J Neurophysiol 118: 2499–2506, 2017.
First published August 16, 2017; doi:10.1152/jn.00439.2017.

RESEARCH ARTICLE | *Sensory Processing*

Perception of the dynamic visual vertical during sinusoidal linear motion

A. Pomante, L. P. J. Selen, and W. P. Medendorp
Radboud University, Donders Institute for Brain, Cognition and Behaviour, Nijmegen, The Netherlands

Submitted 14 June 2017; accepted in final form 11 August 2017

Pomante A, Selen LP, Medendorp WP. Perception of the dynamic visual vertical during sinusoidal linear motion. *J Neurophysiol* 118: 2499–2506, 2017. First published August 16, 2017; doi:10.1152/jn.00439.2017.—The vestibular system provides information for spatial orientation. However, this information is ambiguous: because the otoliths sense the gravitoinertial force, they cannot distinguish gravitational and inertial components. As a consequence, prolonged linear acceleration of the head can be interpreted as tilt, referred to as the somatogravic effect. Previous modeling work suggests that the brain disambiguates the otolith signal according to the rules of Bayesian inference, combining noisy canal cues with the a priori assumption that prolonged linear accelerations are unlikely. Within this modeling framework the noise of the vestibular signals affects the dynamic characteristics of the tilt percept during linear whole-body motion. To test this prediction, we devised a novel paradigm to psychometrically characterize the dynamic visual vertical—as a proxy for the tilt percept—during passive sinusoidal linear motion along the interaural axis (0.33 Hz motion frequency, 1.75 m/s^2 peak acceleration, 80 cm displacement). While subjects (n=10) kept fixation on a central body-fixed light, a line was briefly flashed (5 ms) at different phases of the motion, the orientation of which had to be judged relative to gravity. Consistent with the model's prediction, subjects showed a phase-dependent modulation of the dynamic visual vertical, with a subject-specific phase shift with respect to the imposed acceleration signal. The magnitude of this modulation was smaller than predicted, suggesting a contribution of nonvestibular signals to the dynamic visual vertical. Despite their dampening effect, our findings may point to a link between the noise components in the vestibular system and the characteristics of dynamic visual vertical.

NEW & NOTEWORTHY A fundamental question in neuroscience is how the brain processes vestibular signals to infer the orientation of the body and objects in space. We show that, under sinusoidal linear motion, systematic error patterns appear in the disambiguation of linear acceleration and spatial orientation. We discuss the dynamics of these illusory percepts in terms of a dynamic Bayesian model that combines uncertainty in the vestibular signals with priors based on the natural statistics of head motion.

Bayesian integration model; gravity; perception; somatogravic illusion; subjective visual vertical

SPATIAL ORIENTATION IN DARKNESS depends strongly on how the brain interprets vestibular information (Angelaki and Cullen 2008; Clemens et al. 2011; Haustein and Mittelstaedt 1990; Mittelstaedt 1992, 1996, 1999). The semicircular canals sense angular acceleration, from which head orientation can be derived; the otoliths measure the gravitoinertial force (GIF), i.e., the vector sum of gravity and the experienced force due to linear acceleration of the head in space. Thus the canals subside during constant-velocity rotation, while otoliths provide ambiguous information: they cannot distinguish between the gravity direction and linear acceleration of the head (Glasauer 1992; Mayne 1974; Merfeld 1995; Paige and Seidman 1999; Seidman et al. 1998). Because of the ambiguity of the otoliths, in combination with the intrinsic noise on the vestibular signals, the internal estimate of orientation may not match the actual orientation (Clemens et al. 2011; Laurens and Droulez 2007; MacNeilage et al. 2007).

Spatial orientation can be assessed through the percept of vertical, which can be characterized by asking subjects to judge the orientation of a visual line with respect to gravity (Glasauer 1995; Tarnutzer et al. 2014). Various studies evaluated vertical perception while the head and body were tilted but stationary, i.e., when the rotation effects in the canals have decayed, and the otoliths are only stimulated by gravity. For small tilts (<30°), errors in vertical perception are typically small and opposite to the direction of the tilt (called the E-effect, Müller 1916) while for larger head tilts (>60°), there are substantial biases in the direction of the tilt (known as A-effect, Aubert 1861), as if subjects underestimate their head tilt relative to gravity (Mittelstaedt 1983; Tarnutzer et al. 2009).

To explain this error pattern, it has been suggested that the brain processes the otolith signal according to the rules of Bayesian inference (Clemens et al. 2011; De Vrijer et al. 2009; MacNeilage et al. 2007). Within this account, the percept of vertical follows from an optimal combination of a noisy otolith signal and an a priori probability distribution of head orientation in space, which is centered at upright. The effect of this prior is a reduction of the uncertainty in the estimate of the vertical, but at the expense of a systematic bias at larger tilts (De Vrijer et al. 2009; MacNeilage et al. 2007; Vingerhoets et al. 2009).

While this sensory integration model allows for a good characterization of the percept of vertical in static situations, it does not consider the sensory dynamics and physical laws that dictate verticality perception in dynamic situations. For example, horizontal acceleration stimulates the otoliths in the same way as head tilt. As a consequence, horizontal acceleration in darkness induces the percept of being transported over a small hill, referred to as the somatogravic or hilltop illusion (Glasauer 1995; Graybiel and Clark 1965), although cognitive signals could suppress this effect (Wertheim et al. 2001.

Address for reprint requests and other correspondence: A. Pomante, Donders Institute for Brain, Cognition and Behaviour, Radboud University Nijmegen, Montessorilaan 3, 6525 HR Nijmegen, The Netherlands (e-mail: a.pomante@donders.ru.nl).

It is commonly accepted that vestibular perception in such dynamic conditions depends not only on the sensory transfer functions, but also on internal models to resolve sensory ambiguities. For example, an internal model of spatial orientation assumes that the disambiguation of the GIF into linear and gravitational components depends on the canal signal (Angelaki et al. 2004; Bos and Bles 2002; Merfeld et al. 1999). Recently, Laurens and Droulez (2007) developed a dynamic Bayesian inference model of vestibular processing, which deals with noisy sensory cues and incorporates an internal model that assumes priors of low angular velocity and low inertial accelerations. It has been shown that this model can explain perceptual observations in several motion paradigms including centrifugation and off-vertical-axis rotation (Benson and Bodin 1966; Graybiel and Clark 1965; Guedry 1965; Merfeld et al. 2001).

According to this model, sensory noise on both the otoliths and canals in combination with a priori assumptions about linear acceleration and angular velocity determine the gain and phase of the somatogravic illusion during sinusoidal linear accelerations. More specifically, even without rotation, there is uncertainty in the canal signal, which affects the internal processing during pure otolith stimulation. As a result, the model predicts that the somatogravic effect has low-pass dynamics with a time constant of ~1.7 s.

As a proxy for the amount of perceived tilt, Glasauer (1995) measured how subjects dynamically adjust a luminous line to their subjective visual vertical (SVV) during sinusoidal linear accelerations at various frequencies (0.0083–0.33 Hz). While the perception of tilt decreased with increasing oscillation frequency, i.e., it had a low-pass gain, which is in accordance with the dynamic Bayesian model, Glasauer also reported phase shifts close to zero, nearly independent of motion frequency. The latter is in disagreement with both the predictions of the dynamic Bayesian model and with a low-pass filter description of the somatogravic illusion. Glasauer suggested that this discrepancy is due to the involvement of a predictive component in the adjustments of the line. However, whether this predictive component actually reflects the central processing of vestibular information or rather relates to an anticipatory effect imposed by the cyclic nature of the adjustment task is unclear.

Here we revisit the dynamics of the somatogravic illusion by developing a novel psychometric task that provides measures of both the bias and variability of vertical perception at different phases of a passively induced sinusoidal body motion. Our results, collected on a moment-to-moment basis, provide a dynamic characterization of the somatogravic illusion during pure otolith stimulation. Our experimental findings support the model of Laurens and Droulez (2007), suggesting that vestibular processing is consistent with Bayesian computations in which sensory noise levels and a priori assumptions affect the dynamics of vertical perception.

MATERIALS AND METHODS

Subjects. Ten naive participants (7 women, 3 men), aged between 21 and 32 yr old, provided written, informed consent to participate in the experiment. The study was approved by the ethics committee of the Faculty of Social Sciences of Radboud University Nijmegen, The Netherlands. All participants were free of any known vestibular or neurological disorders and had normal or corrected-to-normal visual acuity.

Before the experiment, subjects received careful instructions. During the experiment, participants never received any feedback about their performance. One subject did not show consistent task performance and was excluded from further data analyses.

Setup. Participants were sitting on a custom-built vestibular sled that moved side-to-side along a magnetic track, aligned to the subject's interaural axis. The sled was driven by a linear motor (TB15N; Technotion, Almelo, The Netherlands) that was controlled by a Kollmorgen S700 drive (Danaher, Washington, DC). The body of the subject was tightly fixed using a five-point seat belt. In addition, Velcro straps restrained both legs and feet, and an ear-fixed mold firmly held the head in a natural upright position for looking straight ahead and kept the head-on-body orientation fixed at 0°. Emergency buttons at either side of the sled chair enabled subjects to stop the sled motion immediately. The sled moved sinusoidally, with an amplitude of 0.4 m (0.8 m peak-to-peak displacement) and a period of 3 s, resulting in peak velocity and peak acceleration of 0.84 m/s and 1.75 m/s^2, respectively. A motor-controlled laser (stepping motor of 0.0125° angular resolution) was mounted on the sled and projected a green fixation dot and a red line of 17 cm length (angular subtense 20°) on a black plate attached to the sled 75 cm in front of the participant's eyes. The green fixation dot and the rotation point of the red line were at eye level. The laser line was calibrated with respect to gravity, using a plumb line, before the start of the experiment. Sled motion and stimuli were controlled using custom written Python code.

Experiment. Experiments were conducted in complete darkness, except for the fixation point and the visual line. Each run started with the onset of the fixation point, to be fixated for the entire duration of the run. To avoid discontinuous acceleration at motion onset, sled velocity was linearly increased over one sinusoidal cycle (see Merfeld et al. 2005 for a similar approach). Once the steady-state sinusoidal motion was reached, the visual line was presented for 5 ms at one out of eight possible phase angles (from 0° to 315° in steps of 45°) of the motion. Each phase corresponds to a different combination of acceleration and velocity (see phase plot in Fig. 1*A*).

Subjects had to indicate, as quickly as possible, whether they perceived the orientation of the flashed line as clockwise (CW) or counterclockwise (CCW) with respect to gravity, by moving a joystick to the right (indicating CW) or left (indicating CCW). For each phase, the line orientation was randomly selected from a set of 13 line orientations centered around the gravitational vertical −5°, −3°, −1°, −0.7°, −0.5°, −0.3°, 0°, 0.3°, 0.5°, 0.7°, 1°, 3°, 5°, where positive values indicate a CW orientation relative to gravity.

For each phase, each line orientation was probed 10 times, yielding 130 trials in total. Subsequent trials were tested 1.125 motion cycle apart, i.e., testing at a phase that was shifted 45° forward compared with the former, so the minimum time between trials was 3.37 s (1.125 × 3 s). In total, every subject performed 1,040 trials (8 phases × 13 line orientations × 10 repetitions), in two experimental sessions, lasting ~45 min each, collected on separate days. Each session was divided into five runs of 104 trials, lasting ~5 min. Lights were turned on for 1 min at the end of each run to prevent dark adaptation.

Sensory integration model. The otolith organs sense the joint effect of linear acceleration and gravity, the so-called gravitoinertial force (GIF). As a consequence, they are equally stimulated by a linear acceleration or a tilt of the head, which defines an ambiguity problem, that if resolved incorrectly results in illusory percepts of visual vertical. Figure 1*B* shows the direction of the illusory visual vertical percept in response to linear motion. When the subject is moving to the right with a constant acceleration (+*A*), the inertial force, as detected by the otoliths, is in a leftward direction (−*A*) which yields a GIF that is oriented clockwise relative to the true gravity direction. If the brain interprets the GIF as identical to the direction of gravity (*G*), it must infer that the head is tilted counterclockwise relative to *G*. If this is the case, an earth-vertical visual line will be perceived in the same counterclockwise direction, which means that a visual line must

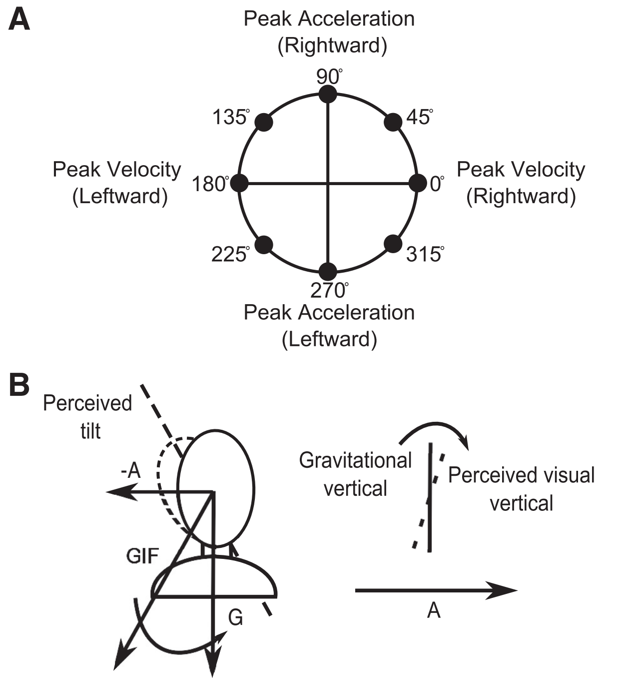

Fig. 1. *A*: phase-plane plot, showing the combination of acceleration and velocity (i.e., phase) at which the visual lines was presented. *B*: the gravito-inertial force (GIF). For a linear translation to the right (A), the inertial acceleration component points to the left (−A). The GIF is deviated clockwise from actual gravity. If the direction of the GIF is interpreted as the direction of gravity, the head must be tilted counterclockwise. An earth-vertical visual line will be perceived in the same counterclockwise direction. A visual line must be presented in the opposite, clockwise orientation relative to actual gravity, to be perceived as earth vertical.

be present in the opposite, clockwise orientation relative to the true gravitational vertical, to be perceived as earth-vertical.

Laurens and Droulez (2007) developed a dynamic Bayesian model to describe how the otolith signal is decomposed into its gravitational and accelerative components during nonstationary stimulation. We used this model as a theoretical basis for the experimental paradigm and the interpretation of the behavioral response.

Figure 2*A* shows a schematic illustration of the model, which we will first explain in heuristic terms. At a peripheral level, when the head rotates there is a flow of the endolymph within the canals, causing a deflection of the cupula (C) that is related to physical head angular velocity (ω) via high-pass filter characteristics. Linear acceleration of the head (A) is sensed by the otoliths but always in combination with the pull of gravity (G), resulting in the GIF. To disambiguate the gravitational and inertial components of the GIF, the brain needs to know the head orientation (θ), in space which can be inferred from the canal signal. However, sensory noise in the canal signals leads to uncertainty in the percept of head orientation ($\hat{\theta}$), which in combination with an a priori assumption of no motion will bias the final estimate of the motion. Even in conditions without actual rotation, optimal observer theory assumes that there is still uncertainty in the canal signal, affecting the internal computations of the vestibular processing during pure otolith stimulation. Note that for estimating linear acceleration and rotational velocity, the model assumes that the brain also takes into account prior information, i.e., the probability of a certain observation based on earlier experiences. For example, the presence of a prior probability over linear acceleration, stating that low sustained translational accelerations are a priori more likely, results in a perception of tilt because the signaled GIF is more likely to be interpreted as a change of the direction of gravity in a head-centered reference frame (i.e., tilt) than as a nonzero linear acceleration.

In mathematical terms, the relationship between physical head angular velocity ω and displacement of the cupula is modeled as a high-pass filter $\frac{\mathrm{d}C}{\mathrm{d}t} = -\frac{1}{T_c}C - T_{can}\frac{\mathrm{d}\omega}{\mathrm{d}t}$. The matrix $\boldsymbol{T}_{can}$ describes the orientation of the canal planes with respect to a head-centered reference frame (Raphan and Cohen 2002). The deflection C of the cupula is converted into a neural signal V by adding independent Gaussian noise ~$N(0,\sigma_V)$ to represent uncertainty accumulated over the neural pathways. So, the noisy neural signal is described as $V = C + N(0,\sigma_V)$.

For a linear acceleration stimulus A, the otoliths detect the resultant GIF, given by $G-A$ in world coordinates, where G is the gravity vector. This information is then converted into a head-centric reference frame using a rotation matrix H, which describes the true orientation of the head with respect to a world fixed frame. Thus $\mathrm{GIF}_h = H^{-1}(G-A)$ is the signaled GIF in head coordinates. The rotation matrix H depends on the estimated head orientation and thus on the canal signal. Because the canal signal is noisy, this noise also influences the otoliths via the coordinate transformation.

Now, in the model, there are two neural/vestibular signals ($S = [V,\mathrm{GIF}_h]^T$) available to infer the two movement states ($\varepsilon = [\omega,A]^T$) that caused them. The model uses Bayes rule to make this inference:

$$P(\varepsilon|S) \propto P(S|\varepsilon)P(\varepsilon)$$

in which $P(\varepsilon|S)$ is the inferred posterior probability based on the likelihood $P(S|\varepsilon)$ and the prior probabilities over movement variables $P(\varepsilon)$. Priors are defined as Gaussian distributions centered at zero over linear acceleration and angular velocity. The widths of the linear acceleration prior (σ_A) and rotational velocity prior (σ_ω) are assumed equal to 5 m/s^2 and 30°/s, respectively. Sensory uncertainty on the rotational velocity is set to 10°/s (Laurens and Droulez 2007).

Because the model is nonlinear, it has no straightforward analytical solution and is implemented using particle filtering. We further adapted the model to simulate the perceptual response to a sinusoidal interaural linear acceleration with an amplitude of 1.75 m/s^2 and a period of 3 s and the actual head orientation being upright, the same as in the experiment. Figure 2*B* shows the predicted roll tilt percept in response to this sinusoidal whole-body acceleration. With the parameters set as above, the predicted bias modulation follows a sinusoidal profile with an amplitude of 2.7° and a phase shift of ~74° with respect to the actual GIF.

Data analysis. Data were analyzed using MATLAB (MathWorks). We quantified choice preference by calculating the proportion of CW responses as a function of line orientation for each phase of motion. We fit a cumulative Gaussian function including a lapse rate parameter to summarize the psychometric data of each participant, at each phase:

$$P(x = CW|s) = \lambda + (1 - 2\lambda)\frac{1}{\sigma\sqrt{2\pi}}\int_{-\infty}^{x} e^{-(y-\mu)^2/2\sigma^2}\mathrm{d}y$$

in which x represents the subject's response and s is the line orientation. Parameters μ and σ are directly related to the bias and uncertainty in verticality estimates, respectively. We assumed σ to be independent of phase. Parameter λ, representing the lapse rate, is independent of stimulus levels and phase and accounts for subjects' lapses or inadvertent mistakes. As a result, the whole data set of a subject can be characterized with 10 parameters: one lapse rate λ, one sigma σ, and eight μ values. This characterization does not introduce any constraint on the relationship between the μ-values for the different phases.

To test the predictions of the Bayesian model, especially the phase shift of the bias modulation, we also evaluated a sinusoidal relationship between μ and phase: $\mu(\boldsymbol{phase}) = \mathrm{A}*\sin(\boldsymbol{phase} - phase0) + \mathrm{B}$. In this way, we only need five parameters (amplitude A, offset B, phase shift *phase*0, uncertainty σ, and lapse rate λ) to account for the

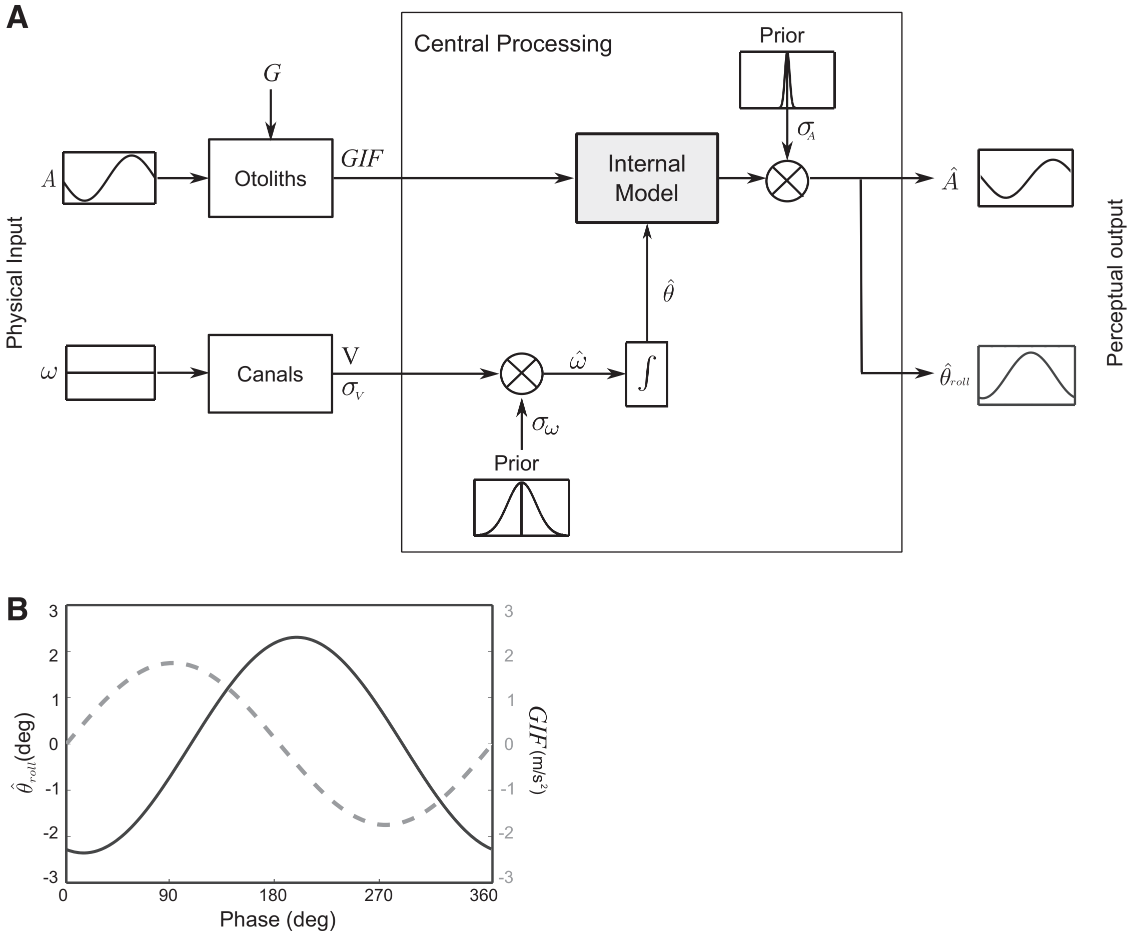

Fig. 2. *A*: model from Laurens and Droulez (2007). Vestibular input (A,ω) to the model was chosen to be comparable to the one tested experimentally: in response to a sinusoidal linear acceleration (A) the otoliths measure the gravitoinertial force (GIF) which can be interpreted either as tilt or translation, or a combination of both. An internal model assumes that canal information about head orientation in space ($\hat{\theta}$) is used to disambiguate the otolith signal ($\text{GIF} = \hat{G} - \hat{A}$, $\frac{dG}{dt} = -\omega \times G$). Notice that if the canals are not stimulated ($\omega = 0$), the cupula in the canals is not displaced ($C = 0$). Nevertheless, the signal is noisy (σ_V). The noise on perceived head angular velocity ($\hat{\omega}$) propagates to the estimation of $\hat{\theta}$ via temporal integration. This noisy signal will influence the estimated acceleration ($\hat{A}$) and tilt ($\hat{\theta}_{\text{roll}}$). Notice that no additive noise is acting on the otoliths signal. This is because canal noise also affects the otoliths via the coordinate transformation. Computationally, adding noise to the otoliths or considering the effect of canal noise acting on them would be the same, but the latter case has the advantage of reducing the number of free parameters in the model. Prior probabilities over ω and A are modeled as Gaussians centered at zero and with a certain variance (σ_ω, σ_A) and together with the noisy canal information are thought to bias and delay perceptual responses: *B*: model prediction. For the experimentally tested sinusoidal linear acceleration (peak acceleration 1.75 m/s^2, frequency 0.33 Hz) (dashed gray line), the model predicts a tilt percept (black line) which is also sinusoidal, with an amplitude of ~2.7° and a phase shift of ~74° with respect to stimulus onset. Note that for the chosen frequency this phase shift corresponds to 616 ms [(3s * 74°)/360°).

full data set of each subject. For comparison, we tested a model that assumes μ to be constant, $\mu(\boldsymbol{phase}) = K$, $K \in \mathbb{R}$ irrespective of phase, which needs only three free parameters (K, σ, λ) to characterize a subject's data set.

We fitted all three models using maximum-likelihood estimation. We minimized the negative log-likelihood using the MATLAB routine *fmincon*, restricting the amplitude A of the sinusoidal model, the uncertainty σ, and the lapse rate λ of the psychometric curve to positive values. For all fits, the fitting procedure was repeated for 792 different initial parameter sets (11 equally spaced values for the amplitude A from 0° to 1°, 9 for the offset B from −0.8° to 0.8°, and 8 for the phase shift *phase*0 from 0° to 315°). From these fits, we selected the one(s) with the lowest negative log-likelihood and assumed that this was the global optimal solution.

To compare the sinusoidal and constant model, we used the Akaike information criterion (AIC), which evaluates the likelihood of the data, by penalizing model complexity. The AIC is defined as $\text{AIC} = -2^*\log L + k$, in which $\log L$ is the log-likelihood of the data for the given model, and k is the number of parameters necessary to define the model. Therefore, lower AIC values are indicative of a better fit to the data.

RESULTS

We used a two-alternative forced-choice task to test the bias and precision of subjective vertical percepts at various phases of sinusoidal whole body translation, i.e., at different combinations of instantaneous velocity and acceleration. Figure 3 shows response data from an example subject. The panels show the proportion of CW responses (black circles) as a function of line orientation relative to gravity for the eight phases of the whole-body motion.

The solid lines depict the psychometric fits that match the observed responses best. The respective psychometric curves were fitted with independent means (μ), but with a common

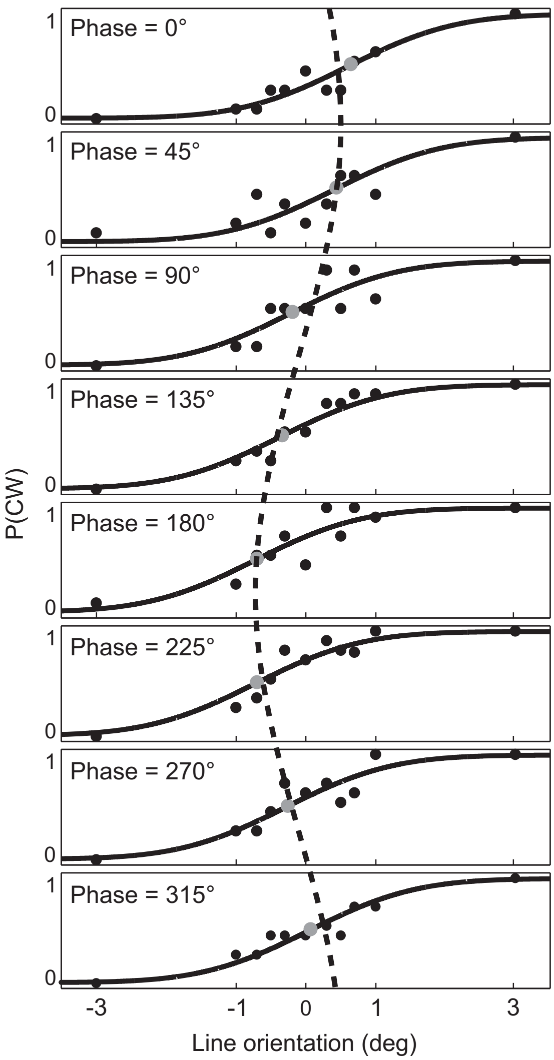

Fig. 3. Single-subject results. Each panel shows the proportion of CW responses for each line orientation (black dots) and the corresponding independently fitted psychometric curve (black line). The gray dot is the associated bias (μ-value) defined as the value of line orientation that the subject perceives as vertical. By assuming a sinusoidal modulation of the μ-values across phase conditions, the whole data set for that subject can be fitted by a sinusoidal function (black dashed curve).

slope (σ, the standard deviation) and lapse rate (λ). While in an observer with exact knowledge of head orientation in space all curves would resemble a step centered at zero, the panels show shallow slopes and clear phase-dependent biases, indicating nonperfect precision and accuracy in task performance, respectively. For the extreme line orientations, i.e., furthest away from the true vertical ($\pm 3°$ and $\pm 5°$; not shown), the judgments were consistently correct, irrespective of phase. For orientations closer to upright ($< |1°|$), subjects made more erroneous judgments. The line orientations for which these psychometric curves predict chance level performance are indicated by the gray circles.

The dashed line, superimposed over all panels, represents the fit to the psychometric data under the assumption of a sinusoidal phase-bias relationship. In accordance with the prediction by the model of Laurens and Droulez (2007), the bias modulation with phase can indeed be described as a sinusoidal relationship. Furthermore, if verticality perception would follow the instantaneous direction of the GIF vector, we would expect a CCW bias at peak acceleration to the left, when the subject crossed the right turning point (thus at phase 90°). Analogously, we would expect a CW bias when the subject crossed the left turning point (phase 270°), accelerating to the right (see Fig. 1*B*). However, the perceptual modulation in this subject shows a phase shift relative to the imposed sinusoidal acceleration, and thus relative to the direction of the true GIF.

The results of this subject are exemplary for all subjects. Figure 4*A* plots the independently estimated μ-values (black dots) as a function of phase for the individual subjects (exemplar subject of Fig. 3 is S1). For all subjects, there is a sinusoidal relationship of the bias with the phase of the body motion. To test this further, we fitted a model that assumes a sinusoidal modulation of the bias (Fig. 4*A*, black line) and a model that assumes a phase-independent bias.

We compared the model fits using the AIC, which accounts for the difference in degrees of freedom of the models. Figure 4*B* shows that the AIC difference between the two models is positive for seven of nine subjects, indicating that a sinusoidal bias-phase relationship provides a better description of the data than a constant bias-phase relation.

Now that we have shown that the bias is sinusoidally modulated, we can examine the parameters of this modulation: amplitude A, phase shift (*phase*0), and offset B (Fig. 5). The amplitude of the sinusoidal modulation has an average value of 0.31° ($\pm$0.06° SE), which is significantly smaller (*t*-test, $P < 0.05$) than the 2.7° amplitude predicted by the model. Parameter B describes the offset of the sinusoidal modulation of

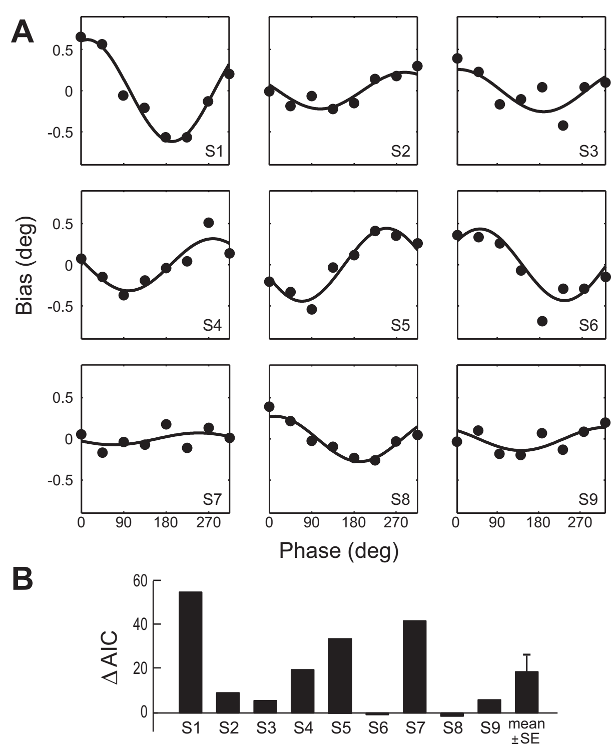

Fig. 4. *A*: bias as a function of phase for all subjects. Black dots: independently fitted psychometric curves for each phase. Continuous line: assumption of a sinusoidal modulation of the bias with the phase. Data and fits are offset corrected. *B*: model comparison. Difference between Akaike information criterion (AIC) values of constant and sinusoidal model for each subject. Positive values indicate that the sinusoidal model provides a better description of the data.

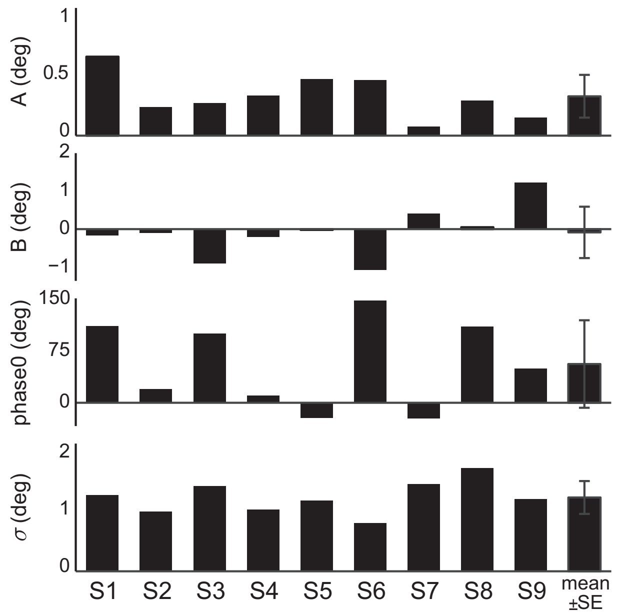

Fig. 5. Best fit parameters of the sinusoidal model. Amplitude A, offset B, phase shift *phase*0, and sigma values were obtained by fitting the whole data set of each subject under the assumption of sinusoidal modulation of the bias with phase. Lapse rate was small and is not shown.

verticality perception and might be related to a generic bias of the verticality percept, irrespective of motion. Across subjects, this parameter did not significantly differ from zero (t-test, $P > 0.05$). Finally, the phase shift of the response curve with respect to the whole-body acceleration was 52° on average (range −20° to 137° across subjects), which is not significantly (t-test, $P > 0.05$) different from the model prediction of 74°.

DISCUSSION

We studied the visual vertical—a proxy for the somatogravic illusion—at various phases of passively induced sinusoidal whole-body translation along an interaural axis. For the sinusoidal acceleration imposed ($f = 0.33$ Hz, 1.75 m/s^2 peak acceleration, 80 cm peak-to-peak displacement) a dynamic Bayesian inference model of spatial orientation, devised by Laurens and Droulez (2007) and adapted to the present experiment, predicts a sinusoidal modulation of the perceived direction of the gravitational vertical. The model also predicts that the phase shift between the acceleration profile and the perceptual response depends on both the sensory noise levels of the vestibular signals and on prior assumptions about natural statistics of head motion.

Previous experiments by Glasauer (1995) probed the perception of verticality during whole-body acceleration, at several frequencies, using a continuous line adjustment task. In all cases the phase offset between the acceleration pattern and the responses remained close to zero. However, it would be premature to take this observation as an argument against the Bayesian model. First, the continuous-tracking method employed in that study provides measurements that are not independent and, second, the continuous adjustments could anticipate on the cyclic nature of the motion, causing a predictive element in the indicated perceived vertical (see also Correia Grácio and Bos 2012; Keusch et al. 2004; Merfeld et al. 2001). In the present study, this problem was avoided by using a psychometric approach in which a briefly flashed line was used to measure the bias and variability of verticality perception at different phases of a passively induced sinusoidal body motion.

We found a phase-shifted sinusoidal modulation of the bias in verticality perception in response to a whole body lateral acceleration. Across subjects, the mean phase shift of the perceived vertical was 52°, which matched well with the model's prediction of 74°, using the parameters provided by Laurens and Droulez (2007). However, this phase shift varied substantially across subjects (from −20° to 137°), reminiscent of observations by Glasauer (1995). The Bayesian model may offer an explanation for this variation in terms of subject-specific sensory noise characteristics and reliance on prior knowledge. In the model, both the prior and sensory noise affect the emergent phase shift. This is illustrated in Fig. 6, showing the phase shift as function of the sensory noise magnitude and the width of the prior over linear acceleration (the prior on angular velocity was kept constant at a value of 30°/s). A large phase shift is explained by either low sensory noise or relatively large prior uncertainty, whereas a small phase shift reflects the reverse, i.e., high signal noise and stronger reliance on prior assumptions about head motion. Note though that the simulated range of phase shifts (40° to 80°) cannot fully account for the experimentally observed range, which is larger. We think, however, that this should not discard the model structure per se; estimating the phase in the experimental data is error prone, especially with smaller signal-to-noise ratio (see, e.g., *subject 7* or *9*).

A key strength of our psychometric approach is that very small deviations of the perceived vertical from the actual gravity direction can be measured. The amplitude of the modulation of the perceived vertical direction was 0.31 ± 0.17° (mean ± SD), which is smaller than the 2.7° predicted by the Bayesian model. Converting the measured amplitude to a gain measure (perceived tilt angle/peak acceleration), it yields a value of 0.18°/(m/s^2), which is of similar order as the value of 0.31°/(m/s^2) reported by Glasauer (1995) at the frequency under investigation.

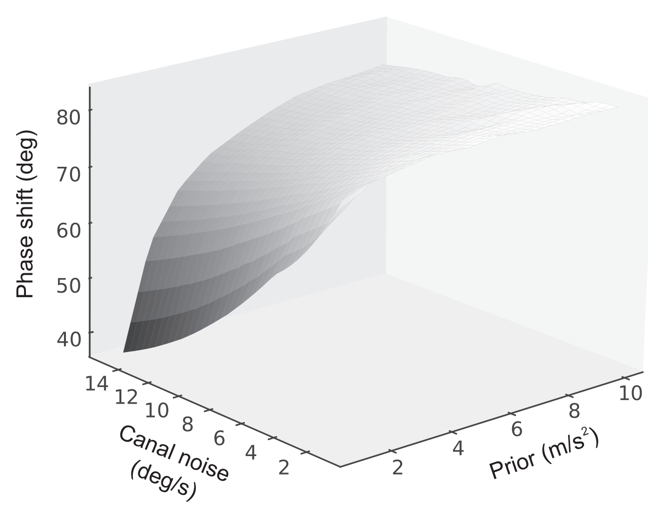

Fig. 6. Influence of noise levels on the estimated phase shift. As predicted by the model, a large phase shift can be interpreted as a consequence of low level of sensory noise and high uncertainty over prior assumptions, whereas as the sensory noise increases and the reliability of prior knowledge increases, the phase shift decreases.

A possible explanation of the discrepancy between the experimentally observed amplitude and the model's prediction is that the model only concerns the processing of vestibular signals, while there may also be other sensory signals, such as pressure sensors in the skin, that contribute to resolving the vertical (Au Yong et al. 2007; Seidman 2008). These other sensors will signal that the body and head are upright, dampening the effect of the vestibular mediated somatogravic illusion. Also, cognitive factors could play a role in gravity perception. For example, it has been shown that if subjects know the movement axis of the apparatus by which they are moved, i.e., realizing that it cannot tilt, their tilt perception will be reduced (Wertheim et al. 2001). Such a cognitive factor could be modeled in terms of a sharp prior for upright head orientations, which will reduce the modulation of verticality percept.

The existence of such an upright prior in the computation of the subjective visual vertical has been suggested before for the static case. For example, several studies have shown that roll-tilted subjects estimate their subjective body tilt (SBT) rather accurately but show systematic errors in their vertical percepts (Clemens et al. 2011; Kaptein and Van Gisbergen 2004; Mast and Jarchow 1996; Mittelstaedt 1983). To explain this observation, Clemens et al. (2011) suggested that prior knowledge is used in the visual vertical but not in body tilt perception. In the same vein, Vingerhoets et al. (2008) reported a similar dissociation between the SVV and SBT during multiple-cycle dynamic roll rotation, also suggesting a prior is used only in the SVV and not for body-tilt estimation. They argued that a prior increases precision at the expense of accuracy, which may be important for reasons of visual stability, yielding a more stable percept of visual orientation than can be derived from the sensory signal alone.

Compared with the numerous studies on verticality perception during static roll tilt, there are only few studies on the visual vertical in dynamic conditions. Most of the dynamic studies involved a rotation of the body around an earth-horizontal axis (Mittelstaedt 1989), an earth-vertical axis (Merfeld et al. 2001; Pavlou et al. 2003), or an off-vertical axis (Vingerhoets et al. 2007; Wood et al. 2007). All these studies emphasized the importance of the canal signal in verticality perception during whole body rotation.

Merfeld et al. (2001) tested the subjective visual horizontal in subjects exposed to either fixed-radius or variable-radius yaw rotation in a centrifuge. In the fixed-radius condition, the subject was seated at a constant radius from the centrifuge rotation point while the rotation speed varied to yield changes in the centrifugal force experienced by the otoliths. In the variable-radius condition, the rotation speed of the centrifuge was held constant while the radius varied to generate the same centrifugal force profile of the fixed-radius condition. The relevant difference between the two paradigms was that the variable-speed fixed-radius condition involved the contribution of the canals. In both cases subjects experienced illusory roll tilt during pure yaw rotation, but the perceived tilt considerably lagged behind the centrifugal or GIF during the fixed-radius condition and not in the variable-radius condition. The observed phase lag in the fixed-radius condition followed the decay of the canal signal, providing evidence that the nervous system uses internal models to estimate motion and spatial orientation.

The use of an internal model in vestibular perception finds also evidence in the perceptual responses during off-vertical axis rotation, i.e., in the time course of an illusory linear acceleration component and the dynamic underestimation of body tilt (Vingerhoets et al. 2007). Vingerhoets et al. (2007) found that the errors in the visual vertical increased exponentially to an asymptotic value, reached at ~60 s after rotation onset, which could be explained as a consequence of the involvement of the canals in resolving the ambiguous otolith cues. The effect of the noise levels in the canal signal, however, has been evaluated only theoretically, using computer simulations. MacNeilage et al. (2008) simulated velocity storage using the Bayesian model of Laurens and Droulez (2007). They found the time constant of velocity storage to depend on the noise in the canal signal and the width of the angular velocity prior. In the present study, we provide further evidence for the involvement of an internal model that combines uncertainties from sensory signals and prior assumptions about acceleration and rotation based on experimental evidence that the somatogravic illusion is modulated by sinusoidal motion. The crucial part of our study is that although the canals were not directly stimulated, they still influence the interpretation of the otolith signals. However, further studies are needed to understand the Bayes-like computations in the dynamic estimation of the visual vertical as well as their implementation by the brain.

To conclude, although our findings do not offer proof, they are consistent with the computational link between the noise components in the vestibular system and the characteristics of dynamic visual vertical. That the magnitude of this modulation was smaller than predicted, suggests that other, nonvestibular signals also contribute the dynamic visual vertical. Despite their dampening effect, we suggest, supported by simulations, that the observed variation in the dynamics of the visual vertical is (at least partly) explained by individual levels of sensory noise and prior assumptions about natural statistics of head motion.

ACKNOWLEDGMENTS

We thank Dr. Laurens for graciously providing the MATLAB code of the particle filter.

GRANTS

The research leading to these results has received funding from the European Union Seventh Framework Programme (FP7/2007–2013) under grant agreement no. 604063 (A. Pomante, W. P. Medendorp). The work has also been supported by the Netherlands Organization for Scientific Research, no. NWO-VICI 453-11-001 (W. P. Medendorp).

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

A.P., L.P.S., and W.P.M. conceived and designed research; A.P. performed experiments; A.P. analyzed data; A.P., L.P.S., and W.P.M. interpreted results of experiments; A.P. prepared figures; A.P. drafted manuscript; A.P., L.P.S., and W.P.M. approved final version of manuscript; L.P.S. and W.P.M. edited and revised manuscript.

REFERENCES

Angelaki DE, Cullen KE. Vestibular system: the many facets of a multimodal sense. *Annu Rev Neurosci* 31: 125–150, 2008. doi:10.1146/annurev.neuro.31.060407.125555.

Angelaki DE, Shaikh AG, Green AM, Dickman JD. Neurons compute internal models of the physical laws of motion. Letters to nature. *Nature* 430: 560–564, 2004. doi:10.1038/nature02754.

Aubert H. Eine scheinbare bedeutende drehung von objecten bei neigung des kopfes nach rechts oder links. *Virkows Arch* 20: 381–393, 1861.

Au Yong N, Paige GD, Seidman SH. Multiple sensory cues underlying the perception of translation and path. *J Neurophysiol* 97: 1100–1113, 2007. doi:10.1152/jn.00694.2006.

Benson AJ, Bodin MA. Interaction of linear and angular accelerations on vestibular receptors in man. *Aerosp Med* 37: 144–154, 1966.

Bos JE, Bles W. Theoretical considerations on canal-otolith interaction and an observer model. *Biol Cybern* 86: 191–207, 2002. doi:10.1007/s00422-001-0289-7.

Clemens IAH, De Vrijer M, Selen LPJ, Van Gisbergen JAM, Medendorp WP. Multisensory processing in spatial orientation: an inverse probabilistic approach. *J Neurosci* 31: 5365–5377, 2011. doi:10.1523/JNEUROSCI.6472-10.2011.

Correia Grácio BJ, Bos JE. Measuring dynamics of the subjective vertical and tilt using a joystick. *J Vestib Res* 22: 181–189, 2012.

De Vrijer M, Medendorp WP, Van Gisbergen JAM. Accuracy-precision trade-off in visual orientation constancy. *J Vis* 9: 1–15, 2009.

Glasauer S. Interaction of semicircular canals and otoliths in the processing structure of the subjective zenith. *Ann N Y Acad Sci* 656: 847–849, 1992. doi:10.1111/j.1749-6632.1992.tb25272.x.

Glasauer S. Linear acceleration perception: frequency dependence of the hilltop illusion. *Acta Otolaryngol Suppl* 115, *Suppl* 520: 37–40, 1995. doi:10.3109/00016489509125184.

Graybiel A, Clark B. Validity of the oculogravic illusion as an indicator of otolith function. *Aerosp Med* 36: 1173–1181, 1965.

Guedry FE Jr. Orientation of the rotation-axis relative to gravity: its influence on nystagmus and the sensation of rotation. *Acta Otolaryngol* 60: 30–48, 1965. doi:10.3109/00016486509126986.

Haustein W, Mittelstaedt H. Evaluation of retinal orientation and gaze direction in the perception of the vertical. *Vision Res* 30: 255–262, 1990. doi:10.1016/0042-6989(90)90041-I.

Kaptein RG, Van Gisbergen JAM. Interpretation of a discontinuity in the sense of verticality at large body tilt. *J Neurophysiol* 91: 2205–2214, 2004. doi:10.1152/jn.00804.2003.

Keusch S, Hess BJM, Jaggi-Schwarz K. Direction specific error patterns during continuous tracking of the subjective visual vertical. *Exp Brain Res* 155: 283–290, 2004. doi:10.1007/s00221-003-1733-9.

Laurens J, Droulez J. Bayesian processing of vestibular information. *Biol Cybern* 96: 389–404, 2007. doi:10.1007/s00422-006-0133-1.

MacNeilage PR, Banks MS, Berger DR, Bülthoff HH. A Bayesian model of the disambiguation of gravitoinertial force by visual cues. *Exp Brain Res* 179: 263–290, 2007. doi:10.1007/s00221-006-0792-0.

MacNeilage PR, Ganesan N, Angelaki DE. Computational approaches to spatial orientation: from transfer functions to dynamic Bayesian inference. *J Neurophysiol* 100: 2981–2996, 2008. doi:10.1152/jn.90677.2008.

Mast F, Jarchow T. Perceived body position and the visual horizontal. *Brain Res Bull* 40: 393–397, 1996. doi:10.1016/0361-9230(96)00132-3.

Mayne RA. Systems concept of the vestibular organs. In: *Handbook of Sensory Physiology*, edited by Kornhuber H. New York: Springer, vol. VI/2, p. 493–580, 1974.

Merfeld DM. Modeling the vestibulo-ocular reflex of the squirrel monkey during eccentric rotation and roll tilt. *Exp Brain Res* 106: 123–134, 1995.

Merfeld DM, Park S, Gianna-Poulin C, Black FO, Wood S. Vestibular perception and action employ qualitatively different mechanisms. I. Frequency response of vor and perceptual responses during translation and tilt. *J Neurophysiol* 94: 186–198, 2005.

Merfeld DM, Zupan L, Peterka RJ. Humans use internal models to estimate gravity and linear acceleration. *Nature* 398: 615–618, 1999. doi:10.1038/19303.

Merfeld DM, Zupan LH, Gifford CA. Neural processing of gravito-inertial cues in humans. II. Influence of the semicircular canals during eccentric rotation. *J Neurophysiol* 85: 1648–1660, 2001.

Mittelstaedt H. A new solution to the problem of the subjective vertical. *Naturwissenschaften* 70: 272–281, 1983. doi:10.1007/BF00404833.

Mittelstaedt H. The role of the pitched-up orientation of the otoliths in two recent models of the subjective vertical. *Biol Cybern* 61: 405–416, 1989. doi:10.1007/BF02414902.

Mittelstaedt H. Somatic versus vestibular gravity reception in man. *Ann N Y Acad Sci* 656: 124–139, 1992. doi:10.1111/j.1749-6632.1992.tb25204.x.

Mittelstaedt H. Somatic graviception. *Biol Psychol* 42: 53–74, 1996. doi:10.1016/0301-0511(95)05146-5.

Mittelstaedt H. The role of the otoliths in perception of the vertical and in path integration. *Ann N Y Acad Sci* 871: 334–344, 1999. doi:10.1111/j.1749-6632.1999.tb09196.x.

Müller GE. Über das Aubertsche Phänomen. *Z Sinnesphysiol* 49: 109–246, 1916.

Paige GD, Seidman SH. Characteristics of the VOR in response to linear acceleration. *Ann N Y Acad Sci*: 123–135, 1999. doi:10.1111/j.1749-6632.1999.tb09179.x.

Pavlou M, Wijnberg N, Faldon ME, Bronstein AM. Effect of semicircular canal stimulation on the perception of the visual vertical. *J Neurophysiol* 90: 622–630, 2003. doi:10.1152/jn.00960.2002.

Raphan T, Cohen B. The vestibulo-ocular reflex in three dimensions. *Exp Brain Res* 145: 1–27, 2002. doi:10.1007/s00221-002-1067-z.

Seidman SH. Translational motion perception and vestiboocular responses in the absence of non-inertial cues. *Exp Brain Res* 184: 13–29, 2008. doi:10.1007/s00221-007-1072-3.

Seidman SH, Telford L, Paige GD. Tilt perception during dynamic linear acceleration. *Exp Brain Res* 119: 307–314, 1998. doi:10.1007/s002210050346.

Tarnutzer AA, Bockisch C, Straumann D, Olasagasti I. Gravity dependence of subjective visual vertical variability. *J Neurophysiol* 102: 1657–1671, 2009. doi:10.1152/jn.00007.2008.

Tarnutzer AA, Bockisch CJ, Straumann D, Marti S, Bertolini G. Static roll-tilt over 5 minutes locally distorts the internal estimate of direction of gravity. *J Neurophysiol* 112: 2672–2679, 2014. doi:10.1152/jn.00540.2014.

Vingerhoets RAA, De Vrijer M, Van Gisbergen JAM, Medendorp WP. Fusion of visual and vestibular tilt cues in the perception of visual vertical. *J Neurophysiol* 101: 1321–1333, 2009. doi:10.1152/jn.90725.2008.

Vingerhoets RAA, Van Gisbergen JAM, Medendorp WP. Verticality perception during off-vertical axis rotation. *J Neurophysiol* 97: 3256–3268, 2007. doi:10.1152/jn.01333.2006.

Wertheim AH, Mesland BS, Bles W. Cognitive suppression of tilt sensations during linear horizontal self-motion in the dark. *Perception* 30: 733–741, 2001. doi:10.1068/p3092.

Wood SJ, Reschke MF, Clément G. Tilt and translation motion perception during off-vertical axis rotation. *Exp Brain Res* 182: 365–377, 2007. doi:10.1007/s00221-007-0994-0.