Earth-Gravity Congruent Motion Benefits Visual Gain For Parabolic Trajectories

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Abstract

There is evidence that humans rely on an earth gravity (9.81 m/s²) prior for a series of tasks involving perception and action, the reason being that gravity helps predict future positions of moving objects. Eye-movements in turn are partially guided by predictions about observed motion. Thus, the question arises whether knowledge about gravity is also used to guide eye-movements: If humans rely on a representation of earth gravity for the control of eye movements, earth-gravity-congruent motion should lead to improved visual pursuit. In a pre-registered experiment, we presented participants (n=10) with parabolic motion governed by six different gravities (-1/0.7/0.85/1/1.15/1.3g), two initial vertical velocities and two initial horizontal velocities in a 3D environment. Participants were instructed to follow the target with their eyes. We tracked their gaze and computed the visual gain (velocity of the eyes divided by velocity of the target) as proxy for the quality of pursuit. An LMM analysis with gravity condition as fixed effect and intercepts varying per subject showed that the gain was lower for -1g than for 1g (by -0.13, SE = 0.005). This model was significantly better than a null model without gravity as fixed effect ($p<0.001$), supporting our hypothesis. A comparison of 1g and the remaining gravity conditions revealed that 1.15g (by 0.043, SE=0.005) and 1.3g (by 0.065, SE=0.005) were associated with lower gains, while 0.7g (by 0.054, SE=0.005) and 0.85g (by 0.029, SE=0.005) were associated with higher gains. This model was again significantly better than a null model ($p<0.001$), contradicting our hypothesis. Post-hoc analyses reveal that confounds in the 0.7/0.85/1/1.15/1.3g condition may be responsible for these contradicting results. Despite these discrepancies, our data thus provide some support for the hypothesis that internalized knowledge about earth gravity guides eye movements.

Introduction

There is a growing corpus of research indicating that humans use their knowledge of earth gravity in a broad range of tasks, such as grasping (Verheij, Brenner, & Smeets, 2013), catching and interception (Bosco, Delle Monache, & Lacquaniti, 2012; Jörges, Hagenfeld, & López-Moliner, 2018; Lacquaniti et al., 2013; McIntyre, Zago, & Berthoz, 2001; McIntyre, Zago, Berthoz, & Lacquaniti, 2003; Senot, Zago, Lacquaniti, & McIntyre, 2005; Senot et al., 2012; Zago et al., 2004; Zago, McIntyre, Senot, & Lacquaniti, 2009; Zago & Lacquaniti, 2005), duration estimation (Moscatelli & Lacquaniti, 2011) or the perception of biological motion (Jokisch & Troje, 2003; Maffei et al., 2015; Simion, Regolin, & Bulf, 2008), while arbitrary accelerations are generally neglected (Benguigui & Bennett, 2010; Benguigui, Ripoll, & Broderick, 2003) or used insufficiently. Here we examined ocular pursuit and spatial estimation in a linear prediction motion task that emphasized extrapolation of occluded accelerative object motion. Results from the ocular response up to occlusion showed that there was evidence in the eye position, velocity and acceleration data that participants were attempting to pursue the moving object in accord with the veridical motion properties. They then attempted to maintain ocular pursuit of the randomly-

ordered accelerative object motion during occlusion but this was not ideal, and resulted in undershoot of eye position and velocity at the moment of object reappearance. In spatial estimation there was a general bias, with participants less likely to report object reappearance being behind than ahead of the expected position. In addition, participants' spatial estimation did not take into account the effects of object acceleration Humans seem to rely on their knowledge of earth gravity to predict target motion in space and/or time. This predictive information is then combined with online information in order to estimate relevant variables of the environment (such as time-to-contact or location of interception). On the other hand, eye movements have been shown to be partially guided by predictive mechanisms (Simon J. Bennett & Benguigui, 2013; Diaz, Cooper, Rothkopf, & Hayhoe, 2013). If gaze behavior is influenced by prediction and an "internal model of gravity" (Zago & Lacquaniti, 2005) or "earth gravity prior" (Jörges & López-Moliner, 2017) drives prediction in many different computations, then this internal representation of 1g should allow humans to follow targets more closely when their trajectories are governed by earth gravity. And indeed, this line of reasoning has recently been brought into focus: (Delle Monache, Lacquaniti, & Bosco, 2014) presented participants with targets moving along parabolic trajectories that were generally governed by earth gravity. In the second half, a perturbation with 0g or 2g could occur. The trajectories were presented in a 2D scene with pictorial cues. Participants tracked targets less successfully during the 0g perturbations than during 2g perturbations or trials without perturbation, which can be taken as some evidence for the role of a representation of earth gravity being used in gaze behavior. While this should, in principle, also impact gaze following during the 2g perturbations, the 2D presentation may have affected the recruitment of an internal model of gravity negatively (Moscatelli & Lacquaniti, 2011; Zago, La Scaleia, Miller, & Lacquaniti, 2011).

To our knowledge, human gaze behavior has not been studied for parabolic motion with uniform gravities throughout the trajectory, that is, for trajectories that obey one gravity value from beginning to end, rather than generally being governed by 1g interwoven with perturbations with earth-discrepant gravities.

This is of special interest because smooth pursuit of curved trajectories is a demanding task that requires a complex interplay of ocular muscles. It would thus be particularly beneficial to employ all available information, including a strong prior for earth gravity, to plan and execute these movements.

Based on the above considerations, the present papers tests the hypothesis that participants should follow targets on parabolic trajectories more successfully when they are governed by earth gravity rather than by earth-discrepant gravities.

Furthermore, we tested whether we can replicate previous results that knowledge of earth gravity is used to extrapolate motion information for occluded stimuli.

Both hypotheses have been pre-registered (https://osf.io/8vg95/), and any other, exploratory analyses of our data are clearly marked as such and should be treated with the due caution.

Methods

Participants

A total of eleven (n = 10) participants performed the task, among them one of the authors (BJ). All had normal or corrected-to-normal vision. The remaining participants were in an age range of 19 and 51 years and five (n = 5) were female. We did not test their explicit knowledge of physics, as previous studies suggest that explicit knowledge about gravity has no effect on performance in related tasks

(Flavell, 2014; Kozhevnikov & Hegarty, 2001). All participants gave their informed consent. The research in this study is part of an ongoing research program that has been approved by the local ethics committee of the University of Barcelona. The experiment was conducted in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

Stimuli

We presented participants with targets of tennis ball size (radius = 0.033 m), shape and texture that moved on parabolic trajectories. The trajectories were determined by the gravity levels (0.7,0.85,1,1.15,1.3g,-1g), the initial vertical velocities (4.5 and 6 m/s) and the initial horizontal velocities (3 and 4 m/s). The different kinetic profiles, as well as the occlusion condition (Short Occlusion: last 20-25%; Long Occlusion: last 45-50% of the trajectory), were presented in random order, but the method guaranteed that each combination was presented the same amount of times. The parabolas were presented in the fronto-parallel plane with no change in depth. Air resistance was simulated to provide a more realistic stimulus. For description of the parabolas, we use a coordinate system where the observer's position is defined as x = y = z = 0; the x axis runs from left to right, the y axis from down to up and the z axis away from the observer in depth. The starting y position was half a meter above the ground (y = 0.5 m) for positive gravity values (0.7-1.3g) and 3.5 m for negative gravity values (-1g), while the starting x position was moved to the left from the middle of the scene by half of the overall length of the trajectory (x = -length/2 m). The target travels to the right, such that the peak of the parabola was always reached at x = 0 m (or the lowest point for the inverted parabolas). The ball's z position remained constant at z = -6.15 m. The target disappeared at a random point between 20% and 25% (Short Occlusion) or 45% and 50% (Long Occlusion) of the time it would take for it to return to the initial height (y = 0.5 m or y = 3.5 m, respectively). The y end position was marked with an elongated table that was displayed in the target area of the room for targets with positive gravities; it was marked with an elongated lamp hanging from the ceiling for inverted stimuli. We presented the trajectories in a rich environment that provided 3D cues about the object's position in depth and used a known object (a tennis ball) as target to recruit prior knowledge consistent with the geometry on display This has been shown to help recruit the internal model of gravity (Lacquaniti et al., 2013; Zago, La Scaleia, Miller, & Lacquaniti, 2011), that we have previously suggested to be an earth gravity prior (Jörges & López-Moliner, 2017). This environment was constructed such that no low-level cues such as differences in brightness and contrast with the target differed significantly between the different trajectories.

Apparatus

Participants were first instructed pursue the target closely with their gaze and to indicate via mouse button click when they believed the target returned to the starting level (y = 0.5 m/y = 3.5 m). We familiarized subjects with 48 training trials (each combination of experimental variables once), in which the ball reappeared upon mouse click, thus indicating the spatial error. Then, we calibrated the eye-tracker and started data collection. We presented the stimuli in four blocks: 3 blocks of 320 trials each (5 gravities from 0.7g to 1.3g; 2 initial vertical velocities; 2 initial horizontal velocities; 2 occlusion conditions; 8 repetitions per combination), and one block of 384 trials (2 gravities – 1g and -1g –; 2 initial vertical velocities; 2 initial horizontal velocities; 2 occlusion conditions; 24 repetitions per combination) for a total of 1344 trials. After each block, participants could take a break, after which the calibration of the eye-tracker was repeated to avoid that potential displacement of the eye-tracker on the subjects' head contaminated the data. Five subjects received the 1g/-1g block as first block, while the other five subjects received it as last block.

Justification of Sample Size

The relative contribution of participants and number of observations to overall power differs according to the ratio of inter-subject variability and intra-subject variability (Rouder & Haaf, 2018). We assume that the effect is relatively homogeneous between subjects, with variability thus stemming mostly from trial-to-trial differences. Figure 1 visualizes this relationship for two effect sizes (a very small 0.05 difference in gain versus a small 0.1 difference in gain), while assuming that intra-subject variability is 6 times higher than inter-subject variability. A combination of about 60 observations per condition and 10 subjects should thus provide sufficient power to capture any relevant effect. However, in order to power potential post-hoc analyses for possible interactions between gravities and initial speeds, we choose to repeat each combination of 2 vertical velocities, 2 horizontal velocities, 2 occlusion conditions and 5 gravities 24 times, making for a total of 2*2*2*5*24 = 960 trials. We compare 1g and -1g parabolas in a separate block, again with 2 vertical velocities, 2 horizontal velocities and 2 occlusion conditions, which adds another 2*2*2*2*24 = 384 trials. This way, we also satisfy the generic recommendation of total observations per condition issued by (Brysbaert & Stevens, 2018) in order to achieve a properly powered experiment.

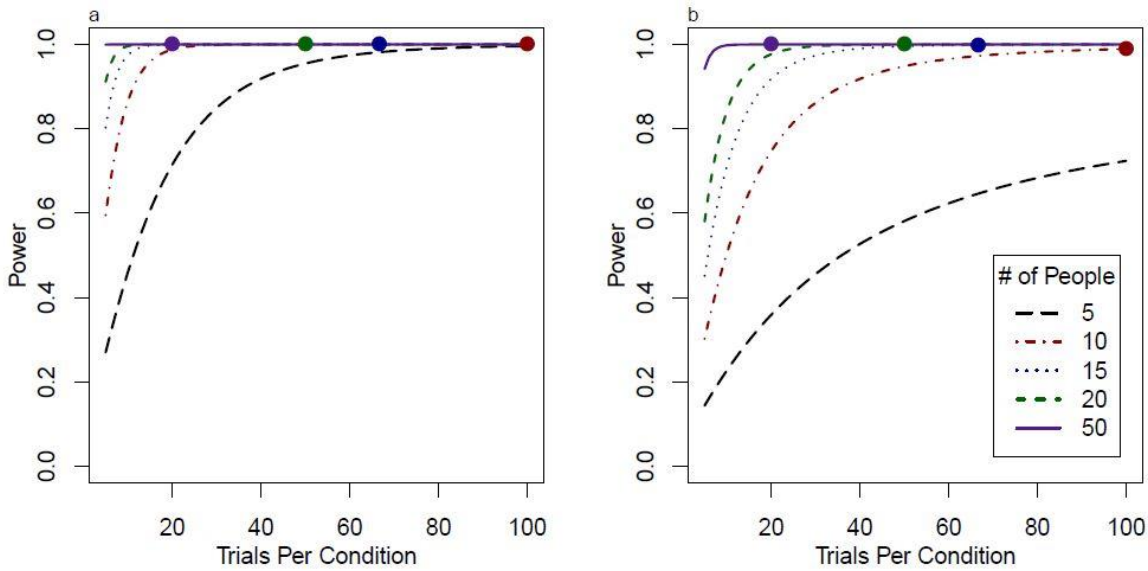

Figure 1: Power for different design scenarios. Panel 1A visualizes power for a very small effect (0.05 mean difference between gains) as a function of trials per condition for different numbers of participants. Panel 1B visualizes the same for a small effect (0.1 mean difference between gains). The calculations are based on the script https://github.com/PerceptionAndCognitionLab/stat-sampsize/blob/public/papers/amppsSub/fig-pow.R.

Apparatus

Two Sony laser projectors (VPL-FHZ57) were used to provide overlaid images on a back-projection screen (244 cm height and 184 cm width) with a resolution of 1920x1080 pixels. The frequency of refresh of the image was 85 Hz for each eye. Circular polarizing filters were used to provide stereoscopic images. Participants stood at 2 m distance centrally in front of the screen and used polarized glasses to achieve stereoscopic vision of the visual scene and the target. The shown disparity was adapted to each participant's inter-ocular distance. Eye-movements were recorded with a Pupil Labs eye-tracking device working at 200 Hz (Kassner, Patera, & Bulling, 2014). We employed the surface-tracker technology provided in the Pupil Labs Software to map eye-tracking data directly to the real-world coordinates of our display. The pupil labs eye-tracker achieves generally an accuracy of below 1° visual degrees (see pupil labs documentation under https://docs.pupil-labs.com/#notes-on-calibration-accuracy). In our setup, we achieved accuracies of < 0.5° for most of our participants; whenever the calibration was > 1°, we adjusted the cameras and repeated the calibration. The stimuli

were programmed in PsychoPy (Peirce, 2007); we added the code to our pre-registration (https://osf.io/8vg95/).

Data Preparation and Analysis

Pre-registered Hypothesis I: Visual Gains – We used the Visual Gain, defined as v_{target}/v_{eyes}, as a proxy for quality of visual pursuit. To calculate the Gain from our data, we employed the following method, which you can also view in the R (R Core Team, 2017) code we uploaded in our preregistration (https://osf.io/8vg95/). There, you can also find the final code that we used for data analysis to allow for a transparent comparison with the pre-registered code. With the surface tracker technology, the pupil labs eye tracking system saves the data in the real world coordinates of the defined display. We first excluded all data points where the confidence reported by the pupil labs system was < 0.9 (6.4% of all frames), or where the gaze was outside of the display ($y_{eyes} > 1$ or < -0.3; $x_{eyes} > 1$ or < 0; 2.2% of the remaining frames). Furthermore, we excluded frames with missing data (0.1% of the remaining data).. We then employed a series of computations to transform the data, which pupil labs reports in the coordinates of the display, into real world data of the visual scene, scaling the gaze positions on the surface to the depth of the stimulus. Therefore, gaze velocities are reported in terms of where the gaze hit in the z plane of the stimulus. We then smoothed the gaze position data locally with a Gaussian filter. Next, we calculate the tangential velocities with a lag of 9, and in a second step we calculate the acceleration as derivative of the velocity in time with a lag of 5. We defined as saccades those parts of the trajectory where acceleration was > 300 m/s² and/or where the velocity of the eyes was > 1.5*$velocity_{target}$. This is a relatively low value, but as Figure 2 shows, the algorithm identifies saccades with high accuracy. For each trial, we then calculated the average gain as $v_{tangential(eyes)}/v_{tangential(target)}$ for those parts of the trajectory (1) after the first catch-up saccade after motion onset, (2) that were not classified as saccades, (3) before the occlusion.

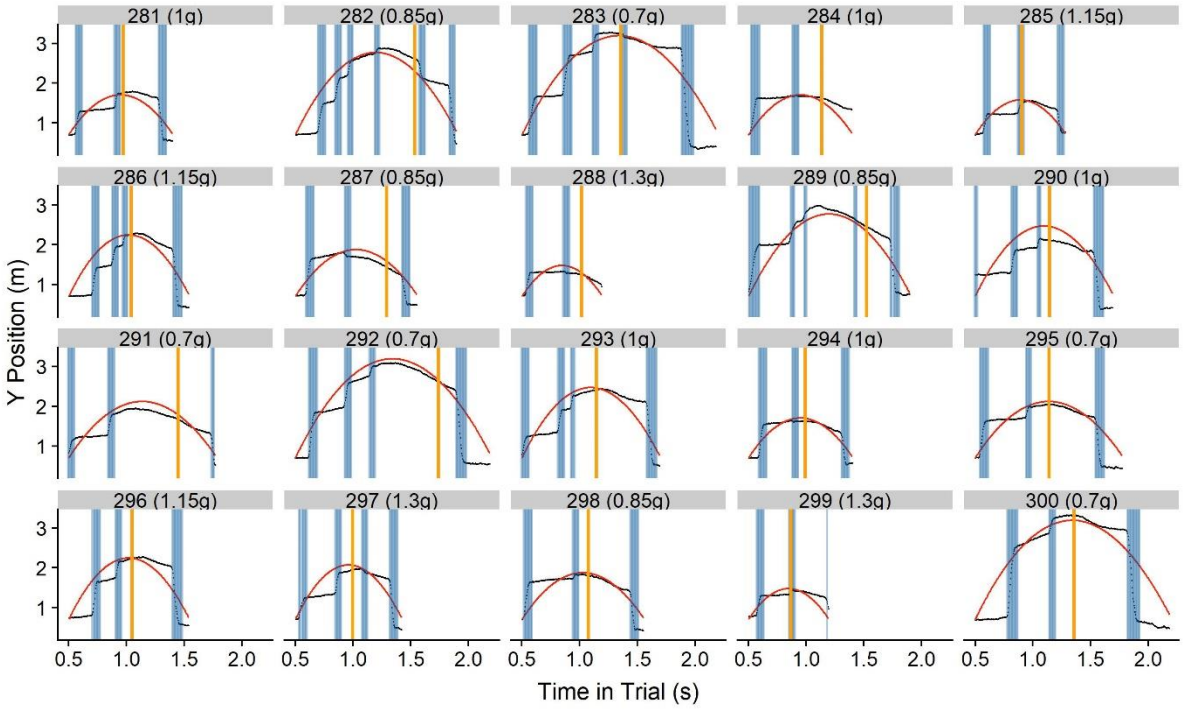

Figure 2: Eye behavior for 24 randomly chosen trials. The black dots indicate the recorded gaze behavior. The red line until the yellow vertical line is the actual trajectory of the ball. The red line after the yellow vertical line is the hypothetical trajectory the ball would follow after the occlusion. The vertical yellow lines indicate occlusion onset, while areas shaded in blue indicate behavior that our algorithm marked as saccades.

To test our hypothesis, we employed Linear Mixed Modeling on the pursuit gain as dependent variable to compare a model with subjects as grouping variable and gravity as fixed effect and intercepts as random effects to a Null Model. We analyzed the block where we compared 1g and -1g separately from the other blocks where we presented 0.7-1.3 g trajectories.

Pre-registered Hypothesis II: Timing Error – We exclude trials where the timing error was >= 0.5 s as outliers. Then, we employ Linear Mixed Modeling to compare a model with subject as grouping variable, Gravity, Occlusion Condition and their interaction as fixed effects and intercepts as random effects to a null model without Gravity as fixed effect.

Exploratory Analysis: Saccades as indicator for spatial predictions – We furthermore explored the possibility that the first saccade after occlusion onset could serve as indicator of spatial predictions. To this end, we identified the x position of the gaze after the first saccade and subtracted it from the x position where the ball hit the table. A negative error thus means that the target location of the saccade was to the left of the point of coincidence, while a positive error means the saccade went to its right. We discarded the error in y direction because subjects had the table as a reference for the height, which should overrule any predictive information.

Results

The hypotheses described under the subheadings "Visual Gains" and "Timing Error" were preregistered as confirmatory hypotheses, the exception being the analysis where we compared bins of similar presentation times, which was added afterwards. The analyses described under "Modelling the Timing Error" and "Saccades as indicators of spatial predictions" are exploratory.

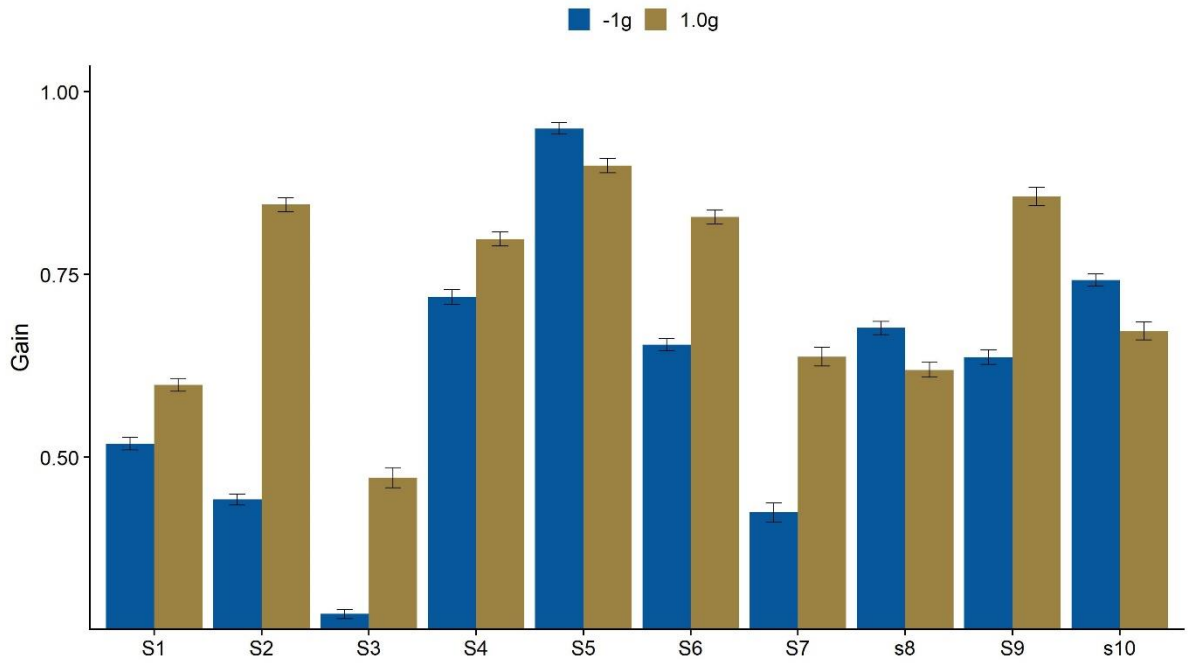

Figure 3: Average Gains for -1g and 1g per subject. Vertical lines on top of the bars indicate the standard error (+/- 1 SE). S1, S3, S5, S7 and S9 received the -1g block first. S2, S4, S6, S8 and S10 received the 0.7-1.3g block first.

Visual Gains – We compared a Linear Mixed Model (LMM) with subjects as grouping variable, gravity as fixed effect and intercepts per subject as random effects to a Null Model. For the 1g/-1g model, an

ANOVA confirmed that the LMM was significantly better than the Null Model ($p < 0.001$). The difference in gain was -0.13 (SE = 0.005), confirming our hypothesis. Figure 3 visualizes the average gains per gravity condition for each subject.

For the 0.7g-1.3g model, an ANOVA confirmed that it was better than the Null Model ($p < 0.001$). However, the effect partially goes in the wrong direction: gain was higher for 0.7g (by 0.053, SE = 0.0054) and 0.85g (by 0.029, SE = 0.0054) than for 1g, and lower for 1.15g (by 0.043, SE = 0.0054) and 1.3g (by 0.065, SE = 0.0054), going against our hypothesis. The effect was much more homogeneous than for 1g/-1g; we thus visualize it grouped together for all subjects in Figure 4.

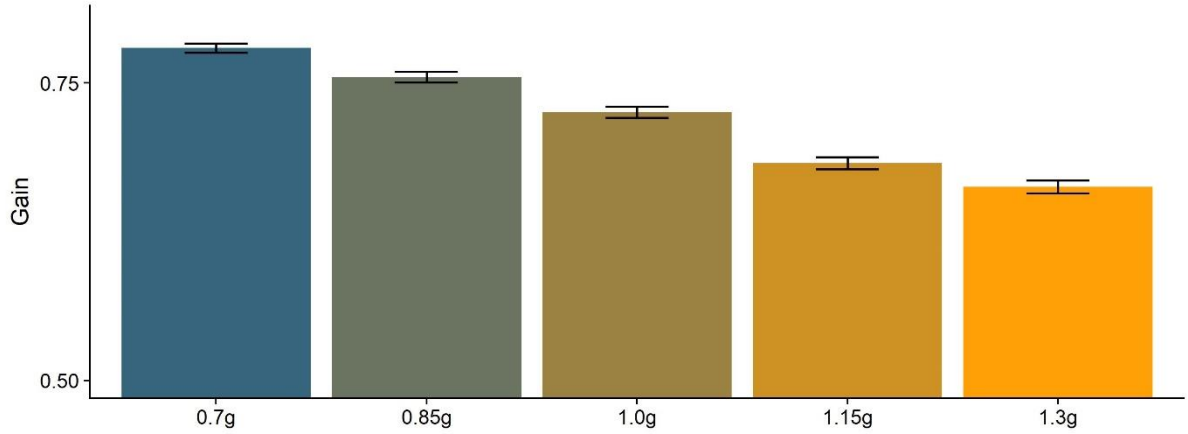

Figure 4: Gains averaged across subjects and gravity level. Lines on top of the bars indicate the Standard Error (+/- 1 SE).

Considering the unexpected result for the 0.7g-1.3g condition, we further analyzed whether this effect could be attributed to gravity, or if there were other factors at play. We discarded average speed because there are virtually the same across gravities. We further tested whether differences in presentation time could lead to this effect. We used the variability we had in our presentation times due to the different occlusion times to compare trajectories with similar presentation times, but different gravities (see Figure 5). Within the bins, there still seem to be differences according to gravity levels; however, as different percentages of the trajectories are occluded, average velocities per trajectory necessarily differ, which may introduce a new bias.

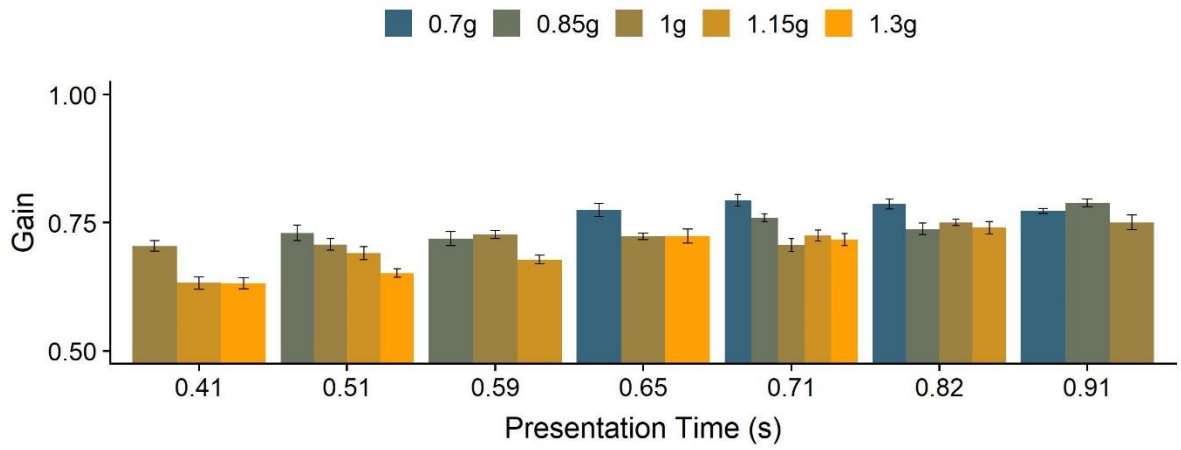

Figure 5: Gains for different presentation times, divided by gravity level. The variey in presentation times stems from the different combinations of gravity and initial vertical velocity, the Occlusion condition (long or short) and the variability in the occlusion length within each occlusion condition. We binned presentation times into seven bins with the same number of

trials each, which resulted in the bins 0.44s, 0.51s, 0.59s, 0.65s, 0.72s, 0.73s and 0.82s. We calculate the average gains per gravity and presentation time as well as the Standard Errors; the black lines on top of the bars indicate +/- SE.

Timing Error – According to the pre-registration, we were going to compare a Linear Mixed Model (LMM) with subjects as grouping variable, Gravity, Occlusion Category and their interaction as fixed effects and intercepts per subject as random effects to a Null Model. However, for the 0.7g-1.3g condition, we found that a simpler model, with subjects as grouping variable, Gravity as fixed effect and intercepts per subject as random effects was not significantly worse than the model we had pre-registered ($p = 0.11$ for the 0.7g-1.3g model). For the -1g/1g condition, the original model was better than the simpler model ($p < 0.001$). We thus proceeded with the simpler model for thr 0.7/0.85/1/1.15/1.3g condition and with the more complex model for the -1g/1g condition. For the -1g/1g model, an ANOVA confirmed that the LMM was significantly better than the Null Model ($p < 0.001$). For -1g, subjects pressed the mouse button later than for 1g, an effect that was stronger for the long occlusion condition (the regression line is given by Y = 0.04*Gravity Category+0.005*Occlusion Category+0.02*Gravity Category*Occlusion Category+0.1), confirming our hypothesis. Figure 6 visualizes the average timing errors across all participants per gravity condition.

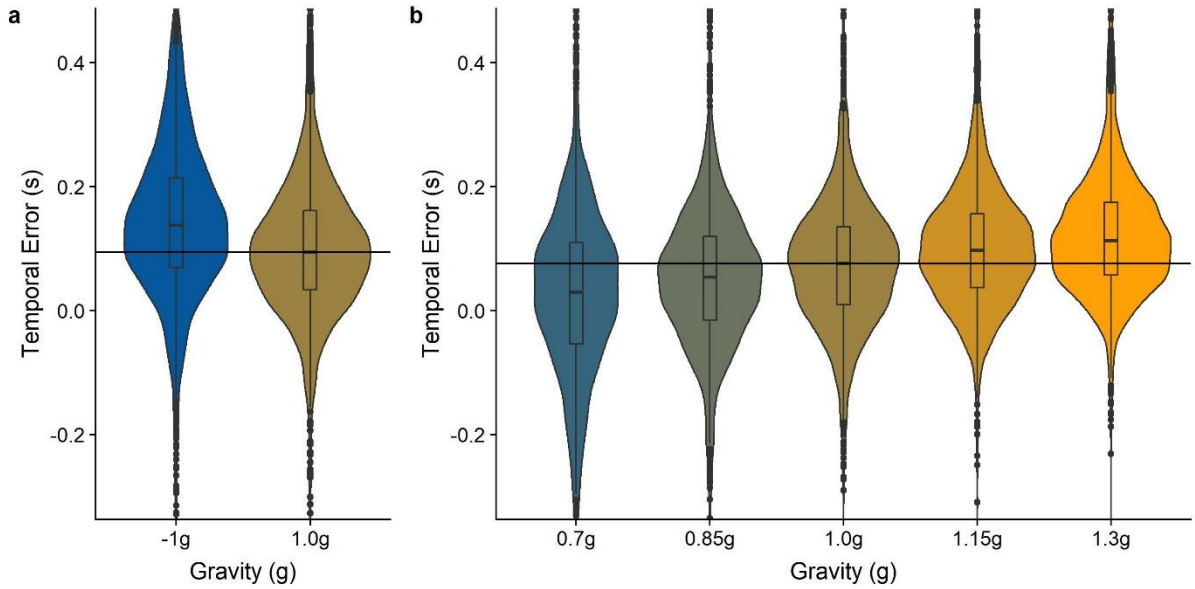

Figure 6: Temporal errors per gravity condition. Negative values indicate that subjects pressed the button too early with regards to the moment of impact. Positive values indicate that the button was pressed too late. Boxplots in the middle of each structure indicate the percentiles and the median, while the wings represent the distribution of responses. The horizontal black line represents the median of the responses for 1g. Figure 6a visualizes data from the -1g/1g blocks, while Figure 6b visualizes data from the 0.7/0.85/1/1.15/1.3g blocks.

For the 0.7g-1.3g model, an ANOVA confirmed that it was significantly better than the Null Model ($p < 0.001$). Subjects pressed the mouse button earlier for 0.7g (by 0.05 s, SE = 0.0035 s) and 0.85g (by 0.024 s, SE = 0.0035 s), and later for 1.15g (by 0.023 s, SE = 0.0035) and 1.3g (by 0.040 s, SE = 0.0034 s), confirming our hypothesis. See Figure 6 for a visualization of the differences.

Modelling the Timing Error – Both the mean temporal error for 1g in the 0.7/0.85/1/1.15/1.3g condition ($p < 0.001$, $t = 27.153$) and in the -1g/1g condition ($p < 0.001$, $t = 34.516$) are significantly different from zero. This is likely due to delays in the projectors.

To verify to what extend the observed temporal error are consistent with the use of an earth gravity prior to extrapolate motion during the occlusions, we simulated the temporal errors assuming the last

vertical velocities observed by the participants and a gravity of 9.81 based on the physical formula for travelled distance from initial velocity and acceleration (Equation 1), solved for time (Equation 2).

$$d_y = \frac{g_{earth}}{2} * t^2 + v_y * t \qquad [1]$$

$$t_{1/2} = \frac{-v_y \pm \left(v_y{}^2 - 4 * \frac{g_{earth}}{2} * d_y\right)^{0.5}}{2 * \frac{g_{earth}}{2}} \qquad [2]$$

d_y is the remaining distance in y direction, g_{earth} is the value earth gravity (9.81 m/s²) and v_y is the last observed velocity in y direction. As we are interested in future positions, we discard negative solutions of Equation 2 for t (that is, the version of the formula where the discriminant is subtracted).

Figure 8a depicts the observed errors as a function of the error predicted from our simple model. The overall correlation between simulated and observed temporal error was r = 0.31, while it rose to r = 0.37 when only considering the long occlusion condition and dropped to r = 0.17 for the short occlusion condition. This indicates that gravity becomes more important as a source of information as the occlusion becomes longer and motion has to be predicted for a bigger time frame. In Figure 8B, we illustrate the median simulated error and the median standardized observed error for the two occlusion conditions and each gravity value. We standardized the observed error by subtracting the median error from the 1g condition from each value in order to compensate for the delays we encountered in our apparatus. As apparent from the plot, the observed data fit the predictions very well, indicating that humans indeed rely on earth gravity to guide temporal coincidence responses.

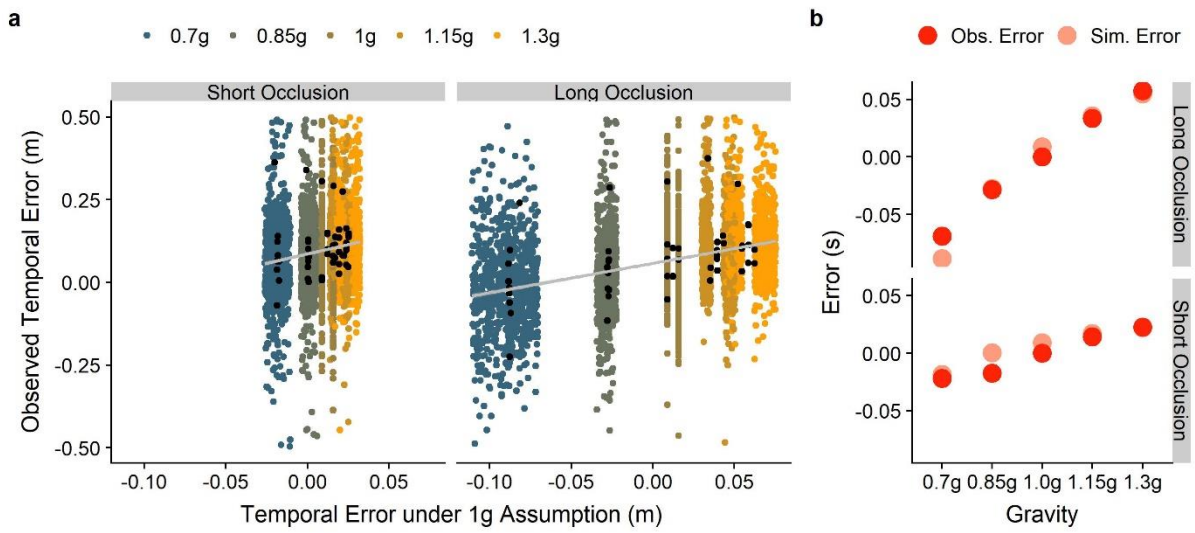

Figure 7: A. Empirically Observed temporal errors as a function of the error predicted by our model. We display the data separately for the short and the long occlusion conditions and color coded for gravity. The black dots are the median values per subject. The grey line is the regression line, while the (very) faint grey area around it marks +/- 1 standard error. Due to the amount of data points, the standard error is really small and barely visible in the plot. B. Median observed errors per gravity condition (red) and median simulated errors per gravity conditions (light red).

Saccades as indicators for spatial predictions – Apart from the two pre-registered hypotheses, we tested whether the first saccade after occlusion onset would reveal gravity-based spatial predictions. This error was computed as target x position of the first saccade after occlusion onset minus the position where the ball hit the table (see also code available under https://osf.io/8vg95/). We compared a Linear Mixed Model (LMM) with subjects as grouping variable, Gravity as fixed effects and intercepts per subject as random effects to a Null Model. As we did not expect any spatial bias for -1g, we applied this model only to the 0.7-1.3g condition. An ANOVA showed that the model was significantly better than the Null Model ($p < 0.001$). In comparison to 1g trajectories, subjects executed

their first saccade after occlusion onset more to the left for 0.7g (0.77 m, SE = 0.042 m) and 0.85g (0.29 m, SE = 0.042 m) trajectories, and more to the right for 1.15g (0.12 m, SE = 0.042 m) and 1.3g (0.29 m, SE = 0.042 m) trajectories. This effect is consistent with assuming 1g for the occluded part of the trajectory. Figure 6 visualizes this effect.

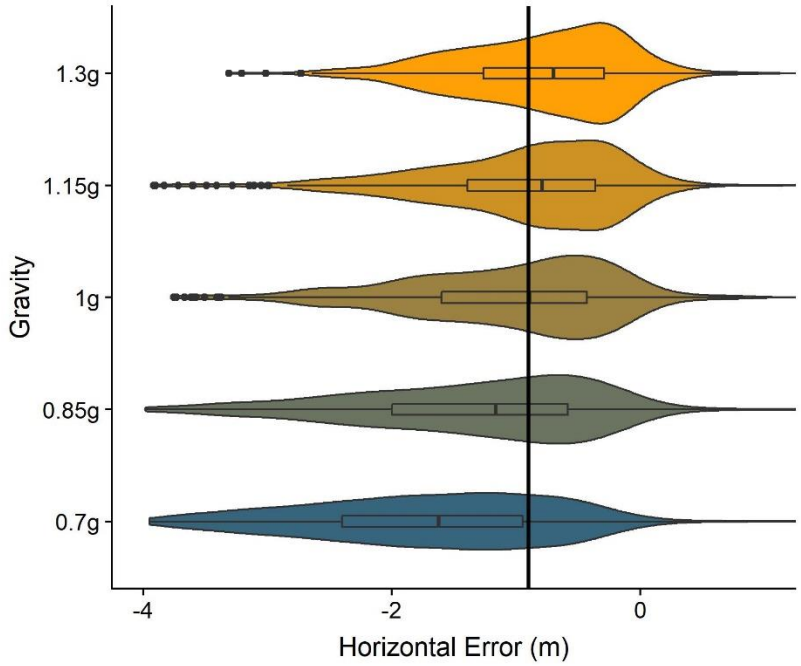

Figure 8: Spatial Error per gravity level. Negative values represent an undershoot, that is, the saccade lands further to the left than the spot where the ball hits the table. Positive values in turn signify an overshoot. Boxplots in the middle of each structure indicate the percentiles and the median, while the wings represent the distribution of responses. The black line represents the median of responses for 1g.

Discussion

Visual Gains

Our results show that humans use their earth gravity prior to guide their smooth pursuit eye movements, and possibly also to guide saccades. This effect is clearly visible in the 1g/-1g condition, which we consider to be the stronger test of our hypothesis as it minimizes confounds. The results from the 0.7g-1.3g condition are less clear: we observed a correlation between gravity value and gains, which goes against our original prediction that the highest gains should be observed for 1g trajectories, with lower gains for both lower and higher gravities.

An alternative is a post hoc adjustment of the original hypothesis – which, for this reason, should be treated with the due caution: Since the gains are calculated to the bigger part of ascending trajectories, employing earth gravity to guide smooth pursuit would mean that the gaze is lagging behind for higher gravities, and slightly ahead of the target for lower gravities. This is exactly the direction of effect we found in the data. However, if taken seriously, this interpretation would mean that gains should be around 1 for 1g, below 1 for 1.15 and 1.3g and above 1 for 0.7 and 0.85g. As gains are generally below 1, our data can't be taken as strong evidence for this interpretation of the original hypothesis. Also, after further analyzing the data, we believe that the effect is an artifact of our design, where higher gravities entailed lower presentation times. Lower presentation times could impact pursuit because subjects have less time to adjust to the trajectory. It is, unfortunately, virtually impossible to match every relevant dimension of the stimulus: to match the presentation time while

maintaining gravity, the initial vertical velocity would have to be adjusted, which may incur new problems.

Our results also shed light on what information the visual system relies upon to make predictions about observed motion in order to guide eye-movements. Generally, it has been found that motion estimates are taken into account to predictively guide eye movements (Maffei, Macaluso, Indovina, Orban, & Lacquaniti, 2010; de Xivry, Missal, & Lefevre, 2008), wave forms are pursued more closely than neural delays would allow without prediction (Bahill, Iandolo, & Troost, 1980) and curvilinear paths were followed throughout an occlusion (Mrotek & Soechting, 2007). Arbitrary accelerations are taken into account qualitatively at best (Benguigui & Bennett, 2010; Bennett, de Xivry, Barnes, & Lefevre, 2007; Bennett & Benguigui, 2013). The control of eye movements has also been described in an active inference framework (Adams, Aponte, Marshall, & Friston, 2015; Adams, Perrinet, & Friston, 2012), and neural bases have been suggested (Fukushima, 2003; Fukushima, Yamanobe, Shinmei, & Fukushima, 2002) for predictive mechanisms. By demonstrating that congruency with earth gravity improves visual pursuit gains, we show that, in addition to the aforementioned sources of information, also an earth gravity prior is recruited to guide eye movements.

Timing

We furthermore aimed to replicate the known effect that internalized knowledge of gravity is used to extrapolate motion information for interception tasks (pre-registered hypothesis II). Our data support this notion: subjects generally clicked too late for higher gravities and too early for lower gravities (for the 0.7g-1.3g), and too late for -1g, indicating that they expect objects to accelerate/decelerate according to earth gravity.

Moreover, to our knowledge, this is the first time a continuous, quantitative effect of an internal model of gravity has been shown. Studies have generally focused on comparing 1g to 0g or -1g motion to tease out the impact of our knowledge of gravity (Bosco et al., 2015; La Scaleia, Zago, & Lacquaniti, 2015; McIntyre et al., 2003; Zago, Iosa, Maffei, & Lacquaniti, 2010). By analyzing the effect across a range of values (0.7/0.85/1/1.15/1.3g), we add an understanding of how our internalized representation of 1g affects coincidence timing across a range of gravity values. To help capture this quantitative aspect, we present a very simple model that estimates the temporal error based on the last observed vertical velocity before occlusion and earth gravity. The model explains responses very well, which can be taken as additional evidence that humans maintain and access a representation of gravity that is very accurate and nearly immutable.

As the results for 0.7-1.3g are roughly symmetric, it could be argued that our timing results are due to a regression to the mean. However, the dispersion is not uniform across conditions, which makes a regression to the mean effect less likely.

Spatial Error

When analyzing the data, we realized that many subjects made a saccade right after the object disappeared. As exploratory analysis, we verified whether also this saccade may be informed by earth gravity. Figure 9 illustrates that this may well be the case, and our LMM analysis confirmed that the data support this interpretation. In our data set, the effect is much stronger for lower gravities than for higher gravities, which might reflect a confound: for our stimuli, lower gravities meant that the point of coincidence was much further to the left than for higher gravities. Therefore, also the distance that needed to be covered during the saccade was much higher, resulting in an additional undershoot for higher gravities. In fact, a similar behavior has been shown for smooth pursuit (Becker & Fuchs,

1985; Mrotek & Soechting, 2007), where during a transient occlusion the gaze decelerated and stabilized at a lower velocity, lagging behind the hypothetical path of the target. In occlusion scenarios, saccades seem to be executed to compensate for lagging smooth pursuit, realigning the gaze with the position of the target. (de Xivry, Bennet, Lefèvre, & Barnes, 2005). Also independently of smooth pursuit, humans directed saccades to the expected position of a target after an occlusion (Barborica & Ferrera, 2004). We thus believe that the overall undershoot we are observing for all conditions is not a general trend of saccadic behavior for occlusions, but rather a consequence of our experimental design. All in all, especially because lower gravities required bigger saccadic amplitudes to reach the locus of coincidence, the data should be treated as suggestive rather than conclusive. The notion that not only smooth pursuit, but also saccades are partially guided by an earth gravity prior, deserves nonetheless further, confirmatory research.

Conclusions

In our study, we test the hypothesis that an earth gravity prior is used by humans to guide their smooth pursuit eye movements. We furthermore replicated a known effect where this earth gravity prior lead to systematic timing errors for interceptive timing. This effect had so far been study mostly qualitatively, on which we add by demonstrating that a larger deviation from earth gravity leads to larger timing errors. Moreover, in an exploratory analysis, we show that also saccades may be guided by earth gravity-based predictions.

Future research should confirm that saccades are guided by the earth gravity prior. More ambitiously, it would be interesting to delve deeper into quantitative aspects of the internal model of gravity: Do the introduced biases get stronger the further we are moving away from 1g? Are subjects able to adjust manual or ocular responses when given feedback and enough opportunity to learn? Is it, generally, more useful to envision our representation of earth gravity qualitatively as an internal model, or should we call it a gravity "prior", invoking a Bayesian framework of perception and action?

Author Contributions and Notes

BJ conducted and analyzed the experiment and wrote the paper. JLM provided the initial research question and provided overall advice. BJ and JLM programmed the stimuli in a joint effort.

The authors declare no conflict of interest.

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