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Temporal constancy of perceived direction of gravity assessed by visual line adjustments

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Abstract

Here we investigated how well internal estimates of direction of gravity are preserved over time and if the subjective visual vertical (SVV) and horizontal (SVH) can be used inter-changeably. Fourteen human subjects repetitively aligned a luminous line to SVV, SVH or subjective visual oblique (± 45°) over 5min in otherwise complete darkness and also in dim light. Both *accuracy* (i.e., the degree of veracity as reflected by the median adjustment error) and *precision* (i.e., the degree of reproducability as reflected by the trial-to-trial variability) of adjustments along the principle axes were significantly higher than along the oblique axes. Orthogonality was only preserved in a minority of subjects. Adjustments were significantly different between SVV vs. SVH (7/14 subjects) and between +45° vs. −45° (12/14) in darkness and in 6/14 and 14/14 subjects, respectively, in dim light. In darkness, significant drifts over 5min were observed in a majority of trials (33/56). Both accuracy and precision were higher if more time was taken to make the adjustment. These results introduce important caveats when interpreting studies related to graviception. The test re-test reliability of SVV and SVH can be influenced by drift of the internal estimate of gravity. Based on spectral density analysis we found a noise pattern consistent with $1/f^{\beta}$ noise, indicating that at least part of the trial-to-trial dynamics observed in our experiments is due to the dependence of the serial adjustments over time. Furthermore, using results from the SVV and SVH inter-changeably may be misleading as many subjects do not show orthogonality. The poor fidelity of perceived ± 45° indicates that the brain has limited ability to estimate oblique angles.

Keywords

Subjective visual vertical; subjective visual horizontal; vestibular; otolith organs; self-similarity

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1. Introduction

An accurate internal estimate of the direction of gravity is essential to staying upright, navigating in and interacting with the environment(see [8] for review). Besides vision and proprioception (skin pressure sensors, joint sensors, visceral body sensors, muscle spindles), the labyrinthine otolith organs provide key information about the direction of the pull of gravity [33,42]. Signals from the labyrinth are forwarded along the ascending central graviceptive pathways [44] to the multisensory “vestibular” cortex and integrated with input from the other sensory systems [6,15], weighted based upon the relative reliability of these cues [2].

Internal estimates of gravity can be assayed using ocular motor, postural and perceptual paradigms. Reflexive compensatory torsional eye movements – called ocular counterroll (OCR [9,11]) – in response to sustained lateral head roll are mediated by various brainstem structures and heavily depend upon otolith input under static conditions [17]. On the other hand, paradigms that assess internal estimates of the direction of gravity based on perception reflect central processing in a more widespread network including areas in the brainstem such as the vestibular nuclei, the deep cerebellar nuclei [4,7,34], the thalamus [14] and the multisensory “vestibular” cortex [27].

Whereas the assessment of torsional eye position is limited in its clinical applicability due to its technical demands [37], the perception of vertical or horizontal can easily be determined by asking subjects to align a luminous line to their subjective visual vertical (SVV) or horizontal (SVH) in darkness [26]. Deviations in SVH or SVV are sensitive markers of lesions along the central vestibular pathways [13]. Due to its relatively simple implementation and portability [57] measurements of SVV and SVH are used broadly in clinical settings.

Here we investigated internal perceptual estimates of gravity using visual cues and focused on the temporal consistency and inter-changeability of SVV and SVH in the upright position. A drift of perceived direction of gravity has been found when subjects were roll-tilted both for ocular motor [38] and perceptual [29,42,53] paradigms, whereas no consistent drift has been reported when upright. Most studies implementing the SVV or SVH for clinical or basic research, however, were not designed to detect small drifts in the upright position. For example, mean ±1 standard deviation (SD) are often obtained from few trials without a time constraint for making each adjustment, and results obtained using either SVV or SVH are directly compared. This approach may be problematic as subjects may be more accurate and precise when spending more time on single trials. Whether or not the SVV and SVH can be used inter-changeably is controversial. In roll-tilted positions average non-orthogonalities of up to 7° [5] and ~12° [49] were reported, while no consistent differences were found with subjects in the upright position [5,19,40]. Unfortunately, drift over time has not been reported using the SVH. Therefore it is unclear whether or not modulations in sensed vertical and horizontal run in parallel over time, which would be an explanation for non-orthognailityas suggested by Betts and colleagues [5]. If so, the inter-changeable use of SVV and SVH in the upright position would not be justified.

Furthermore, the performance of line adjustments may depend on the desired orientation. The natural environment is enriched with vertical and horizontal visual cues [10,45], upon which the human brain may mainly rely because they are common and directly indicate vertical or horizontal. Based on this observation one would predict superior performance in estimating earth-vertical and earth-horizontal than other, oblique axes in the presence of usual visual orientation cues. How this transforms to estimates of spatial orientation in the absence of visual cues has not been reported.

2. Material and methods

2.1. Subjects

Fourteen healthy human subjects,aged 22 to 38 years (7 women, 7 men; median age: 27.5 years) were studied. All but two were unaware of the underlying motivation and hypotheses of this study. Five subjects completed the experiments without corrected vision (i.e., impaired vision has been previously confirmed but they did not wear their glasses or contact lenses during the experiments), the remaining nine had normal visual acuity (six of those nine subjects did not require visual correction; three wore their glasses/contact lenses). Informed written consent of all participants was obtained after explanation of the experimental procedure. The protocol was approved by the Johns Hopkins Institutional Review Board, and was in accordance with the Declaration of Helsinki for research involving human subjects.

2.2. Experimental setup

All data was collected with subjects sitting upright with their head fixed by an individually molded bite-bar in the straight-ahead position. The head was horizontal by definition when a horizontal laser line was parallel to both lower lids. A luminous laser line (length: 80 cm), covering the central 16° of the binocular visual field, back-projected on a semi-transparent screen placed 140 cm away from the subject's eyes was used for all paradigms. The spatial resolution of the roll orientation of this laser line was approximately 0.02°. In the center of rotation of the laser line a red laser dot was back-projected and subjects were asked to look at this laser dot when performing the adjustments. The line orientation was controlled by rotating a track ball with the right hand. Adjustments were confirmed by pushing a button with the left hand. To control for the direction of rotation, which by itself may affect the accuracy of SVH and SVV adjustments [32], trials were intermixed that required either clockwise (CW) or counter-clockwise (CCW) rotations. CW/CCW rotations were defined as seen by the subject and referred to the top pole of the laser line.

2.3. Experimental setting

All 14 subjects participated in four different paradigms that were recorded in random order in a first session in darkness and in a second session in dim light (15 lux at the center of the screen facing the subject, provided by two light sources mounted onto the ceiling). In the dim light condition the subjects could depict the horizontal and vertical outline of the frame holding the tangent screen in front and details of the furniture of the recording room. In all paradigms subjects were asked to orient the laser line parallel to perceived direction of the horizon (SVH), parallel to perceived direction of gravity (i.e., the direction along which objects fall towards the ground; SVV) or 45° oblique (i.e., the average between perceived horizontal and perceived vertical) depending on the paradigm, by rotating it along the shortest path within five seconds, otherwise the line disappeared and a brief auditory beep indicated failure. Before any paradigm, subjects practiced so that they could complete trials within the time limit. We chose a short time limit to reduce the duration of each trial in favor of collecting more trials in a given interval and to minimize effects of varying adjustment time on accuracy (i.e. how close the subject's estimate was to true vertical) and precision (i.e. how consistent were the responses from trial to trial) of adjustments. Nonetheless the amount of time (within the time allowed) each subject spent to make a judgment differed among subjects; these ranges will be used for analyzing effects of time on trial performance.

2.4. Data analysis

The orientation of the laser line was collected at a frequency of 1000 Hz and stored on a hard-drive for offline processing using interactive programs written in Matlab 7.0 (The MathWorks, USA). Outliers were defined as data points differing by more than three SD from the mean. Less than 0.1% of all trials were discarded. Since the data did not meet criteria of a Gaussian distribution (using Lilliefors test), we applied non-parametric statistics for further analysis including Kruskal Wallis tests for non-parametric analysis of variance (ANOVA) with multiple comparisons (using Tukey-Kramer to compensate for multiple tests). The drift amplitude – referring to the average difference of adjustments within the first and the last (fifth) minute of each run – was determined in all runs. Drifts over time were also analyzed using least-square linear regression analysis that takes outliers into consideration (robust-fit, Matlab 7.0, The MathWorks). Whenever both variables considered for correlation analysis are dependent variables, i.e., measured with error, principal component analysis (PCA) providing major axis regression was chosen instead. This procedure is equivalent to Orthogonal Linear Regression or Total Least Squares, which minimizes the perpendicular distances from the data points to the fitted model [50]. As a measure of the goodness of fit we provide the R^2 value. To estimate the sampling distribution of the slope of the fit obtained by PCA, we used bootstrapping to construct 1,000 resamples and calculated the 95% confidence interval (CI). The correlation between the dependent variables was considered significant whenever the CI did not include zero.

Trial-to-trial dynamics for each recording period of 5 min were evaluated using spectral density analysis. Generally, consecutive behaviors that show robust serial correlations (reflecting fractal features such as ‘self-similarity’ and ‘scale-invariance’) are considered to be part of a special class known as $1/f^{\beta}$ noise and occur throughout a wide range of different biological systems, (see [48] for an extensive review of serial correlations). Decay of serial correlations related to $1/f^{\beta}$ noise has been found to be so slow that the generating system is called persistent or long-range dependent [48]. The spectral density analysis was applied to individual data sets for all conditions and subjects and linear regression analysis (robustfit.m) was performed to estimate the slope β of the fit. For a $1/f^{\beta}$ process the log-log power spectrum is linear with a slope of $-\beta$ typically being in the range of 0.5 to 1.5 [48]. Consecutive behaviors that are independent yield a slope of 0, while random serial behaviors result in a slope of –2.

3. Results

The overall median individual number of trials and its inter-quartile range (IQR) in darkness (99/33; median/IQR) and in dim light (93/30) was not significantly different ($p > 0.05$) and there was no main effect of the paradigm type (SVV, SVH, +45°, −45°) in either darkness or dim light. Furthermore, there was no main effect of direction of line rotation on adjustment errors (ANOVA, $p > 0.05$) and on the individual IQRs. Therefore trials with either CW or CCW line rotations were pooled.

3.1. Accuracy of adjustments based on absolute adjustment errors

Individual median adjustment errors (see Fig. 1A) in darkness ranged between −4.3 and +3.7° (SVV) and between −4.4 and +6.1° (SVH), whereas for adjustments along +45° (range: −9.4° to +13.5°) and −45° (range: −9.1° to +6.3°) considerably more inter-individual variability was observed. In dim light the range of individual median adjustment errors along both SVV (ranging from −0.8 to +0.8°) and SVH (−0.3° to +0.5°) was considerably smaller (see Fig. 1B) compared to those ranges obtained in darkness; this was also true along +45° (range: from −5.7° to +8.9°) and along −45° (range: from −10.0° to +4.1°), although inter-individual variability was still high.

As a measure of accuracy individual median absolute adjustment errors were calculated. Statistical analysis showed that both in darkness and dim light the accuracy for SVV vs. SVH was not significantly different (ANOVA, $p > 0.05$), whereas accuracy for +45° was significantly (ANOVA, $p < 0.05$) less than for −45° (Fig. 2). Compared to the oblique axes, accuracy along the principle axes was significantly greater ($p < 0.05$) in either condition. With visual orientation cues accuracy increased significantly ($p < 0.05$) for all four paradigms.

3.2. Precision of adjustments based on the inter-quartile range(IQR)

In both darkness and dim light precision was about five times greater (being statistically significant, $p < 0.05$) along the principle axes than along the oblique axes (see Fig. 3) whereas no significant differences were found between the principle (SVV vs. SVH) or the oblique (+45° vs. −45°) conditions. Providing visual orientation cues reduced IQRs by 17 to 39% but they were significant only for the −45° task.

3.3. Temporal constancy of adjustments over periods of five minutes

We noted significant ($p < 0.05$) drift of individual adjustments over time in 33 of 56 runs (14 subjects,four paradigms per subject) in darkness. The drift pattern in all four paradigms in darkness is shown for two typical subjects in Fig. 4. Subject BJ showed significant drift in three of four paradigms but subject DF showed no significant drift.

For each of the four desired line orientations, at least seven subjects had significant drifts; however, a majority of these 33 runs had low ($R^2 < 0.3$; $n = 17$) or moderate ($R^2 > 0.3$ and < 0.7, $n = 9$) R^2 values (Fig. 5A). When providing visual orientation cues, there was still significant drift in 24 of 56 runs (Fig. 5B). Compared to the drift amplitudes observed in darkness, the amplitudes in dim light were significantly smaller ($p < 0.05$) along the principle axes. Furthermore, we found no significant differences ($p > 0.05$) between drift amplitudes (Fig. 6) in the SVV vs. SVH condition and in the +45° vs. −45° condition, therefore we pooled individual drift amplitudes obtained from the principle axes and from the oblique axes for further analysis. The drift amplitudes in darkness were significantly larger for adjustments along the oblique axes (3.6°, 3.4°; overall median drift, IQR of individual drift amplitudes) than along the principle axes (0.9°, 1.0°). This was true for both the overall median drift and the IQR of individual drift amplitudes in dim light (1.6° and 2.4° vs. 0.2° and 0.3°; oblique vs. principle axes).

Significant drift in darkness was CCW in the majority of subjects along SVV ($n = 6/9$) and SVH ($n = 7/7$), CW in the +45° condition ($n = 8/8$) and equally frequently CW ($n = 4/8$) and CCW ($n = 4/8$) in the −45° condition. In dim light, there was a preference for CCW drift for the SVV (n = 3/5) and the SVH ($n = 4/6$), whereas for the oblique conditions CW and CCW drifts were about equally frequent in +45° ($n = 3/7$ for CW drifts) and −45° ($n = 3/6$) condition. Within subjects, the drift direction was not consistent among the different paradigms (e.g. SVV vs. SVH) and conditions (darkness vs. dim light).

Alertness and attention may decrease over a 5 min test period. To address this potential bias we compared the within-trial variability (assessed as IQR) as a measure of the subject's performance and assumed that a decrease in attention/alertness would result in a decrease in precision (increase in the IQR). When comparing the IQR of the 1st and the 5th (and last) minute of every 5 min block and subject (both in darkness and dim light), there were no significant changes, suggesting that fluctuation in attention/alertness is not a major confound in this paradigm. Potentially, a decrease in alertness/attention may have been compensated by an increase in the trial time (as we have shown that trial time and precision are correlated) leaving the IQR unchanged. However, comparing the median individual trial time (1st minute vs. 5th minute) did not yield any significant differences (Kruskal-Wallis ANOVA, $p > 0.05$) for either the dark or the dim light condition.

3.4. Is orthogonality preserved?

When subtracting individual median SVV values from individual median SVH values differences ranging from −2.8° to +2.6° in darkness were noted in single subjects (see Fig. 7). In dim light, the range of differences was much smaller (−0.6° to +0.7°).

As a whole group ($n = 14$) individual trial adjustment errors along SVV and SVH were not significantly different ($p > 0.05$) in darkness and dim light. However, both in darkness and in dim light many subjects (darkness: $n = 7/14$; dim light: $n = 6/14$) showed significantly ($p < 0.05$) different individual adjustment errors along SVV vs. SVH based on Kruskal Wallis analysis. Along the oblique axes most subjects did not show orthogonality in darkness ($n = 12/14$) or in dim light ($n = 14/14$). As a whole group, adjustment errors along +45° were significantly different ($p < 0.05$) from those along −45° in both conditions.

3.5. Does spending more time for single adjustments improve accuracy and precision?

The median time to complete trials in darkness was 2.7sec (IQR: 1.0sec) and 2.6sec (IQR: 1.2sec) in dim light, and statistical analysis yielded no significant differences in individual median adjustment duration for the different paradigms and conditions ($p > 0.05$). There was no main effect ($p > 0.05$) of the direction of line rotation and of the paradigm on the individual median duration to complete adjustments in either darkness or dim light. To study the effect of adjustment time on the subject's performance PCA was used. Both median adjustment errors and the individual IQR values were inversely correlated with the median time subjects spent for individual adjustments in darkness (see Fig. 8). No significant correlation between adjustment time and the amount of drift over time ($R^2 = 0.26$, slope = −0.23, 95% CI of the slope = −0.38 to 0.34) was noted. For trials in dim light, a similar pattern emerged with inverse correlations between median individual adjustment time and median adjustment errors and the individual IQR values. As in darkness, the time spent on individual trials did not correlate with the amount of drift in individual subjects ($R^2 = 0.23$, $p = -0.28$, 95% CI of the slope = −0.54 to 0.52).

3.6. Spectral density analysis of consecutive behaviors

The log-log power spectrum for both conditions was calculated on an individual subject and individual paradigm basis. As illustrated in the individual data presented in Fig. 9A, the log-log power-spectrum shows linear decay (in this example with a slope $-\beta$ of 1.16).

In condition 1 (darkness) individual slopes of $-\beta$ ranged between 0.05 and 1.64 (median/IQR: 0.72/0.44) for the four different paradigms pooled (see Fig. 9B), being compatible with a $1/f^{\beta}$ process. In condition 2 (dim light), slopes were overall smaller, ranging between −0.31 and 0.96 (median/IQR: 0.45/0.46), indicating that serial correlations were less robust (for an $1/f^{\beta}$ process slope $-\beta$ typically ranges between 0.5 and 1.5). As certain experimental manipulations may systematically change the intensity of $1/f^{\beta}$ noise [48], slopes from both experimental conditions were compared. Non-parametric statistical analysis (Kruskal-Wallis ANOVA) yielded a significant main effect of the condition with $-\beta$ being significantly closer to zero ($p < 0.05$) in dim light than in darkness. Multiple comparisons for a given paradigm (i.e. SVH), however, resulted in significant differences ($p < 0.05$) for SVV and +45° line orientation only, whereas for the remaining two conditions (SVH and −45°) no significant changes in the slope were noted when providing visual cues (condition 2).

4. Discussion

4.1. Temporal constancy of internal estimates of direction of gravity

We used psychophysical paradigms to gain insights into the internal estimates of direction of gravity over time and to evaluate whether they can be used interchangeably or not. A significant drift was found along both principle (i.e., SVV and SVH) and oblique (i.e., +45° and −45°) axes in most subjects, suggesting that internal estimates of the direction of gravity, based on a visual cue, are not stable over time when upright. Perceptual drifts were attenuated and occurred in a smaller fraction when a structured visual feedback was provided, though they did not disappear completely. These findings contrast with previous studies investigating temporal constancy of the perceived vertical. Drifts up to 90° in perceived vertical have been reported for roll-tilted positions over periods of eight minutes [29, 42], however the same groups failed to show such drifts in upright position. How can these discrepancies be explained? Since drifts in the upright position are considerably smaller than those in roll-tilted positions, the experimental setup used by previous groups might not have been sensitive enough to detect changes in perceived vertical in the range of less than one degree. Also considerably fewer trials (32 compared to ~100 here) were obtained by these groups. Due to the trial-to-trial variability observed here least-square linear regression analysis evaluating for significant drift yielded moderate or low R^2 values (< 0.7) underlining the necessity to collect large numbers of trials to obtain a reasonable fit and so discern the drift effect.

In single subjects, drift did not follow a specific pattern (e.g., drifting into the same direction in all four paradigms) and was often distinct in the dim light and the dark condition. This suggests that these drifts are not stable over time and that they do not represent inter-individual differences in processing graviceptive input, but rather the result of continuous modulation of the internal estimate of direction of gravity at a very low frequency, raising the question about underlying mechanisms. Potentially, drift could emerge from the sensors themselves (e.g., vision, otolith organs, proprioceptors), occur while centrally processing and integrating sensory information or when performing the motor task of adjusting the line.

Van Rijn noted fluctuations of conjugate torsional eye position up to one degree over periods of 32 seconds [51]. Based on previous work we assume that fluctuations noted in ocular motor and in psychophysical paradigms have a common origin. Both the trial-to-trial variability [47] and errors of SVV [54] (or SVH [39]) were found to correlate well with torsional eye position. Hence fluctuations in torsional eye position may produce drift in perceived direction of gravity over time in both upright and roll-tilted positions. By providing visual orientation cues the number of runs with significant drifts was reduced, suggesting that retinal input inhibits these drifts. However, at the same time we did not find a significant decrease in the amplitude of drifts comparing the individual drift amplitudes in darkness and dim light. This agrees with previous observations by Van Rijn et al. that the stability of cycloversion does not improve when providing a square background pattern [51]. Furthermore, this may explain the persistence of drifts (although with smaller amplitude) in the dim light condition in several subjects noted here and suggests that the drifts in the estimates of the direction of gravity do not emerge solely from lack of visual orientation cues.

Drift amplitude, however, depended on the desired line orientation, yielding significantly larger drifts when performing the oblique paradigms. For both paradigms (principle axes vs. oblique axes) one would expect the spontaneous modulation of torsional eye position to be the same since the orientation of the otolith organs that drive OCR is the same with the head being in a stable upright position. Therefore, fluctuations in torsional eye position alone cannot explain the drifts.

Previous studies have proposed that the brain adapts to proprioceptive cues over time in roll-tilted positions resulting in a drift of internal estimates of gravity [29, 43,53]. For drifts in the upright position, adaptation of proprioceptive input cannot provide an explanation as this proprioceptive input is symmetric and would not result in a directional bias. Adaptation of the otolith afferents as has been proposed to explain torsional drifts when roll-tilted [38] also seems unlikely as subjects held their head upright beforehand and otolith afferents would be expected to be adapted to the upright position already. As discussed above, modulations in torsional eye position while upright [51] may contribute to the drifts observed here, however, there must be other factors to explain the pattern observed. This prompts the hypothesis that more central compensatory mechanisms, possibly emerging from the multisensory vestibular cortex, may play a role in modulating estimated direction of gravity over time.

Consecutive trials in our paradigms are not independent as shown by spectral density analysis. We hypothesize that resultant drift in a majority of trials is related to trial-to-trial dynamics and may underline an important central contribution to the subjects' performance. This is especially true if no external reference is provided (see [48] for an extensive review of serial correlations). Such serial correlations are considered to be part of a special class known as $1/f^{\beta}$ noise and occur throughout a wide range of different systems as for example in cognitive psychology, biology, economics and stock markets [48]. Based on spectral density analysis we found a noise pattern consistent with $1/f^{\beta}$ noise, indicating that indeed at least part of the trial-to-trial dynamics observed in our experimentsis due to the dependence of the serial adjustments over time. When compared to the dark condition, the average values of the fitted slope ($-\beta$) significantly dropped in the light condition, suggesting that a structured visual background reduces the correlation of serial adjustments.

Trial-to-trial dynamics are affected by the subject's strategy to complete the desired task of repetitively estimating a certain direction. A robust serial correlation and trial-to-trial dependency could occur when a given line orientation is produced repetitively from memory -in which a reasonable strategy is to reproduce the line orientation from the previous trial. Distinct approaches however seem possible for a task requiring an internal estimate that is continuously updated (i.e., the internal estimate of direction of gravity). Theoretically the subject could use an updated estimated for each trial, reducing but not eliminating the dependency of individual trials, resulting in a still significant correlation of repetitive adjustments. As noted earlier this behavior is consistent with a $1/f^{\beta}$ process.

4.2. Accuracy and precision of internal estimates of gravity

All but two subjects had median SVV and SVH errors of less than two degrees, which is consistent with previous studies characterizing the accuracy of SVV and SVH [18]. Providing a structured visual background significantly enhanced the accuracy of internal estimates of direction of gravity. For the principle axes, errors were smaller than one degree in all subjects in dim light, which is consistent with previous SVV and SVH data in light [19]. Two subjects, however, showed larger median adjustments errors (~5°) along both SVV and SVH in darkness. In most studies mean or median adjustments in the range of ± 2° to ± 3° are considered normal in darkness [4,13,18,21] and ± 1° in light [19], whereas larger deviations are attributed to lesions along the central vestibular pathways. Based on these criteria, two of our subjects would have a pathological SVV and SVH in darkness. However, there was no evidence for any neurological or vestibular disorder in these two subjects.

The natural environment is enriched with vertical and horizontal visual cues [10,45]. To navigate in space and to estimate direction of gravity, humans heavily rely on visual orientation cues and moving visual fields [12]. We noted superior performance along SVV and SVH than along oblique axes with visual orientation cues, supporting the hypothesis that the human brain preferentially relies on such visual cues presumably because of their frequent appearance and their direct indication of vertical or horizontal. Such meridional anisotropy (termed ‘oblique effect’) yielding poorer psychophysical performance when the stimulus is obliquely oriented – instead of horizontal or vertical – has been extensively studied [1,3,36,55]: and described for a wide range of experimental paradigms related to visual processing [36], transparent motion detection [20] and smooth pursuit [28].

The oblique effect has been attributed to the properties of orientation-selective neurons at early stages of visual processing, where retinotopic mapping is preserved [1,24,31,35,41,52]. Others, however, reported evidence that the modulations induced by orientation-selective neurons may be insufficient to generate the oblique effect and proposed that the meridional anisotropy could emerge in more advanced stages of visual processing [23,25,30]. Recent work suggests that the middle temporal visual area MT contributes to the oblique effect as cardinal orientations have been found to be overrepresentedcompared to oblique orientations in this area [56]. Perceptual adaptation to visual tilts using prisms [58] and in roll-tilted positions [59] results in a loss of the normal difference in detection threshold for vertical and oblique stimuli, underlining its dependency on the experimental parameters.

In darkness – lacking any visual orientation cues – we found a similar pattern, again with significantly higher accuracy of internal estimates of direction of gravity as assessed by the SVV and SVH compared to the oblique axes. These observations suggest that the brain may be optimized for estimating vertical and horizontal also in the absence of a structured visual background. It is in accordance with previous studies reporting that meridional anisotropy is not restricted to vision-related paradigms, but also emerges in non-visual domains as for example tactile sensitivity [16]. Based on our findings and on previous work by others a more general underlying mechanism for the oblique effect not restricted to visual processing is postulated. Alternatively, distinct independent mechanisms leading to an oblique effect in visual and other, non-visual systems could explain the occurrence of meridional anisotropy in a wide range of systems. Its neurobiological substrate, however, remains to be identified.

Our subjects were more precise in estimating earth-vertical and earth-horizontal than earth-oblique axes by a factor of about five. However, unlike for accuracy, the precision of estimates did not increase significantly when providing visual orientation cues. Potentially, this could be explained by the discrimination threshold for roll stimuli projected onto the retina, the subjects’ motor performance, the spatial resolution of the device used to control the line's roll orientation or a visual surrounding that provides relatively few vertical and horizontal stimuli. The foveal orientation discrimination thresholds for the principle axes (~0.6° [22]), however, are considerably smaller than the inter-quartile range of SVV (~1°) and SVH (~0.9°) adjustments noted here, making this an unlikely explanation. Although the visual environment used here provided relatively few orientation cues, it was sufficient to enhance accuracy of adjustments significantly. Therefore it seems unlikely that precision could not be improved if not for other reasons. To test for a potential limitation due to the subject's motor performance or technical limitations of the device, we obtained control trials where the subject had to adjust the luminous line along a plum line in dim light in two subjects. This task could be achieved with an at least twofold higher precision than the SVV task, making technical or manual limitations an unlikely explanation.

Various sources of noise may contribute to the trial-to-trial variability observed in our study. The findings of the spectral density analysis suggest that the 5 min series of adjustments in our paradigms show robust serial correlations related to $1/f^{\beta}$ noise. Thereby $1/f^{\beta}$ noise may account for a significant proportion of the observed variance, as further elaborated in section 4.1. The origin of $1/f^{\beta}$ noise, however, is not well understood and cannot be linked to specific systems of either the peripheral or central nervous system. Trial-to-trial variability (i.e., precision) eventually depends on the noise characteristics of the involved sensory, integrating and motor systems to complete the task. In case of the tasks studied here – all being related to spatial orientation – it reflects the properties of the sensory organs involved in determining the direction of gravity, the CNS networks in processing and integrating this sensory input and the motor system for generating the output (motor commands to perform the line adjustments). For our paradigm in complete darkness sensory input is mostly from the otolith afferents and skin/joint/muscle proprioceptors. Based on a previous study from Tarnutzer and colleagues trial-to-trial variability in SVV adjustments is most strongly affected by the properties of the otolith organs and to a lesser degree to central processing [46]. Motor commands are unlikely to play a major role. At any of the mentioned steps, serial estimates could be correlated robustly, resulting in $1/f^{\beta}$ noise. From a practical viewpoint, fluctuations of the internal estimate of direction of gravity have an impact on many activities including balance, gait and spatial orientation. In addition, task-related fatigue and lack of interest in the behavioral task may contribute to increasing trial-to-trial variability.

4.3. Orthogonality of perceived vertical and horizontal

Using the SVV and SVH interchangeably may not be advisable even in the upright position since SVV and SVH adjustments in half of our subjects were significantly different from orthogonal, diverging up to ~3° in individual subjects. This finding contrasts with previous studies that compared SVV and SVH in the same population and setup; they reported preserved orthogonality in the upright position [5,19]. In these studies, however, ten or even fewer trials were obtained per condition, relatively few subjects were studied and there was no time limit per trial. Considering these differences, it is not surprising that previous analyses did not reveal significant differences. Furthermore, in these studies orthogonality was assessed only for the entire study group and not for individual subjects. Van Beuzekom and Van Gisbergen reported consistent nonorthogonalities for the entire study population only at small roll-tilt angles [49]. However, on a single subject level the data presented (thin lines in Fig. 2 in their publication, $n = 6$) actually shows differences in adjustment errors for the SVV and SVH (based on ten trials per subject) up to ~4–5° in either direction.

What is the underlying cause of this non-orthogonality? Potentially the drifts observed in a majority of subjects could lead to the non-orthogonalities. Distinct drift patterns (i.e., significant drift along only one of the two principle axes or significant drift along both principle axes into opposite directions) were present in four of seven subjects in whom orthogonality was not preserved and in three of seven subjects in whom orthogonality was preserved. Based on these observations, differences in drift along the principle axes are unlikely to cause non-orthogonality in our study.

4.4. Limitations

Five of the 14 subjects completed the two sessions without wearing their glasses, by which theoretically we might have underestimated their ability to complete the adjustments precisely. However, a comparison of the IQR between subjects who performed the experiment without their visual correction ($n = 5$); subjects with normal vision and subjects who completed the experiment with adequately corrected vision did not show better precision than the group with without their usual visual correction. This suggests that not wearing corrective spectacles in those five subjects did not limit their performance in this experiment. Considering the small number of subjects in each sub-group, however, we emphasize the caveat that these multiple comparisons are limited in their statistical power.

Five subjects reported afterimages of the visual line but also said they did not pay attention to them when making line adjustments. Potentially, subjects may have used afterimages to adjust the line orientation based on the orientation of the line in the previous trial. If gaze is kept straigth-ahead on the projected line during adjustments, the retinal afterimage will provide a retinal-fixed reference. Such a reference could be used to reproduce a given line orientation more precisely from trial to trial, resulting in a decrease of drift of perceived vertical or horizontal over the five minute period. However, from those five subjects, four showed drift in at least one paradigm, supporting their statement that they did not use their afterimages for subsequent trials.

5. Conclusions

With the experimental setting used here we obtained a sufficiently large number of trials both along SVV and SVH to evaluate temporal constancy of internal estimates of gravity. This protocol allowed us to make important new observations that have implications for studies that ask how the brain derives a sense of the direction of the pull of gravity. Despite limiting single trials to five seconds we observed accurate and precise adjustments along the principle axes though both precision and accuracy were better in subjects who spent more time to make their adjustment, underlining the importance of controlling the individual trial duration tightly. Individual subjects may show significant drifts of SVV and SVH over time periods as short as five minutes. Neither adaptation of proprioceptive and otolith afferent input nor fluctuations of torsional eye position can explain completely the modulations in internal estimates of direction of gravity noted here. We therefore hypothesize that these drifts are also related to more central mechanisms possibly located within the multisensory vestibular cortex and related to either adaptation or sensory noise. A robust serial correlation between repetitive adjustments consistent with $1/f^{\beta}$ noise –behavior may explain at least part of the trial-to-trial dynamics observed here. Using SVV and SVH adjustments obtained in the upright position inter-changeably is not advisable; half of our subjects showed significant non-orthogonalities. The origin of these non-orthogonalities is still unclear; however, it is likely not related to the individual drifts over time.

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Abbreviations

CW	clockwise
CCW	counter-clockwise
OCR	ocular counterroll
SVV	subjective visual vertical
SVH	subjective visual horizontal

References

1. Andrews DP. Perception of contour orientation in the central fovea. I: short lines. Vision Res. 1967; 7:975–997. [PubMed: 5615784]
2. Angelaki DE, Gu Y, DeAngelis GC. Multisensory integration: psychophysics, neurophysiology, and computation. Curr Opin Neurobiol. 2009; 19:452–458. [PubMed: 19616425]
3. Appelle S. Perception and discrimination as a function of stimulus orientation: the “oblique effect” in man and animals. Psychol Bull. 1972; 78:266–278. [PubMed: 4562947]
4. Baier B, Bense S, Dieterich M. Are signs of ocular tilt reaction in patients with cerebellar lesions mediated by the dentate nucleus. Brain. 2008; 131:1445–1454. [PubMed: 18477593]
5. Betts GA, Curthoys IS. Visually perceived vertical and visually perceived horizontal are not orthogonal. Vision Res. 1998; 38:1989–1999. [PubMed: 9797945]
6. Brandt T, Dieterich M. The vestibular cortex. Its locations, functions, and disorders. Ann N Y Acad Sci. 1999; 871:293–312. [PubMed: 10372080]
7. Buttner U, Glasauer S, Glonti L, Kleine JF, Siebold C. Otolith processing in the deep cerebellar nuclei. Ann N Y Acad Sci. 1999; 871:81–93. [PubMed: 10372064]
8. Carriot J, DiZio P, Nougier V. Vertical frames of reference and control of body orientation. Neurophysiol Clin. 2008; 38:423–437. [PubMed: 19026962]
9. Collewijn H, van der SJ, Ferman L, Jansen TC. Human ocular counterroll: assessment of static and dynamic properties from electromagnetic scleral coil recordings. Exp Brain Res. 1985; 59:185–196. [PubMed: 4018196]
10. Coppola DM, Purves HR, McCoy AN, Purves D. The distribution of oriented contours in the real world. Proc Natl Acad Sci USA. 1998; 95:4002–4006. [PubMed: 9520482]
11. Diamond SG, Markham CH, Furuya N. Binocular counterrolling during sustained body tilt in normal humans and in a patient with unilateral vestibular nerve section. Ann Otol Rhinol Laryngol. 1982; 91:225–229. [PubMed: 6979286]
12. Dichgans J, Held R, Young LR, Brandt T. Moving visual scenes influence the apparent direction of gravity. Science. 1972; 178:1217–1219. [PubMed: 4637810]
13. Dieterich M, Brandt T. Ocular torsion and tilt of subjective visual vertical are sensitive brainstem signs. Ann Neurol. 1993; 33:292–299. [PubMed: 8498813]
14. Dieterich M, Brandt T. Thalamic infarctions: differential effects on vestibular function in the roll plane (35 patients). Neurology. 1993; 43:1732–1740. [PubMed: 8414023]

15. Dieterich M, Brandt T. Functional brain imaging of peripheral and central vestibular disorders. Brain. 2008; 131:2538–2552. [PubMed: 18515323]
16. Essock EA, Krebs WK, Prather JR. An anisotropy of human tactile sensitivity and its relation to the visual oblique effect. Exp Brain Res. 1992; 91:520–524. [PubMed: 1483524]
17. Fernandez C, Goldberg JM, Abend WK. Response to static tilts of peripheral neurons innervating otolith organs of the squirrel monkey. J Neurophysiol. 1972; 35:978–987. [PubMed: 4631840]
18. Friedmann G. The judgement of the visual vertical and horizontal with peripheral and central vestibular lesions. Brain. 1970; 93:313–328. [PubMed: 5310320]
19. Friedmann G. The influence of unilateral labyrinthectomy on orientation in space. Acta Otolaryngol. 1971; 71:289–298. [PubMed: 5574304]
20. Greenwood JA, Edwards M. An oblique effect for transparent-motion detection caused by variation in global-motion direction-tuning bandwidths. Vision Res. 2007; 47:1411–1423. [PubMed: 17391725]
21. Hafstrom A, Fransson PA, Karlberg M, Magnusson M. Idiosyncratic compensation of the subjective visual horizontal and vertical in 60 patients after unilateral vestibular deafferentation. Acta Otolaryngol. 2004; 124:165–171. [PubMed: 15072418]
22. Heeley DW, Buchanan-Smith HM. Recognition of stimulus orientation. Vision Res. 1990; 30:1429–1437. [PubMed: 2247953]
23. Heeley DW, Buchanan-Smith HM. Directional acuity for drifting plaids. Vision Res. 1992; 32:97–104. [PubMed: 1502816]
24. Heeley DW, Buchanan-Smith HM. Orientation acuity estimated with simultaneous and successive procedures. Spat Vis. 1992; 6:1–10. [PubMed: 1536826]
25. Heeley DW, Buchanan-Smith HM, Cromwell JA, Wright JS. The oblique effect in orientation acuity. Vision Res. 1997; 37:235–242. [PubMed: 9068823]
26. Howard, IP. Human visual Orientation. Wiley; New York: 1982.
27. Kahane P, Hoffmann D, Minotti L, Berthoz A. Reappraisal of the human vestibular cortex by cortical electrical stimulation study. Ann Neurol. 2003; 54:615–624. [PubMed: 14595651]
28. Krukowski AE, Stone LS. Expansion of direction space around the cardinal axes revealed by smooth pursuit eye movements. Neuron. 2005; 45:315–323. [PubMed: 15664182]
29. Lechner-Steinleitner S. Interaction of labyrinthine and somatoreceptor inputs as determinants of the subjective vertical. Psychol Res. 1978; 40:65–76. [PubMed: 635075]
30. Li W, Westheimer G. Human discrimination of the implicit orientation of simple symmetrical patterns. Vision Res. 1997; 37:565–572. [PubMed: 9156200]
31. Mansfield RJ. Neural basis of orientation perception in primate vision. Science. 1974; 186:1133–1135. [PubMed: 4219965]
32. Mezey LE, Curthoys IS, Burgess AM, Goonetilleke SC, MacDougall HG. Changes in ocular torsion position produced by a single visual line rotating around the line of sight–visual “entrainment” of ocular torsion. Vision Res. 2004; 44:397–406. [PubMed: 14659966]
33. Miller EF 2nd, Fregly AR, Graybiel A. Visual horizontal-perception in relation to otolith-function. Am J Psychol. 1968; 81:488–496. [PubMed: 5760030]
34. Mossman S, Halmagyi GM. Partial ocular tilt reaction due to unilateral cerebellar lesion. Neurology. 1997; 49:491–493. [PubMed: 9270583]
35. Orban GA, Kennedy H. The influence of eccentricity on receptive field types and orientation selectivity in areas 17 and 18 of the cat. Brain Res. 1981; 208:203–208. [PubMed: 7470923]
36. Orban GA, Vandenbussche E, Vogels R. Human orientation discrimination tested with long stimuli. Vision Res. 1984; 24:121–128. [PubMed: 6710874]
37. Palla, A.; Straumann, D.; Tarnutzer, AA. Otolith testing: roll plane disorders, in: Vertigo and Imbalance: Clinical Neurophysiology of the Vestibular System. Eggers, SDZ.; Zee, DS., editors. Elsevier; Amsterdam: 2009.
38. Pansell T, Tribukait A, Bolzani R, Schworm HD, Ygge J. Drift in ocular torsion during sustained head tilt. Strabismus. 2005; 13:115–121. [PubMed: 16251140]
39. Pavlou M, Wijnberg N, Faldon ME, Bronstein AM. Effect of semicircular canal stimulation on the perception of the visual vertical. J Neurophysiol. 2003; 90:622–630. [PubMed: 12649316]

40. Pettorossi VE, Bambagioni D, Bronstein AM, Gresty MA. Assessment of the perception of verticality and horizontality with self-paced saccades. Exp Brain Res. 1998; 121:46–50. [PubMed: 9698189]
41. Rose D, Blakemore C. An analysis of orientation selectivity in the cat's visual cortex. Exp Brain Res. 1974; 20:1–17. [PubMed: 4844166]
42. Schoene H, Udo de Haes H. Perception of gravity-vertical as a function of head and trunk position. Z Vgl Physiol. 1968; 60:440–444.
43. Schoene H, Udo de Haes H. Space orientation in humans with special reference to the interaction of vestibular, somaesthetic and visual inputs. Biokybernetik III, Materialien. 2. Internat. Sympos. Biokybernetik, VEB Fischer Jena. 1971:172–191.
44. Shinder ME, Taube JS. Differentiating ascending vestibular pathways to the cortex involved in spatial cognition. J Vestib Res. 2010; 20:3–23. [PubMed: 20555163]
45. Switkes E, Mayer MJ, Sloan JA. Spatial frequency analysis of the visual environment: anisotropy and the carpentered environment hypothesis. Vision Res. 1978; 18:1393–1399. [PubMed: 726283]
46. Tarnutzer AA, Bockisch C, Straumann D, Olasagasti I. Gravity dependence of subjective visual vertical variability. J Neurophysiol. 2009; 102:1657–1671. [PubMed: 19571203]
47. Tarnutzer AA, Bockisch CJ, Straumann D. Head roll dependent variability of subjective visual vertical and ocular counterroll. Exp Brain Res. 2009; 195:621–626. [PubMed: 19415246]
48. Torre K, Wagenmakers EJ. Theories and models for 1/f(beta) noise in human movement science. Hum Mov Sci. 2009; 28:297–318. [PubMed: 19403189]
49. Van Beuzekom AD, Van Gisbergen JA. Properties of the internal representation of gravity inferred from spatial-direction and body-tilt estimates. J Neurophysiol. 2000; 84:11–27. [PubMed: 10899179]
50. Van Huffel, S.; Vandewalle, J. The Total Least Squares Problem. Computational Aspects and Analysis. Society for industrial and applied mathematics; Philadelphia: 1991.
51. Van Rijn LJ, Van der Steen J, Collewijn H. Instability of ocular torsion during fixation: cyclovergence is more stable than cycloversion. Vision Res. 1994; 34:1077–1087. [PubMed: 8160416]
52. Vogels R, Orban GA. The effect of practice on the oblique effect in line orientation judgments. Vision Res. 1985; 25:1679–1687. [PubMed: 3832592]
53. Wade NJ. Effect of prolonged tilt on visual orientation. J Exp Psychol. 1970; 22:423–439.
54. Wade SW, Curthoys IS. The effect of ocular torsional position on perception of the roll-tilt of visual stimuli. Vision Res. 1997; 37:1071–1078. [PubMed: 9196725]
55. Westheimer G. Meridional anisotropy in visual processing: implications for the neural site of the oblique effect. Vision Res. 2003; 43:2281–2289. [PubMed: 12962986]
56. Xu X, Collins CE, Khaytin I, Kaas JH, Casagrande VA. Unequal representation of cardinal vs. oblique orientations in the middle temporal visual area. Proc Natl Acad Sci U S A. 2006; 103:17490–17495. [PubMed: 17088527]
57. Zwergal A, Rettinger N, Frenzel C, Dieterich M, Brandt T, Strupp M. A bucket of static vestibular function. Neurology. 2009; 72:1689–1692. [PubMed: 19433743]
58. Fiorentini A, Ghez C, Maffei L. Physiological correlates of adaptation to a rotated visual field. J Physiol. 1972; 227:313–322. [PubMed: 4646583]
59. Luyat M, Gentaz E. Body tilt effect on the reproduction of orientations: Studies on the visual oblique effect and subjective orientations. J Exp Psychol Hum Percept Perform. 2002; 28:1002–1011. [PubMed: 12190248]

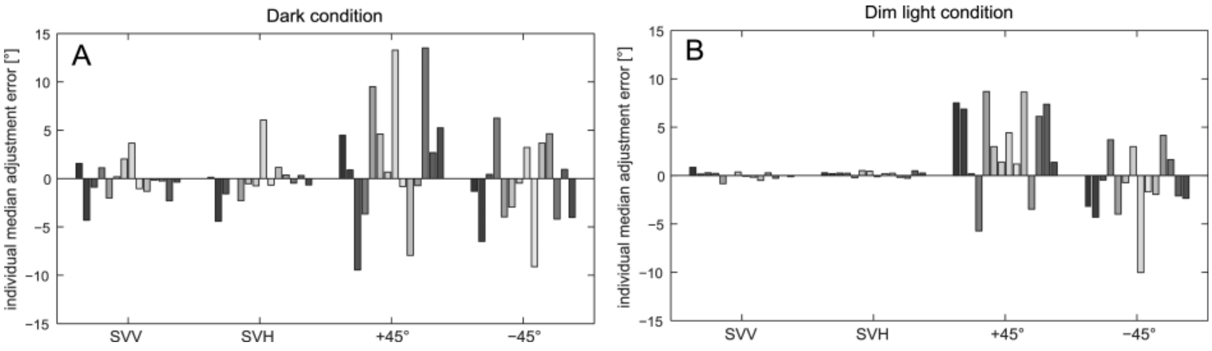

Fig. 1.

Individual median adjustment errors relative to the desired roll orientation for all four paradigms are shown both for darkness (Fig. 1A) and dim light (Fig. 1B) in all 14 subjects. Note that subjects 1 to 5 performed both sessions without glasses whereas subjects 6 to 14 wore glasses/contact lenses or had normal uncorrected vision.

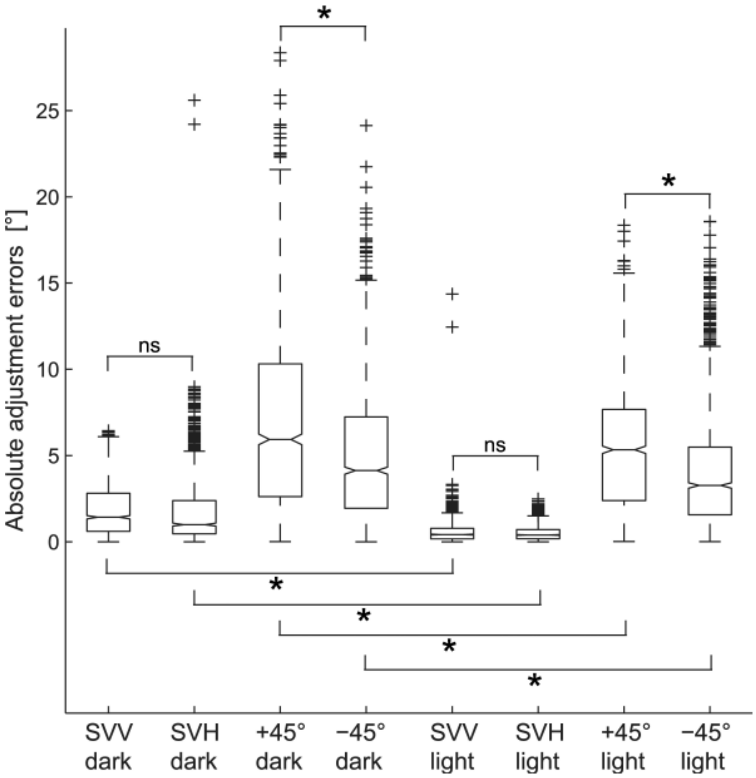

Fig. 2.

The absolute values of the individual median adjustment errors (accuracy) using box and whisker plots. The box has lines at the lower quartile, the median and the upper quartile values. Whiskers extend from each end of the box to the adjacent values in the data; by default, the most extreme values within 1.5 times the inter-quartile range from the ends of the box. Outliers (black + sign) are data with values beyond the ends of the whiskers. Statistical analysis provides pairwise comparison between various conditions, indicated by the horizontal brackets. Significant differences ($p < 0.05$) are indicated by '*', 'ns' refers to non-significant differences.

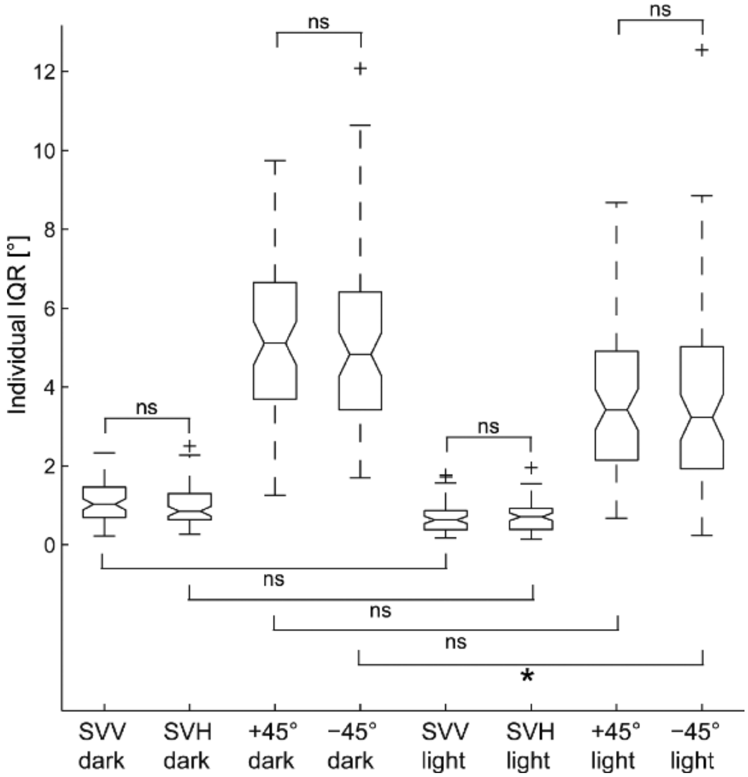

Fig. 3.

Precision of individual adjustments based on the individual inter-quartile range (IQR) for each paradigm and condition using box and whisker plots (for an explanation see legend of Fig. 2) and providing pair wise statistical analysis (see legend of Fig. 2 for details).

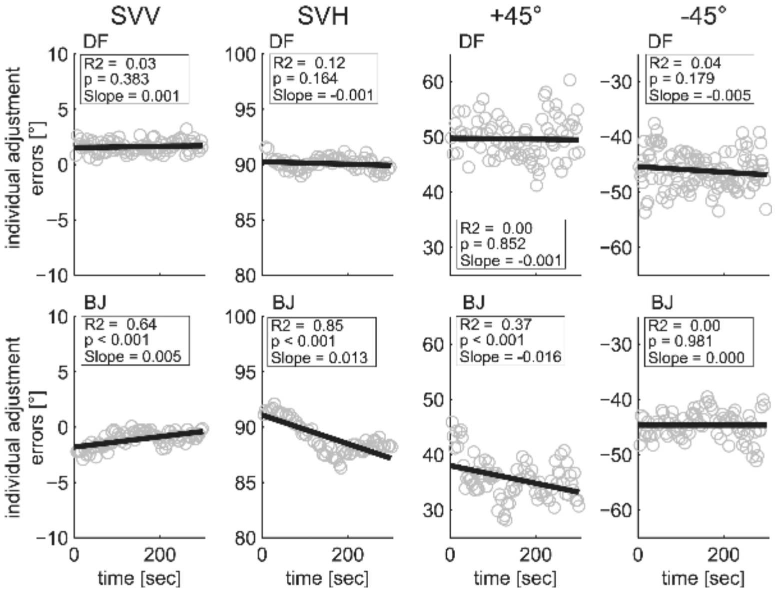

Fig. 4.

Individual adjustments (grey circles) in two typical subjects (DF and BJ) plotted against time for all four paradigms in darkness. Least square linear regression was used to fit a line to the individual trials. Whereas subject DF (top row) showed no drift of adjustments over time, subject BJ (bottom row) yielded significant drift in three of four paradigms.

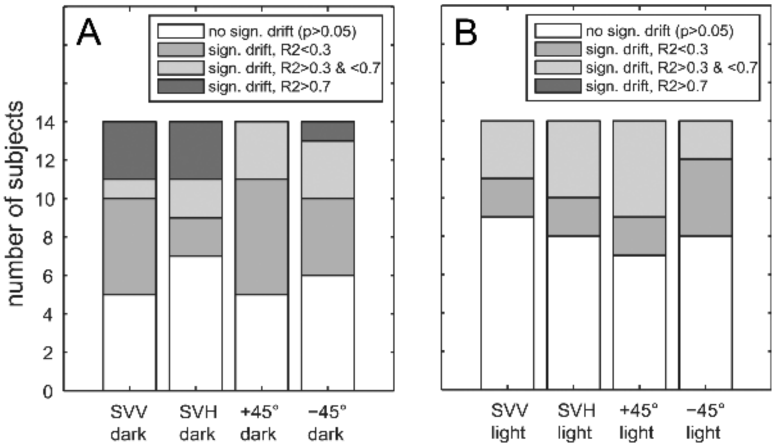

Fig. 5.

Summary of linear regression analysis in darkness (Fig. 5A) and in dim light (Fig. 5B) in all runs and desired line orientations. Runs were categorized based on the goodness of fit (represented by the R^2-value) and whether the slope of the fit was significantly different from zero (based on the p-value).

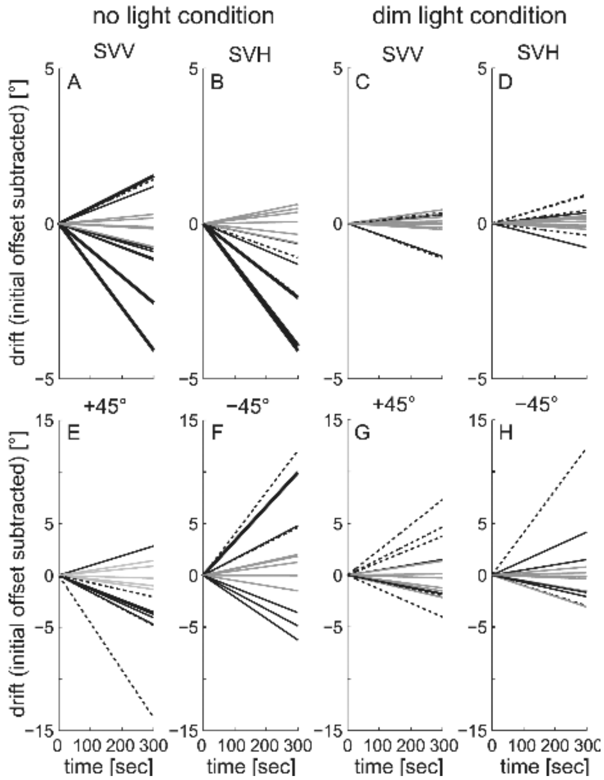

Fig. 6.

Slopes representing the fit to one run of repetitive adjustments in individual subjects are shown both for darkness (panels A, B, E and F) and dim light (panels C, D, G, and H). Note that the initial offset relative to the desired roll orientation was subtracted so that all slopes start at zero offset to allow better comparison between individual subjects and facilitate illustration of the individual drifts. Traces in black refer to runs with significant ($p < 0.05$) drift, traces in grey refer to runs with non-significant ($p > 0.05$) drift. All runs with significant drift were further subdivided into three categories, depending on the goodness of fit. Black thick solid traces: $R^2 > 0.7$; black dashed traces: $0.7 > R^2 > 0.3$; black thin solid traces: $R^2 < 0.3$.

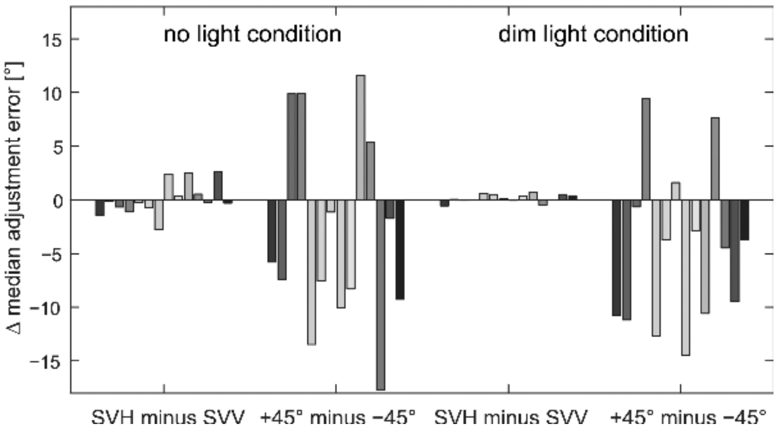

Fig. 7.

Bar plot illustrating differences in median adjustment errors along the principle (SVH minus SVV) and along the oblique (+45° minus −45° condition) axes in individual subjects both for the no light and the dim light condition.

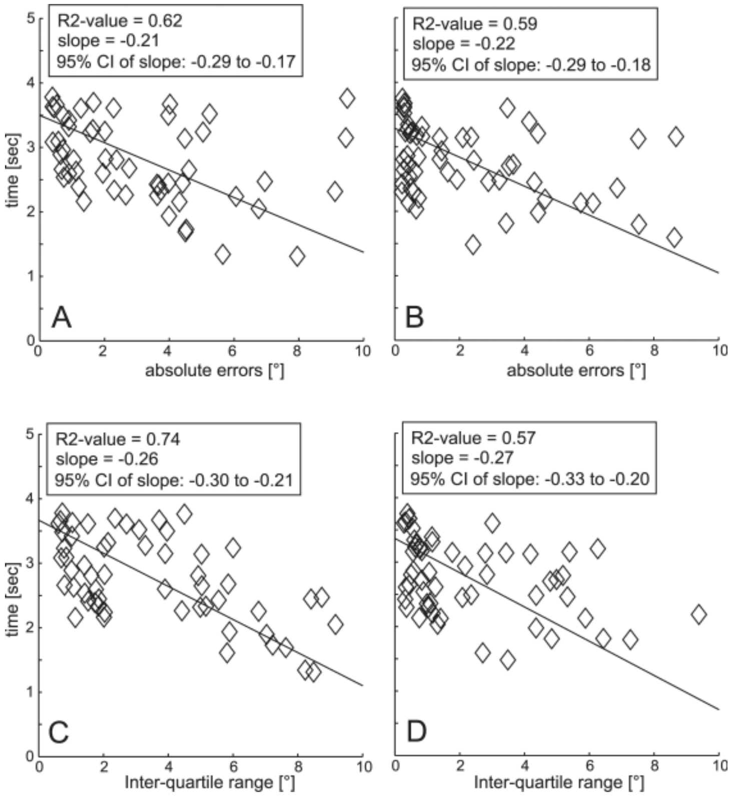

Fig. 8.

Principle components analysis of individual median trials (illustrated by the triangles) showing an inverse relationship between adjustment time and absolute adjustment errors [panel A (darkness) and panel B (dim light)] and between the median individual adjustment time and the inter-quartile range [panel C (darkness) and panel D (dim light)].

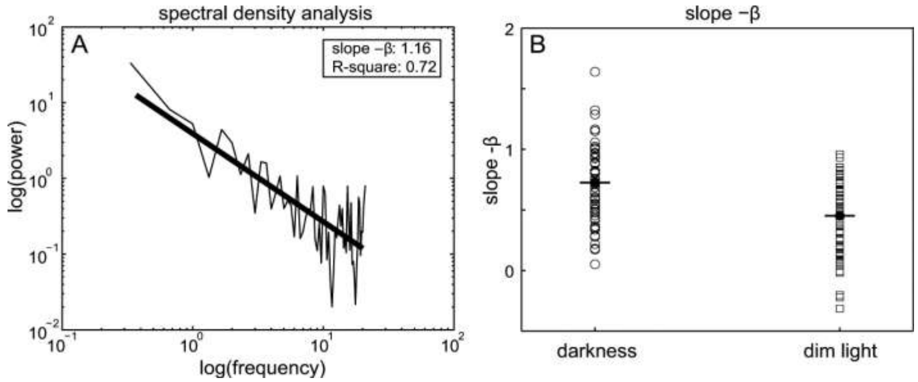

Fig. 9.

Log-log power spectrum analysis of individual repetitive adjustments over periods of 5 min in either darkness or dim light. Panel A shows exemplary data from a single subject (obtained in darkness, desired −45° line orientation) including the linear fit to the spectral density analysis with slope $-\beta$ and the R^2-value. Panel B provides a summary of all slope-values obtained from the spectral density analysis in individual subjects both for darkness (circles) and for dim light (squares). While open circles and open squares refer to individual values of slope $-\beta$, filled circles/squares with a short horizontal bar indicate median values (data pooled for all four different desired line orientations).