The effects of visual parabolic motion on the subjective vertical and on interception

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Abstract

Observers typically present a strong bias in estimating the orientation of a visual bar when their body is tilted $> 60°$ in the roll plane and in the absence of visual background information. Known as *the A-effect*, this phenomenon likely results from the under-compensation of body tilt. Static visual cues can reduce such bias in the perceived vertical. Yet, it is unknown whether dynamic visual cues would be also effective. Here we presented projectile motions of a visual target along parabolic trajectories with different orientations relative to physical gravity. The aim of the experiment was twofold: First, we assessed whether the projectile motions could bias the estimation of the perceived orientation of a visual bar, measured with a classical subjective visual vertical (SVV) task. Second, we evaluated whether the ability to estimate time-to-contact of the visual target in an interception task was influenced by the orientation of these parabolic trajectories. Two groups of participants performed the experiment, either with their head and body tilted 90° along the roll plane or in an upright position. We found that the perceived orientation of the visual bar in the SVV task was affected by the orientation of the parabolic trajectories. This result was present in the tilted but not in the upright participants. In the interception

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task, the timing error increased linearly as a function of the orientation of the parabola. These results support the hypothesis that a gravity vector estimated from dynamic visual stimuli contributes to the subjective visual vertical.
Keywords: Gravity perception, Subjective visual vertical, Linear mixed models

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Introduction

The fundamental constraints set by gravity on any object on Earth—be it still or in motion—shape our perception and provide an important reference for action (Lacquaniti et al., 2015; Jörges and López-Moliner, 2017). Humans often assume downward acceleration even in scenarios where objects move with a constant speed, such as in virtual reality or space flights (Lacquaniti et al., 2013), and base their perceptual judgments of stability and motion on expectations of Earth's gravity (Battaglia et al., 2013). Observers on Earth are more precise in discriminating the motion duration of a target moving downwards, as if falling, than that of a target moving upwards (Moscatelli and Lacquaniti, 2011). They also overestimate motion speed when it moves downward at constant velocity (Moscatelli et al., 2019), as if they expect the acceleration of gravity. Observers are able to correctly judge as consistent with gravity kinematic patterns such as linear motion along an incline (Ceccarelli et al., 2018; Cano Porras et al., 2020), free fall (Zago et al., 2004), pendular motion (La Scaleia et al., 2014) and parabolic trajectories (Bosco et al., 2015; Jörges and López-Moliner, 2019). In addition to visual perception, expectations of gravity shape motor behavior in humans (Lacquaniti et al., 2013; White et al., 2020). For instance, astronauts initiate catching movements earlier in microgravity than on Earth, as if they expect the effects of gravity on target motion even when absent and plan interception accordingly (McIntyre et al., 2001). Interception tasks are also performed better for gravity-congruent trajectories than for gravity-incongruent ones, even when they are partially occluded (Delle Monache et al., 2015). Information about head and body orientation contribute to our internal representation of gravity in interception tasks (La Scaleia et al., 2019), suggesting that vestibular and somatosensory cues in addition to visual cues play a role in modeling the effects of gravity on the estimation of object motion. Taken together, these results support the hypothesis of an internal model of gravity stored in multi-modal networks in the brain (Indovina et al., 2005; Mackrous et al., 2019). Not only is the estimation of gravity important for interaction with falling objects, but it is also critical for orienting our body along the vertical axis (Dyde et al., 2006; Barra et al., 2010; Harris et al., 2011). Under normal gravity conditions, viewing videos that show polarized, natural scenes significantly enhances the effectiveness of vision in determining the perceptual upright (Jenkin et al., 2011). This capacity to use static and dynamic gravity cues is critical in humans, since achieving a bipedal stance and walking requires constant monitoring of the position of the center of mass, and even small uncontrolled deviations of the body midline from a position of equilibrium with respect to the upright can result in instability and ultimately lead to falls (Masani et al., 2013; Cavagna et al., 2000). When humans are asked to estimate the direction of gravity by aligning a visual bar to the perceived vertical, as for example in a Subjective Visual Vertical (SVV) task, they typically make errors if their body midline is not aligned to the direction of gravity (Tarnutzer et al., 2010). In particular, for body tilts above 60°, the SVV is strongly biased towards the body midline (Aubert, 1861; Mittelstaedt, 1986). It has been suggested that this phenomenon, called the Aubert (A-) effect after its first investigator (Aubert, 1861), results from an under-compensation of body-tilt (Van Beuzekom and Van Gisbergen, 2000; Kaptein and Van Gisbergen, 2004; De Vrijer et al., 2008; Clemens et al., 2011; Alberts et al., 2016). The A-effect is not apparent in everyday conditions, as we can usually rely on other cues in the environment, which can provide a reliable reference axis (Coppola et al., 1998; Jenkin et al., 2003; MacNeilage et al., 2007; Vingerhoets et al., 2009; Haji-Khamneh and Harris, 2010).

In a previous study (Balestrucci et al., 2017), we showed that gravity-congruent kinematic patterns are associated with decreased postural sway. We proposed that contribution of these motion patterns to balance might be complementary to that of static visual cues, since visual information regarding the direction and acceleration of gravity is processed in adjacent, interconnected brain regions (Maffei et al., 2016). We might also expect that gravity-congruent visual motion provides cues about the gravity field which are relevant for the estimation of the visual vertical.

In this study, we hypothesized that dynamic visual cues congruent with gravity can modulate the estimation of the SVV. To this end, we presented the participants with videos of a visual target moving along a parabolic trajectory which was either congruent or tilted with respect to Earth's gravity. To ensure that the participants attendeded to the moving target, they were required to click a mouse button to intercept the target when it reached the end of the trajectory, which was marked by a circle. The last segment of the target trajectory was occluded for a variable duration. Throughout the experiment, the axis of symmetry of the parabolic trajectories was rotated systematically between experimental blocks, thereby simulating visual gravity fields with the same magnitude but different directions. The axis of the parabolas remained the same within each block, so that participants were exposed to the same orientation of the simulated visual gravity field for several minutes at a time. After each inteception block, the participants performed a SVV task, where they were requested to align a visual bar to the perceived vertical. Blocks of the adjustment and the inteception task were interleaved within each experimental session. The first aim of the study was to evaluate how the upright or tilted gravitational motion in the interception task would modulate the perceived vertical in the subsequent SVV task. A second aim of this study was to evaluate whether the error in the interception task was influenced by the orientation of the simulated gravitational motion with respect to Earth's vertical.

For the interception task, we chose to use parabolic rather than straight trajectories in order to reduce simple geometric cues such as the "motion streak" lines—i.e., the lines of image smear arising from the temporal integration of the linear motion of a visual target (Geisler, 1999). A group of participants completed the experiment while tilted 90° along the roll plane, and their results were compared against those of an upright group. We implemented the experiment using a between-subject design in order to evaluate the effect of body tilt free of possible confounds introduced by a crossover design (e.g. long-term effects due to double exposure to the task).

Since judgments of the subjective vertical are typically biased when participants are tilted with respect to gravity, whereas on average they remain accurate in the upright position (Schoene, 1964), we expected that an effect related to visual motion would be found mainly in the tilted group. Moreover, since the SVV is not stable over time (Tarnutzer et al., 2009), and the memory of the parabolic motions may rapidly fade, we expected that a putative bias produced by the motor task, which acts as a priming, would reduce across SVV trials. We therefore focused on evaluating the transient after-effects elicited by the block of the interception task in the first trial of the adjustment task.

Materials and Methods

Participants

36 volunteers (18 males and 18 females, age: 27 ± 7 years; mean $\pm$ standard deviation) took part in the experiment. All participants reported no neurological or vestibular disorders, and they all had normal or corrected-to-normal vision. The protocol was approved by the Ethics Committee of the I.R.C.C.S. Fondazione Santa Lucia (Rome, Italy), in accordance with the guidelines of the Declaration of Helsinki. All participants were briefed about the experimental procedures and participated in the study after giving their written consent.

Experimental setup

Visual stimuli were presented on a back projection screen placed 1.5 m from the frontal plane of the participant. The projector (EH-TW9200 by 3LCD) had a resolution of 1920 x 1080 pixels and a refresh rate of 60 Hz, and was placed 3.70 m behind the screen. The area available for projection was significantly wider than the section ultimately used for the experiment. This solution allowed us to keep the frame of the screen away from the central visual field, thus avoiding the geometric references it would otherwise provide. To limit their field of view, all participants looked at the projection screen through a rigid black cylinder of length 100 cm and inner diameter 75 cm, whose center was placed at eye level and in correspondence with the center of the active area of the screen (Fig. 1C). In order to further reduce any additional external reference and possible residual sources of light from outside the active area of the screen, participants wore a custom-made set of goggles with no lenses which further obstructed the peripheral visual field.

All experimental stimuli were programmed in Matlab 8.1.0 (Mathworks, Inc., Natick, MA) and Psychophysics Toolbox version 3.0.11 (Brainard, 1997; Pelli, 1997; Kleiner et al., 2007). Participant responses were acquired using a standard computer mouse (Logitech MX500; polling rate equal to 125 Hz).

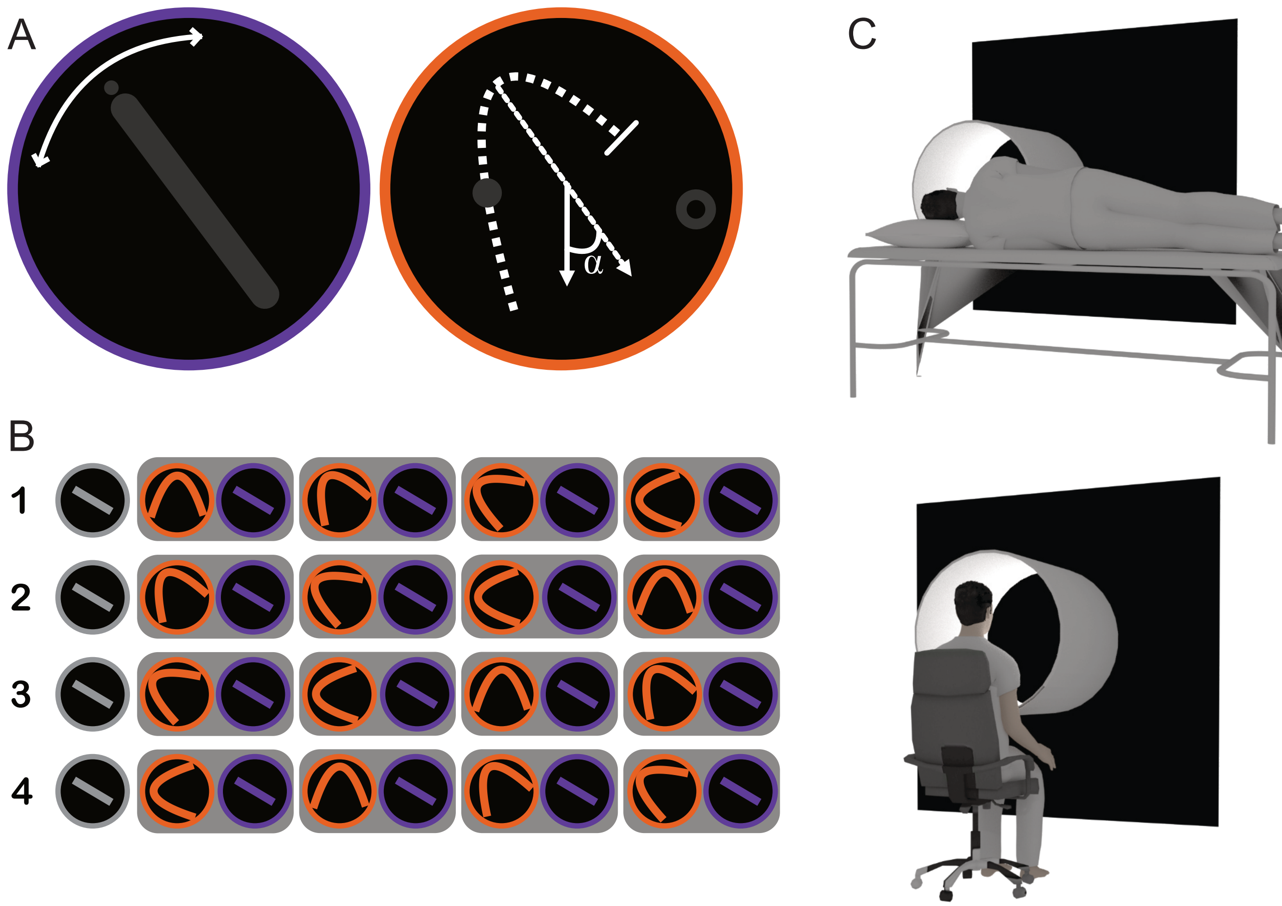

Figure 1: Experimental methods. (A) Experimental tasks. Left: adjustment task. Participants were instructed to orient the grey bar according to the perceived external vertical. Right: interception task. A sphere followed a parabolic trajectory with different orientations α with respect to the external vertical g. The sphere was occluded 100, 200 or 300 ms before intersecting the endpoint of the trajectory marked with a disk. Participants were instructed to press the mouse button at the estimated time of interception. (B) Experimental procedure. After two minutes of habituation in darkness, every session started with a block of adjustment task, followed by four repetitions of pairs of interception + adjustment task. Rows in the matrix represent subsequent experimental sessions. The presentation order of parabola orientations across sessions followed a Latin square design: a "standard order" was presented in the first experimental session, and in subsequent sessions the sequence was generated by applying a permutation to the initial order. For half of the subjects in each experimental group, the initial order consisted in increasing tilts as shown in figure (i.e. 0°, 30°, 60°, 90°.) For the rest of the subjects, the standard order was reversed (i.e. 90°, 60°, 30°, 0°). (C) Experimental groups. The two groups differed based on the participants' body orientation: in the tilted group (top) participants were lying on their left side, with their body axis perpendicular to the vertical direction. In the upright group (bottom) participants were sitting with their body axis aligned with the vertical.

Stimuli and Procedure

The procedure is illustrated in Fig. 1B. The experiment was divided in 4 sessions. Each session is represented as one of the 4 different rows (labelled as 1–4) in the Figure. In the first block of each session, participants performed an adjustment task for the baseline assessment of the Subjective Visual Vertical (see below). Each baseline block consisted of 10 trials and it is depicted as a grey circle in the Figure (leftmost column). Baseline blocks were each followed by four repetitions of pairs of blocks, including a block for the interception task (24 trials each; see below) and a block for the adjustment task (10 trials each). These pairs are depicted as gray rectangles which enclose colored circles (an orange circle with a parabola for the interception task and a purple circle with an oblique line for the adjustment task). Before each session, the lights were turned off and participants rested in darkness for 2 minutes. This allowed participants to adapt to the tilted body position and to dim-light conditions, reducing non-stationarity in the response (Tarnutzer et al., 2013).

Adjustment Task. In the adjustment task, we assessed the angle of subjective visual vertical (SVV) by asking participants to align a bar according to what they perceived to be the physical vertical. To perform this task, participants were instructed to rotate the bar until they were satisfied with its orientation (Figure 1A, left). The grey bar was 11° long and 1.3° wide, and was rendered on a black background. A sphere whose diameter was half the width of the bar was aligned to the long axis and signaled the top. For each trial, the bar appeared on the screen with one of 10 possible orientations on the frontal plane, sampled across all the circumference in steps of 36 degrees. Pressing the right and left mouse button rotated the bar clockwise and counterclockwise, respectively. As long as one button was pressed, the bar rotated smoothly with a constant angular velocity of 20°/s, or with steps of 0.5° for a single button stroke. When participants were satisfied with the obtained adjustment, they pressed the central mouse button to signal their choice and move on to the next trial. No feedback concerning the deviation of the selected angle from the physical vertical was provided.

Interception Task. In the motor task, we measured the participant's performance in intercepting a virtual target moving as a projectile along a parabolic path via button press, with the final part of the target's trajectory being occluded (Fig. 1A, right). To perform the task, participants needed to press the mouse button when they thought that the target would intersect a visible disc if the complete trajectory had been shown. The target consisted of a grey sphere of 0.46° diameter moving against a black background, with no depth cues available. The sphere moved clockwise on the frontal plane along a parabolic trajectory. The final part of the sphere's parabolic movement was masked 100, 200, or 300 ms before intersecting the disc, which had the same diameter as the sphere. To avoid participants completing the task by making assumptions about the symmetry of the parabolic path, as well as to increase the variability of the motion duration of the sphere, the interception disc was placed randomly above or below the coordinate marking the range of the sphere's trajectory within an interval of ±10% of the maximum height of the trajectory. The kinematics and the size of the visual target was consistent with those of a soccer ball seen at a viewing distance of ∼30 m, moving along a parabolic trajectory of ∼10 m range in the frontal plane under the effect of gravity acceleration (g = 9.81 m/s^2). The kinematic properties of the displayed trajectories were derived from the equations describing balistic motion of a projectile launched with initial velocity V_0 and launch angle θ, constrained by constant acceleration g. This corresponds to a target's acceleration of $22°/s^2$ visual angle. The parabolic trajectories were chosen based on their geometric characteristics in terms of maximum height (i.e. the elevation reached by the projectile) and range (i.e. the distance traveled). We presented four parabolic shapes that were determined by doubling one or both of these two parameters: the first consisted in maximum height and range being equal ($V_0 = 16.4°/s$ visual angle, $\theta = 76°$), the second in doubling only the height ($V_0 = 22.6°/s$, $\theta = 83°$), the third in doubling the only the range ($V_0 = 17.8°/s$, $\theta = 63°$), and the fourth in doubling both height and range

($V_0 = 23.1°/s$, $\theta = 76°$).

At the beginning of each trial, only the interception disc was displayed and remained visible for the whole duration of the trial. The participant pressed any mouse button to start the parabolic trajectory and after a small random delay $< 1s$, the ball appeared at its starting position and began moving. The participant pressed a mouse button to intercept the target; the trial ended immediately afterwards. No feedback on the actual time of arrival was provided.

Throughout the experiment, the tilt of the parabola's axis of symmetry (labelled as α in Fig. 1A) was modulated with respect to the physical vertical direction. Four possible orientations of the parabolic path were presented: $\alpha = 0°$ (i.e. the parabolic axis was aligned with the Earth's vertical), 30°, 60°, and 90° (i.e. the parabolic axis was perpendicular to the Earth's vertical). The orientation of the parabolic trajectories was kept constant in each block and varied across blocks, so that all the four orientations were presented in every session but with a different order. The presentation order for the parabola orientations was counterbalanced across sessions by following the model of a *Latin square design* (Fig. 1B).

Each block of interception consisted in 24 trials, which were divided as follows: 1 parabola orientation x 4 shapes of parabolic trajectories x 3 occlusion intervals x 2 repetitions. The different parabolic trajectories and occlusion intervals were presented in random order within each block. As all the 4 parabola orientations were presented once in each of the 4 experimental sessions, this design resulted in 384 trials of interception, which were presented in counterbalanced order during the experiment.

Each experimental session lasted approximately 30 minutes, so that the full experiment took about 2 hours to complete. Between sessions there was a mandatory break of about 10 minutes. For the time of each experimental session, the room was dark, and participants were instructed to avoid standing up or lifting their head until the scheduled break. During the break, the lights were turned on and participants were asked to stand up and rest for a few minutes. Participants were also encouraged to interrupt the experiment and take an earlier break at any time, should it become tiring or uncomfortable. None of the participants reported fatigue or needed to interrupt the experimental session.

Body orientation. Throughout the experiment, participants performed the task either upright, or with their head and body tilted with respect to the physical vertical (Fig. 1C). In each experiment, we tested a total of 20 participants: Thirty-two participants were assigned randomly to the tilted or to upright group (16 participants each), while 4 participants completed the experiment in both upright and tilted position about thirty days apart.

Participants in the *tilted* group underwent all experimental sessions lying on their left side on a declinable medical stretcher, so that they were facing the projection screen with their frontal plane. As a result, their body axis was orthogonal to the physical vertical. A pillow was placed and adjusted under the participant's head to make sure that they would be comfortable, and that the head axis and body axis were aligned. Participants in the *upright* group sat in front of the screen in a chair with a high backrest, so that their body axis was aligned with the external vertical.

Data Analysis

We analyzed participants' responses in the adjustment and in the interception task. For each task, responses that exceeded ± 3 standard deviations from the mean values were considered as outliers and removed from further analyses. Overall, 0.5% of the data for the adjustment task and 1.1% for the interception task was categorized as outliers. Processed data was analysed by means of Linear Mixed Models (LMMs), accounting for the fixed-effects of the experimental variables, and for within- and between-participant variability (Brown and Prescott, 2014; Bates et al., 2015). We analysed separately the data from the adjustment and interception trials. All analyses were performed in R (R version 3.5.2) (R Core Team, 2016). The R packages `lme4`(Bates et al., 2015) and `MixedPsy` (Moscatelli et al., 2012; Moscatelli and Balestrucci, 2017) were used for LMM fitting. Pre-processing of the data and Exploratory Data Analysis (EDA) were performed with `Tidyverse` packages (Wickham and Grolemund, 2016). .

Adjustment task. For each adjustment trial, we computed the SVV angle as the difference in degrees between perceived vertical (i.e. the degree by which the bar was adjusted) and physical vertical. A negative angle stands for a clockwise angular error, a positive angle for a counter-clockwise error. We evaluated separately the different experimental variables affecting the SVV response (i.e. the angle α of the parabolic motion as well as the temporal evolution of the experiment assessed in terms of the sequence of trials, blocks, and sessions).

Analysis of the baseline block. To estimate the baseline value of the SVV angle, we first analyzed the response in the first block of SVV assessments in each session (baseline block), i.e. before any parabolic motion was presented. The model that provided the best fit among those considered for the data in the first assessment of the tilted group was the following:

$$\mathrm{SVV}_{\mathrm{baseline}} = \beta_0 + \beta_1 \log t + Zu \tag{1}$$

where β_0, β_1 are the fixed-effect parameters of the model, t is the trial repetition within the block, and Zu are the random-effect predictors accounting for between–participant variability. We chose the model in Eq. 1 from a pool of nested models based on the lowest Akaike Information Criterion (AIC) score. Significance of the fixed-effect parameters included in the models is evaluated by means of likelihood ratio (LR) tests.

For consistency, we tested the model in Eq. 1 for the baseline data in the tilted and in the upright group. However, since the model was overparameterized for the data of the latter group, we also fitted the data with a second model that provided the best AIC score. The resulting model is the following:

$$\mathrm{SVV}_{\mathrm{baseline}} = \beta_0 + Zu \tag{2}$$

In order to directly compare the SVV in the baseline block between the tilted and the upright group, we fit a LMM to the data, including *Body Tilt* as a fixed-effect categorical predictor, and random-effects predictors accounting for between-participant variability. Here and in all the other between-group analyses, we excluded the participants (N = 4) that completed both experiments to avoid cross-over effects.

Comparison of the first and the last adjustment trial. We tested the hypothesis of an after-effect of the parabolic motion on the SVV. To this end, we used LMMs to analyze the relationship between the SVV and the angle of the parabolic motion α, in the first and last trials of the adjustment blocks. The equation of the LMM was the following:

$$\text{SVV} = \gamma_0 + \gamma_1\alpha + \gamma_2\alpha^2 + \gamma_3 T + \gamma_4(T\alpha) + \gamma_5(T\alpha^2) + Zu \qquad (3)$$

where $\gamma_0, ..., \gamma_5$ are the fixed-effect parameters of the model, α is the angle of the parabolic motion in the previous interception block and T is the dummy variable coding for the first or last trial ($T = 0$ for the first trial and $T = 1$ for the last trial). The model in Eq. 3 was applied separately to the tilted and upright group. Significance of the fixed-effect parameters included in the models is evaluated by means of LR tests.

To further evaluate the effects of the parabolic motion on the SVV, we compared the first and the last trials of the adjustment task in the baseline condition with the first and last trials following the interception task, respectively. By means of LMM models, we tested separately the first and the last trials. We included a variable α' as predictor for the fixed and random effect. In order to compare the SVV in the baseline (BL) condition and after interception, α' was coded as a categorical variable with 5 levels (i.e. "BL", "0", "30", "60", "90", where each numerical value denotes the orientation of the parabola during the interception). As it emerged that the variability between adjustment trials in the upright condition was in general very small, we performed this latter analysis for the tilted group only.

The comparison between the tilted and upright groups was performed by means of a LMM including α, *Body Tilt*, and their interaction as fixed-effect factors, together with random-effects predictors accounting for between-subjects variability. This LMM was evaluated separately for the first and last adjustment trial.

Other effects. Lastly, we evaluated whether other experimental variables (i.e. the order of trials, blocks, and sessions within the experiment) affected the SVV response throughout the experiment. Since we expected a non-stationary response at the beginning of each adjustment block, at least partly dependent on the presentation of parabolic motion in the interception task, we removed the first three trials of each block. We also did not include the response in the first adjustment block (baseline) which was evaluated separately with the model in Eq. 1.

The model that provided the best fit for the data of the tilted group did not include any fixed effects associated with the variables of interest (i.e. trial, block, session and their interactions):

$$\text{SVV} = \delta_0 + Zu \quad (4)$$

Conversely, the model that emerged for the upright dataset was the following:

$$\text{SVV} = \delta_0 + \delta_1 S + Zu \quad (5)$$

where S is the order of sessions within the experiment.

We performed a comparison between the groups by means of a LMM which evaluated the effect of *Body Tilt* as a fixed-effect factor.

Interception task. For each interception trial, we computed the Timing Error (TE) as the difference in milliseconds between the time of the button press and the time in which the (occluded) sphere intercepted the disc:

$$\text{TE} = \text{T}_{\text{press}} - \text{T}_{\text{interc}}$$

Negative TEs denote an underestimation of the target arrival time, positive TEs denote an overestimation.

We evaluated the relationship between participants' TEs and the experimental variables in the tilted group by fitting the response data with the following LMM:

$$\mathrm{TE} = \zeta_0 + \zeta_1\alpha + \zeta_2 t + \zeta_3 \log(t) + \zeta_4 B + Zu \tag{6}$$

where $\zeta_0, ..., \zeta_4$ are the fixed-effect parameters of the model, α is the orientation angle of the parabolic trajectory, t is the trial repetition within the blocks, B is the order of the block within each session, and Zu are the random-effect predictors accounting for between–participant variability. As for the models presented previously, we chose the model in Eq. 6 from a pool of nested models based on the lowest AIC score, and evaluated significance of the fixed-effect parameters by means of LR tests.

For consistency, we used the same model separately for the data of the tilted and upright group. However, the model in Eq. 6 provided an over-fitting for the upright data set (Table 3). Therefore, we also fit the upright data with a second model that resulted as the best model according to AIC score for this data set. The alternative model is the following:

$$\mathrm{TE} = \eta_0 + \eta_1 t + \eta_2 B + \eta_3 S + \eta_4 BS + Zu \tag{7}$$

where $\eta_0, ..., \eta_4$ are the fixed-effect parameters of the model, S is the order of sessions within the experiment and BS the interaction between session and block within each session.

In order to compare the performance in the tilted and upright experiment, as we did for the adjustment task, we fit the full data set of timing errors in the interception task with a LMM, excluding from the analysis the participants who completed both experiments.

Results

Adjustment Task

Analysis of the baseline block. We analyzed the SVV response at the beginning of the experimental sessions, i.e. before any projectile motion was presented. For the tilted group, we found an increase of the SVV angle over trials, while for the upright group the SVV remained roughly constant during the baseline block. Statistically significant differences emerged between the two groups, exposed in detail below in this paragraph.

For the first adjustment block at the beginning of each session (baseline), the model in Eq.1 showed a logarithmic relationship between the angle of SVV and the trial number (t) in the tilted group. Accordingly, the parameter accounting for the effect of $log(t)$—labelled as $\beta 1$ in the model—was significanlty different from zero (estimated β_1 = 2.152 ± 0.458; Estimate ± SE; χ_1 = 15.233, p < 0.001). Pooled data for all participants in the tilted group are illustrated in Fig. 2A where the logarithmic relationship between the SVV and trial repetition, t, can be appreciated. The relationship between the SVV angle and trial number was not statistically significant in the upright group (estimated β_1 = -0.004 ± 0.068; Estimate ± SE. χ_1 = -0.777, p > 0.05). In fact, the model that provided the smallest AIC for the upright group did not have any significant fixed effects (Eq. 2). Accordingly, the difference between the tilted and upright groups estimated by the $Body\ Tilt$ parameter of the LMM was statistically significant (χ_1 = 55.441, p < 0.001. Fig. 2B).

Comparison of the first and the last adjustment trial. To evaluate after-effects of the projectile motion in the interception task on the SVV angle, we analyzed the response in the first and last adjustment trials of each experimental block. In the tilted group, we found a non-linear relationship between the parabola orientation α and the SVV angle in first trials, while this did not depend on α in last trials. Moreover, the first baseline trials were statistically different from the first trials of all parabola orientations, except for $\alpha = 0$. The parabola orientation was not a significant predictor for either first or last trials in the

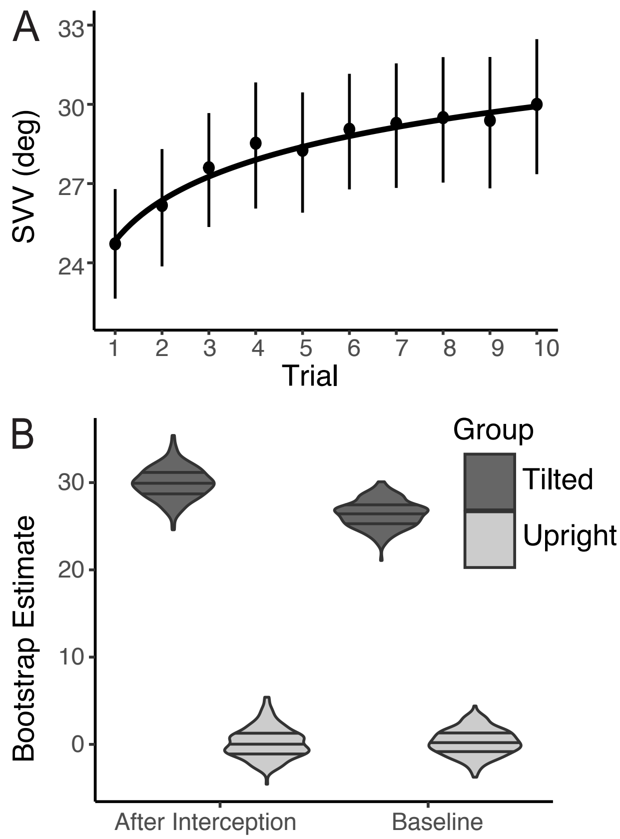

Figure 2: Adjustment task, analysis of the baseline block. (A) SVV angle (mean ± SE across the four experimental sessions) for the pooled participants of the tilted group in the baseline block (i.e. the block preceding all interception blocks in each experimental session). (B) Violin plot of bootstrap-based estimate of the SVV angle in the baseline and in trials 3–10 of all other adjustment blocks, for the tilted (dark grey) and the upright group (light grey). The three horizontal bars on the violins indicate the first quartile, the median, and the third quartile

upright group. Difference in average SVV in the two groups was statistically significant. The analysis is presented in detail below.

First, we evaluated the marginal relationship between the SVV and parabola orientation α by pooling data across all participants, separately in the tilted and in the upright group (Fig. 3A and B, respectively). In the tilted group, a non-linear relationship between α and SVV became apparent for the first but not for the last trial. To test this nonlinear relationship, we fit the data separately for the first and the last trial with a first-order (i.e. linear) LMM and with a second-order polynomial LMM and compared the two models by means of LR tests. In the first trial data (i.e. the trials immediately following an interception block), the polynomial model provided a better fit than both the intercept-only model ($\chi_1 = 8.879$, p = 0.003) and the first-order linear model ($\chi_1 = 5.091$, p = 0.024). For the last trial (trial 10), the polynomial model did not differ significantly from the linear model, and the linear model did not differ from the constant model (polynomial versus first-order model: $\chi_1 = 0.034$, p = 0.853; first-order versus intercept-only model: $\chi_1 = 0.116$, p = 0.734).

We fit the combined first and last trial data with the polynomial LMM in Eq. 3 to test the hypothesis that the after-effect of the interception task affected the SVV in the first but not in the last trials (i.e. that the effect faded over time). There was a statistically significant interaction between α and the dummy variable coding for the first or last trial T. That is, the fixed-effect parameter γ_5 accounting for the interaction between T and α^2 in Eq. 3, was significantly different from zero ($\chi_1 = 6.385$, p = 0.041). This interaction confirmed that the non-linear relationship between α and the SVV angle was significantly different for the first and the last trial. To estimate the effects of α and α^2 in the first and the last trials, we computed the bootstrap-based 95% confidence intervals of the related fixed-effect parameters in Eq. 3. The effects were consistent with those presented for the data pooled across participants (Fig. 3A), with the fixed-effects associated with α and α^2 being significantly different from zero for the first, but not for the last trial (Fig. 5 and Table 1. See Fig. 7 for individual participants).

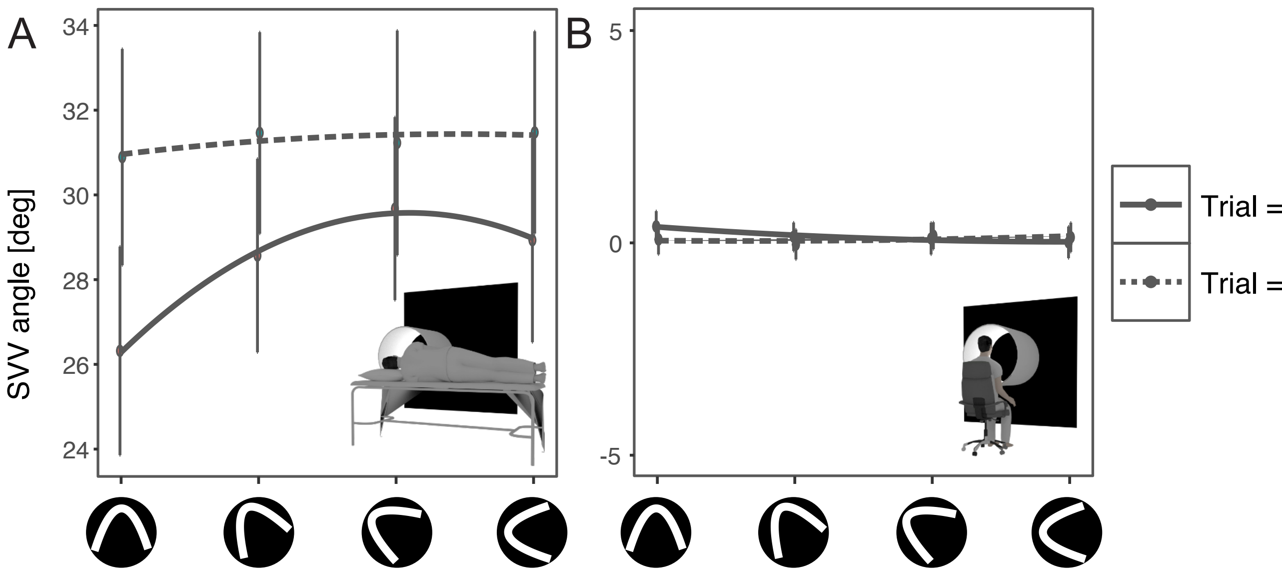

Figure 3: Adjustment task, comparison of the first and the last trial. (A) Marginal relationship between the parabola orientation α and the SVV in the first trial (solid line) and last trial (dashed line), for the pooled data of the tilted group. For the values of the mean and standard deviation of the SVV angle in the different orientation conditions, as well as for values in the baseline, refer to Table 2. (B) Same effects for the pooled data in the upright group.

In the upright group, neither the linear nor the non-linear effect associated with α was significant for the first or the last trial (all p $>$ 0.1). This suggests that for both the first and last trial, the fixed-effect parameters associated with α did not differ significantly from 0 (Fig. 3B). Moreover, the first and last trial did not differ significantly from each other. Accordingly, the parameter γ_5 in Eq. 3 accounting for the interaction between T and α^2 was not significanlty different from zero ($\chi_2 = 2.521$, p = 0.284).

When directly comparing the baseline trials with the SVV following the interception of projectile motion (Table 2), it emerged that the variable α' was a significant predictor for the first but not for the last trial of adjustment (effect of α' for SVV in first trial: $\chi_4 = 16.005$, p = 0.003; in last trial: $\chi_4 = 2.956$, p = 0.565). For the first adjustment trials, the bootstrap-based confidence intervals showed that the differences between the baseline and the SVV following inter-

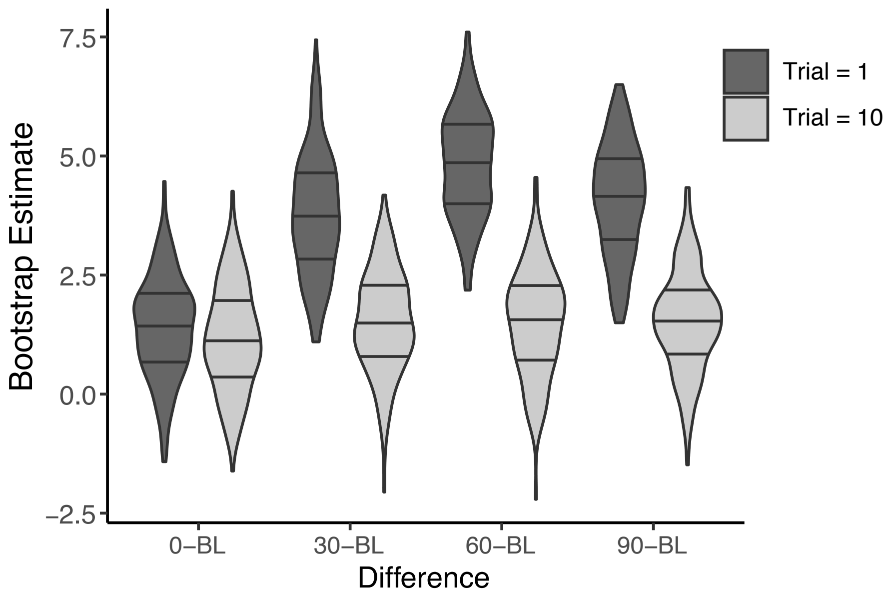

Figure 4: Adjustment task, difference between the baseline condition and the trials following interception task. Violin plots of the differences of the SVV between the baseline and the blocks following interception of parabolic trajectories with different orientations, for first trials (dark grey) and last trials (light grey). Only the values for the tilted group are reported. For mean and SD values of the SVV in tilted and upright group, refer to Table 2.

ception of parabolic motion were significant for all the parabola orientations except for $\alpha = 0$ (Fig. 4). Participants were tested in the baseline trials before the four interception and adjustment pairs, hence, a putative drift in the subjective vertical due to the prolonged body tilted position might also contribute to the result, to some extent. However, this cannot explain the difference between parabola orientations, since the order of the four pairs of interception and adjustment tasks were counterbalanced across sessions.

From the comparison between the tilted and upright groups, a statistically significant interaction emerged between parabola orientation and body tilt for the first trial (effect associated with α $BodyTilt$ for first trial: $\chi_1 = 7.964$, p = 0.005), confirming that the effect of parabola orientation mostly occurred in the tilted group. The interaction was not statistically significant for the last trial (effect associated with α $BodyTilt$ for last trial: $\chi_1 = 0.072$, p = 0.788).

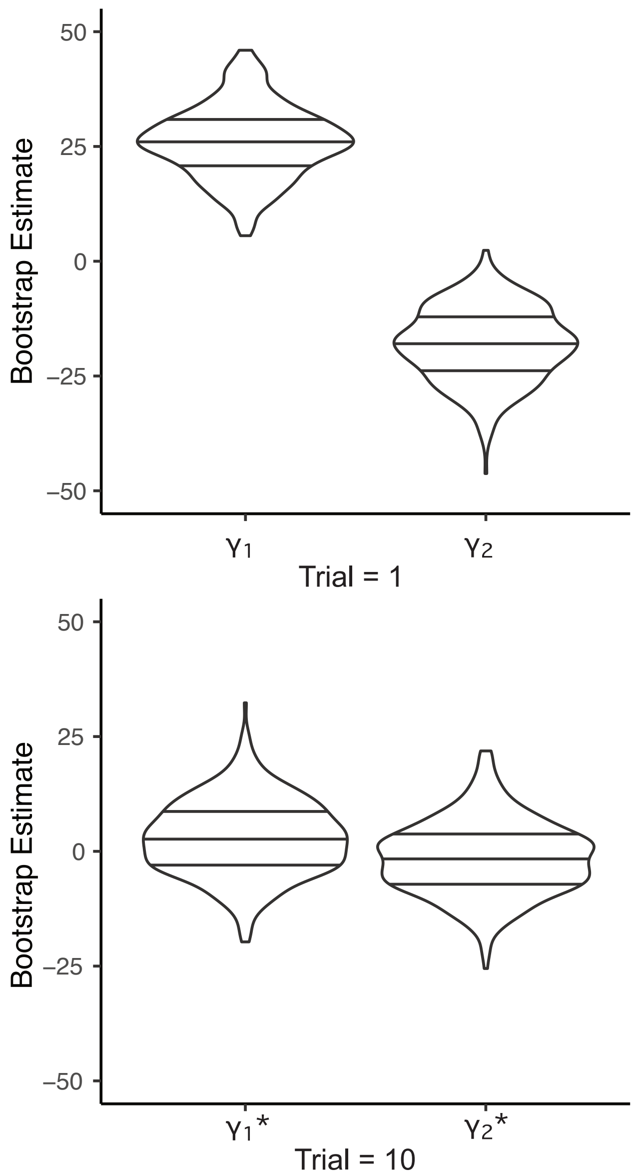

Figure 5: Adjustment task, model parameters for the first and last trial of blocks following interception task. The violin plot shows the bootstrap-based estimates of the two parameters accounting for the effect of parabola orientation. The fixed effect parameters in Eq. 3 accountig for α and α^2 are γ_1 and γ_2 for the first trial, respectively. Instead, for the last trial these are equal to $\gamma_1^* = \gamma_1 + \gamma_4$ and $\gamma_2^* = \gamma_2 + \gamma_5$, respectively. The two parameters are significanlty different from zero in the first (top panel) but not in the last trials (bottom pannel). For details, refer to Table 1.

Other effects. Albeit beyond the main goal of this study, which focused on the after-effect of parabolic motion on the SVV, we also analyzed the change in the SVV across trials after the extinction of non-stationary effects. For the tilted group, none of the variables under consideration provided significant predictors for the data (Eq. 4), while for the upright group we found a significant effect associated with the session. The parameter accounting for the effect of session in Eq. 5 was therefore significant (estimated δ_1: 0.127 ± 0.049, Estimate $\pm SE$. $\chi_1 = 5.723$, p = 0.017). This means that, for the tilted group, the SVV angle was stable across trials, blocks, and sessions in the experiment once the early, non-stationary part of the response was removed. For the upright group, the SVV angle increased slightly over subsequent experimental sessions.

Statistically significant differences emerged when directly comparing the SVV for the tilted and upright group. We found a significant effect associated with *Body Tilt* ($\chi_1 = 54.413$, p < 0.001. Fig.2B), consistent with previous studies (A- effect).

Interception Task

We analysed the relationship between the experimental variables and the timing error. Our main finding (explained below in detail) suggests that the parabola orientation α was a significant predictor for the response in the tilted but not in the upright group.

Using the LMM in Eq. 6, we analysed the timing error (TE) in the tilted and the upright groups. The estimated parameters of the model are reported in Table 3. In the tilted group, the TE during the interception task was significantly affected by the orientation of the parabola. In Eq. 6, the parameter ζ_1 accounting for the effect of the parabola orientation α was statistically significant (χ_1 = 4.901, p = 0.027; Figure 6B. See also Fig. 8 for individual participants). In particular, the greater the deviation of the parabola axis relative to the vertical direction (i.e. the greater α), the larger the delay in TE (estimated $\zeta_1 = 0.221$ $\pm$ 0.093, Estimate $\pm SE$). This is illustrated for the pooled data in Fig. 6A.

In the upright group, the parameter ζ_1 was not statistically significant ($\chi_1 =$

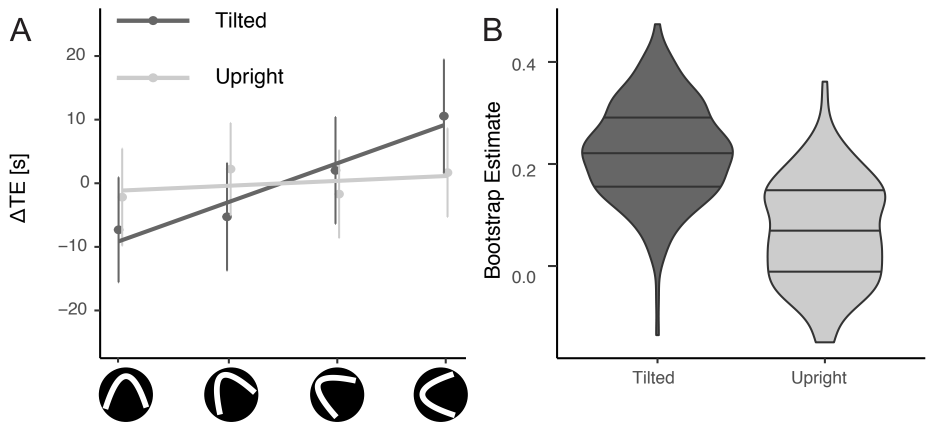

Figure 6: Interception task, fitted model and slopes for the tilted group. (A) Timing error variation (mean $\pm$ SE) as a function of the parabola orientation for the pooled data of the tilted (dark grey line) and upright group (light grey line). (B) Violin plot of bootstrap-based estimates of the slope associated with parabola orientation α in model in Eq. 6, for the tilted (dark grey) and upright group (light grey).

0.604, p = 0.437). Inspecting the random-effect parameter, the values of slopes were equally distributed around zero (Fig. 6A). Next, we fit the responses of the upright group with the simpler LMM in Eq. 7. The estimated parameters of this simpler model are reported in Table 4.

As is apparent from effect sizes and significance levels described in Table 3 and 4, the timing error was modulated by predictors other than the parabola orientation α in both groups. In particular, all participants showed an increase of the TE over trials and blocks within an experimental session. In the tilted group, within each block we observed a non-linear dependency between the response variable and the trial predictor, which is captured in model 6 by the significant linear and logarithmic effects associated with the trial variable. These non-linear aspects of the TE over trials were missing in the upright group, in which a linear increase of TE was still present.

After modeling the TE response of each data set separately, we compared the two groups (upright and tilted) by means of a LMM. We did not find a significant interaction between parabola orientation α and body tilt ($\chi_1 = 1.976$, p = 0.160). This is possibly because a trend similar to the tilted group also occurred in the upright group, albeit non-significantly in the latter (Fig. 6).

Discussion

In this study, we used a SVV task to assess the participants' ability to estimate the direction of the Earth's vertical and to intercept targets along parabolic trajectories with different orientations. The experiment was tested in two body tilt conditions, horizontal and upright. In the the tilted group, in trials immediately following the interception task, the angle of the SVV increased as a function of orientantion of the parabola. The SVV angle was coherent with the angle of the parabolic trajectories in terms of directions, with both angles rotating counterclockwise (i.e. in the direction of the tilted body midline). In the upright group, the SVV angle was close to zero, and the variance very low ($\sim 2.6°$), consistently throughout the experiment. In the interception task, the timing error was greater for larger deviations of the parabola orientation from Earth's vertical. This effect was statistically significant for the tilted but not for the upright group. The findings for the two tasks will be further discussed in separate paragraphs.

Adjustment task

In the adjustment task, we found a strong bias towards the body midline for participants in the tilted condition, consistent with previous reports on the A-effect (Aubert, 1861; Tarnutzer et al., 2009). This bias increased across trials within each experimental sessions (Fig. 2 and Fig. 3A). Since body tilt was maintained at 90° for the whole duration of a session, and visual background information was also minimized, the linear drift of the SVV angle over time can be explained in terms of adaptation of the somatosensory and vestibular systems (Lechner-Steinleitner, 1978). Additionally, we found that the orientation of the parabolic trajectories presented in the interception task was a significant predictor for SVV estimation in the first trial of the adjustment task. In trials preceded by parabolas with axis aligned to the Earth's gravity, the angle bias was smaller, i.e. the subjective vertical was closer to the physical vertical in this condition. SVV angles increased as a non-linear function of the parabola orientation (Fig. 5). This effect cannot be explained in terms of the temporal evolution of the experiment, because the order of interception blocks in different orientations was counterbalanced across sessions (Fig.1B).

Previous studies showed that the perception of the visual vertical is the result of the integration of visual, vestibular, and body-referenced signals (Vingerhoets et al., 2009; De Vrijer et al., 2008; Dakin et al., 2018). Likewise, static visual cues such as straight lines are known to provide a powerful reference for the estimation of the SVV (Vingerhoets et al., 2009). In our case, the motion stimuli in the interception task provided implicit directional information. We can explain the modulation of SVV estimation by parabolic motion by assuming that observers process such motion as gravitational rather than arbitrary. We suggest that observers extrapolate information about the direction of the gravity vector consistent with the displayed parabolic motion, integrating this information with noisy signals from the vestibular and somatosensory systems to estimate the SVV.

According to previous studies, prior knowledge about the world is useful for estimating ambiguous sensory inputs (Ernst and Bülthoff, 2004). For example, 3D shapes from shading are interpreted as concave or convex based on assumptions regarding the overhead placement of sources of light (Adams et al., 2004), and the localization of ambiguous sound sources takes into account the natural distribution of sounds in the environment (Parise et al., 2014). In the same way, if parabolic motion is assumed as gravitational rather than arbitrary motion, this might transiently change the putative gravity prior (which we would otherwise assume to be aligned with Earth's gravity), ultimately reducing the SVV angle bias when participants were exposed to zero-angle parabolic motion (Jörges and López-Moliner, 2017; Moscatelli et al., 2019).

The increase in the A-effect from $0°$ to $60°$ parabolas is consistent with the hypothesis that the dynamic visual cues (i.e. the parabolic accelerate motion) calibrated the subjective vertical toward the apparent gravity direction implied by the target's motion. However, other cues might also contribute to the perceived vertical. The small reduction of the A-effect observed between 60° and 90° may be explained by a dynamic frame line, which becomes salient when the orientation of the parabola is aligned with the body axis.

The effect of visual gravitational motion on the adjustment task was consistent across all tilted participants in the first trial following a block of interception tasks. However, the effect due to the exposure to gravitational motion dissipated over trials, so that the parabola orientation angle was a significant predictor for the SVV angle in the first but not in the last trial of the adjustment task (Fig. 5). During the interception task, observers were exposed to accelerated parabolic motion for several minutes, and we speculate that they adapted to the gravitational vector implied by the visual motion (Day and Wade, 1969). This memorized gravity vector would be a priming stimulus affecting the subsequent adjustment task. Since the projectile motion was present in the interception blocks only, its memory might have faded across the adjustment trials. This would explain the reduction of the effect from the first to the last adjustment trial.

Interception task

In tilted observers, there was a systematic delay in the motor response, which increased as the orientation of the parabolic trajectory deviated from the physical vertical (Fig. 6). Tilted participants were more accurate when estimating time-to-contact of parabolic trajectories whose axis was aligned with the physical vertical.

In a recent study (Miwa et al., 2019), it has been shown that the perception of gravity direction indicated by the visual polarity of a scene affects motion perception when observers are tilted. It has also been suggested that the perception of visual gravitational motion is the result of the integration of gravitational cues, visual polarity, and body orientation. Our findings that the timing error for interception is smaller for gravity-congruent motion are in line with this hypothesis. However, in our case we did not provide information about scene polarity. Instead, the direction of the gravitational vector was implied in the kinematics of the visual stimuli. Similarly, Claassen and colleagues (2016) showed that motion perception is not affected by body orientation when objects are likely to move as an effect of gravity. Since we found smaller timing errors for gravity-congruent parabolic trajectories, and increasing errors for larger deviations of the path orientations from the physical vertical, we can confirm this hypothesis.

In summary, we found evidence that visual gravitational motion contributes to the estimation of the subjective visual vertical, likely because the life-long visual experience with the effects of the Earth's gravity field is used as a prior to disambiguate noisy sensory signals. Visual information on the direction and magnitude of the gravity field is associated with the activation of a distributed neural network (Indovina et al., 2005; Lacquaniti et al., 2013; Maffei et al., 2016). Accordingly, this study has shown that dynamic stimuli can offer additional cues which contribute to vertical estimation when other visual static information is less reliable.

Tables

	Estimate	Inferior	Superior
α (trial = 1)	25.540	10.784	41.697
α^2 (trial = 1)	−18.248	−32.196	−0.057
α (trial = 10)	3.425	−11.686	20.412
α^2 (trial = 10)	−1.222	−17.204	14.339

Table 1: Estimate and bootstrap-based 95% confidence interval for the effects associated with model in Eq. 3 in the tilted group. The fixed effect parameters accountig for α and α^2 are γ_1 and γ_2 if $T = 0$, respectively. Instead, for $T = 1$ these are equal to $\gamma_1 + \gamma_4$ and $\gamma_2 + \gamma_5$, respectively.

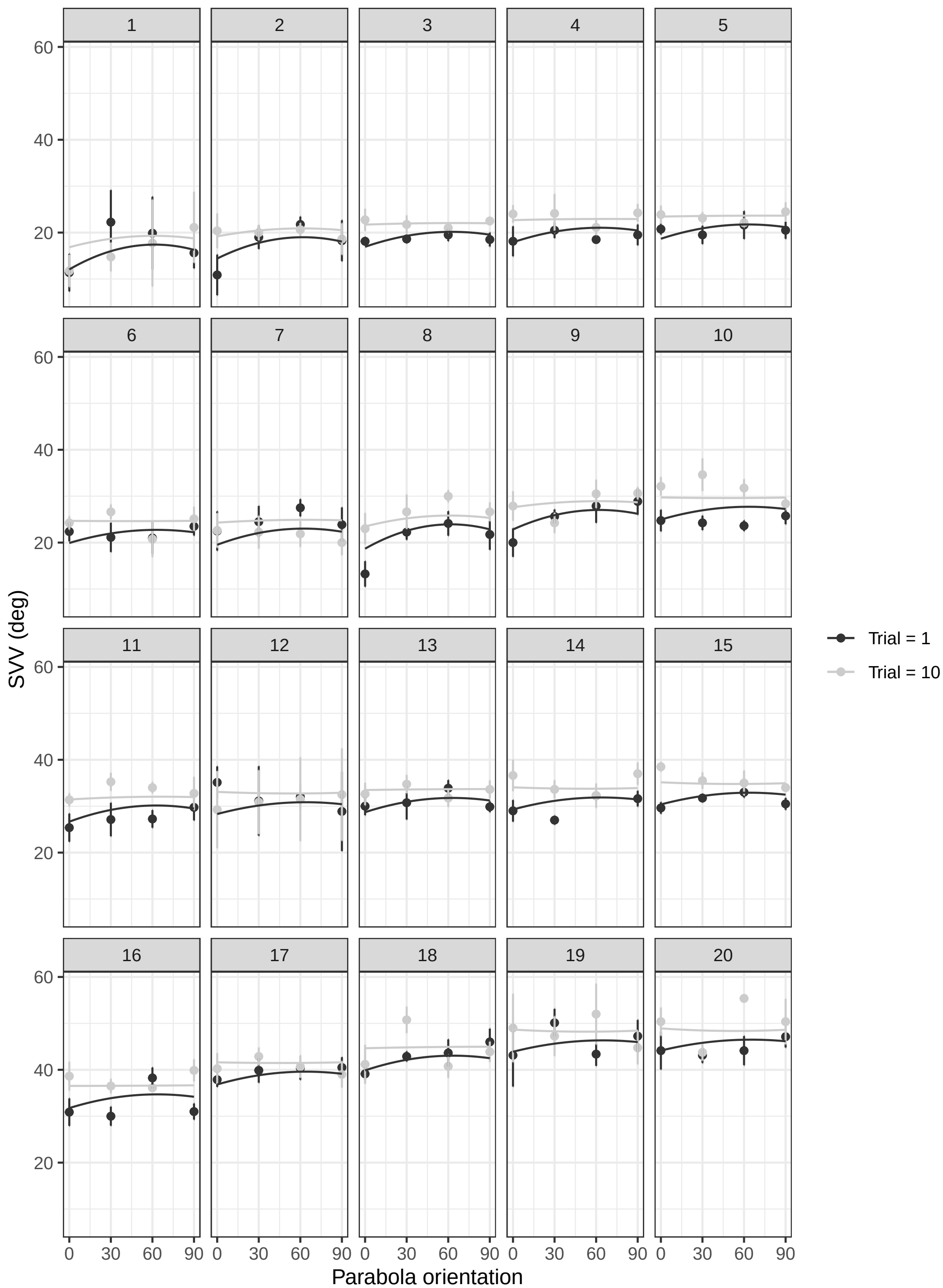

Figure 7: Adjustment task in the body tilted group. Raw data and LMM fit of twenty participants, sorted by intercept value. First and Last trials are illustrated in black and in grey, respectively.

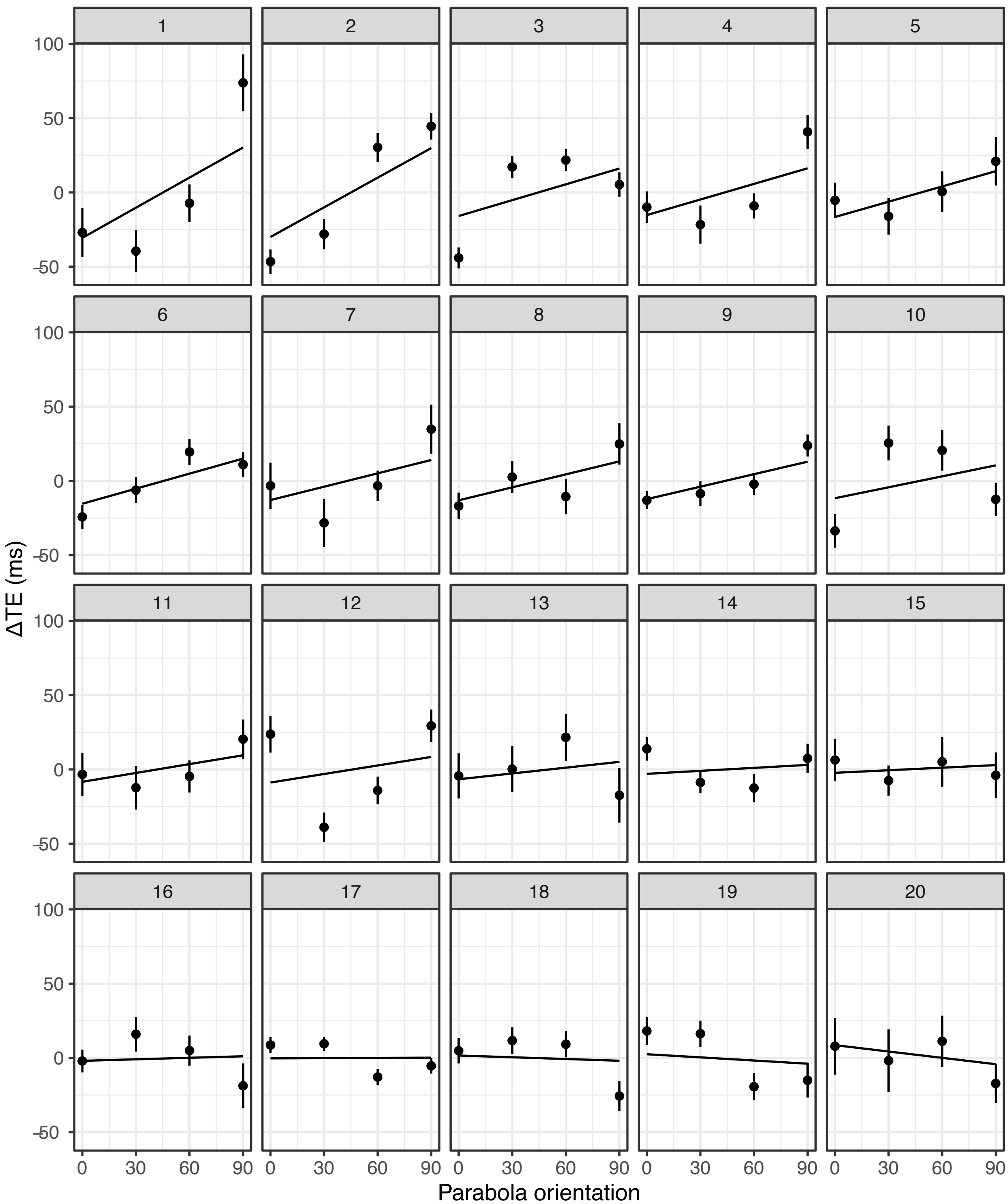

Figure 8: Interception task in the body tilted group. Raw data and LMM fit of twenty participants, sorted by slope.

	α'	*Trial = 1* mean	SD	*Trial = 10* mean	SD
Tilted	BL	24.93	8.22	29.91	9.67
	0	26.32	10.00	31.02	9.95
	30	28.57	9.04	31.46	9.72
	60	29.68	8.67	31.35	10.32
	90	28.93	9.69	31.48	8.94
Upright	BL	0.34	0.77	0.10	0.91
	0	0.39	1.10	0.08	0.98
	30	0.14	0.86	-0.04	0.92
	60	0.11	1.16	0.17	0.84
	90	0.01	1.24	0.13	1.01

Table 2: Mean and standard deviation of the first and last trials of the adjustment task for tilted and upright group.

	Tilted				*Upright*			
	Est.	SE	LRT	p	Est.	SE	LRT	p
ζ_1	0.22	0.09	4.61	0.03	0.08	0.10	0.60	0.44
ζ_2	-1.26	0.51	4.99	0.03	0.28	0.48	0.31	0.57
ζ_3	20.81	4.19	23.94	<0.001	3.44	3.54	0.88	0.35
ζ_4	9.40	2.20	12.86	<0.001	7.47	1.94	11.00	<0.001

Table 3: Estimate of the coefficients and relative significance levels of the LMM (Eq. 6) for the TE response in the tilted and upright group.

	Upright			
	Est.	SE	LRT	p
η_1	0.73	0.30	5.51	0.02
η_2	11.55	5.10	4.91	0.03
η_3	15.05	3.08	20.42	<0.001
η_4	-2.62	0.88	8.89	<0.01

Table 4: Estimate of the coefficients and relative significance levels of the LMM model in Eq. 7, fitted to the TE response in the upright group.

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