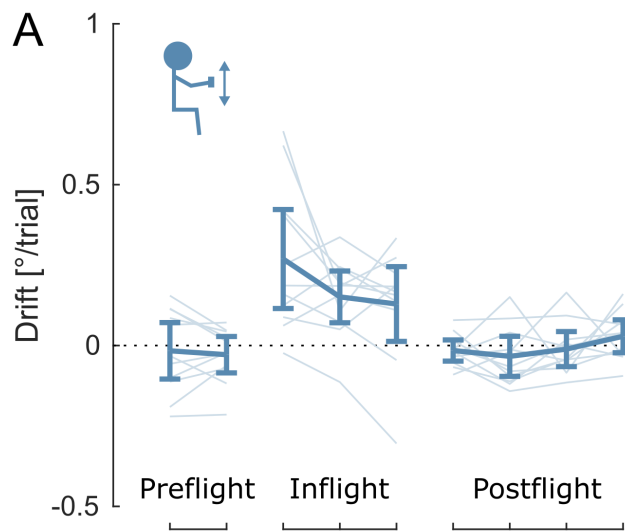
702 **Figure 5:** Across-subject correlations in drift between movement conditions. A: Drift in
703 0g in supine posture vs. seated posture, in the two axis conditions. B: Drift in 0g during
704 Longitudinal vs. Sagittal movements, in the two posture conditions. C: Drift in the
705 Supine Longitudinal condition in 0g vs. 1g. Each point is the mean value of one
706 participant. In panel C, filled disks show the data of first-time flyers, while empty disks
707 show the data of second-time flyers. Panels A and B show the average of the three
708 inflight sessions, while panel C only show the data of the Early inflight session versus
709 the average of all ground sessions.

710 **Figure 6:** Results of the complementary experiment. A: Path orientation as a function
711 of time in the two Delay conditions performed in supine posture with eyes closed. In the
712 Short-Delay condition, 24 movements were performed over 48s. In the Long-Delay
713 condition, 6 movements were performed in the same time interval. Error bars show the
714 mean \pm SEM across participants (N = 18) while grey lines show data from individual
715 participants. B: average drift in path orientation (mean \pm 95% CI), expressed as a
716 function of time [$^{\circ}$ /s]. C: average drift in path orientation expressed as a function of trial
717 number [$^{\circ}$ /trial] (**p < .001).

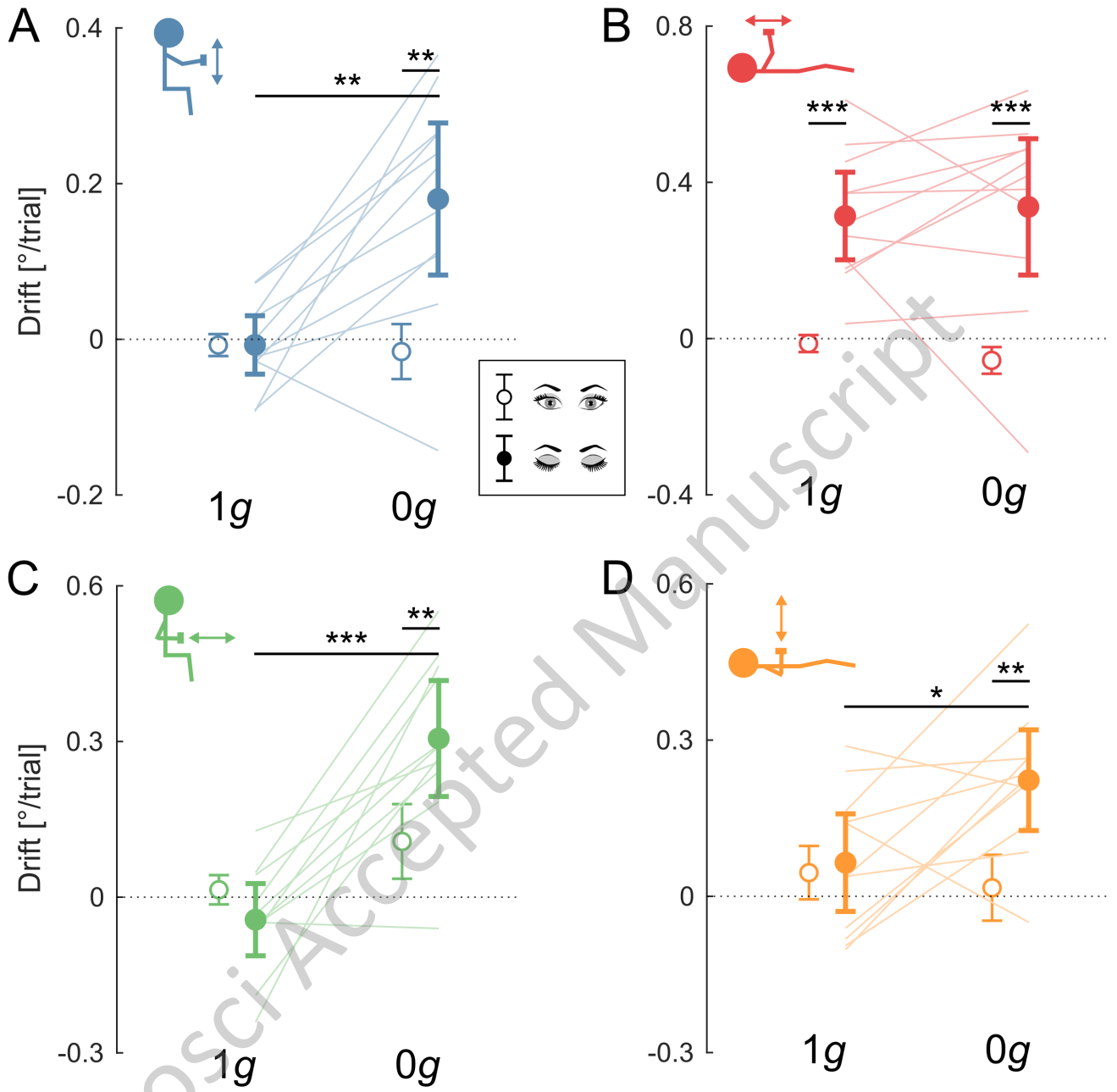
718 **Figure 7:** illustration of the singularities inherent to an inverted pendulum and of the
719 raised arm holding a mass against gravity. (A) Singularity of the upright posture, where
720 the gravitational torque is zero and the head is unstable. Small rotations of the
721 pendulum away from vertical result in divergent net torques that increase the farther
722 one gets away from vertical. (B) Singularity when pushing on an object against a
723 constant external force (vertical) with an articulated arm. The relationship between joint
724 torques ($\vec{\tau}$) and the driving force produced by the hand is given by $\vec{F} = (J^T(\Theta))^{-1}\vec{\tau}$,
725 where $J(\Theta)$ is the Jacobian of the transformation between joint angles Θ and Cartesian
726 hand position. If the torques generated at the shoulder and elbow remain constant,
727 small displacements of the hand from the intended line of motion cause rotation of the
728 force applied by the hand on the manipulandum, creating a net force perpendicular to
729 the intended line of motion (Mussa-Ivaldi et al., 1985; McIntyre et al., 1996). Solid
730 arrows indicate forces acting on the hand-held object (black/grey: gravity; colors: forces
731 applied by the hand). Dashed arrows indicate accelerations perpendicular to the
732 intended line of motion due to uncorrected rotations of the hand force. The sketch
733 illustrates this for a particular configuration of the arm, close to the configuration of the
734 Supine Sagittal configuration. It can be shown through simulation that when pushing an
735 object upward against gravity the horizontal component of the net force is divergent
736 (unstable) more-or-less whenever the hand is located above the shoulder joint.

737

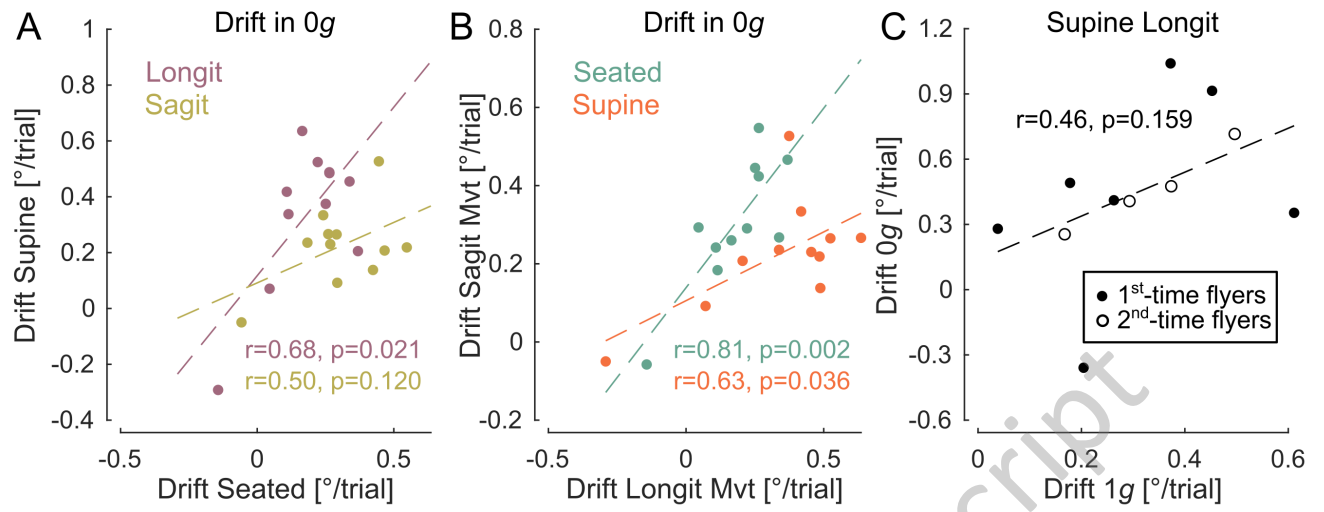




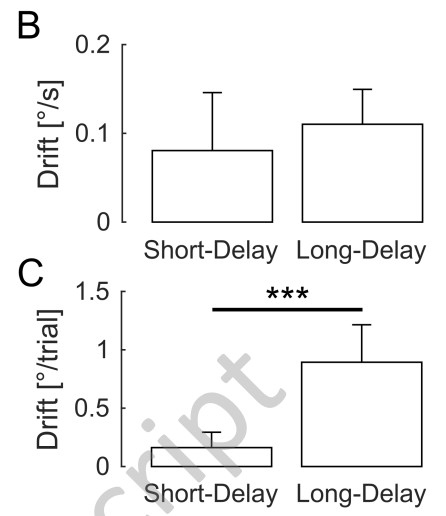
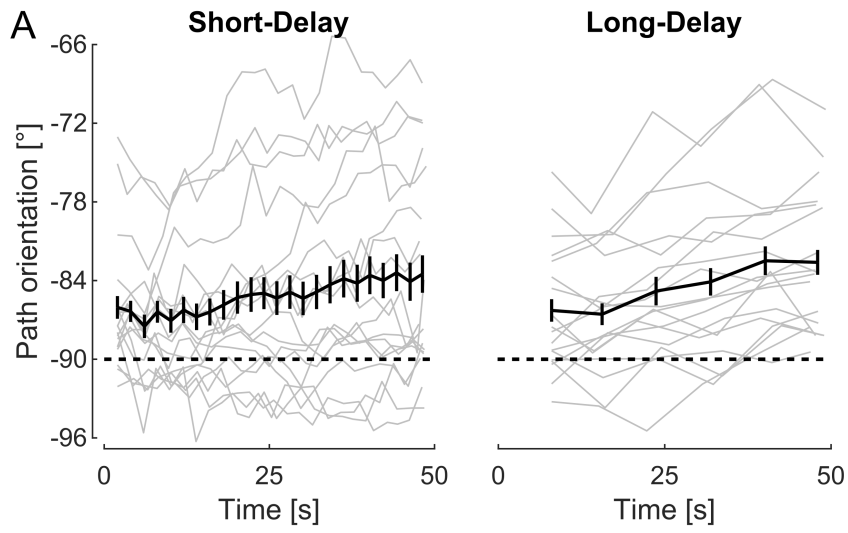
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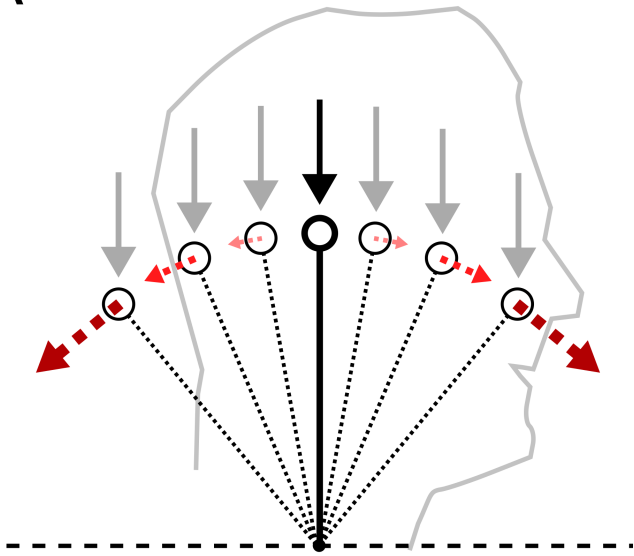


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