

A Singular Theory of Sensorimotor Coordination: On Targeted Motions in Space

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Gravity has long been purported to serve a unique role in sensorimotor coordination, but the specific mechanisms underlying gravity-based visuomotor realignment remain elusive. In this study, astronauts (nine males, two females) performed targeted hand movements with eyes open or closed, both on the ground and in weightlessness. Measurements revealed systematic drift in hand-path orientation seen only when eyes were closed and only in very specific conditions with respect to gravity. In weightlessness, drift in path orientation was observed in two postures (seated, supine) for two different movement axes (longitudinal, sagittal); on Earth, such drift was only observed during longitudinal (horizontal) movements performed in the supine posture. In addition to providing clear evidence that gravitational cues play a fundamental role in sensorimotor coordination, these unique observations lead us to propose an “inverted pendulum” hypothesis to explain the saliency of the gravity vector for eye–hand coordination—and why eye–hand coordination is altered during body tilt or in weightlessness.

Key words: gravity; motor control; multisensory integration; sensorimotor coordination

Significance Statement

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

Introduction

Since the pioneering work of Paillard (1971) describing the theoretical and empirical bases of sensorimotor behavior, the direction of gravity has been assigned a primary role in the encoding of spatial relationships within the nervous system. Paraphrasing

Paillard, maintaining the body upright creates a critical reference position specific to states of vigilance and alertness, the true basis of any sensorimotor intervention in the surrounding environment. The ubiquitous and constant presence of gravity is proposed to provide a reliable cue for calibrating visual, vestibular, and proprioceptive representations of the so-called “body scheme” with respect to the environment (Gurfinkel et al., 1988; Paillard, 1991; Berthoz and Pozzo, 1994; Tagliabue and McIntyre, 2014).

Indeed, gravity represents a common signal that can be detected across sensory modalities. While it is generally accepted that the vestibular system can signal the orientation of the head with respect to gravity (Angelaki et al., 2004; Angelaki and Laurens, 2020), gravity can also be sensed through proprioceptive cues [the weight of an outstretched arm pulling it downward (Worringham and Stelmach, 1985)] and tactile signals [pressure on the soles of the feet (Carriot et al., 2004), direction of the forces on fingers holding an object (Birznies et al., 2001; Delhay et al.,

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2021)]. One can even “see” gravity by the constraints that it imposes on objects and motions (Asch and Witkin, 1948; Sciutti et al., 2012; Scotto Di Cesare et al., 2014): walls are typically vertical so as not to topple over, objects fall downward toward the center of the Earth. The cross-modal nature of gravity perception makes this signal a prime candidate for aligning the reference frames that the CNS employs to perform coordinated actions (Soechting and Flanders, 1989; Buneo et al., 2002; Cohen and Andersen, 2002; McGuire and Sabes, 2009).

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

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

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

Materials and Methods

Participants. Thirteen astronauts were recruited to participate in the experiment. Two of them were obliged to drop out after their first preflight session due to operational constraints and were thus excluded from the analyses, leaving a sample of 11 astronauts (aged 33–51 at the time of their first preflight session; nine males, two females; all right-handed). They were tested onboard the International Space Station (ISS). Seven had never before experienced long-term exposure to microgravity, whereas the other four had previously participated to one mission to the ISS. All astronauts stayed at least 5 months on the ISS (min, 157 d; max, 272 d). The experimental protocol was approved by the Medical Board of the European Space Agency, the Institutional Review Board

of the National Aeronautics and Space Administration, and the Human Research Multilateral Review Board. All astronauts provided written informed consent prior to testing.

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

Each sequence consisted of 19 point-to-point movements, 10 in one direction and 9 in the other, and lasted ~30 s. In the eyes-open condition, the participant moved the manipulandum between two targets with both hand and target visible at all times. In the eyes-closed condition, the hand movements were performed to the remembered location of the two targets, with the eyes kept closed during the whole movement sequence. At the beginning of each sequence, the participant was instructed to grip the manipulandum at its center, to place it to the right of the start target (the lowest of the two targets for longitudinal movements and the closest of the two targets for sagittal movements), and to align the center of the object with the position of the target. Once the manipulandum was positioned correctly, the other target turned on. The participant was then instructed to either keep their eyes open or to close them until the end of the sequence, depending on the defined vision condition. Each movement was then triggered by an audible signal, with the time delay between go signals varying randomly between 1.0, 1.3, 1.6 and 1.9 s. The participant was instructed to move the manipulandum quickly

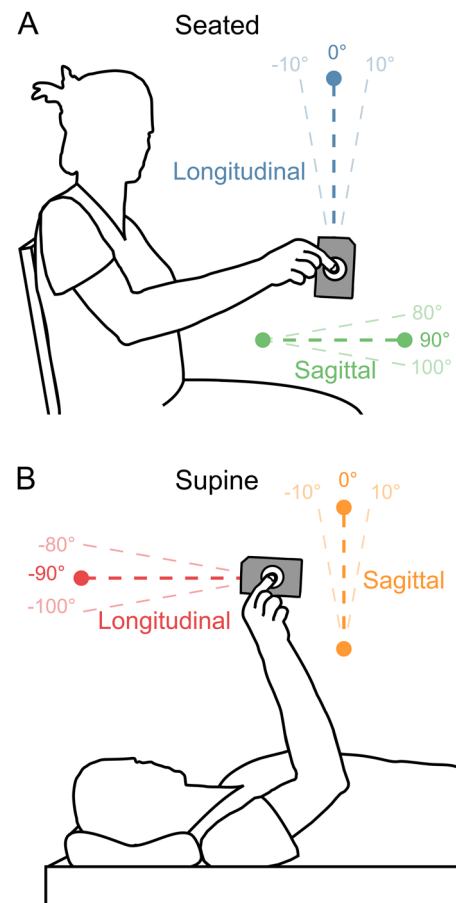


Figure 1. Participant's posture in the Seated (A) and Supine (B) conditions. The colored disks depict the position of the targets in the Longitudinal and Sagittal conditions. The dashed lines illustrate the convention used for path orientation.

and accurately to the target after each go signal, to mark a full stop at the target and to wait for the next go signal to perform the next movement in the opposite direction.

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

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

After learning to execute the required targeted motions in a separate training session, the astronauts completed two preflight sessions, three inflight sessions, and five postflight sessions. One preflight session was performed 65–274 d prior to launch, the other 43–173 d prior to launch, with a minimum of 27 d between the first and second sessions. The Early inflight session was performed between flight day (FD) 4 and 12; the Middle inflight session between FD 70 and 91; and the Late inflight session between FD 132 and 146 (except for the supine condition of one participant, which was performed on FD 196, as noted above). Three Early postflight sessions were conducted, the day after the return to the ground ($R+1$) as well as on $R+5$ (± 2) and on $R+11$ (± 3). Finally, two Late postflight sessions were performed between $R+46$ and $R+152$ and between $R+63$ and $R+410$, respectively, to check for return to the preflight baseline. Due to time and safety constraints, only the seated posture was tested on $R+1$. One participant did not perform the last Late postflight session due to time constraints.

Complementary experiment. Based on our results from the main experiment, we asked whether observed drift was related to a cumulative effect of movement repetition or a temporal drift related to the time elapsed since the eyes were closed. A group of 18 additional participants (aged 21–65, median age 27; 7 males, 11 females; 17 right-handed) performed the same Seated Longitudinal and Supine Longitudinal conditions as the astronauts but varied the number of discrete movements performed in blocks of fixed duration by varying the delay between consecutive movements (dictated by an audible signal). In the Short-Delay condition, the delay between movements was equal to 2 s on average (chosen pseudorandomly between 1.5, 1.7, 1.9, 2.1, 2.3, and 2.5 s from trial to trial) such that 24 movements (12 in each direction) were performed over the 48 s that lasted each block. In the Long-Delay condition, the delay was equal to 8 s on average (chosen pseudorandomly between

6.0, 6.8, 7.6, 8.4, 9.2, and 10.0 s from trial to trial), such that only six movements (three in each direction) were performed in these blocks (which also lasted 48 s). After a short training, during which the participants were familiarized with the task and the two delay conditions, the participants performed four blocks in each combination of posture (Seated or Supine) and delay (Short- or Long-Delay). As in the main experiment, blocks 1 and 3 were always performed with eyes open, while blocks 2 and 4 were always performed with eyes closed. The order of the posture and delay conditions, however, was counterbalanced across participants.

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

The manipulandum was an instrumented object of dimensions $102 \times 50 \times 62$ mm, mass 400 g, and grip aperture 40 mm. It was covered with eight infrared markers. Two motion-tracking units (Codamotion CX-1 units adapted for spaceflight requirements; Codamotion) were used to track the position of these markers in 3D, at 200 Hz. The manipulandum was additionally equipped with an accelerometer and a gyroscope to measure linear acceleration and angular velocity of the object in 3D, at 1,000 Hz, allowing continuous recording of the trajectory despite occasional occlusions of the infrared markers. The position of the center of mass of the manipulandum was reconstructed using the measured position of the eight infrared markers combined with the accelerometer and gyroscope signals using custom routines. The accelerometer and gyroscope signals were low-pass filtered using a Butterworth filter of order four with a cutoff frequency of 50 Hz. After reconstruction, the position of the center of mass was low-pass filtered using a Butterworth filter of order four with a cutoff frequency of 7 Hz and then differentiated numerically to compute object velocity.

For the complementary experiment, the position of the participant's hand was recorded with a motion-tracking system (two CX-1 unit, Codamotion) tracking the 3D position of an infrared marker attached to the nail of the participant's index finger. As in the main experiment, the participants held a small mass (125 g, $8.5 \times 2 \times 3$ cm) between the thumb and index finger of the right hand and had a pillow under their head in the supine posture for comfort, as was used by astronauts during testing on ground.

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

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

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

To further investigate if the determinant independent variable was indeed trial number or if it was rather the time elapsed since closing the eyes, for the complementary experiment we computed the drift in

path orientation with respect to movement repetition (°/trial) as above, and with respect to time (°/s) by computing the slope of a linear regression between path orientation and elapsed time. In both cases, a positive (negative) slope indicates that the path rotated clockwise (counterclockwise) in the parasagittal plane when looking toward the participant's right side.

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

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

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

Results

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

To quantify the drift, we computed for each movement sequence the slope of the linear regression that best fitted the path orientation as a function of trial number. This slope gives an approximation of the rate at which path orientation changed, in degrees per trial. Based on previous work revealing asymmetries in the characteristics of movements performed with or against gravity (Atkeson and Hollerbach, 1985; Papaxanthis et al., 2005; Le Seac'h and McIntyre, 2007; Gaveau et al., 2016), we compared drift as a function of movement direction (forward/backward) within each posture-axis condition and found no significant differences ($p > 0.05$). We therefore pooled all trials of a given sequence together independent of movement direction. We found no significant changes in drift over pre- and postflight ground sessions in the Eyes-Closed condition ($p > 0.05$ in all conditions), justifying our decision to average across all ground sessions for subsequent statistical analyses. We did find a significant change between inflight sessions, but only in the Seated Longitudinal condition with eyes closed ($F_{(2,20)} = 4.17$, $p = 0.03$). As shown in Figure 3, the drift was slightly larger during the Early session than during the other sessions in that condition, but the effect was small and did not survive the post hoc Holm corrections applied when comparing the three inflight sessions pairwise. In subsequent analyses, we therefore pooled results from all preflight and postflight sessions and pooled data from the three inflight sessions for each of the vision/posture/axis combinations.

Figure 4 shows the average of the path-orientation drift in each condition after collapsing the different sessions. The omnibus statistical test used to test the effect of the different conditions on the drift revealed strong interaction effects between vision, posture-axis, and gravity. More specifically, we found significant interaction effects between gravity and vision ($F_{(1,10)} = 15.2$, $p < 0.005$, $\eta^2 = 0.13$), between posture-axis and vision ($F_{(3,30)} = 19.9$, $p < 0.001$, $\eta^2 = 0.20$), and between gravity and posture-axis ($F_{(3,30)} = 20.2$, $p < 0.001$, $\eta^2 = 0.12$) on the drift. There was also a marginal second-order interaction effect between these three factors ($F_{(3,30)} = 2.7$, $p = 0.06$, $\eta^2 = 0.02$). These interaction effects reflect the fact that path orientation drifted only in specific conditions, as detailed below.

On the ground, a significant effect of vision on the drift in path orientation was found only in the Supine Longitudinal condition ($t_{(10)} = 6.7$, $p < 0.001$, $d = 2.02$). In that condition, the drift was significantly greater than zero when the eyes were closed ($t_{(10)} = 6.24$, $p < 0.001$, $d = 1.88$). In all other conditions on the ground, the drift was not significantly different from zero, whether the eyes were open or closed. During spaceflight, closing the eyes caused a significant increase in path-orientation drift in the four posture-axis conditions, compared with eyes open (Seated Longitudinal: $t_{(10)} = 4.6$, $p < 0.005$, $d = 1.37$; Seated Sagittal: $t_{(10)} = 4.0$, $p < 0.005$, $d = 1.21$; Supine Longitudinal: $t_{(10)} = 4.8$, $p < 0.001$, $d = 1.43$; Supine Sagittal: $t_{(10)} = 3.2$, $p < 0.01$, $d = 0.96$). With eyes closed, the drift was significantly greater than zero in all four conditions (Seated Longitudinal: $t_{(10)} = 4.11$, $p < 0.005$, $d = 1.24$; Seated Sagittal: $t_{(10)} = 6.1$, $p < 0.001$, $d = 1.84$; Supine Longitudinal: $t_{(10)} = 4.3$, $p < 0.005$, $d = 1.30$; Supine Sagittal: $t_{(10)} = 5.1$, $p < 0.001$, $d = 1.55$). Furthermore, the drift was significantly larger than on the ground in the Seated Longitudinal ($t_{(10)} = 4.36$, $p < 0.005$, $d = 1.31$; Fig. 4*A*), Seated Sagittal ($t_{(10)} = 5.9$, $p < 0.001$, $d = 1.77$; Fig. 4*C*) and Supine Sagittal ($t_{(10)} = 2.8$, $p < 0.05$, $d = 0.83$; Fig. 4*D*) conditions. No significant difference between Ground and Spaceflight was found in the Supine Longitudinal condition, since in that case the drift was high in both gravity conditions ($t_{(10)} = 0.33$, $p = 0.74$, $d = 0.10$; Fig. 4*B*).

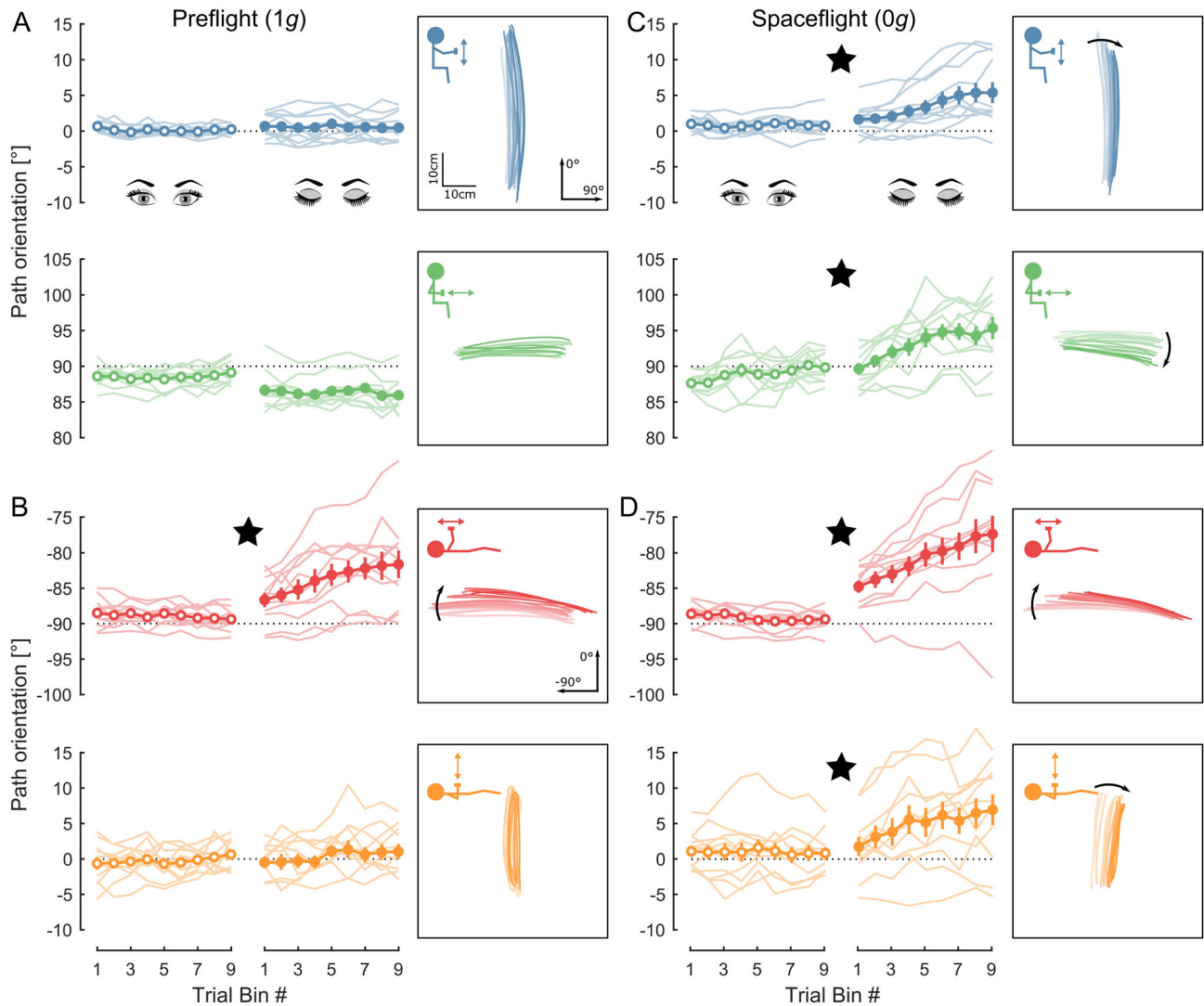


Figure 2. Hand-path orientation across individual trials as a function of body posture (seated or supine), visual feedback (eyes open or closed), target movement axis (longitudinal or sagittal), and gravitational context (ground or spaceflight). **A**, Seated posture on the ground (first preflight session).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

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

Finally, the complementary experiment was used to test whether observed drift was related to a cumulative effect of movement repetition or a temporal drift related to the time elapsed since the eyes were closed. A group of nonastronaut subjects performed a greater or lesser number of discrete movements within a given time window, i.e., with a larger or smaller average inter-movement time delay. We first confirmed that the effects of visual feedback (eyes open vs closed) and posture (seated vs supine) on path-orientation drift were consistent with results obtained on the ground in our main experiment with astronauts: there was a significant main effect of Vision ($F_{(1,17)} = 18.1, p < 0.001, \eta^2 = 0.17$) and Posture ($F_{(1,17)} = 18.5, p < 0.001, \eta^2 = 0.11$) on the drift measured in $^\circ/s$, as well as a significant interaction effect between these two factors ($F_{(1,17)} = 14.3, p < 0.005, \eta^2 = 0.14$) reflecting the fact that path orientation drifted in the supine posture, but not in the seated posture, as was the case with the astronauts on Earth. Regarding the effect of movement repetitions, we found that the delay condition (Short Delay vs Long Delay) did

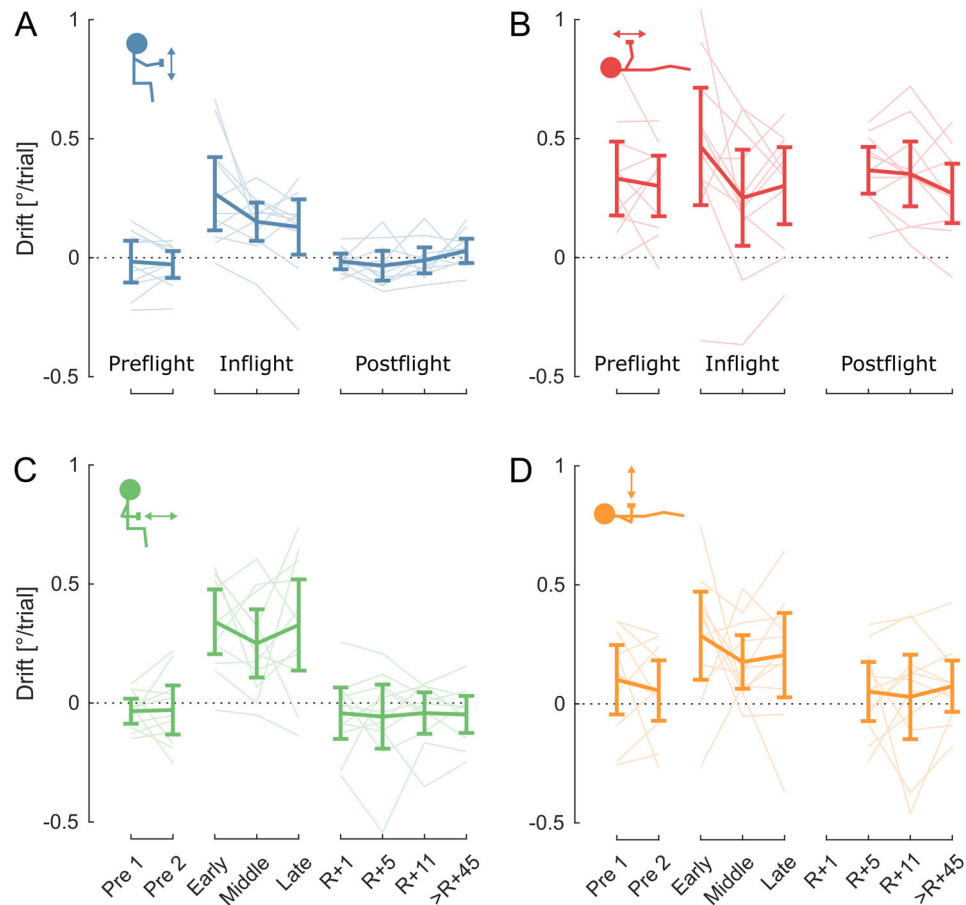


Figure 3. Drift of hand-path orientation in the Eyes-closed condition over preflight, inflight, and postflight sessions for the Seated Longitudinal (**A**), Supine Longitudinal (**B**), Seated Sagittal (**C**), and Supine Sagittal (**D**) posture-axis conditions. Thick dark traces show the mean across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

not significantly affect drift when the drift was expressed relative to time (main Delay effect: $F_{(1,17)} = 0.84$, $p = 0.37$; $p > 0.05$ for all interaction effects involving the Delay factor). Figure 6A shows the evolution of path orientation over time in the two delay conditions in the Supine posture with eyes closed: path orientation drifted over time at a similar rate ($t_{(17)} = -0.94$, $p = 0.36$; Fig. 6B) whether participants performed 6 or 24 movements in the same time interval. In contrast, when expressing the drift as the amount of change in path orientation per trial (instead of per second), a highly significant effect of Delay appeared ($t = -4.98$, $p < 0.001$, $d = -1.5$; Fig. 6C), as more time elapsed between two consecutive movements in the Long-Delay compared with the Short-Delay condition. Thus, we have shown that path orientation drifts as a function of time, not as a function of movement repetition.

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

Discussion

Our results show that in the absence of gravitational and visual cues, humans fail to reproduce constant path orientations during repeated point-to-point hand motions. But if gravity is a key

anchoring cue in the absence of vision, why did it not suppress drift for all postures and movement directions on Earth? Here we propose a new hypothesis, based on the singularity of an unstable, inverted pendulum, to explain the saliency of the gravity vector for maintaining proprioceptive alignment with the external world.

Singular hypothesis

A standing human body or an upright head can be modeled in their simplest form as inverted pendulums (Stoffregen and Riccio, 1988). When perfectly aligned with gravity, a pendulum is at an unstable singular point (Fig. 7A). No torque at the pivot is needed to resist gravity, but any small misalignment from the vertical will generate gravitational torque that, if not opposed, will cause it to tumble. Heightened vigilance is needed due to the unpredictable direction of the fall from this singular position. At the same time, the sensorimotor system should be most sensitive to deviations from this posture, where change in gravitational torque per change in tilt is maximal, allowing fine discrimination of nearby orientations (Butts and Goldman, 2006). According to Weber's law (Ekman, 1959), the perceptual system will be more sensitive to deviations when the underlying signal is small. We postulate that on Earth, the singular configuration of the head on shoulders provides an unambiguous indicator as to when the head is upright, reducing errors in sensorimotor transformations (Paillard, 1991; Burns and Blohm, 2010; Tagliabue et al., 2013; Bernard-Espina et al., 2022).

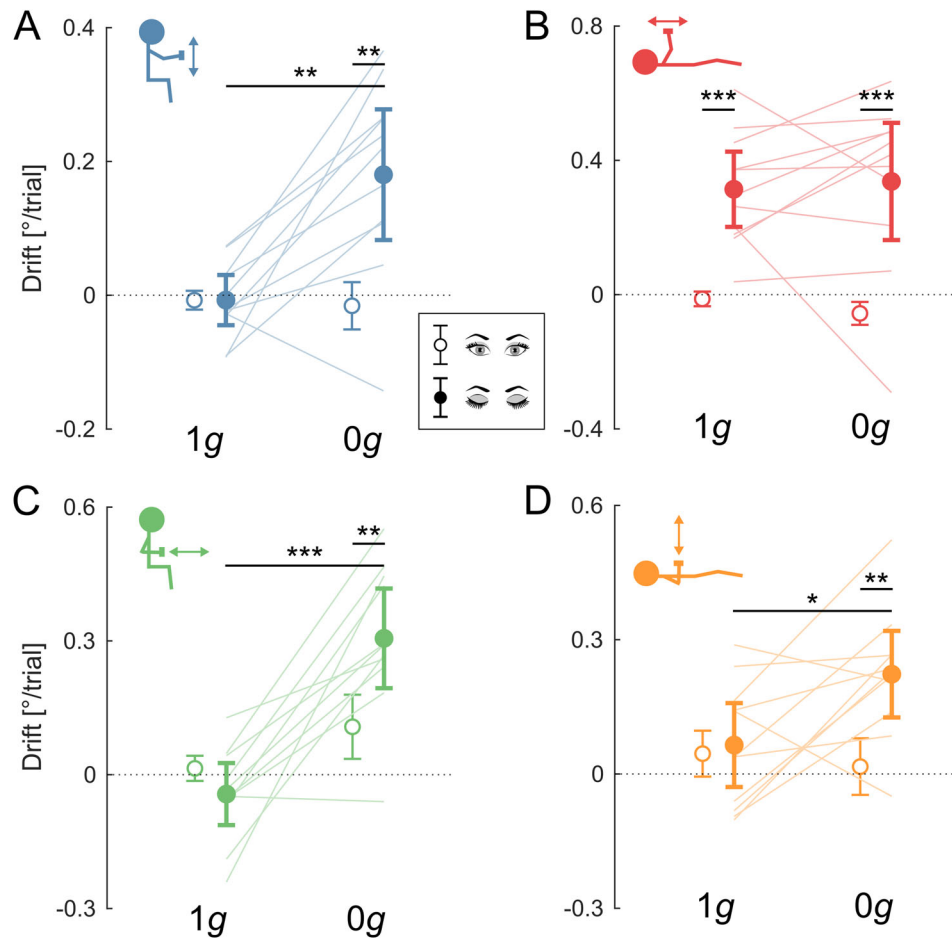


Figure 4. Path orientation drift in the Seated Longitudinal (**A**), Supine Longitudinal (**B**), Seated Sagittal (**C**), and Supine Sagittal (**D**) posture-axis conditions. Disks (open, eyes open; filled, eyes closed) and error bars show the mean and 95% confidence interval of the mean across participants ($N = 11$). Thin light lines show the eyes-closed data of individual participants. Stars emphasize significant differences between 0 and $1 \times g$ or between Eyes Open and Eyes Closed (paired t tests: $*p < 0.05$; $**p < 0.01$; $***p < 0.001$).

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

The unstable nature of holding the head upright or pushing directly against gravity requires, therefore, heightened vigilance in the form of muscle co-contraction (Hogan, 1984; Burdet et al., 2001; Berret and Jean, 2020), augmented reflex activity (Damm and McIntyre, 2008), grip force adjustments

(Johansson and Westling, 1984; Hadjiosif and Smith, 2015), or increased visual attention. At the same time, deviations of head orientation or hand displacement from the singular direction determined by gravity are the easiest for the CNS to detect. We posit, therefore, that the singularities created by a constant gravitational field induce a "pop-out" effect (Treisman and Gelade, 1980), such that unstable postures and movements brought on by gravity serve as critical markers for multisensory alignment. Absent gravity and vision, hand-path orientation will drift regardless of posture or target axis, as we observed.

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

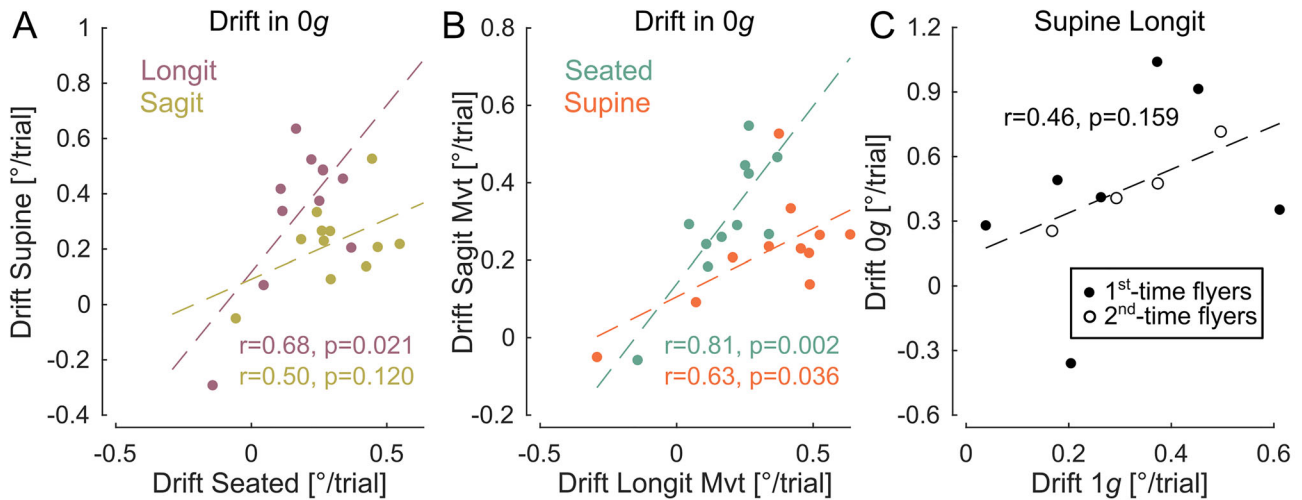


Figure 5. Across-subject correlations in drift between movement conditions. **A**, Drift in $0 \times g$ in supine posture versus seated posture, in the two axis conditions. **B**, Drift in $0 \times g$ during Longitudinal versus Sagittal movements, in the two posture conditions. **C**, Drift in the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

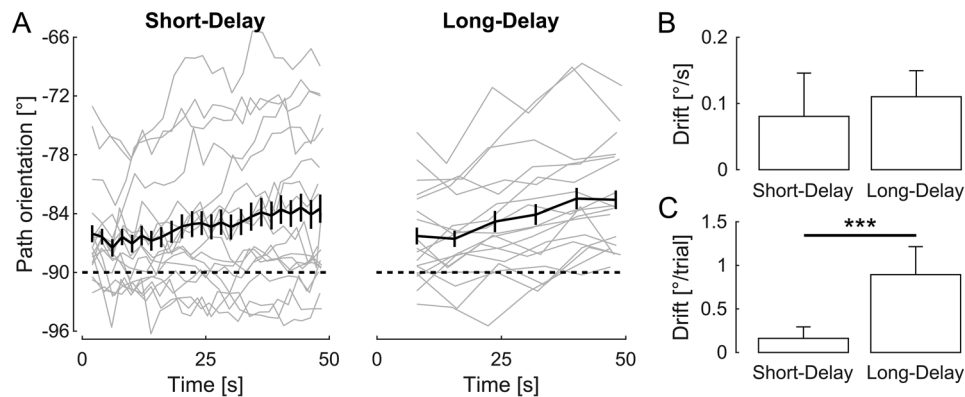


Figure 6. Results of the complementary experiment. **A**, Path orientation as a function of time in the two Delay conditions performed in supine posture with eyes closed. In the Short-Delay condition, 24 movements were performed over 48 s. In the Long-Delay condition, six movements were performed in the same time interval. Error bars show the mean $\pm$ SEM across participants ($N = 18$) while gray lines show data from individual participants. **B**, Average drift in path orientation (mean $\pm$ SEM), expressed as a function of time [°/s]. **C**, Average drift in path orientation expressed as a function of trial number [°/trial] (***) $p < 0.001$.

McIntyre, 2007) and why near-vertical arm movements can ameliorate verticality perception (Tani et al., 2021).

Potential causes of drift

While our theory explains how biomechanical singularities engendered by gravity can suppress drift in movement path orientation, it provides no explanation as to why these paths go adrift when this anchor disappears. One might postulate that in weightlessness, or in the infrequent supine posture, the CNS incorrectly computes gravity-tuned motor commands habitually used to achieve the desired hand displacement, with a subsequent accumulation of errors in the absence of visual feedback (Bock et al., 1992). But in our complementary experiment path orientation drifted at a consistent rate with respect to the time elapsed since closing the eyes, irrespective of the number of movement repetitions and irrespective of the direction of movement along the path (forward or backward). Furthermore, occurrence of drift persisted over several months spent on orbit, despite ample opportunities in the astronauts' daily lives to learn the unfamiliar force fields of weightlessness through visually guided movement

(Ohashi et al., 2019). We conclude that drift does not stem from an accumulation of errors in the motor command used to follow the path.

Instead, we believe that the drift arises in the mapping from remembered target locations to intended hand paths. Subjects show systematic bias when visually (Aubert, 1861; Mittelstaedt, 1983) or haptically (Bauermeister et al., 1964) reporting their perception of vertical and misreport the orientation of their body axis when tilted with respect to gravity (Bauermeister, 1964; McIntyre and Lipshits, 2008) or when faced with vestibular disorders (Saj et al., 2013). Biases in the perceived vertical are purported to arise from prior assumptions in the absence of salient orientating cues (De Vrijer et al., 2008; Sinnott et al., 2023) or from unbalanced vestibular signals (Mittelstaedt, 1983; Glasauer and Mittelstaedt, 1998), while visual and proprioceptive reference frames appear to rely on different estimates of gravity (Fraser et al., 2015). In addition, remembered arm postures in a gravitational field can be biased toward the resting state of the limb (Han et al., 2024). Under these effects, vision and proprioception may fall out of register. According to Bayesian

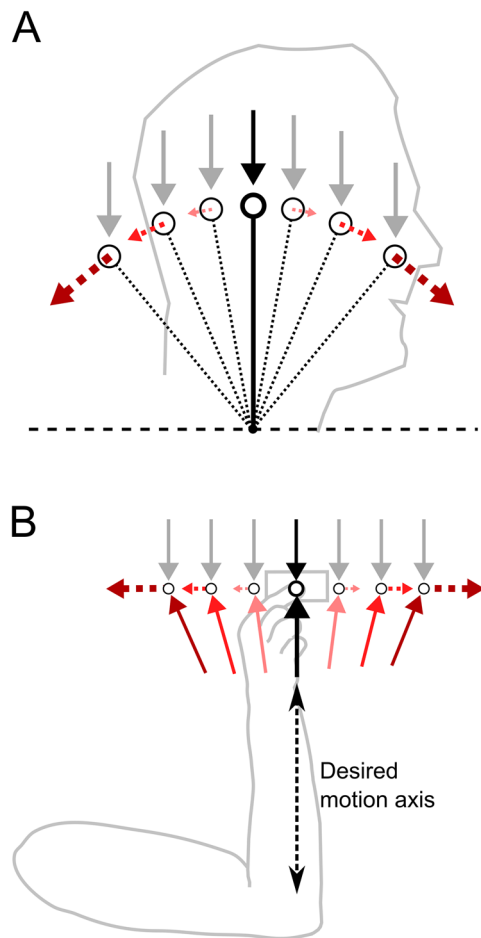


Figure 7. Illustration of the singularities inherent to an inverted pendulum and of the raised arm holding a mass against gravity. **A**, Singularity of the upright posture, where the gravitational torque is zero and the head is unstable. Small rotations of the pendulum away from vertical result in divergent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

models of multisensory integration, the rotation of the hand paths that we observed could stem from a gradual shift in weighting between misaligned visual and proprioceptive representations of the targeted motion as the visual representation degrades in memory, a concept that has been used to explain translational drift in hand path when vision of the hand is removed (Smeets et al., 2006). Visual-vestibular reweighting might also explain why the subjective vertical deviates gradually over ~ 20 s when a biasing visual stimulus is removed (Gibson, 1937; Dichgans et al., 1972). Alternatively, the mapping from an allocentric representation of the targets in memory to egocentric representation of the required motion might change

gradually due to drift in the estimation of body orientation with respect to the world. Indeed, when human participants are tilted in the dark, perception of the visual vertical rotates progressively, with time constants on the order of several minutes (Wade, 1970; Tarnutzer et al., 2013). Computational models that include the effects of biased signal from the semicircular canals would predict such drift in the estimation of head/body orientation (Laurens and Angelaki, 2011) in the absence of the anchoring cues provided by gravity.

Open questions

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

Conclusions

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

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