Fusion of Visual and Vestibular Tilt Cues in the Perception of Visual Vertical


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Submitted 1 July 2008; accepted in final form 20 December 2008

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. First published December 31, 2008; doi:10.1152/jn.90725.2008. We investigated the effect of visual and vestibular body-tilt cues on the subjective visual vertical (SVV) in six human observers at roll tilts of 0, 60, and 120°. Subjects adjusted a small luminous test line parallel to the perceived direction of gravity, in the presence of a large peripheral visual frame line. These settings, referred to as the frame SVV, were compared with the SVV in complete darkness (dark SVV). The frame SVV was virtually identical to the dark SVV for frame lines parallel or orthogonal to the dark SVV. Away from these neutral positions, the frame induced a periodic SVV modulation, which was small in upright observers, but became quite pronounced when subjects were tilted. For upright, where the dark SVV was very accurate, the frame SVV showed errors in both directions, following a roughly symmetrical pattern. At 120° tilt, where the dark SVV invariably showed tilt undercompensation (A-effect), the frame effect became asymmetrical, with a stronger tendency to improve than to worsen accuracy. We tested whether our findings could be explained by two spatial orientation models: Mittelstaedt’s idiotropic model and a Bayesian scheme with a stage for the processing of visual cues. Both models show a periodic frame effect that becomes stronger with increasing body tilt and can explain why frame lines parallel or perpendicular to the dark SVV are ineffective. Based on their performance, we conclude that perception of the visual vertical is based on a centrally weighted fusion of visual, vestibular, and egocentric references.

IN TRO D U C T I O N

In this study, we investigate how the orientation of a peripheral visual frame and lateral body-tilt signals affect the subjective visual vertical (SVV) and test whether two alternative models can account for the data. The literature contains numerous reports on the effects of each of these factors in isolation, but combined studies, particularly those with a modeling background, are very rare. To provide a survey of the important concepts, we first review current knowledge about visual frame effects on the SVV in upright observers, then discuss previous SVV studies with tilted observers in the absence of a visual frame, and conclude by reviewing previous work on the interaction of frame and body-tilt signals.

Natural scenes have an overrepresentation of world-horizontal and world-vertical orientations (Coppola et al. 1998; Switkes et al. 1978; Van der Schaaf and Van Hateren 1996) and typically contain polarity cues indicating which direction is up. Strong effects of a rich panoramic stimulus have been found in experiments where upright subjects adjusted a luminous line to the perceived direction of gravity while viewing a tilted furnished room (Asch and Witkin 1948a; Howard and Childerson 1994). However, also in more impoverished stimulus conditions—for example, when using a simple square frame devoid of obvious polarity cues—average verticality settings clearly deviate in the direction of the tilted frame (Witkin and Asch 1948). This phenomenon, known as the rod-and-frame effect, has been confirmed by many other studies (see Beh et al. 1971; Chan et al. 2001; DiLorenzo and Rock 1982; Dyde and Milner 2002; Ebenholtz 1977; Ebenholtz and Benzschawel 1977; Spinelli et al. 1991; Wenderoth and Beh 1977; Zoccolotti et al. 1992). Spinelli et al. (1991) found a cyclical modulation of the SVV when the orientation of the frame was varied across a 90° range. Recently, Li and Matin (2005a,b) reported that even a single peripheral line can be as effective as a complete square, with the same 90° periodicity, indicating that the square configuration is not crucial. In this context, the cyclical modulation of the SVV seems to suggest that a single line or a frame is an ambiguous indicator of four potential up directions: two corresponding to its orientation and two perpendicular to it. Matin and Li (1995) suggested that these effects stem from a rather primitive global vision system that interprets an anisotropic orientation distribution in the visual field as an ambiguous body tilt signal that combines with the nonvisual tilt cues provided by the vestibular system to determine the SVV.

Before discussing the nature of this visuo-vestibular fusion process in more detail, we first provide some background about the peculiarities of the SVV in roll-tilted observers, in the absence of panoramic visual stimuli. At large tilt angles, the orientation of a luminous test line is misperceived, even without a frame. This was first described by Aubert (1861) and, ever since, this phenomenon has been extensively investigated. Numerous experiments, testing the ability of roll-tilted subjects to adjust a luminous line to the perceived direction of gravity in an otherwise dark room have found a consistent pattern of tilt undercompensation at tilts 60°, known as the Aubert or A-effect, whereas at smaller tilts the opposite effect (E-effect) may occur (Kaptein and Van Gisbergen 2004; 2005; Mittelstaedt 1983; Schöné 1964; Udo de Haes 1970; Van Beuzekom and Van Gisbergen 2000). A widely accepted explanation for the A-effect at large tilts holds that the SVV reflects a compromise between the direction of gravity indicated by the tilt sensors and an egocentric reference, corresponding to the long-body axis. Models incorporating this concept have taken two different forms. Mittelstaedt (1983) proposed that the A-effect is linked to a so-called idiotropic vector, an internal bias expressing the tendency to assume that the subjective vertical is aligned with the head axis. In this model, the SVV setting is a compromise between the tilt signal of the otoliths.
and the idiotropic vector. Recently, alternative models using Bayesian signal processing have been formulated (De Vrijer et al. 2008; Eggert 1998; MacNeilage et al. 2007) in which the SVV depends on the statistical properties of the various signals that are involved. More specifically, these models incorporate a priori information, that body-tilt is usually small, in the form of a prior probability distribution centered at zero. Furthermore, the sensory tilt signal in the model is assumed to be noisy and the outcome of the Bayesian estimator is an optimal compromise based on the mean and the width of the sensory signals and the prior distribution (De Vrijer et al. 2008; Eggert 1998; MacNeilage et al. 2007).

Given the topic of this report, a crucial question is how the effects of a visual frame combine with those of body tilt in the perception of the visual vertical. Several studies have shown that the frame effect becomes more pronounced when the observer is tilted (Asch and Witkin 1948b; Bischof 1974; Bischof and Scheerer 1970; Corbett and Enns 2006; Dyde et al. 2006). Bischof and Scheerer (1970) studied the combined effect of body tilt and visual frame tilt by testing the effect of a slowly rotating parallel-stripe pattern on the SVV settings, at various roll-tilt angles of the observer. The stripe pattern acted as an attacker when its orientation deviated slightly from the subjective vertical. Further rotation of the pattern gradually reduced the attraction effect until a new attraction effect emerged around 90°. Bischof and Scheerer (1970) suggested that the lines thus provide a fourfold ambiguous indicator of which way is up, an interpretation that gained later support from Li and Matin (2005a,b).

Mittelstaedt (1986) studied the effect of a visual frame on the SVV at 90° roll tilt. He found that a visual frame with a polarization direction aligned with the SVV does not affect the setting of a small luminous line, whereas other visual frame orientations clearly modulate the SVV. To account for these observations, Mittelstaedt (1986, 1988) extended his original model (Mittelstaedt 1983) by conceiving the SVV as a weighted sum of the otolith signal, the idiotropic vector, and an additional vector that points in the upward direction defined by the visual frame of reference. Herein, we will refer to this extended model as the Mittelstaedt model.

Eggert (1992, 1998) reformulated the Mittelstaedt model to account for the influence of visual–vestibular interactions on the SVV in Bayesian terms. In the present study, we combined the De Vrijer et al. (2008) model and the Eggert model to construct a Bayesian model that incorporates head-tilt cues derived from visual-frame information in a statistically optimal fashion. We will refer to this model as the Bayesian model. Our objective is to offer a thorough assessment of Bayesian modeling in this domain of multisensory integration, which has traditionally been dominated by more heuristic approaches. In addition, we compare performance of the Bayesian model with the vector component model of Mittelstaedt (1986) and discuss the structural similarities between both schemes (see METHODS for full description of both models).

We put both models to the test by investigating the effect of a visual frame, consisting of a single peripheral visual line, on the SVV at three different body-tilt angles (0, 60, and 120°). These tilt angles were combined with a broad range of visual frame angles (−90 to 90°) in steps of 10° to determine the frame SVV. For comparison, we also determined the SVV in complete darkness (dark SVV). In the experiment, subjects were rotated in complete darkness to the tilt angle chosen for testing, where they were then shown the visual frame line. Subsequently, after a short viewing period, they adjusted a short luminous test line parallel to the perceived direction of gravity. Consistent with both models, our results show a 90° periodic modulation on the frame SVV, which increases when the body is tilted away from upright. Our data also confirm that visual frames aligned with or perpendicular to the dark SVV do not affect the frame SVV. Although the two models cannot capture all aspects of the data, we conclude that they provide valuable insights into the centrally weighted fusion of visual, vestibular, and egocentric signals in human spatial orientation.

METHODS

Subjects

Six subjects [four male, two female, ages between 23 and 64 yr (mean ± SD: 32 ± 16 yr)] gave informed consent to participate in this study. All subjects were free of any known vestibular disorder and had normal or corrected-to-normal vision. All participants except two (JG and MV) were naive with respect to the purpose of the experiments. Before the experiment began, subjects were carefully instructed about the task and were given a few practice runs. They never received feedback about their performance. Vision was always binocular.

Setup

The subject was seated in a computer-controlled vestibular chair with nested gimbals that was configured to rotate subjects about their roll axis. The subject’s head, positioned at the rotation center, was restrained in a natural upright position relative to the torso using a padded helmet. The torso was secured with seat belts and adjustable shoulder and hip supports. The legs and feet were fixated with Velcro straps and a foot rest.

The SVV was tested using a uniformly illuminated line with an angular subtense of 20° mounted on the vestibular chair at about 90 cm, straight ahead in front of the subject. The SVV test line was polarized by a bright dot at one end and could be controlled by computer with an angular resolution of 0.5°. The rotation axis of the test line coincided with the cyclopean eye of the subject and the rotation axis of the chair, so that it rotated in the frontoparallel plane. The observer adjusted the orientation of the test line with a joystick to indicate the SVV, both in the presence and in the absence of a visual frame stimulus. We will refer to the SVV determined in otherwise complete darkness as the “dark SVV,” whereas the SVV in the presence of the frame line will be denoted as “frame SVV.”

The visual frame stimulus was a line (to be denoted as “frame line”) with an angular subtense of 108° whose center was located 54° eccentric relative to the rotation axis. The visual frame line and SVV test line were mounted on separate but aligned axes, such that the two lines could rotate to different orientations in the frontoparallel plane. Both the test line and the frame line consisted of a roughened glass fiber (diameter: 2 mm) that was lit over its entire length by a white light-emitting-diode at a luminance of 0.4 cd/m² (Model 1980a, Spectra Pritchard Photometer). The frame line was presented at orientations ranging from −90 to 90° relative to the dark SVV at 10° intervals, yielding a total of 18 different frame-line orientations (see Fig. 1). An orientation of 0° denoted that the frame line was parallel to the dark SVV. When the frame line was oriented at 90 or −90°, it was perpendicular to the dark SVV. Subjects were instructed that the frame line could have any orientation in space and thus provided no reliable clue as to the direction of gravity.

SVV experiment

In each run, the initially upright subject was rotated clockwise (seen from behind) about the roll axis to the tilt angle chosen for testing (0,
that are normally reserved for judgments in the dark, but will be used.

In our experiments, A-effects yielded positive errors in SVV (completely dark room). Error in SVV (\(\gamma\) in degrees) is defined as the angular difference between the final orientation of the SVV test line and the direction of gravity. Angles \(\rho\) and \(\gamma\) are defined as positive in the clockwise direction, seen from behind the subject. Example shows body-tilt angle (\(\rho\)) of 120°, with a clear Aubert effect (A-effect) in the test-line setting.

The chair rotated with a constant velocity of 30°/s, using a peak acceleration and deceleration of about 50°/s². Once the desired tilt position was reached, there was a 30-s waiting period before SVV testing began to allow rotational signals to subside. Subsequently, the test line was presented in a random orientation and the subject adjusted its orientation parallel to the perceived direction of gravity with the dot pointing upward in space. After the subject completed the adjustment, a new test line appeared at a random orientation. The time available for each adjustment was 15 s. After five consecutive adjustments the subject was returned back to upright to remain there for 45 s with the room lights on to allow reorientation.

Each session of about 45 min started by testing the dark SVV. This was done extensively in the first session (three measurements for each tilt angle) and only once to check for stability in later (second to fourth) sessions. Runs testing the frame SVV differed in two aspects: the size of the A-effect was allowed to vary across subjects to account for differences in the size of the A-effect in the dark SVV. In the simple case that the visual frame is a highly polarized visual scene, its effect can be modeled by a single vector \(P\), pointing in the polarization direction of the visual scene. In this special case, the model determines the percept of vertical (SVV) by adding vectors \(G\), \(M\), and \(P\), as shown in Fig. 2A. In the following, we translate this graphical account into mathematical terms to allow for the handling of more ambiguous visual frames, such as a single line.

### Data analysis

Response error (\(\gamma\)) was defined as the difference between the true direction of gravity and the SVV setting of the subject (see Fig. 1). Errors (\(\gamma\)) in the clockwise (CW) direction, seen from behind the subject, were defined as positive. Accordingly, for the right-ear-down tilts used in our experiments, A-effects yielded positive \(\gamma\) values and E-effects yielded negative \(\gamma\) values. A-effect and E-effect are terms here to denote errors that occur in the presence of a visual stimulus as well.

### Model simulations

As we shall see in RESULTS, both the degree of body tilt and the orientation of the frame line affected the perception of vertical. Mittelstaedt (1986, 1988) proposed a model to account for both effects. In the following we first provide an outline of this model and then describe an alternative Bayesian framework for visual frame processing (De Vrijer et al. 2008) that shares several features with models developed by Eggert (1998) and MacNeilage et al. (2007).

### Mittelstaedt’s model

Mittelstaedt (1986, 1988) proposed a framework (Fig. 2) incorporating the effects of the estimated direction of gravity, the idiotropic vector, and vector panoramic cues on the percept of vertical. As explained in the INTRODUCTION, the idiotropic vector represents the tendency to assume that the SVV is aligned with the long-body axis. Figure 2A illustrates the idea behind the model in schematic fashion. The direction of gravity sensed by the otoliths (G), the idiotropic vector (M), and the direction of visual panoramic cues (P) are modeled by vectors with lengths proportional to their relative weights. The internal representation of gravity, assumed to be veridical, is represented by an upward pointing unit vector. The idiotropic vector, pointing along the long-body axis, has a weight that can vary across subjects to account for differences in the size of the A-effect in the dark SVV. In the simple case that the visual frame is a highly polarized visual scene, its effect can be modeled by a single vector \(P\), pointing in the polarization direction of the visual scene. In this special case, the model determines the percept of vertical (SVV) by adding vectors \(G\), \(M\), and \(P\), as shown in Fig. 2A. In the following, we translate this graphical account into mathematical terms to allow for the handling of more ambiguous visual frames, such as a single line.

Mittelstaedt (1986, 1988) defined vectors \(G\), \(M\), and \(P\) in a head-fixed coordinate system in which the \(x\)-axis is aligned with the nasoccipital
axis, the y-axis corresponds to the interaural axis, and the z-axis is the vertical axis. The three vectors can then be written as: \( G = (0, \sin \rho, \cos \rho), M = (0, 0, M), \) and \( P = (0, V \sin \theta_V, V \cos \theta_V) \), where gravity is normalized: \( |G| = 1, \rho \) is the tilt angle of the body, \( M \) is the length of the idiotropic vector, and \( V \) is the length of vector \( P \). For simplicity, we ignore ocular torsion so that the angle between the upward direction of the visual scene and the head’s z-axis equals the orientation of the visual scene on the retina, denoted by \( \theta \). The luminous line, serving as an indicator of the SVV, is also considered as a vector: \( L = (0, \sin \beta, \cos \beta) \), in which \( \beta \) is the angle between body and SVV. When the observer rotates indicator \( L \) until it is aligned with \( G \), this is equivalent to reducing the cross-product between \( L \) and \( G \) to zero, which yields

\[
\sin \beta \cdot \cos \rho - \cos \beta \cdot \sin \rho = 0
\]

Note that this equation is based on the work by Mittelstaedt (1986) on the visual frame effect. Mittelstaedt (1988) later discussed the possibility that the otolith signals from the utricle and sacculle have different weights, i.e., \( G = (u \sin \rho, s \cos \rho) \); for simplicity we did not include this. Including the notion that the SVV setting is a compromise between the actual tilt signal of the otoliths and the idiotropic vector yields

\[
\sin \beta (\cos \rho + M) - \cos \beta \sin \rho = 0
\]

which represents the condition without additional visual cues (dark SVV). To add the effect of panoramic cues, indicated by vector \( P \), to the equation we can write

\[
\sin \beta (\cos \rho + M + V \cos \theta_V) - \cos \beta (\sin \rho + V \sin \theta_V) = 0
\]

Before we can apply the model to our testing conditions, it should be realized that \( P \) has four ambiguous polarization directions in the case of a single frame line. In contrast to a rich panoramic scene, the frame line yields the same effect when rotated by 90 or 180° (Li and Matin 2005a,b). To incorporate this 90° periodicity effect of the frame line, the following equation can be derived (see APPENDIX A)

\[
\sin \beta (\cos \rho + M + V \sin \theta_V) + \cos \beta \cdot \sin \rho + V_s \sin (\beta - \theta) = 0
\]

In this equation, the third term represents the visual frame effect, with \( V_s \) denoting the length of the vector that represents the four effective orientations of the visual frame. The factor 4 in this term expresses the fourfold periodicity across 360°, corresponding to the four polarization directions (represented by four vectors of length \( V_s \)) associated with the frame stimulus. When the subject adjusts \( \beta \) so that the cross-product reduces to zero, the resulting SVV can be regarded as the vector sum of \( G \) and \( M \) and the two \( P \) vectors closest to their resultant.

Model predictions of the frame SVV (solid line) in Fig. 2B show that the error pattern for upright is 90° periodic with positive peaks around −63, 27, and 117° and negative peaks around −27 and 63°. Note that, due to factor \( \beta - \theta \), the predicted error pattern deviates from a symmetric sine wave. The horizontal dashed line, indicating the error in the dark SVV, shows that the model predicts an accurate dark SVV when the body is upright. Since the dark SVV can be regarded as the orientation that is perceived as vertical, we also indicated it as a vertical dashed line in the plot to illustrate the orientation at which the frame line is aligned with the dark SVV. For the two tilted conditions, the periodic error pattern is superimposed on a constant bias representing the A-effect in the dark SVV, caused by the idiotropic vector (M). Furthermore, the error pattern is shifted to the right and thus no longer symmetric around the vertical axis through the origin (y-axis). This shift reflects the model prediction that a frame line aligned with the vector sum of \( M \) and \( G \) (i.e., the dark SVV) has no effect on the percept of vertical, which means that the error pattern now becomes symmetric around the orientation parallel to the dark SVV indicated by dashed lines. Finally, the panels express the model prediction that the effect of the frame line increases slightly with tilt angle, as indicated by the larger peak-to-trough distance in the body-tilt conditions.

In testing the quality of this model, the best-fit parameters \( M \) and \( V_s \) were found by minimizing the sum-of-squared-errors, with the constraint that only positive \( V_s \) values were allowed.

**BAYESIAN MODEL.** De Vrijer et al. (2008) recently developed a Bayesian model to simulate the dark SVV in tilted observers. As in Eggert (1998) and MacNeilage et al. (2007), computation of the dark SVV in their scheme is based on the vestibular head-tilt signal, which is assumed to be veridical but corrupted by noise, and an a priori assumption that the head is usually nearly upright. Unlike Eggert (1998) and MacNeilage et al. (2007), De Vrijer et al. (2008) made the additional conjecture that the visual noise is independent of line orientation on the retina and that body-tilt noise increases with tilt angle, which allowed them to simulate the nonlinear behavior of the dark SVV across the full tilt range. Herein, we extend the De Vrijer model with a new additional stage for the processing of visual-frame cues, as shown in Fig. 3. The inputs to the extended model are head orientation in space (\( \rho \)) and the retinal orientations of the SVV test line (\( \phi_\rho \)) and of the visual frame line (\( \phi_\theta \)). The crucial signal in the model is \( \beta \) (defined as in Fig. 2), the central tilt signal that ultimately transforms retinal signals to spatial coordinates. Since the model is designed to combine noisy signals in an optimal fashion, it deals with probability distributions instead of deterministic signals.

**Body-tilt signal and prior.** We first describe how the model works in the absence of panoramic cues. We followed the assumption in De Vrijer et al. (2008), that head-tilt signal \( \rho \), provided by extraretinal sensors, such as the otoliths and the canals, has a linear relation with input angle \( \rho \) and that its noise level increases with tilt angle. As a result, a given tilt angle \( \rho \) yields a distribution \( \beta_\rho \). The probability of obtaining a given neural signal for a given tilt angle is illustrated in Fig. 3A, bottom left. The brain must solve the inverse problem of determining which tilt angle caused the given sensory signal, indicated by the horizontal dashed line. Because of the noise in the system, there is no unique solution and a statistical approach is required. The Bayesian scheme applies knowledge of the forward \( \rho \rightarrow \beta \) relationship to compute the probability that any particular tilt angle produced the incoming sensory signal. The result of this computation, the vestibular likelihood function \( P(\beta | \rho) \), which comprises all nonretinal tilt signals, is based exclusively on the sensory evidence \( \beta \), which comprises all nonretinal tilt signals, and is modeled by a Gaussian centered at \( \rho \) with standard deviation \( \sigma_\rho \). To obtain a statistically optimal tilt estimate, the Bayesian model also takes into account prior knowledge. In line with earlier work (De Vrijer et al. 2008; Eggert 1998; MacNeilage et al. 2007) we incorporated the prior \( P(\rho) \), a Gaussian with standard deviation \( \sigma_\rho \), centered on zero head tilt, to account for the fact that small head tilts are most common. In our model, we assume that the prior is always the same, irrespective of information about recent motion and high-level cognitive knowledge about orientation. For a particular tilt angle, the combination of sensory evidence and prior knowledge yields the posterior probability \( P(\rho | \beta) \) distribution according to Bayes’ rule: \( P(\rho | \beta) = kP(\beta | \rho)P(\rho) \), where \( k \) is a constant that serves to normalize the posterior distribution. The location of the peak of the posterior distribution \( P(\rho | \beta) \) is denoted by \( \beta \) and lies in between the peaks of the prior and the vestibular likelihood (see Carandini 2006; MacNeilage et al. 2007). Compensatory tilt signal \( \beta \) is defined by the relative widths of the prior and the likelihood following De Vrijer et al. (2008)

\[
\beta(\rho) = \frac{\sigma_\rho^2}{\sigma_\rho^2 + \sigma_{\beta|\rho}^2}
\]

Note that this is simply a form of optimal sensor fusion by weighting sensory estimates by their reciprocal variances, which has been used in many other models (Bays and Wolpert 2007; Ernst and Banks 2002;
To account for the nonlinear increase of the A-effect with tilt angle, the model assumes that the noise in the tilt signal ($\sigma_{\text{tilt}}$) increases linearly with tilt angle

$$\sigma_{\text{tilt}}(\rho) = a_0 + a_1|\rho|$$  \hspace{1cm} (6)

The visual frame stage. To adapt the model to the present testing conditions, it was extended with a stage for the processing of visual panoramic cues. The scheme proposes that a frame line affects the model assumes that the noise in the tilt signal ($\sigma_{\text{tilt}}$) increases linearly with tilt angle

$$\sigma_{\text{tilt}}(\rho) = a_0 + a_1|\rho|$$  \hspace{1cm} (6)

The associated frame likelihood function is a circular distribution with one peak at the presented line angle and other peaks at 90° intervals (middle column, second panel). In other words, each frame line leads to an ambiguous head-tilt estimate where four possibilities stand out as most likely. The strength of the frame cue is reflected by the sharpness of the four peaks and the modulation depth in the frame likelihood function. In case of a visual frame with many randomly oriented lines, the angular distribution would be a perfect circle and the frame likelihood function would become entirely flat, indicating that, based on the visual frame information, all head tilts are equally likely.

To express the fourfold periodic influence of the frame line, we represented the frame likelihood by a von Mises distribution with one peak at the frame line orientation and the other peaks at 90° intervals (see Fig. 3A)

$$P(\hat{\theta}_r|\rho) = \exp \left\{ V \cdot \cos \left[ 4(\hat{\theta}_r - \rho) \right] \right\}$$  \hspace{1cm} (8)

in which $2\pi$ is a normalization factor, $I_0$ denotes the modified Bessel function with the order zero, and $V$ is a concentration parameter, which can be regarded as the inverse of the variance. The von Mises distribution was chosen because it is the circular analog of the normal distribution (Evans et al. 2000) and therefore the most simple approach apart from a simple normal distribution. Also, the von Mises distribution approaches the image statistics of natural scenes, where
the likelihood of oblique orientations is somewhat smaller than the likelihood of orientations in the direction parallel or orthogonal to gravity (see Switkes et al. 1978).

Although technically sound, using Eq. 8 makes it impossible to find an analytical expression for $\beta$ similar to Eq. 5. We therefore calculated the prior, the frame likelihood, and the vestibular likelihood numerically using MATLAB 7.0 (The MathWorks) and simply multiplied them to obtain the posterior distribution. As a last step, we took the tilt angle with the highest probability, i.e., the maximum a posteriori (MAP), as the final model prediction of the head-tilt signal, an approach also followed by MacNeilage et al. (2007). The perceived orientation of the test line in space, $\hat{\varphi}$, is obtained by combining the compensatory tilt signal $\hat{\beta}$ with the perceived orientation of the test line on the retina $\varphi_r$.

Figure 3B, depicting model predictions obtained with the parameter values $\sigma_\varphi = 15^\circ$, $V = 4$, $a_0 = 1.5^\circ$, $a_1 = 0.040$ (chosen to be representative for fit outcomes in RESULTS), shows that the predicted effect of the frame line is very small for upright. However, more clearly than in the Mittelstaedt model, the effect becomes more manifest for the tilted conditions. In these conditions, the frame effect is superimposed on a constant bias induced by the prior. Note that predicted errors show a skewed pattern that can also be seen in the predictions of the Mittelstaedt model. This similarity is understandable because Eggert (1998) has shown that both models have essentially the same structure. APPENDIX B describes the close relationship between the two models in more detail.

The Bayesian model was fitted to the experimental data with the least-squares method using the routine fmincon (MATLAB 7.0). Since leaving all four parameters free for each subject caused overfitting, parameters $\sigma_\varphi$ and $\sigma_\beta$ and the increase of the noise in the tilt signal ($a_1$; see Eq. 6) were fitted at the population level, whereas the offset of the tilt-signal noise ($a_0$) was allowed to vary freely among our subjects. Fitting parameter $a_0$ at the population level and $a_1$ individually did not yield different conclusions and will not be discussed further.

RESULTS

The goal of the present study was to investigate how tilt cues provided by a visual frame and by the vestibular system contribute to the SVV. We first assessed the effect of frame line orientation on the SVV at three different roll tilt angles and then explored how well these data were fitted by the two models described in METHODS.

Overview of main findings

To introduce our results, we first describe the first row of Fig. 4, which plots frame SVV errors in subject FW as a function of frame-line orientation in space, for each body-tilt angle. The horizontal gray band denotes sign and magnitude of the error ($\pm 1$SD) in the dark SVV, with positive errors indicating an A-effect and negative errors indicating an E-effect (see Figs. 2B and 3B for corresponding model predictions). The vertical gray band represents the orientation of the dark SVV in space ($\pm 1$SD). For upright, these bands almost coincide with the $y$- and $x$-axes, indicating that the dark SVV is almost flawless. In this subject, the dark SVV showed a small A-effect at 60° tilt and a more pronounced A-effect at 120° tilt, which is consistent with previous reports (Kaptein and Van Gisbergen 2004, 2005; Schöne 1964; Udo de Haes 1970; Van Beuzekom and Van Gisbergen 2000).

Judged from the vertical distance of the data points to the center of the horizontal gray bands, which represents the induced changes with respect to the dark SVV, the frame effect depends on two factors: the orientation of the frame line and the degree of body tilt. There was only a modest 90° periodic SVV modulation with the subject in upright position, but a more robust frame effect emerged at 60 and 120° body tilt. Note that frame lines parallel to the dark SVV (see vertical gray band), and those perpendicular to it, yield a frame SVV equal to the dark SVV. The effect of other frame-line orientations, in the tilted conditions, shows modulations with a vertical asymmetry. Unlike the situation with the subject upright, the periodic response pattern has a downward bias. To illustrate: in the 60° tilt panel, varying the frame orientation has a stronger capacity to elicit small E-effects than to increase the A-effect seen in the dark SVV. Similarly, in the 120° condition, the maximum decrease in the A-effect clearly exceeds the maximum increase induced by other frame orientations.

The complete data set from all subjects shows common features along with intersubject differences. First, the dark SVV (gray bands) is almost flawless for upright, but shows small A-effects in some subjects (JG, MV, and SP) and E-effects in others (FW and JK) at 60° tilt. At 120° tilt, all subjects have a clear A-effect of at least 20° in their dark SVV. In all subjects, the effect of the frame line is small when the subject is upright, but becomes more pronounced in tilted subjects where the frame line modulates the SVV with an approximate periodicity of 90°, as in Li and Matin (2005a). In line with the observations in subject FW, the complete data set also illustrates the downshift in the tilted conditions (60 and 120° tilt), with more data points below the horizontal gray band than above. This indicates that varying the frame orientation mostly tends to decrease A-effects and to increase E-effects. Finally, it should be noted that, in the largest tilt condition, the frame-induced downward transitions in the error pattern were more abrupt than upward changes, in several subjects (FW, JG, and SP). This pattern is reminiscent of the skewed profile predicted by both models (see Figs. 2B and 3B).

The black, red, and blue lines in the figure denote the fits, which will be discussed in the following text.

Detailed analysis of frame effect

EFFECT OF BODY TILT. To quantify the magnitude of the frame effect using a descriptive approach that could also capture the skewness predicted by the models, we fitted the following series of two harmonic functions to our frame SVV data for each subject and condition separately

\[
SVV = F_0 + F_1 \cdot \sin(2\theta_r - \Delta \Phi_1) + F_2 \cdot \sin(4\theta_r - \Delta \Phi_2)
\]

(9)

In this equation $F_0$ is the vertical offset of the sinusoid, whereas the other terms represent the modulation with amplitudes $F_1$ and $F_2$ and phase shifts $\Delta \Phi_1$ and $\Delta \Phi_2$ caused by varying the orientation of the frame line in space ($\theta_r$; see Fig. 1).

The black lines in Fig. 4, representing the fits, provide a reasonable description of the data. We used the peak-to-peak amplitude of the fit as a measure for the magnitude of the frame effect. Figure 5 shows that the effect depends on tilt angle. We found a consistent increase from 0 to 60° tilt in all subjects, but when the tilt angle was further increased to 120°, the effect remained roughly constant, with a slight increase in a few subjects and some decrease in others. A paired t-test confirmed that the differences between the 0 and 60° tilt condition ($P < 0.040$).
0.001) and the 0 and 120° tilt condition (P = 0.003) were significant, whereas the difference across subjects between 60 and 120° tilt was not significant (P = 0.73). These findings are roughly in line with previous findings by Bischof and Scheerer (1970) in a slightly different paradigm. These authors observed that the modulating effect of the visual orientation stimulus increased steeply from 0 to 60° tilt, then remained roughly constant up to 120°, followed by a decay at still larger tilt angles.

**A-effects are smaller with than without frame line.** Figure 4 revealed that the complete data set had a downward shift in the tilted conditions (60 and 120° tilt), with most frame SVV data points showing decreased A-effects and increased E-effects. To explore this phenomenon, which was not predicted by either model, Fig. 6 plots the population average of the frame SVV error pattern (solid line) and the population average of the dark SVV (white line), each with the SE (gray band). In upright subjects, the average error is small for all frame line orientations. The average response curves for the tilted conditions further corroborate the impression of a downward shift in Fig. 4. For 60° tilt, the mean response curve is shifted downward and has negative peaks reflecting increased E-effects. Furthermore, the frame SVV at 120° tilt seems to be improved by a broad range of visual frame cues, whereas the frame line almost never deteriorates performance. This indicates that A-effects are generally smaller with the frame line present, in
contrast to the model predictions, which suggested a vertically symmetric modulation.

FRAME LINE PARALLEL TO DARK SVV HAS NO EFFECT. Previous findings in the literature (Mittelstaedt 1986, 1988) suggest that the frame line has no effect when it is aligned with the dark SVV. This observation is confirmed by Fig. 4, which shows that, in almost all subjects and tilt conditions, the frame SVV is close to the intersection of the gray bands indicating the dark SVV. To test this further, Fig. 7 shows a scatterplot of the dark SVV against the frame SVV when the frame line was aligned with the dark SVV. A linear regression revealed a significant correlation ($r = 0.97; P < 0.001; n = 18$), a slope that differed not significantly from unity ($0.96 \pm 0.06$), and an intercept not significantly different from zero ($-0.6 \pm 0.9$). This confirms that a frame line parallel to the dark SVV does not change the perception of visual vertical.

SUBJECTIVE UPRIGHT OF FRAME LINE AND TEST LINE ARE IDENTICAL. As explained in METHODS, subjects estimated the perceived orientation of the frame line on a clock scale before the SVV test line was lit and the adjustment task began. The panels in Fig. 8 present the verbal orientation estimates from subject FW as a function of the actual orientation in space, for each body-tilt angle separately. The solid lines denote a linear fit through the data. All data points scatter along the regression line with a slope close to one. The intercept in the 120° tilt condition, which clearly deviates from zero, denotes a systematic error (A-effect) in the perceived orientation. This analysis was done for all subjects and the resulting intercepts were compared with their dark SVV obtained using the test line. The intercepts were submitted to a two-way ANOVA with the factors “tilt angle” ($\rho = 0$, 60, 120°) and “measurement method” (SVV adjustment, clock estimate), which did not reveal a significant interaction ($P = 0.47$) or a main effect of the measurement method ($P = 0.59$). This analysis suggests that visual space in a tilted observer is rotated but not distorted, confirming earlier work by Van Beuzekom et al. (2001) and Vingerhoets et al. (2008) for a short luminous line. The results show that the visual frame used in our study is subject to the same A-effect (or E-effect) as a short luminous line tested in isolation (dark SVV).

Model fits

Although the harmonic function fits (Fig. 4) yielded a reasonable first-order account of the characteristics in the data, they served only a descriptive purpose and do not provide a conceptual explanation of the present observations. With the latter objective in mind, we have described two conceptual frameworks in METHODS, whose explanatory power will now be tested. In short, the Mittelstaedt model proposes that the perception of visual vertical is constructed by a weighted addition of the gravity vector, the idiotropic vector, and a visual panoramic vector. The Bayesian model computes a statistically optimal estimate of body tilt based on visual and vestibular likelihoods and a prior.

MITTELSTAEDT MODEL. Figure 4 (blue lines) also presents fits of Mittelstaedt’s model to the observed frame SVV error patterns. The model predicts two effects: a positive constant error (A-effect) that increases with tilt angle, due the idiotropic vector, and a periodic modulation that depends on the orientation of the visual frame line. This is indeed the general picture arising from the data. For example, the model predicts no systematic error and only small effects of the frame line in upright subjects. In the tilted conditions, the model is generally capable of matching the increased size of the modulation. Yet,

FIG. 6. Population average of frame effect and dark SVV. Gray bands, SE. For upright the frame effect is small. The frame effect is larger in 60 and 120° tilted subjects. At 60° tilt, the frame can induce larger E-effects; at 120° tilt the frame reduces the A-effects.
the individual fits are not always convincing. For example, the constant offsets are not fitted well in some subjects. The reason is that several subjects show substantial E-effects at 60° tilt, which cannot be reproduced by the model. Across tilt conditions, the model’s $R^2$ scores range from 0.17 to 0.71 (mean SD: 0.34 ± 0.19) as listed in Table 1. This table also shows that the weight of the idiotropic vector ranges from 0.01 to 0.52 (mean SD: 0.23 ± 0.17) across subjects. The effect of this parameter is best understood by comparing subjects JK ($M = 0.01$) and JG ($M = 0.52$) at 120° tilt. Whereas the fit for JK is almost symmetric around the x-axis, the fit curve of JG for this condition shows a substantial vertical offset of about 30°. Fit parameter $V_4$ represents the effect of the frame line. Its value, which ranges from 0.03 to 0.17 (mean SD: 0.11 ± 0.05), highlights the difference between subjects that depend heavily (e.g., JG) or only slightly (e.g., MV) on the visual frame.

BAYESIAN MODEL. To prevent overfitting (see METHODS), we allowed only noise parameter $a_0$ to vary among subjects, whereas the remaining three parameters ($\sigma_0$, $V$, and $a_1$) were determined as a best-fit value across subjects. The fit results are shown in Fig. 4 (red lines). Table 2 shows the fit values for $\sigma_0$, $V$, and $a_1$, corresponding to 15.2°, 3.9, and 0.038, respectively. The positive value for parameter $a_1$ indicates that the noise in the tilt signal must increase with tilt angle if the model is to explain the data. Parameter $a_0$, which represents the vestibular noise level when the subject is upright, ranges from 0.5 to 4.6° (mean SD: 1.9 ± 1.4°). The Bayesian model combines the vestibular likelihood, the frame likelihood, and the prior distribution to obtain the posterior distribution. We assumed that the Bayesian observer uses the peak of the posterior as the best estimate of head tilt (maximum a posteriori [MAP]). Since parameter $a_1$ is positive, the tilt noise increases with tilt angle so that the vestibular likelihood becomes less peaked and broader. As a result, the prior and the frame likelihood are weighted more heavily, causing the constant offset (A-effect) and the frame effect to increase with tilt angle, as shown in all model fits. Along the same lines, when parameter $a_0$ is larger in a particular subject, the vestibular likelihood is already broader at upright and again the frame likelihood and the prior have more weight. This is exemplified by subject JG, who has the largest $a_0$ value and thus a relatively noisy vestibular tilt signal. Consequently, this subject shows the largest bias, induced by the prior, and the strongest visual frame effect, induced by the frame likelihood. For all subjects, fit lines and data match best for 0 and 120° tilt, as in the Mittelstaedt model.
subject, ranging from 0.27 to 0.77 (mean the Mittelstaedt model fit (paired t-test, shown in Table 2, are significantly lower than those of Bayes-ian fits, consistent with data obtained in tilted subjects by Mittelstaedt and Bischof (1974), Bischof and Scheerer (1970), and Eggert (1998).

The model does not entirely replicate the sharp transitions in subjects FW, JG, PB, and SP. The model also has difficulties in accounting for the 60° tilt data, which is mainly due to its inability to simulate the E-effects regularly found at this tilt angle. Yet, everything being taken into account, the Bayesian model provides a better fit to the data than Mittelstaedt’s vector model, as illustrated by the higher $R^2$ values in each individual subject, ranging from 0.27 to 0.77 (mean ± SD: 0.60 ± 0.19). Also, the root-mean-squared error values based on the Bayesian fits, shown in Table 2, are significantly lower than those of the Mittelstaedt model fit (paired t-test, $P < 0.05$).

**DISCUSSION**

**Main findings and relation to earlier studies**

We studied the interaction between the effects of body tilt and a visual frame line on the subjective visual vertical (SVV) at three different tilt angles using a broad range of visual frame orientations. For comparison, we also collected SVV settings in full darkness. In line with earlier reports on the SVV (Kaptein and Van Gisbergen 2004, 2005; Schöne 1964; Udo de Haes 1970; Van Beuzekom and Van Gisbergen 2000), we found that the dark SVV was almost flawless in upright subjects, showed small A-effects or even E-effects at 60° tilt, and large A-effects at 120° tilt. With regard to the frame SVV we made the following observations.

First, frame lines aligned with or perpendicular to the dark SVV had no effect on the perception of vertical. This result is consistent with data obtained in tilted subjects by Mittelstaedt (1986) and by Eggert (1998).

Second, we found that the frame line acted as an attractor for small deviations from the dark SVV, whereas frame line tilts beyond 45 and up to 90° relative to the dark SVV repelled the frame SVV. At a frame tilt of 90° there was no effect. Thus a single frame line modulates the SVV in a cyclical fashion with a 90° period, as if indicating two potential up directions corresponding to its orientation and two perpendicular to it. This 90° periodicity is in agreement with results from Bischof (1974), Bischof and Scheerer (1970), and Eggert (1998), who tested the effect of a stripe pattern on the perception of visual vertical of roll-tilted subjects. In addition, this fourfold periodicity was also observed by Li and Matin (2005a) who tested the SVV in upright observers using a single frame line. The observation by Bischof (1974) that the axis perpendicular to a parallel stripe pattern has a weaker attracting effect than the main axis was not seen in our data.

Our third finding was that the effect of the frame line, while retaining the 90° periodicity, became substantially larger in tilted subjects. The larger frame effect in tilted subjects has also been reported earlier in studies using tilt angles smaller than those in the present study (Asch and Witkin 1948b; Corbett and Enns 2006). This finding is also consistent with reports by Bischof and Scheerer (1970) and Bischof (1974) showing that the effect of the stripe pattern increased with body tilts up to 60°, then leveled off and decreased again beyond tilts of 120°.

Finally, we found that the frame line in tilted conditions usually led to a reduction of the A-effect. At 60° tilt, this trend took the form of E-effects in some subjects. Furthermore, we made the novel observation of steep discontinuities in the frame SVV error pattern in several subjects in the 60 and 120° tilt conditions.

We will now discuss these observations in terms of the two spatial orientation models central to this study.

**Modeling aspects**

**OPTIC–VESTIBULAR INTERACTIONS SUBSERVING SPATIAL VISION.** The vestibular sensors that are involved in spatial orientation have some limitations. For example, the otoliths cannot discriminate inertial forces caused by tilt or translation and the semicircular canals work as a high-pass filter and thus cannot sense low-frequency rotations. It has therefore been proposed that the brain combines information from both sensors to obtain optimal estimates of the motion variables (Droulez and Darlot 1989; Glasauer and Merfeld 1997; Merfeld et al. 1993; Vingerhoets et al. 2006, 2007, 2008; Zupan et al. 2002). Studies of the SVV indicate that canal signals play a role in the computation of the vestibular head-tilt signal (Jaggi-Schwartz and Hess 2003; Lorincz and Hess 2008). Whereas these studies have been mainly concerned with vestibular interactions, our present study focuses on the visual–vestibular interactions. That optic flow information can be used to complement the head angular velocity signal of the canals to determine orientation was shown by Dichgans and colleagues (1972). They reported that upright subjects, viewing a large visual pattern rotating about the roll body axis, felt as if they were moving continuously in the opposite direction and that the visual vertical could deviate by as much as 15° from true vertical.

Likewise, optostatic cues can complement the head-tilt signals provided by vestibular sensors and thus affect the tilt percept. This effect is exploited in amusement parks where tilted houses are used to impose a percept of body tilt in actually upright observers. That simpler visual orientation cues such as a square frame or even a large single visual line can...
affect the percept of vertical probably has an ecological basis. Natural scenes contain an overrepresentation of world-horizontal and world-vertical orientations (Coppola et al. 1998; Svitk es et al. 1978; Van der Schaaf and Van Hateren 1996). The brain can use this information, inferring that the optostatic cues most likely represent world-horizontal or world-vertical orientations. Accordingly, when asked to set a line parallel to the direction of gravity, the setting will deviate in the direction indicated by the visual frame. Before discussing how this notion is implemented in the two models, we first point out that Li and Matin (2005) found no evidence that the Gestalt properties of a rectangle or a square frame have special importance rather than being simply a collection of lines, which implies that the configuration of the frame, as such, has no special significance for its effect. Therefore the two models could, at least in principle, be extended to work for any configuration based on the summed contributions of individual lines, as indicated by Li and Matin (2005).

OPTIC–VESTIBULAR SENSOR FUSION IN THE MITTELSTAEDT AND THE BAYESIAN MODELS. Mittelstaedt (1986, 1988) extended his model to incorporate the effect of visual frame cues on the SVV. In his model, the frame SVV is a weighted sum of three factors: the direction of gravity, the idiotropic vector, and the upward direction indicated by the visual scene. Mittelstaedt tested this model only in 90° tilted subjects. In the present study we extended the test conditions to three different tilt angles: 0°, 60°, and 120°. Along with Mittelstaedt’s idiotropic vector model, we also explored a Bayesian model. Bayesian frameworks have successfully been applied to explain performance in various perception and action domains (Ernst and Banks 2002; Knill and Pouget 2004; Niemeier et al. 2003; Stocker and Simoncelli 2006; Weiss et al. 2002). These models combine various sources of information, to optimize performance in the context of optimal observer theory. A Bayesian interpretation of the idiotropic vector was first formulated by Eggert (1998). More recently, MacNeillage et al. (2007) and De Vrijer et al. (2008) also adopted a Bayesian approach to model the perception of visual vertical. In our Bayesian model, the percept of vertical is based on the vestibular tilt signal, which is assumed to be veridical but corrupted by noise, an a priori assumption that the body is usually upright, and a four-peak frame likelihood representing an inbuilt assumption that natural visual contour distributions have peaks at orientations that are parallel and perpendicular to gravity.

Both models have much in common. In the Mittelstaedt model the A-effect is explained by the idiotropic vector that represents the tendency of tilted subjects to include the long-body axis as a reference for the direction of gravity. In the Bayesian model, the A-effect is the result of including prior knowledge that one is most likely to be upright (see also MacNeillage et al. 2007). Although the formulation is different, Eggert (1998) has shown that the idiotropic vector and the prior are closely related (see APPENDIX B, Structural similarity between Mittelstaedt model and Bayesian model). With certain assumptions, his Bayesian scheme can yield identical results as the Mittelstaedt (1983) model. In addition, Eggert (1998) included visual–vestibular interactions in his model and was able to reproduce the model simulations from Mittelstaedt (1986). This shows that the visual frame stages of both models are also quite similar, by relying on a feedforward structure where the vestibular and the visual signal are combined in a relatively simple way.

The basic idea can best be understood at upright. In this situation, the G and M vectors in the Mittelstaedt model are aligned and, consequently, changing the P vector has a negligible effect. Likewise, in the Bayesian model the peaks of the vestibular likelihood and the prior coincide, leading to a limited influence of the frame likelihood. Along this line, it is interesting to recall that the frame effect is larger in the tilted conditions (see Fig. 5), suggesting that the brain assigns relatively more weight to the visual information when tilted than when upright. Both models can replicate this effect.

The difference between both models originates mainly in the underlying assumptions. Mittelstaedt (1983) proposed that the egocentric bias serves to correct for putative systematic errors in the tilt signal caused by unequal numbers of hair cells in the saccule and the utricle. The Bayesian scheme offers an entirely different alternative without the need to assume that the tilt signal is distorted. In this model, the prior is an element in an optimal strategy to handle noisy tilt signals (De Vrijer et al. 2008; Eggert 1998; MacNeillage et al. 2007). The result of the combination of prior information and sensory information is that the final percept is very stable when the prior and the sensory information are compatible, in this case for tilt angles close to upright. This is useful when the brain has to combine the relatively noisy tilt information with the very precise retinal information about line orientation. Because these small tilt angles occur most often, this would be a smart strategy to optimize performance in daily life. The downside of this computational strategy is that it goes at the expense of systematic errors at large tilt angles that occur only rarely.

Both models performed well in explaining the increase of the frame effect with tilt angle and both replicated the fourfold periodicity in our data. The prediction of both models that a frame line aligned with the dark SVV has no effect was also borne out by the data. From a statistical perspective, the Bayesian model performed somewhat better than the Mittelstaedt model, with an average R² value of 0.60 (SD: 0.19) versus 0.34 (SD: 0.19). This makes the Bayesian model a viable alternative in the understanding of the visual vertical.

It is also important to point out that the models could not explain all the idiosyncrasies of the data, in particular the downward shift in the frame effect (see Fig. 4). It is unlikely that this was caused by stray light of the frame line since we found a high correlation between the dark SVV and the SVV in the presence of a parallel frame line (Fig. 7). Moreover, if stray light was responsible, performance would be improved irrespective of the frame line orientation, which is not what we found. Nonetheless, we cannot exclude that our experimental testing procedure may have caused adaptation because the dark SVV was measured only at the beginning of each experiment. Thus we cannot rule out that the dark SVV has changed during the course of the experiment. For a more decisive conclusion on model performance, measurements at a broader range of tilt angles and keeping track of the dark SVV will be required in the future work.

Another limitation of both models in their present form is that they are unable to account for the E-effect at 60° tilt. In the models, we assumed that the orientation of the frame line and
the SVV test line are perceived without any systematic bias caused by ocular counterroll that occurs during head tilt (Bockisch and Haslwanter 2001; Miller 2nd and Graybiel 1971). However, Wade and Curthoys (1997) concluded that ocular counterroll does affect the SVV, which could explain the E-effects that we observed at 60° tilt. A further refinement of the models could be made by adding a provision for ocular counterroll.

At any rate, both models—which commonly suggest that the percept of vertical is based on visual, vestibular, and egocentric references—provide an inspiring background to guide further investigation of the optic vestibular signal fusion underlying perception of the visual vertical.

**APPENDIX A**

*Mittelstaedt model*

As outlined in Methods, Mittelstaedt (1986, 1988) proposed that the effect of visual cues, the idiotoropic vector, and gravity on the SVV can modeled by representing these cues as vectors: \( G = (0, \sin \rho, \cos \rho) \), \( M = (0, 0, M) \), and \( P = (0, V \sin \theta, V \cos \theta) \). The luminous line that serves as indicator of the SVV is also conceived as a vector: \( L = (0, \sin \beta, \cos \beta) \).

These definitions of \( P \) and \( L \) hold only when both the visual scene and the indicator are uniquely polarized in one direction. The visual frame lines used in our experiment, however, have the same influence on the percept of vertical when they are rotated by 180 or 90° (see Li and Matin 2005a,b) and thus may elicit effects that are functions of multiples of \( \theta \). To account for the 90° periodicity, \( L \) and \( P \) can be extended as follows

\[
L = \left[ 0, \sum_{n=1}^{4} L_n \sin (n\beta), \sum_{n=1}^{4} L_n \cos (n\beta) \right]
\]

and

\[
P = \left[ 0, \sum_{n=1}^{4} P_n \sin (n\theta), \sum_{n=1}^{4} P_n \cos (n\theta) \right]
\]

In the model, the observer rotates the indicator \( L \), until the following cross-product equals zero

\[
L \times (G + M + P) = L \times (G + M) + L \times P = 0 \quad (A1)
\]

Further specification of the first term, denoted as the gravito-idiotoropic term, yields

\[
\sum_{n=1}^{4} L_n \sin (n\beta) \cdot (G \cos \rho + M) - \sum_{n=1}^{4} L_n \cos (n\beta) \cdot G \sin \rho \quad (A2)
\]

Similarly, specifying the second term gives

\[
\sum_{n=1}^{4} P_n \sin (n\beta) \cdot \cos (n\theta) - \sum_{n=1}^{4} P_n \cos (n\beta) \cdot \sin (n\theta) \quad (A3)
\]

which can be simplified to

\[
\sum_{n=1}^{4} P_n L_n \sin [n(\beta - \theta)] \quad (A4)
\]

In Mittelstaedt’s model, gravity is normalized \( (G = 1) \) and it is assumed that only the first-order term of the gravito-idiotoropic contribution adds to the complete equation that determines the SVV

\[
sin \beta \cdot (\cos \rho + M) - \cos \beta \sin \rho + \sum_{n=1}^{4} V_n \sin [n(\beta - \theta)] \quad (A5)
\]

with \( V_n = P_n L_n / L_1 \). In line with the findings from Li and Matin (2005a,b) we found a fourfold periodicity, which implies that components \( V_1, V_2, \) and \( V_3 \) of our simple frame stimulus did not contribute significantly to our fits. In the present testing conditions, Eq. A5 can therefore be simplified to

\[
sin \beta \cdot (\cos \rho + M) - \cos \beta \sin \rho + V_4 \sin 4(\beta - \theta) = 0 \quad (A6)
\]

**APPENDIX B**

*Structural similarity of Mittelstaedt model and Bayesian model*

In Methods we have portrayed the Mittelstaedt model and the Bayesian model as two distinct approaches for describing the visual vertical in the presence of visual frame cues (Eggert 1998). At a more abstract level, however, Eggert (1998) has shown that both model structures are very closely related. This similarity can be understood if we first rearrange terms and rewrite Eq. 4 (the Mittelstaedt model) as follows

\[
M \sin \beta + \sin (\beta - \rho) + V_4 \sin 4(\beta - \theta) = 0 \quad (B1)
\]

In our Bayesian model, we took the tilt angle with the highest probability, i.e., the maximum a posteriori (MAP), as the final model prediction of the head tilt signal. To find the maximum of the posterior of the Bayesian model (Eq. 7), we differentiate the logarithm of Eq. 7 with respect to \( \rho \) and rewrite it as

\[
\frac{\partial}{\partial \rho} \ln k + \frac{\partial}{\partial \rho} \ln [P(\rho|\beta)] + \frac{\partial}{\partial \rho} \ln [P(\theta|\beta)] + \frac{\partial}{\partial \rho} \ln [P(\rho)] = 0 \quad (B2)
\]

In this equation we can substitute the Gaussians for the prior and the vestibular likelihood and the von Mises distribution \( (Eq. 8) \) for the frame likelihood. With \( \beta \) the solution to this equation, it follows that

\[
\frac{\beta}{\sigma_{r}^2} + \left( \frac{\beta - \rho}{\sigma_{\theta}^2} \right) + V_4 \sin 4(\beta - \theta) = 0 \quad (B3)
\]

which is structurally identical to Eq. B1. Note also that Eq. B3 does not have one parameter more than Eq. B1 because by multiplying both sides of Eq. B3 by \( \sigma_{\theta}^2 \) it can be recognized that \( M \) corresponds to \( \sigma_{\theta}^2 / \sigma_{r}^2 \) and \( V_4 \) to \( V^* \sigma_{\theta}^2 / \sigma_{r}^2 \). These correspondences imply \( M > 0 \).

**ACKNOWLEDGMENTS**

We thank H. Kleijnen, G. van Lingen, S. Martens, and G. Windau for technical support and the anonymous referees for many valuable suggestions to improve an earlier version of this manuscript.

**GRANTS**

This work was supported by Nijmegen Institute for Cognition and Information and Faculteit der Natuurwetenschappen, Wiskunde en Informatica of Radboud University Nijmegen. Further support came from grants of the Netherlands Organisation for Scientific Research and the Human Frontier Science Program awarded to W. P. Medendorp.

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