Verticity Perception During Off-Vertical Axis Rotation

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Vingerhoets RA, Van Gisbergen JA, Medendorp WP. Verticity perception during off-vertical axis rotation. J Neurophysiol 97: 3256–3268, 2007. First published February 28, 2007; doi:10.1152/jn.01333.2006. During prolonged rotation about a tilted yaw axis, often referred to as off-vertical axis rotation (OVAR), a perception of being translated along a conical path slowly emerges as the sense of rotation subsides. Recently, it was found that these perceptual changes are consistent with a canal–otolith interaction model that attributes the illusory translation percept to improper interpretation of the ambiguous otolith signals. The model further predicts that the illusory translation percept must be accompanied by slowly worsening tilt underestimates. Here, we tested this prediction in six subjects by measuring the time course of the subjective visual vertical (SVV) during OVAR stimulation at three different tilt-rotation speed combinations, in complete darkness. Throughout the 2-min run, at each left-ear-down and right-ear-down position, the subject indicated whether a briefly flashed line deviated clockwise or counterclockwise from vertical to determine the SVV with an adaptive staircase procedure. Typically, SVV errors indicating tilt underestimation were already present at rotation onset and then increased exponentially to an asymptotic value, reached at about 60 s after rotation onset. The initial error in the SVV was highly correlated to the response error in a static tilt control experiment. The subsequent increase in error depended on both rotation speed and OVAR tilt angle, in a manner predicted by the canal–otolith interaction model. We conclude that verticity misjudgments during OVAR reflect a dynamic component linked to canal–otolith interaction, superimposed on a tilt-related component that is also expressed under stationary conditions.

INTRODUCTION

To ensure perceptual stability and a veridical percept of verticity, we use information about self-orientation and self-motion from various sensory modalities, in particular the visual and vestibular system. The vestibular system has specialized organs for detecting rotational acceleration (the semicircular canals) and for sensing linear acceleration (the otoliths). Like any linear accelerometer, the otoliths sense both inertial and gravitational accelerations, so that their signal is ambiguous as to the source of the gravitoinertial force (GIF). For a correct interpretation, the brain has to solve the nontrivial inverse problem of determining whether the otolith signal was caused by tilt, by translation, or by a combination of these motions.

Previously it was suggested that the brain resolves the ambiguity problem by using frequency filtering of the otolith signal. According to this account, low-frequency otolith components are interpreted as the result of gravitational acceleration (tilt), whereas high-frequency components are attributed to inertial accelerations (Mayne 1974; Paige and Seidman 1999; Paige and Tomko 1991; Seidman et al. 1998; Telford et al. 1997). An alternative hypothesis proposes that the brain disambiguates otolith information by exploiting information from the canals (Angelaki et al. 1999; Droulez and Darlot 1989; Glasauer 1992; Glasauer and Merfeld 1997; Merfeld et al. 1993; Merfeld and Zupan 2002; Zupan et al. 2002). This so-called canal–otolith interaction model assumes that otolith signals accompanied by a canal signal are caused by head tilt, whereas otolith signals in the absence of rotational canal cues reflect inertial accelerations arising from translations of the head. Merfeld et al. (2005a,b) found support for either hypothesis in different domains. The filtering hypothesis best explained otolith disambiguation in the action domain (i.e., the vestibuloocular reflex), whereas perception data appeared more compatible with a canal–otolith interaction model. Because the present study focuses on perception, the filtering model will not be considered further.

A schematic representation of the canal–otolith interaction model is shown in Fig. 1A. The core of this scheme, the internal model, transforms inputs from the canals and the otoliths into three internal variables that play crucial roles in disambiguation in verticality perception during motion, which is the main topic of the present investigation. Merfeld et al. (2001) tested the subjective visual horizontal in subjects who were seated upright while being subjected to fixed-radius yaw rotation in a centrifuge. As expected from earlier studies (Clark and Graybiel 1966; Curthoys 1996; Graybiel and Brown 1951), these subjects experienced tilt, but their horizontality settings clearly lagged behind the rotation of the GIF. Merfeld et al. (2001) also performed a variable-radius centrifuge experiment
where subjects were first rotated on axis for several minutes. The radius was then varied to yield the same centrifugal force profile as that in the fixed-radius trials. In contrast with the lag observed in the fixed-radius experiment, such a delay was no longer found. An important difference between the variable-radius and fixed-radius trials is the presence of canal cues in the latter, which were therefore held responsible for the lag observed in the fixed-radius paradigm (Merfeld et al. 2001). In other words, Merfeld et al. (2001) interpreted the delay in terms of a gradually disappearing sensory conflict between the canal and otolith signals. The canal cues initially indicate yaw rotation, whereas the otoliths sense a change of the GIF in the roll plane. Only when the canal activity has dissipated, the sensory conflict is resolved and the otolith signals are reluctantly interpreted as due to tilt.

These centrifuge experiments suggest that a change in the GIF vector induced by linear acceleration may be centrally interpreted as a change in tilt. Can tilt also be interpreted as translation? A paradigm where this might occur is off-vertical axis rotation (OVAR), where subjects are rotated in yaw at a constant velocity about an axis that is tilted relative to the direction of gravity (Fig. 2A). Because of the tilted axis, head orientation changes continuously with respect to gravity, as the body alternates between roll and pitch tilt. In a recent study (Vingerhoets et al. 2006), following up on earlier investigations by Denise et al. (1988) and Guedry (1974), we showed that the initially veridical rotation percept during prolonged OVAR decays gradually (Fig. 2B) and that a percept of circular head translation against the actual direction of movement emerges concurrently (Fig. 2C and D). We found that the illusory translation percept matched the predictions of the canal–otolith interaction model fairly well, provided that a leaky integrator was included in the translation pathway (see Fig. 1A).

Unless there are phase shifts between perceived tilt and actual tilt, the canal–otolith interaction model implies that when decomposition of the GIF vector errs toward overestimating translation, the tilt estimate will have an opposite bias.
Thus the canal–otolith interaction hypothesis predicts that the gradually developing illusory translation percept during OVAR (Fig. 2D) must be accompanied by a gradually emerging underestimation of tilt. The present study tested this specific prediction quantitatively, using the OVAR stimulation paradigm. We also tested whether these experiments would support the extension of the canal–otolith interaction model with the idiotropic mechanism (h in Fig. 1A) that has been proposed on the basis of static tilt experiments (Mittelstaedt 1983). In its original form, the model predicts that subjects in static roll-tilt conditions have correct percepts about the direction of gravity after a transient period (see black line in Fig. 1C). However, many reports showed that stationary subjects, tilted sideways in darkness, make systematic errors when adjusting a luminous line parallel to the perceived direction of gravity. At large tilt angles, the subjective visual vertical (SVV) deviates toward the long-body axis [Aubert effect (SVV)] deviates toward the long-body axis [Aubert effect (A-effect)], as if tilt is underestimated, with errors amounting to 35° when the body is tilted 120° (Kaptein and Van Gisbergen 2004, 2005; Mittelstaedt 1983, 1989; Schöne 1964; Udo de Haes 1970; Van Beuzekom and Van Gisbergen 2000). For small body tilts (<30°), these errors are generally much smaller and may even reverse sign [Müller effect (E-effect)]

Most of these static tilt studies have suggested that the computation of the SVV depends heavily on the otoliths, whose signal in stationary conditions reflects the pull of gravity (Eggett 1998; Mittelstaedt 1983, 1989; Schöne 1964). There is no reason to hold disambiguation errors responsible for the A-effect because it has never been reported that stationary tilted subjects experience an illusory awareness of being translated. Instead, Mittelstaedt’s original model (Mittelstaedt 1983), which does not incorporate a solution for the ambiguity problem, explained the A-effect as the result of a bias signal, known as the idiotropic vector. This head-fixed vector was seen as a computational strategy to mitigate the effect of a putative imbalance in the otolith signal at small tilts, at the expense of large systematic errors at the rarely encountered large tilt angles. As in Mittelsteadt et al. (1989) and Zupan et al. (2002), we incorporated a head vector contribution in the scheme of Fig. 1A, which explains the static A-effects in verticality perception. Inspired by several studies (Dyde et al. 2006; Groen et al. 2002; Mittelstaedt 1983; Zupan and Merfeld 2005; Zupan et al. 2002), we modeled the subjective vertical as a weighted vector sum of the estimated direction of gravity and the direction of the long-body axis (\( \hat{g} = \hat{g} + w \cdot h \); see Fig. 1B). Parameter \( w \) is a tilt-independent variable, which represents the relative weights of these two vectors and can vary across subjects. Head vector \( h \) has virtually no effect on verticality perception when estimated head tilt is small.

The ability of the extended model to account for the static A-effect is illustrated in Fig. 1C, showing both the actual roll-tilt angle and \( \hat{g} \). The dashed line indicates a constant velocity roll rotation to a final tilt angle of 45°. With a moderate weight \( (w = 0.2) \) of head vector \( h \), the model replicates the well-known finding in the SVV literature that the roll-tilt angle implied by \( \hat{g} \) (gray line) is substantially smaller than the actual tilt angle (38 instead of 45°). This systematic error in the SVV, which has been confirmed experimentally from 2 to 90 s after rotation stop (Jaggi-Schwarz and Hess 2003), cannot be reproduced by the original canal–otolith interaction model, lacking the bias signal \( (w = 0) \), as shown by the black line.

Predictions of the extended model for one of our OVAR experiments, are shown in Fig. 1D. Perceived roll tilt, reflected in the SVV, demonstrates that tilt is increasingly underestimated as time during OVAR proceeds and that the head-referenced bias \( (w \cdot h) \) induces an additional underestimation (gray line), right from rotation onset. Because the effect of head vector \( h \) depends on \( \hat{g} \), it is not entirely constant over time. The other panels illustrate that an illusory percept of translation develops slowly over time, whereas rotation perception decays exponentially to nonzero values.

To test the SVV predictions of the extended model, we investigated whether the SVV in extreme roll-tilt positions during OVAR indeed shows a gradually developing underestimation of tilt, superimposed on a tilt-related bias. To do so, we used three different combinations of tilt angle and rotation speed, testing how the time course of the SVV depends on these factors. We also assessed the SVV in a static tilt experiment, for comparison with the possible tilt-related error component in the dynamic data. Our results suggest that the canal–otolith interaction model can explain the SVV data during OVAR when extended by an idiotropic mechanism.

**METHODS**

**Subjects**

Six subjects (five male, one female), whose ages ranged between 25 and 62 yr (mean ± SD: 33 ± 14 yr), gave written informed consent to participate in the experiments. Four of them (JG, NK, RV, and SP)
also participated in our previous OVAR study (Vingerhoets et al. 2006). Four subjects (MV, NK, SP, and TG) were totally naïve regarding experimental goals. Subjects did not have any known visual, vestibular, or other neurological disorders.

**Setup**

Subjects were seated comfortably in a motor-driven and computer-controlled vestibular chair. The apparatus consisted of three adjustable, nested frames that could be arranged to allow subject rotation about any axis in space. For the present experiments, the setup was configured to rotate subjects in yaw about an off-vertical axis. In the chair, subjects were secured with safety belts, hip and shoulder supports, and Velcro straps around the feet. The head was firmly fixated in a natural upright position for looking straight ahead, using a padded adjustable helmet. The rotation axis of the chair was aligned with the center of the interaural axis, parallel to the long-body axis. The right eye was patched to prevent double vision.

A uniformly illuminated line with an angular subtense of 22° was attached to the chair at 0.80 m in front of the subject. The line could be controlled by computer with an angular resolution of 0.5°. The rotation axis of the line, which was parallel to the subject’s nasoocipital axis and intersected the subject’s skull midway between the two eyes, was perpendicular to the rotation axis of the chair, so that the line could be rotated in the frontoparallel plane. At the time when tests were taken, at each left-ear-down (LED) and right-ear-down (RED) position, this plane was perpendicular to the floor. The line was polarized by a bright dot at one end and served to determine the subjects’ dynamic and static SVV.

**Experimental paradigms**

The subjective visual vertical was tested under both dynamic and static conditions, in two separate series of experiments. All experiments took place in complete darkness. Subjects were allowed to move their eyes freely at all times.

**DYNAMIC SVV.** In the dynamic experiments, subjects were rotated clockwise (CW) (seen from above) about the yaw axis, which was tilted (15 or 45°) relative to the earth-vertical (i.e., off-vertical axis rotation (OVAR)). After the subject was restrained, the chair was pitched backward to the tilt angle chosen for the experiment and then rotated to the LED starting position. After 10 s of rest in that position, the chair was accelerated within 1 s to the constant velocity (30 or 50°/s) to be tested in the experiment, which was then maintained for 2 min.

To test the subjects’ SVV at various points in time after rotation onset, we used an adaptive yes/no procedure. Each time during the run when the subject passed through the LED and RED phase, the luminous line in the frontoparallel plane was flashed for 10 ms at a certain orientation specified by computer. Shortly after the flash, subjects used a toggle switch to indicate whether the line deviated from either the CW or the counterclockwise (CCW) direction from their perceived direction of the vertical. An adaptive staircase procedure used the set of responses collected in the series of trials from a given run to update the orientation of the line to be presented at the same test points in the next run (for further details see Adaptive-staircase procedure). The purpose of this procedure was to adjust the orientation of the line in small steps, run after run, until it appeared earth-vertical to the subject.

Because subjects were tested in the LED and RED phases, where physical roll tilt was maximal (see Fig. 2C), the interval between the sequential line flashes was 6 s for the 30°/s runs and 3.6 s for the 50°/s runs. Between runs, subjects were stationary in the nose-up position for 90 s, with the room lights on, to allow reorientation. Subjects were tested for three combinations of tilt angle and rotation velocity: 45° tilt at 30°/s, 45° tilt at 50°/s, and 15° tilt at 50°/s in separate sessions. We will refer to these conditions as the large-tilt & high-speed condition, the large-tilt & high-speed condition, and the small-tilt & high-speed condition, respectively. Testing in each condition consisted of 20 runs, subdivided in two experimental sessions of about 40 min each. Because of the potentially nauseous nature of the OVAR stimulus, the first experimental session of each subject tested the least provocative condition (45° tilt at 30°/s). Subjects never received feedback about their performance.

**STATIC SVV.** We used the static paradigm to examine the subjective vertical during static roll tilt. The subject was first pitched backward (15 or 45° relative to gravity) and then rotated by 90° at 20°/s about this off-vertical axis to either the LED or the RED position, in alternating runs. Once this stationary tilt position was reached, there was a 10-s waiting period before testing began. To determine the static SVV, we used the same yes/no design as in the dynamic experiment, except that testing in a given run was now limited to five consecutive flashes. Subsequently, the subject was rotated back to the nose-up orientation for a 30-s rest period with the room lights on to allow reorientation. In two separate sessions, subjects were tested at the two different tilt angles (15° LED/RED and 45° LED/RED). Each session took about 45 min and consisted of 15 runs.

**Definition of angles**

Because subjects were tested in the LED and the RED phases of rotation, the amount of physical head roll-tilt equaled the tilt angle of the rotation axis. Accordingly, head roll-tilt, denoted by ρ, was −15 or −45° for LED and +15 or +45° for RED. Response error, indicated by γ, was defined as the angular difference between the SVV and the true vertical (see inset Fig. 3A). SVV deviations in the CW direction (seen from behind the subject) were taken as positive. Accordingly, an SVV setting biased in the direction of body tilt (A-effect) yields a positive γ value in the RED phase (Fig. 3A, inset) and a negative γ value in the LED phase. A bias in the opposite direction (E-effect) yields negative and positive γ values for the RED and LED phase, respectively.

**Adaptive-staircase procedure**

In both paradigms, we used a sequential set of adaptive staircases to determine the time course of the subject’s SVV after the onset of OVAR stimulation. Each adaptive staircase in this set was designed to test the SVV repeatedly, across runs, at one particular point in time after OVAR onset. Each new run added a further test step to all staircases by presenting the luminous line at an orientation based on the response at that same point in time in the previous run. Thus if the subject’s response to the first line stimulus testing the SVV at time Tn was “clockwise,” the line testing the SVV at Tn in the next run would be presented at a more counterclockwise orientation (see definition of step size below), and so on, until the response to the Tn trial in a subsequent run reversed to “counterclockwise.” Such a response reversal then started a series of adjustments in the opposite direction until the next response reversal occurred. After many runs, the accumulated set of responses across all sequential runs invariably showed an adaptive staircase pattern that converged on the line orientation that the subject considered vertical at a particular point in time after rotation onset. The SVV was defined as the line orientation at which the response in repeated trials fluctuated between “clockwise” and “counterclockwise.” Applying this procedure of gradually completing a sequential set of independent staircase procedures allowed us to sample the dynamic evolution of the SVV in time intervals of a few seconds (6 s for 30°/s runs and 3.6 s for the 50°/s runs; see above). The staircase began with a 8° step size ±1° scatter that was reduced to 4° ±1° scatter after two reversals and further reduced to 2° step size ±1° scatter after four reversals. In all subjects, the staircase results from the dynamic experiments yielded at least six reversals (typically 8 to 14). In the static experiments, where only 15
IMPROVED MODEL PARAMETERS. We used Matlab 7.0 and Simulink 6.0 (The MathWorks) to simulate the canal–otolith interaction model outlined in Fig. 1A. This scheme is based on the model proposed by Merfeld and Zupan (2002), but extended with a stage including a weighted head vector (h) (Mittelstaedt et al. 1989; Zupan et al. 2002). In model version C3, which emerged as optimal in Vingerhoets et al. (2006), the four internal model parameter values were \( k_a = -4 \), \( k_f = 2 \text{s}^{-1} \), \( k_{sv} = 8 \text{s}^{-1} \), and \( k_w = 8 \). In the previous study, we reported that this model version provided a good fit to the observed translation percepts during OVAR. However, in testing the model’s performance, we overlooked one of its important features—the predicted phase lags. These can be quite substantial and should be taken into account in a proper model evaluation. In the present study, we therefore decided to recalculate the best-fit parameters for all rotation and translation data of Vingerhoets et al. (2006) but now taking the phase shift into account. As in Vingerhoets et al. (2006) we first determined the best-fit time constant of the leaky integrator by minimizing the sum of squared errors, keeping the internal model parameters fixed at values published in Merfeld et al. (2005a). Accounting for the phase shift led to a longer time constant of the leaky integrator of 0.06 s. Subsequently, we searched within a limited parameter space (testing values of \(-0.5, -1, -2, -4, \) and \(-8\) for \( k_a \) and \( 0.5, 1, 2, 4, \) and \( 8 \) for the other parameters) for the internal model parameter set that yielded the smallest sum of squared errors. The parameters that provided the best description were \( k_a = -4, k_f = 4 \text{s}^{-1}, k_{sv} = 8 \text{s}^{-1}, \) and \( k_w = 8 \), which means that only parameter \( k_w \) was changed from 2 to 4 in comparison with model C3 from Vingerhoets et al. (2006). The corrected-fit curves, showing only minute differences with the originals shown in Fig. 15, A and B of our previous paper, match these data quite well. The revised parameter set was held fixed for all subjects, leaving only the weight of the head vector as a free parameter among individual subjects.

We could not obtain a best-fit parameter set based on rotation, translation, and tilt percepts in individual subjects because not all subjects participated in both OVAR studies. We therefore determined the best-fit parameters across the group of subjects because we sought to include data on all percepts.

MODEL PREDICTIONS. The model prediction for the SVV was based on the vector sum of the orientation of gravity with respect to the head and a weighted head vector (i.e., \( \mathbf{g} \equiv \mathbf{g} + w \mathbf{h} \)). Vector \( \mathbf{h} \) points downward along the main body axis with a magnitude of 1 G and parameter \( w \) denotes its weight (see Fig. 1B). Because the SVV responses yielded only the directional error of \( \mathbf{g} \), not its amplitude, we could determine only the relative weighting of the two vectors. Therefore we fixed the gain of \( \mathbf{g} \) to unity and allowed \( w \) to vary freely across subjects. The model prediction for the SVV data was taken as \( \text{SVV} = \text{atan} (\mathbf{g} / \hat{w}) \).

Model predictions for the SVV depend on OVAR conditions and the weight of the head vector. The left column of Fig. 4 shows the actual roll tilt of the chair (solid line) and the predicted perceived roll tilt (dashed line), defined as \( \text{atan} (\hat{g} / \hat{w}) \). The model predicts a gradually worsening underestimation of tilt and a steadily increasing phase lag for all conditions. Both the underestimation of tilt and the phase lag are more pronounced for higher speeds. Measurements were taken at the physical LED and RED positions, but because of the phase lag, there is a time shift with respect to the perceived LED and RED positions predicted by the model. This phase shift (\( \Delta \theta \)) is plotted in the insets in the right panels, which show that phase shift increases exponentially in time and levels off at a value depending on rotation speed and tilt angle. The lag is not constant because it depends on the model’s estimate of angular velocity (\( \omega \)), which declines slowly. In the model, angular velocity is determined using the canal signals, which dissipate during prolonged rotation with a given time constant. An internal feedback loop, which takes the angular difference between the GIF measured by the otoliths and estimated GIF as a measure for angular velocity, extends this time constant, but underestimation will ultimately ensue. Because the phase shift between \( \hat{g} \) and \( g \) depends on
the cross-product of \( \hat{\omega} \) and \( \hat{g} \), a time-varying \( \hat{\omega} \) will lead to a time-varying phase shift.

The predicted errors for LED and RED are indicated in the right panels of Fig. 4, showing predictions with \( (w = 0.2) \) and without \( (w = 0) \) head vector contribution. In the absence of a tilt-related bias \( (w = 0, \) thin line), the model, based on signal \( \hat{g} \), predicts relatively small errors in the large-tilt & low-speed condition. Predicted errors show an exponential increase to a substantially larger asymptotic value of about 12° in the large-tilt & high-speed condition and to 7° in the small-tilt & high-speed condition. Thus predicted dynamic effects are more prominent for the high-speed conditions. As shown by thick lines, involvement of the head vector \( (w = 0.2) \) adds a bias that is already present at rotation onset. For the large-tilt conditions this bias is about 8°, whereas for the small-tilt condition it is limited to about 3°. Note that the effect of the head vector is largest at rotation onset and decreases slightly when the direction of \( \hat{g} \) approaches \( \hat{h} \) later in the run.

MODEL EVALUATION. In the RESULTS section we compare the performance of three model versions. The first two model versions, one with and one without an idiotropic mechanism, are outlined earlier and in Fig. 4. A third version of the model, which is not discussed in Fig. 4, is inspired by the original model proposed by Mittelstaedt (1983). This version assumes no dynamic disambiguation error, but only a constant bias from the idiotropic mechanism. The model versions were compared with actual data using the root mean squared error (RMSE), the variance-accounted-for percentage (VAF), and the Bayesian Information Criterion (BIC). The RMSE is defined as the square root of the mean quadratic distance between the data points and the corresponding model prediction

\[
RMSE_i = \sqrt{\frac{1}{N} \sum_{n=1}^{N} [\Psi(n) - \hat{\Psi}(n)]^2}
\]

where \( \Psi(n) \) is data point \( n \), \( \hat{\Psi}(n) \) is the corresponding value estimated from model \( i \) and \( N \) is the number of data points. Accordingly, smaller RMSE values indicate a better fit. The VAF provides a normalized measure for how well the model predicts the variance of the data and is defined as:

\[
VAF_i = \frac{1}{1 - \text{var}\{\Psi - \hat{\Psi} / \text{var}\{\Psi}\}} \times 100
\]

where \( \Psi \) represents the data and \( \hat{\Psi} \) is the model prediction from model \( i \) (Cullen et al. 1996; Green and Angelaki 2003). A value closer to 100 indicates a better fit. The BIC, which provides a measure of the adequacy of the number of model parameters, is defined as:

\[
\text{BIC}_i = \log \left( \frac{1}{N} \sum_{n=1}^{N} [\Psi(n) - \hat{\Psi}(n)]^2 \right) + (P/2) \log (N/N)
\]

where \( P \) is the number of fit parameters (Green and Angelaki 2003; Schwarz 1978). A more appropriate model is characterized by a lower BIC value.

RESULTS

We studied the sense of verticality during OVAR to test the extended canal–otolith interaction model presented in Fig. 1A. The model predicts errors in the SVV, stemming from two different sources (Fig. 4). First, the decay of rotational cues from the canals during prolonged OVAR causes misinterpretation of the otolith signals in the form of gradually worsening tilt underestimation. Second, the idiotropic mechanism \( (\hat{h}) \) causes further tilt underestimation by biasing the subjective vertical toward the long-body axis, right from rotation onset onward, particularly at larger tilts. We will first report the SVV results in static conditions of 15 and 45° roll tilt to document the idiotropic effect. Subsequently, we present the data on the SVV during OVAR and test whether errors from both origins can be identified.

Static SVV

Classical descriptions of the SVV in tilted subjects (Mittelstaedt 1983; Schöne 1964; Udo de Haes 1970) report A-effects for large-tilt angles and reduced A-effects or E-effects for small-tilt angles. We saw the same trend in our static paradigm...
of tilt angle on the SVV in each subject \([F(1,16) > 8.2; P \leq 0.01\) for each subject\]. In five out of six subjects, there was a significant effect of tilt direction (LED/RED) on the SVV settings \([F(1,16) > 8.7; P \leq 0.01\) for these five subjects\], confirming the suggestion of response asymmetry in Fig. 5.

**Dynamic SVV**

As mentioned earlier, the model (Fig. 1A) predicts two types of errors during dynamic OVAR conditions: an offset that is most prominent in the large-tilt conditions and a dynamic, time-dependent component that is most pronounced in the high-speed conditions (Fig. 4). Figure 6 shows the time course of the SVV errors from subject MV. All three testing conditions caused tilt underestimation, expressed as positive errors for RED and as negative errors for LED. As in the static experiment, LED and RED responses were not precisely symmetric. Close inspection of the two large-tilt conditions (Fig. 6, A and B) reveals that the response, in both LED and RED positions, already shows an A-effect right at rotation onset, indicating a tilt-related bias. The high-speed responses comply with the model (Fig. 4) by showing substantial dynamic effects. In both panels, errors in the SVV increase exponentially with time to a steady-state value after about 60 s. As predicted, the dynamic component was more striking in the high-speed conditions, whereas the bias was more obvious in the large-tilt conditions. In summary, the data from this subject support the model predictions by showing a dynamic response error pattern that seems superimposed on a tilt-related offset. The bold lines in Fig. 6 represent model predictions (discussed later in this section).

**Relation between dynamic and static results**

We observed that virtually all subjects already made systematic SVV errors at the onset of rotation. If this error has the same size as the static error shown in Fig. 5, this would suggest the expression of a head bias in dynamic conditions, in line with the scheme in Fig. 1A. To investigate this, in a lumped comparison across all subjects, we plotted the error observed in the static tilt paradigm (static SVV error) against the error in the first measurement after rotation onset in the dynamic

![Figure 5](image1.jpg)

**FIG. 5.** Bar plot of mean SVV errors (±SD) during the static experiment. White bars: LED; black bars: RED. Signs of SVV errors for LED were inverted for illustrative purposes. Positive errors denote an A-effect; negative errors indicate a Müller effect (E-effect). A: errors in the static experiment at 45° tilt. Apart from NK and TG, all subjects show A-effects for both RED and LED. Mean error for LED 3.3°; mean error for RED 5.2°. B: errors in the static experiment at 15° tilt. A-effects became smaller or even reversed to E-effects, compared with the 45° tilt condition. Mean error for LED −1.8°; mean error for RED −2.6°.

![Figure 6](image2.jpg)

**FIG. 6.** Time course of errors in SVV during OVAR. Open circles: LED trial data; filled circles: RED trial data; solid line: model fit with \(w = 0.2\). Data from subject MV. A: errors in the 30°/s and 45° tilt condition do not start at zero and show a slight increase as rotation continues. B: errors are already present at \(t = 0\) in the 50°/s and 45° tilt condition; dynamic increase in tilt underestimation is about 15°. C: in the 50°/s and 15° tilt condition, errors are initially smaller but again show a slight increase with time.
paradigm (initial dynamic SVV error), at corresponding tilt angles. In this analysis, shown in Fig. 7, we inverted the sign of the LED data to allow pooling with RED data.

A linear regression, which quantified the apparent relationship, revealed a significant correlation ($r = 0.76; P < 0.001; n = 36$), a slope not significantly different from unity ($0.81 \pm 0.12$), and an intercept close to zero ($-2.4 \pm 1.0^\circ$). This suggests that the errors occurring at OVAR onset, whether expressed as an A-effect or an E-effect, resemble those in corresponding static tilt conditions. In other words, the A- and E-effects found in static conditions reflect a tilt-related mechanism that also comes into play when the same tilt angle is tested dynamically.

The dynamic component

In the previous section it was shown that the bias in the SVV in dynamic conditions is quite similar to the SVV in static tests at the same tilt angle. We will now explore whether the remaining time-dependent part of the response can be explained by the canal–otolith interaction model ($w = 0$). To this end, we isolated the dynamic component by subtracting the static response from the total response in each subject and then pooled the result over subjects. Figure 8 shows that the population average (solid line) has a clear dynamic component, which is quite well matched by the predictions of the canal–otolith interaction model (dashed line). Both model and data show a weak dynamic effect in the large-tilt & low-speed condition that becomes more substantial for the small-tilt & high-speed condition and is most pronounced in the large-tilt & high-speed condition. Thus for the pooled data, the time-dependent component of verticality judgments observed during OVAR may be regarded as a genuine manifestation of improper disambiguation of the otolith signal. The evaluation of the combined model on a more individual basis is presented in the next section.

Evaluation of combined model

The notion, that SVV errors during prolonged OVAR contain a static contribution, which can also be observed in stationary (nonmoving) subjects, and a disambiguation contribution that depends on tilt angle and rotation speed, will now be tested further. To test the dependency of the SVV ($\tilde{g}$) on these two factors quantitatively, we fitted parameter $w$ in the extended model to the data from each subject separately

$$\tilde{g}(t) = \tilde{g}(t) + w \cdot h$$  

In this equation $\tilde{g}(t)$ is the internal representation of gravity, $h$ is the head vector, and $w$ represents the weight of the head vector, used as a free parameter. As an example, using $w = 0.2$, the thick lines in the right column of Fig. 4 (labeled Combined) illustrate predictions of this model. The panels clearly show the offset and the dynamic effect.

For comparison, we also computed the residual error between data and original model, without the idiotropic mechanism

$$\tilde{g}(t) = \tilde{g}(t)$$  

In essence, this equation is identical to Eq. 1 with $w = 0$. Figure 4 also shows predictions of this version (thin lines, labeled Dynamic only) where only the dynamic effect remains. Likewise, to assess whether the dynamic contribution is essential, we fitted a version with only the idiotropic mechanism

$$\tilde{g}(t) = \tilde{g}(t) + w \cdot h$$  

In this equation $\tilde{g}_0$ is the true direction of gravity represented in a head-fixed coordinate frame. This model version assumes no disambiguation errors, only the constant bias from Eq. 1.

We obtained the error in the SVV, predicted by each of the three model versions, by taking the difference between actual roll tilt and roll tilt reflected by the SVV, computed as atan ($\tilde{g}_y/\tilde{g}_x$). Fits were simultaneously performed on all static and dynamic data. From our experiments, we obtained a total of 20 static data points and 88 dynamic data points for each subject. To give equal weight to the static and dynamic data in our fit procedure, we extended the static data points with the mean of the five measurements such that the number of data points in the static condition matched the number of data points in the corresponding dynamic paradigm.

As a measure of how well each model version fitted the data, we used the root mean squared error (RMSE), the variance-

![Figure 7](http://www.jn.org)  
**Figure 7.** Correlation between initial dynamic error and error in static experiment. Errors for the same tilt angle are plotted against each other.
accounted-for percentage (VAF), and the Bayesian Information Criterion (BIC). To calculate the BIC we used \( P = 1 \) for the combined and bias-only models and \( P = 0 \) for the dynamic-only model. As explained in METHODS, a model is preferable above a competing scheme if its RMSE and BIC values are smaller and the VAF percentage is higher. Figure 9A shows RMSE values for each model and each subject separately. The combined model (Eq. 1) clearly outperformed the reduced versions specified by Eqs. 2 and 3, respectively, in four of six subjects. As can be seen, depriving the model from the head vector contribution led to a consistent increase in RMSE (Combined vs. Dynamic only). Leaving out the dynamic mechanism reflecting canal–otolith interaction (Combined vs. Bias only) also caused a clear increase in RMSE, except in subject TG. The same conclusions can be drawn for the BIC and VAF values. Higher VAF percentages were found for the model that includes dynamic and bias effects (Combined) in all subjects, except TG. Similarly, we found the lowest BIC values, indicating a better model, for the combined model in all subjects but TG. In addition to subject TG, who is clearly an outlier, one may note that the combined model is only marginally better in subject NK. All in all, the results show that the combined model is definitely better in four of six subjects. A two-way ANOVA with model (combined/bias only) and measurement phase (RED/LED) as factors confirmed that the differences in RMSE and BIC between the combined model and the bias-only model were significant \( F(1,20) > 10.9; P < 0.004 \), whereas the differences in VAF were not significant \( F(1,20) < 0.45; P > 0.51 \). In addition, there was no significant main effect of measurement phase or a significant interaction, confirming that the model performed equally well for LED and RED data. We therefore conclude that the mean errors in the subjective visual vertical during OVAR, based on population data, reflect imperfect otolith disambiguation and a tilt-related bias.

Figure 10 presents fits of the extended model for the RED measurements in each subject, for each of the three dynamic conditions. Best-fit lines for both LED and RED in one subject (MV) are shown in Fig. 6. According to the combined model, we should observe two effects: a time-dependent increasing SVV error that is most pronounced in the high-speed conditions and an initial bias that is largest for the large-tilt conditions. Although this is indeed the general picture arising from the data, individual fits may not always be convincing in all aspects. For example, in the large-tilt & low-speed condition, the model correctly predicts no substantial dynamics, but the bias in the first collected SVV sample is not always matched correctly. Also, the temporal dynamics of the small-tilt & high-speed condition in the data is less convincing than that in the model. On the other hand, for the large-tilt & high-speed condition both effects are clearly present in all subjects except TG. Moreover, even though the intersubject differences in time course are not captured, the model generally gives a very reasonable account of the data. Together with the model analysis shown in Fig. 9, this suggests that the combined scheme is currently the best model to describe our data. To fit the initial bias, all subjects required a weight \( (w) \) that was significantly different from zero \( (t\text{-test}, P < 0.05) \). As shown in the right margin of Fig. 10, weights ranged from \(-0.18\) to \(0.49\) with a mean value of \(0.13\) (SD: 0.23), indicating considerable intersubject variability. In two subjects, NK and TG, the fit assigned a negative weight to the head vector to account for the predominant E-effect in their data (see Fig. 5).

As a final note, we investigated whether a substantially better fit could be obtained if the best-fit parameters of the internal model were determined only by the dynamic component of the present SVV data, rather than by the Vingerhoets et al. (2006) data. To this end, we searched for the best-fit parameters for the dynamic component of the SVV data. Importantly, this best-fit tilt-only parameter set–yielding values \( k_a = -4, k_r = 2 \text{ s}^{-1}, k_{fo} = 8 \text{ s}^{-1} \), and \( k_w = 2 \)– provided no substantial fit improvement in the dynamic SVV component pooled across subjects and conditions as shown in Table 1. Moreover, as Table 1 further shows, this model was clearly inferior for the translation and rotation data. On this basis, we conclude that the adopted parameter set, with \( k_a = -4, k_r = 4 \text{ s}^{-1}, k_{fo} = 8 \text{ s}^{-1} \), and \( k_w = 8 \), provides the best description for motion percepts during OVAR.

**D I S C U S S I O N**

In a previous study (Vingerhoets et al. 2006) we found that the illusory translation percepts during OVAR are consistent with predictions from an adapted version of the canal–otolith interaction model originally proposed by Merfeld and Zupan (2002). The present study was designed to test an extended version of this model (Fig. 1A) by measuring verticality perception during prolonged OVAR. The extended model predicts a combination of two types of errors: a dynamic time-dependent error resulting from improper interpretation of the ambiguous otolith signal and a response bias related to tilt angle. To test this prediction, we implemented an adaptive staircase paradigm to assess the SVV both dynamically during OVAR and under static tilt conditions. In the dynamic experiments, the SVV showed an error pattern that typically started off from a nonzero value and then increased further toward a steady-state error after about 60 s. These dynamic results, in combination with the static results, confirm the predicted superposition of the two effects. We will first discuss our approach to quantify
the time course of verticality perception. Next, we relate the two observed effects to previous investigations in the literature. Finally, we will consider a possible alternative modeling approach to the present data.

Methodological aspects

We tested verticality perception during OVAR using an adaptive psychophysical procedure to adjust a luminous line in iterative fashion until it appeared world-vertical to the subject. Our staircase procedure has a clear advantage when compared with a continuous-tracking method. The latter was used by Keusch et al. (2004), who asked subjects to continuously align a luminous line with the direction of gravity while they were being rotated. With this approach, measurements at different tilt angles are clearly not independent and the time needed for the adjustment may affect the time course of the response. In the present study, these problems were avoided by applying a staircase procedure over runs in combination with a flashed line.

Another methodological aspect with relevance for the interpretation of our results concerns the fact that the subjective visual vertical is not necessarily a direct reflection of our percept of body orientation in space. Several earlier investigations showed that roll-tilted subjects may have a rather accurate estimate of body tilt but may yet show a large A-effect in their SVV settings (Kaptein and Van Gisbergen 2004; Mast and Jarchow 1996; Mittelstaedt 1983). Mittelstaedt (1983) attributes this apparent disparity to the tendency to use the body axis as a partial reference for verticality judgments in the context of the SVV task, but not in the perception of body tilt. A possible indication that body-tilt percepts during OVAR may differ from SVV results comes from experiments from Denise et al. (1988), who asked subjects to verbally estimate the cone angle during OVAR. Denise and coworkers reported that subjects perceived a cone angle greater than the actual tilt angle. This is clearly in contrast with our SVV data, which indicate a slight underestimate of body tilt. For more decisive conclusions, body-tilt percepts would have to be tested more quantitatively, but an appropriate method to do this remains to be developed.

Evaluation of the combined model

We have demonstrated that the combined model, proposed in Fig. 1A, provides the best fit to our data for the majority of our subjects. This finding suggests that both disambiguation
The disambiguation process. As linear accelerometers, the otoliths sense gravitoinertial force (GIF), i.e., the vector sum of gravitational force and inertial force arising from linear acceleration. For reliable spatial orientation the brain must disambiguate the otolith signal into a tilt and a translation component. The canal–otolith interaction model suggests that these components are inversely linked, which implies that an increase of one should lead to a decrease of the other (Merfeld et al. 2005a). Such inverse linkage was previously demonstrated in monkey and human oculomotor studies (Hashwanter et al. 2000; Paige and Seidman 1999; Wood 2002).

Against this background, we wondered whether similar complementary trends can be discerned in the perceptual domain during OVAR stimulation. In a previous study (Vingerhoets et al. 2006) we quantified the time course of the illusory translation percept during OVAR. Simulations showed that this translation percept was described fairly well by the canal–otolith interaction model in Fig. 1A. In the present study we found that the dynamic component of the verticality percept during OVAR also conformed with the model’s predictions. In addition, in the previous study (Vingerhoets et al. 2006) we observed that the translation percept increased with rotation speed; the present study showed a parallel trend for tilt underestimation. On this basis, we conclude that, overall, tilt and translation perception during OVAR are mutually coupled, consistent with the idea that canal–otolith interactions play an important role in motion perception during OVAR. That is not to say that there are no discrepancies between the time courses of these two perceptual variables. For example, our previous study (Vingerhoets et al. 2006) showed that the onset of the translation percept could be delayed by as much as 50 s, whereas the present SVV data never showed any sign of a delay. We cannot provide an explanation for this difference.

Another aspect of the disambiguation process concerns the possible occurrence of phase shifts. In an earlier OVAR study, Denise et al. (1988) reported that their subjects felt being in the nose-up position 0 to 50° before they actually reached this position, which indicates a perceptual phase lead. By contrast, as shown in Fig. 4, the present canal–otolith interaction model predicts phase lags of about 24° in the large-tilt & low-speed condition, 34° in the large-tilt & high-speed condition, and 41° in the small-tilt & high-speed condition. Preliminary results from three subjects in one of our testing conditions (large tilt and high speed), yielded no evidence for either a phase lag or lead. However, it would seem premature to dismiss Merfeld’s model because it conflicts with Denise et al. (1998) and our preliminary data. Clearly, more work is necessary to establish conclusive evidence concerning the perceptual lags or leads during OVAR stimulation.

### Table 1. Model performance with two different parameter sets

<table>
<thead>
<tr>
<th>Parameter Values</th>
<th>Fit Residuals (RMSE)</th>
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<tr>
<td></td>
<td>Translation and Rotation Data, deg/s</td>
</tr>
<tr>
<td>Parameters Based On:</td>
<td></td>
</tr>
<tr>
<td>Rotation and translation data</td>
<td>5.6</td>
</tr>
<tr>
<td>Dynamic SVV component</td>
<td>8.2</td>
</tr>
</tbody>
</table>

One parameter set was based on rotation and translation data from Vingerhoets et al. (2006); the other set was based on the dynamic SVV component from the present study. Models perform comparably on SVV data, but the adopted model performs best for translation and rotation data. RMSE values are averages across subjects and conditions. Dimensions: $k_x, s^{-1}$; $k_f, s^{-1}$; $\tau_{\text{leaky}}$, s. Parameters $k_x$ and $k_f$ are dimensionless.

Tilt-related bias. It is well established that subjects, when tilted sideways in darkness, make systematic errors in judging visual verticality (Kaptein and Van Gisbergen 2004, 2005; Mittelstaedt 1983; Schöne 1964; Udo de Haes 1970; Van Beuzekom and Van Gisbergen 2000). Mittelstaedt (1983, 1989) interpreted these errors as the manifestation of a neural strategy that effectively compensates for an imbalance in the number of hair cells on the utricule and the saccule. This strategy relies on an internal bias signal, called the idiotropic vector, which causes a tendency to align the visual line with the long-body axis. In Mittelstaedt’s scheme, the SVV is the vector sum of the estimated gravity vector in head coordinates and a weighted vector pointing downward along the body-axis, in line with the fact that gravity usually pulls in this direction (see Fig. 1B). A similar approach was followed by others (Dyde et al. 2006; Groen et al. 2002; Zupan and Merfeld 2005; Zupan et al. 2002). The average weight found in this study, $w = 0.13$, is quite comparable to the value of 0.2 observed by Dyde et al. (2006). Importantly, how the brain solves the ambiguity problem of the otoliths, which later became a topic of keen interest in the field (Angelaki et al. 1999, 2001; Merfeld and Zupan 2002), is not considered in Mittelstaedt’s original model. This scheme, widely used as an explanation for the A-effect in stationary tilt, is basically a static model with no provisions to account for the dynamic changes in the SVV that we found in the course of OVAR stimulation. On the other hand, it appears that canal–otolith interactions, which successfully account for the time course and the magnitude of the dynamic SVV component (see Fig. 8), do not explain the occurrence of systematic errors in static tilt (Fig. 1C). Our finding of a tilt-related effect in dynamic conditions supports the basic notion of a head bias as an additional element in the canal–otolith interaction model (Fig. 1A).

### Further modeling aspects. We experimentally distinguished two contributions to the subjective visual vertical during OVAR. One contribution stems from a mechanism that
generates tilt-dependent systematic errors; the other originates from the process of otolith disambiguation. The model in Fig. 1A incorporates both effects. The model can also simulate the illusory translation percepts during OVAR if extended with a leaky integrator. Taken together, the model captures important aspects of the neural strategies that underlie orientation and motion perception during OVAR.

That being said, it cannot be denied that further improvements of the model would be needed. For example, the model would gain explanatory power if it could account for the simultaneous occurrence of E-effects at small-tilt angles and A-effects at large-tilt angles. Also, it is not immediately clear how the model could explain the putative additive canal effects on the SVV during yaw rotation, observed by Pavlou et al. (2003). Nevertheless, in retrospect, the canal–otolith interaction model, first suggested about 15 yr ago by Merfeld et al. (1993), has been of great value in understanding the central computations involved in vestibular signal processing. However, it has become clear that its original formulation cannot fully explain motion perception during OVAR. Previously we found that a leaky integrator had to be incorporated to obtain a more accurate explanation of the translation percepts. The present work prompted the addition of a head bias to improve the predictions of verticality percepts. These extensions, although technically sound, nevertheless raise the question of whether an alternative modeling approach could provide a more unified account of these central computations. For example, Bayesian frameworks have been successfully applied recently to explain performance in various perception and action domains (Ernst and Banks 2002; Knill and Pouget 2004; Körding and Wolpert 2004; Niemeier et al. 2003; Stocker and Simoncelli 2006; Weiss et al. 2002). Bayesian models combine various sources of information, to optimize performance in the context of optimal observer theory. A statistically optimal alternative for current canal–otolith interaction models was proposed by Laurens and Droulez (2006). The basic idea is that the brain makes assumptions about the probability of various body motions and applies Bayesian inference to disambiguate the vestibular signals. An a priori assumption in their model entails that low rotation velocities and small accelerations are most probable in daily life.

A Bayesian alternative for the idiotropic vector concept was formulated by Eggert (1998). In his theory, the SVV computation is based on the otolith signal, which is corrupted by noise, and the a priori assumption that the body is usually upright. With certain assumptions about the otolith noise and the prior, Eggert’s model yields predictions similar to those of the idiotropic vector model proposed by Mittelstaedt (1983). Whether these interesting developments can be combined into a general framework—allowing a unified explanation of the data observed in this study—remains a topic for further investigations.

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