Properties of the Internal Representation of Gravity Inferred From Spatial-Direction and Body-Tilt Estimates

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Van Beuzekom, A. D. and J.A.M. Van Gisbergen. Properties of the internal representation of gravity inferred from spatial-direction and body-tilt estimates. *J Neurophysiol* 84: 11–27, 2000. One of the key questions in spatial perception is whether the brain has a common representation of gravity that is generally accessible for various perceptual orientation tasks. To evaluate this idea, we compared the ability of six tilted subjects to indicate earth-centric directions in the dark with a visual and an oculomotor paradigm and to estimate their body tilt relative to gravity. Subjective earth-horizontal and -vertical data were collected, either by adjusting a visual line or by making saccades, at 37 roll-tilt angles across the entire range. These spatial perception responses and the associated body-tilt estimates were subjected to a principal-component analysis to describe their tilt dependence. This analysis allowed us to separate systematic and random errors in performance, to disentangle the effects of task (horizontal vs. vertical) and paradigm (visual vs. oculomotor) in the space-perception data, and to compare the veridicality of space perception and the sense of self-tilt. In all spatial-orientation tests, whether involving space-perception or body-tilt judgments, subjects made considerable systematic errors which mostly betrayed tilt underestimation [Aubert effect (A effect)] and peaked near 130° tilt. However, the A effect was much smaller in body-tilt estimates than in spatial pointing, implying that the underlying signal processing must have been different. Pointing results obtained with the visual and the oculomotor paradigm were not identical either, but these differences, which were task-related (horizontal vs. vertical), were subtle in comparison. The tilt-dependent pattern of random errors (noisy scatter) was almost identical in visual and oculomotor pointing results, showing a steep monotonic increase with tilt angle, but was again clearly different in the body-tilt estimates. These findings are discussed in the context of a conceptual model in an attempt to explain how the different patterns of systematic and random errors in external-space and self-tilt perception may come about. The scheme proposes that basically similar computational mechanisms, working with different settings, may be responsible.

INTRODUCTION

Background: current issues in spatial perception

In this paper we investigate the ability of human subjects to indicate the cardinal directions (horizontal and vertical) of external space when tilted sideways at various angles. A classical test of the subjective earth-reference frame requires the subject to align a visual line either to the perceived direction of gravity, or to the estimated direction of the horizon, in an otherwise dark environment. To perform this task, the brain has to reconstruct the position of the head in space, which is not immediately available from the raw vestibular input signals. Recent work on the vestibuloocular reflex has strongly suggested that the brain is able to construct an earth-centric representation of head velocity and head position (Angelaki and Hess 1994; Hess and Angelaki 1997; Merfeld 1995; Pettorossi et al. 1999), and various models on how this might be done have been proposed (Angelaki et al. 1999; Glasauer and Merfeld 1997; Merfeld et al. 1999; Raphan and Sturm 1991).

Earlier studies on the subjective earth-reference frame, mostly concentrating on the subjective visual vertical, have shown that the ideal of veridical performance is not achieved. When tested in darkness, subjects show a remarkable pattern of systematic errors at tilts beyond 60°, as if body tilt is undercompensated or underestimated (A effect). At smaller tilt angles, errors with an opposite sign (E effect) may occur (for review see Howard 1982, 1986). These consistent deviations from orientation constancy have received much attention as potential clues to the underlying neural mechanisms (Mittelstaedt 1983). Qualitatively similar deviations from orientation constancy have been observed in the behavior of optokinetic afternystagmus at various tilt angles (Dai et al. 1991). This similarity suggests that spatial perception and reflexive eye movements may rely on a shared gravicentric signal as has been proposed on more general grounds (Glasauer and Merfeld 1997).

Objectives of the present study

To explore the notion of a common gravicentric signal, we have studied whether the subjective earth-reference frame is similar when tested with two different paradigms. We performed two series of experiments where subjects used either their visual system or their oculomotor system to tap their gravicentric signals. The experiments made use of the visual-line paradigm and of saccadic pointing both to assess the subject's estimate of the direction of gravity and the subjective horizontal. If both paradigms indeed get their signals from a common gravicentric representation, one would expect the results to be very similar. Earlier work, where the visual and the oculomotor pointing paradigm were used in isolated experiments (references in the following text), appears inconclusive. It is unclear whether the different results that were ob-

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tained are paradigm related or due to differences in experimental conditions. Our results, obtained for the first time in the same conditions and the same subjects, show that both paradigms yielded comparable results in many important respects.

A further issue investigated in these pointing experiments is whether the subjective earth-reference frame is nonorthogonal as indicated by two earlier oculomotor studies that yielded clear differences in performance depending on whether the task required verticality or horizontality judgments (Pettorossi et al. 1998; Wood et al. 1998). This result led Pettorossi et al. to propose that the percept of verticality may be more primal and therefore more veridical. However, in similar experiments with the visual paradigm (Betts and Curthoys 1998), the nonorthogonality was smaller, less consistent, and reversed in sign. Again a major difficulty in interpreting these various results is that the experimental conditions in all three studies were different, making it impossible to assess whether performance is really task dependent (horizontal vs. vertical) and to what extent the conflicting results reflect the use of a different paradigm (visual vs. motor). To isolate these factors, we used both paradigms and both tasks in the same subjects in otherwise identical experimental conditions. Rather than concentrating on a limited set of tilt angles, like in these earlier studies, we investigated the entire range (from −180 to 180°).

Attractive as the notion of a shared gravity signal may seem as an economical computational strategy, some data in the literature suggest that its actual application by the brain may be subject to unexpected restrictions. In the domain of spatial-perception studies, it has been emphasized that tilted subjects are quite good at estimating their body tilt in space while making large systematic errors in earth-centric orientation judgments (Mast and Jarchow 1996; Mittelstaedt 1983). To investigate whether these earlier results, which were only collected at a single tilt angle (90°), are representative for the entire range, we have obtained verbal body-tilt estimates at all tilt angles from the same subjects in the same trials as where the pointing responses were obtained. While the results confirm earlier findings that errors in body-tilt estimates and earth-centric judgments are clearly different in magnitude, our analysis suggests that they may nevertheless reflect essentially similar computational mechanisms with different settings.

METHODS

Subjects

Six healthy subjects (5 male, 1 female), aged between 20 and 54 yr, participated in the experiments. Three of them (*AB*, *JG*, and *MS*) had knowledge about the purpose of the experiments, whereas the others were naive.

Setup

Seated in a computer-controlled vestibular stimulator in a dark room, the subject was rotated about his nasooccipital roll axis to a new tilt position using a constant velocity of 15°/s. Roll position was measured using a digital position encoder with an angular resolution of 0.04°. The subject's seat was adjusted in height so that the cyclopean eye coincided with the axis of rotation. The trunk was tightly fixed with seat belts and adjustable shoulder and hip supports; the legs were restrained by Velcro straps. The head was firmly stabilized in the natural upright position for looking straight ahead with a padded adjustable helmet.

In the oculomotor sessions, two-dimensional eye position was measured with the coil technique (Collewijn et al. 1975) using oscillating magnetic fields generated by two sets of orthogonal coils (0.77 × 0.77 m) inside the vestibular stimulator. The signals from the eye coil were amplified, demodulated and low-pass filtered (200 Hz) and sampled at 500 Hz per channel.

An array of red light-emitting diodes (LEDs) was used for eye-coil calibration. Its center LED served as a fixation light during the oculomotor task. Other LEDs were positioned on the intersections of three circles at 11, 22, and 31° and 12 meridians. The screen was attached to the vestibular stimulator with the center LED on the subject's roll axis at 1.15 m from the cyclopean eye. For calibration, subjects fixated the central fixation LED and each of 36 peripheral targets.

In visual-line experiments, the subject adjusted the orientation of a linear array of five equally spaced LEDs with an angular subtense of 17°, mounted at a 1.00-m distance. The line could be set accurately by remotely controlled rotation in either direction at adjustable speed. The rotation axis intersected the center LED and was collinear with the subject's roll axis. Its setting was measured using a digital position encoder with an angular resolution of 0.35°.

Experiments

Roll angle (ρ) was defined as the angle of the longitudinal body axis with the earth vertical, taken positive for right-ear-down rotations. All subjects were given a few practice runs to get used to the vestibular stimulation and the paradigm.

In all experiments, we tested 37 roll angles equally distributed across the entire range. Roll-tilt trials started from the upright position ($\rho = 0$) and alternated between clockwise and anticlockwise; final tilt angle was varied randomly. To allow most of the postacceleration effects in the semicircular canals to subside, tasks did not start until 24 s after completion of the rotation. After taking measurements in the tilted position, the chair returned to the initial position. Subsequently, room lights were switched on for ~10 s to give the subject the possibility to reorient. In all experiments, vision was binocular. Subjects never received feedback about their performance.

We used three different paradigms to test the subject's ability to judge orientations in external space relative to gravity as well as his perception of body tilt.

VISUAL-LINE PARADIGM. In these experiments, the task was to align the visual line with either the estimated earth horizontal or earth vertical in separate sessions. In darkness, the visual line was first set in a random orientation by the experimenter. After the 24-s waiting period in the tilted position (see the preceding text), the visual line was switched on for 12 s. Within this period the subject had to align the visual line according to instruction with the horizontal or vertical by remote control.

OCULOMOTOR PARADIGM. In the oculomotor paradigm, saccadic eye movements were used to indicate the perceived earth horizontal and vertical. Following the waiting period in the tilted position, the center fixation LED was presented for 2 s. The subject's task was to first fixate the LED until it extinguished, then to shift gaze to a peripheral position on the estimated horizontal. After 1.5 s, the center LED again lit for 1 s as a cue to reset gaze whereupon the subject made a saccadic-pointing response in the opposite direction along the subjective horizontal. The third requested refixation was upward (to the ceiling) and the final one downward (to the floor). The result of this task, when properly performed, was a cross-like figure whose arms were aligned with the gravity vector and the earth horizontal.

BODY-TILT ESTIMATION PARADIGM. In both oculomotor and visual-line sessions, the subject was requested to verbally report his estimated tilt position immediately after the 24-s waiting period, using a clock scale as if his body were the minute hand. Accordingly, an estimated 90° right-ear-down tilt was reported as 15 min past the hour.

Data analysis

Horizontal and vertical eye-coil signals were calibrated off-line using the fixation data obtained in the eye-coil calibration run (see the preceding text). Two neural networks, one for each position component, were trained to fit the raw fixation data to the target locations (Melis and Van Gisbergen 1996). Each network consisted of two input units (representing the raw horizontal and vertical signal), three hidden units, and one output unit (representing the desired calibrated horizontal or vertical position signal). Raw eye-coil signals were subsequently calibrated by applying the resulting feedforward networks. Calibration errors were typically $<0.5°$ on average.

Saccade detection was performed on the calibrated eye position signals on the basis of separate velocity and acceleration/deceleration criteria for saccade onset and offset, respectively. Detection markings were adjusted by the experimenter, if necessary.

The visual-line setting was defined as the smallest angle between the final orientation of the line and the gravitational vertical, in the visual vertical experiments, and between the line and the earth horizontal in the visual horizontal experiments. The direction of the oculomotor responses was described in a similar fashion. Each arm of a saccadic cross (left, right, up, and down) typically consisted of a sequence of saccades. The direction of such a response was defined as the direction of the most eccentric saccade endpoint relative to the center LED. Rightward and leftward direction were then defined as the angle between the earth horizontal and the direction of the rightward and leftward response, respectively. Upward and downward responses were defined relative to the physical vertical. The mean of the leftward and rightward response in a given trial will be denoted as oculomotor horizontal, the average vertical response as oculomotor vertical.

Trials in which the visual line was still being adjusted after the LEDs had been switched off were discarded from further analysis. Similarly, we excluded oculomotor trials in which the subject did not fixate the center LED accurately ($>5°$ error) or in which the response amplitude was too small (most eccentric saccadic end point $<10°$). The rare trials ($<2\%$) where subjects had obviously mixed up the sequence of required horizontal and vertical responses were left out. Sessions in which more than three trials did not meet the criteria were rejected altogether.

To compare the results from different tasks and paradigms and to characterize intersubject differences, we applied a principal-component analysis to the visual line and oculomotor data (Sokal and Rohlf 1981). The purpose was to characterize how the result from any given paradigm in a particular session, to be denoted as $\gamma(\rho)$, deviated from the overall mean response in all sessions, $M(\rho)$, calculated from the pooled data of all different tests (visual horizontal and vertical, oculomotor horizontal and vertical, verbal body-tilt estimates). Accordingly, the difference $\kappa(\rho) = \gamma(\rho) - M(\rho)$ was computed for the spatial perception results and the verbal estimates obtained in each session, yielding an $m \times n$ matrix K where $m = 60$ equals the total number of $\kappa(\rho)$ profiles and $n = 37$ equals the number of tested roll angles. The principal components, $P_1(\rho)$, $P_2(\rho)$, . . . , $P_n(\rho)$, correspond to the eigenvectors of the covariance matrix of K. The accompanying eigenvalues $\{\lambda_1, \ldots, \lambda_n\}$ express how much each particular principal component contributes to the description of differences among individual responses. Thus principal components with larger eigenvalues capture more of this variability than the higher-order components that have smaller eigenvalues.

The response from each session can be exactly described as a combination of $M(\rho)$ and n scaled principal components

$$\gamma(\rho) = M(\rho) + a_1 \cdot P_1(\rho) + a_2 \cdot P_2(\rho) + \cdots + a_n \cdot P_n(\rho) \qquad (1)$$

Note that $P_1(\rho)$, $P_2(\rho)$, . . . , $P_n(\rho)$ and $M(\rho)$ are common for all subjects and that $\gamma(\rho)$, and a_1, a_2, . . . , a_n are test and session specific. The contributions of the principal components describe deviations from the overall mean (M).

Since there were small differences (typically less than a few degrees) in applied roll angles among sessions, the data were linearly interpolated to roll angles at 10° intervals (−180, −170, . . . , 180), to allow the principal-component analysis that requires measurements at equal roll angles.

RESULTS

We will first give a qualitative survey of the results from in the different types of experiments, concentrating on the pattern of systematic and random errors.

Qualitative observations on performance in various tasks

The responses of all six subjects in the subjective horizontal and vertical tasks are shown in Fig. 1, *top four rows*, both for the visual line and the oculomotor paradigm. The body-tilt estimates (*bottom*) will be discussed later. Figure 1, *left*, contain the responses from all sessions, and Fig. 1, *right*, shows the accompanying mean and standard deviations. The vertical axis, $\gamma(\rho)$, shows the deviation of the actual response from the required response. For example, in the *top left panel*, we see a clear tendency for clockwise deviations (shown as positive) when subjects were tilted right ear down (ρ positive) in excess of 60°. This means that their subjective vertical deviated from the true vertical in the same direction as their body was tilted. Thus this scale gives a direct representation of the orientation of the actual setting that was made. Similarly for large left-ear-down tilts, we again see large errors, biased in the direction of body tilt. This kind of responses is known as the Aubert effect (A effect for short) that has frequently been described for large tilt angles. We will use the term A effect to denote errors of this type, also when they occurred at small tilt angles, as was sometimes the case. The term E effect will denote errors of the opposite type, again regardless of the tilt angle where they occurred. The patterns of errors in the horizontal and vertical responses obtained with the visual-line method were rather similar. Neither the mean visual horizontal nor the mean visual vertical showed systematic E effects, but clear A effects were present for roll tilts beyond 60°.

In the oculomotor paradigm, response curves again show clear A effects at large tilt angles, in line with the visual data. Also outside this range, there is a striking similarity between the subjective horizontal results obtained with either paradigm. In both data sets, we only see A effects, which become gradually smaller as tilt decreases. Inspection of the mean oculomotor vertical response shows right away that these data deviate from the oculomotor horizontal data. On close inspection, the trend toward smaller A effects, or even the emergence of E effects at small tilts, visible in the vertical results is also recognizable in the visual data. As the mean oculomotor vertical curve shows, the phenomenon is much more pronounced here. These points, related to the issue of nonorthogonality (see INTRODUCTION), are further considered in the next section.

In most sessions, subjects were asked to report their estimated body tilt (see METHODS). As can be observed in Fig. 1, *bottom*, their performance was generally far from flawless. Like in the pointing experiments, the body-tilt-perception data

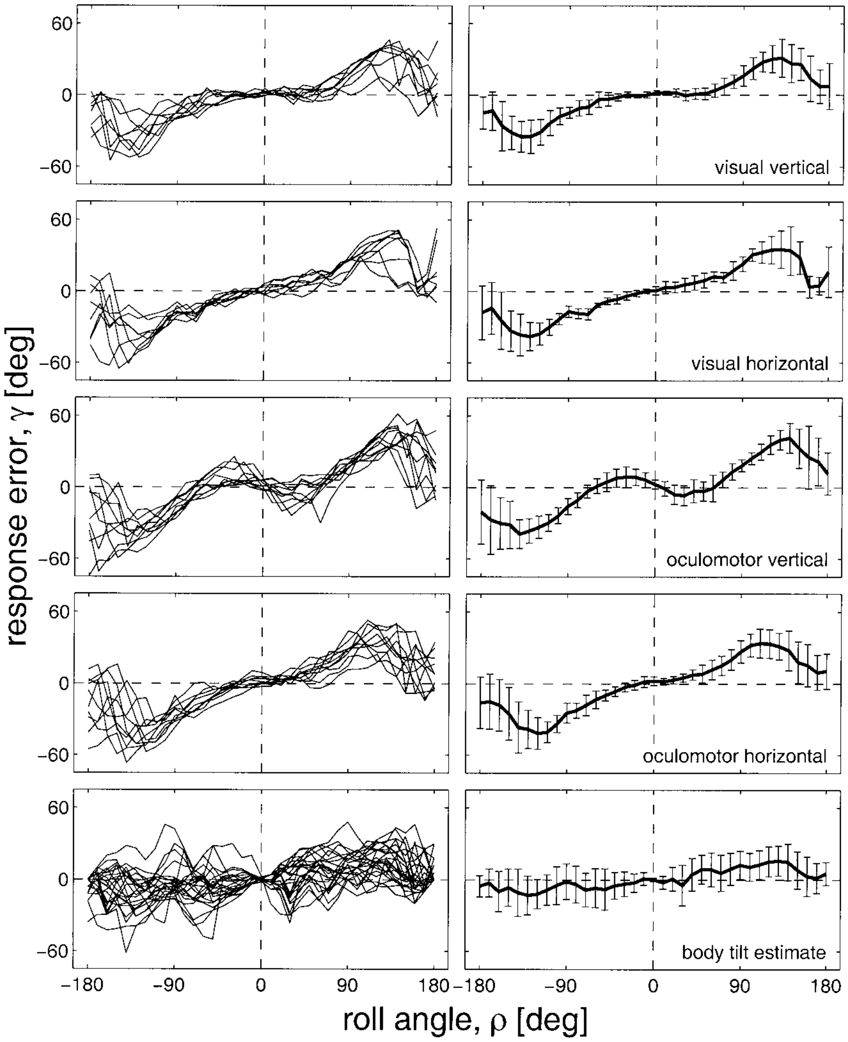

FIG. 1. Response errors in the visual, oculomotor, and body-tilt estimation paradigms. Six subjects were examined at least once in each paradigm. Since some were tested more often (see Table 1), the various panels contain a different number of sessions (visual vertical 8, visual horizontal 8, oculomotor vertical 10, oculomotor horizontal 10, verbal report of estimated body tilt 24). *Left*: response error in separate sessions plotted as a function of roll angle. Note that in both pointing paradigms (visual and oculomotor) considerable Aubert effects (A effects) were present for the large tilt angles. In both oculomotor vertical and body tilt estimates, some subjects showed a clear E effect (errors with an opposite sign) at small tilt angles. Some body-estimate profiles also displayed E effects for the large tilt range. *Right*: mean errors and SDs computed from the data in the *left panels.* Error bars denote 1 SD. Note that the mean errors in the body-tilt estimates were smaller than those in the pointing paradigms.

show systematic errors in the direction of tilt underestimation (A effect). Along with this similarity, two striking properties of the verbal responses are worth noticing: mean systematic errors are clearly much smaller but the scatter in responses seems actually larger, at least in the small tilt range.

NONORTHOGONALITY. The fact that the response curves for the horizontal and vertical tasks have different shapes means that they are nonorthogonal. As a measure of this internal inconsistency, Fig. 2 shows the difference between the two response curves from the same subject. As can be seen, the difference curves for both paradigms show equal-sign deviations from perfect orthogonality (i.e., a 0 difference) in the range of modest tilts. In the visual data, the effect is quite modest and only systematic at small angles of tilt, reaching a maximum of not more than 11.7° in the average (bold curve). The oculomotor orthogonality, which has the same sign as found by Pettorossi et al. (1998) and Wood et al. (1998), is clearly more robust (maximum in the mean: 16.9°) and more consistent.

Quantitative analysis of task performance

By raising the question to what extent session differences are task, paradigm, and subject related, the data in Fig. 1 portray a major challenge for further analysis that now has to be faced. An appropriate assessment of paradigm- and task-related differences, which also can take into account intersubject variability, necessitates an analysis that extracts relevant characteristics from the large data set available. Principal-component analysis nicely meets these requirements.

PRINCIPAL-COMPONENT ANALYSIS. We used principal-component analysis to characterize the differences among the individual responses (see METHODS). In this way, a set of independent, orthogonal basis functions, which describe the variability in the data most economically and without a priori assumptions, was calculated. To be useful for our purpose, however, it is important that the first few principal components can already account for much of the variability. This point will be considered first.

The principal-component analysis, performed on the pooled pointing and verbal data, yielded 37 principal components equaling the number of tested roll angles (see METHODS). The normalized ordered eigenvalues (λ) are shown in Fig. 3. An eigenvalue of 0.10 means that the associated principal component can account for 10% of the variability in the data set. Note the steep decrease in eigenvalue as a function of the order of the principal component. The data in Fig. 3 suggest that the contributions of the higher-order principal components ($k > 3$), with very small eigenvalues, may represent mainly noisy per-

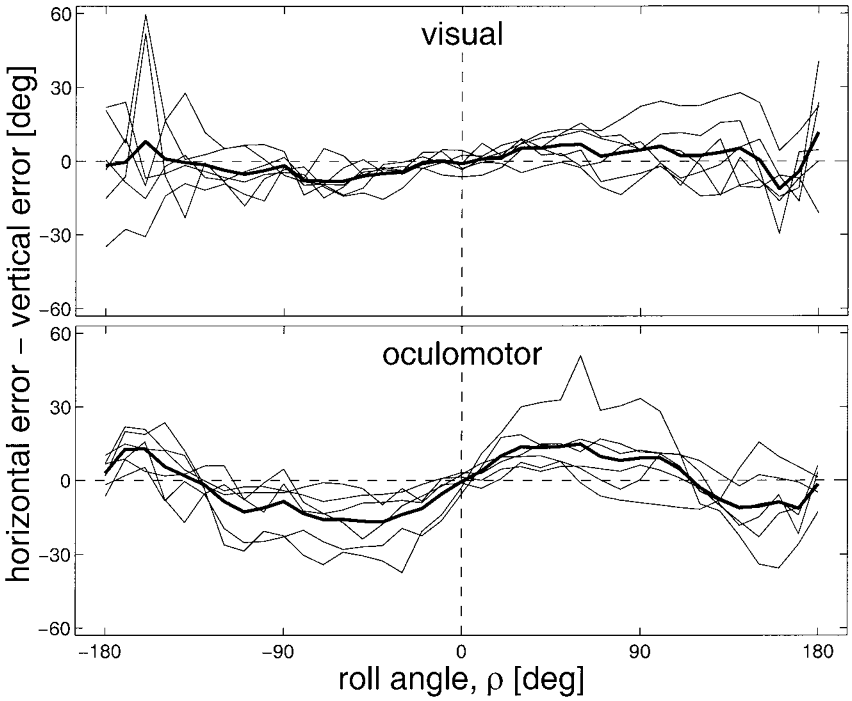

FIG. 2. Degree of orthogonality in the visual and oculomotor paradigm responses. To test the orthogonality of responses in both paradigms, the difference between the horizontal and vertical errors is shown as a function of roll tilt (thin line). In cases where a subject was tested more than once, the average difference between the horizontal and vertical response curves was calculated. Both overall mean difference curves (thick line) show generally the same pattern of deviations from orthogonality, with a change of sign for the large roll angles, showing that the nonorthogonality is not constant. The nonorthogonalities in the visual data (*top*) are quite small, and only consistent for small tilts. A more distinct and systematic pattern can be observed in the oculomotor data (*bottom*). A weak correlation ($r = 0.22$, $n = 6$) was present between the orthogonality in both paradigms (not significant).

formance variations rather than systematic trends in the data. Before considering this point further, we first examine the general features of the most dominant principal components that characterize the differences among individual session results relative to the overall mean (see METHODS, *Eq. 1*).

In Fig. 4, the overall mean response as well as the first three normalized principal components are shown together with their eigenvalues. The overall mean response (M) was calculated from the pooled data containing all pointing results and body-tilt estimates. Note that M roughly resembles the mean visual horizontal and vertical settings as well as the mean oculomotor horizontal responses but that it lacks the pronounced E effects present in the oculomotor-vertical data (see Fig. 1). The fact that the −180 and 180° data show opposite offsets means that

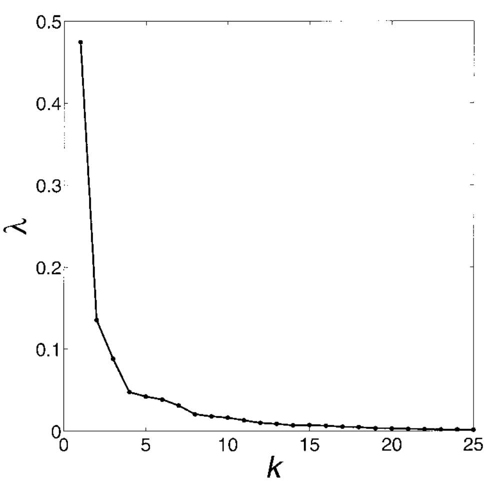

FIG. 3. Normalized eigenvalues of principal components. The eigenvalue (λ) denotes how much each principal component contributes to the complete description of the variance in the data. Parameter *k* denotes the rank order of principal components based on the size of their eigenvalue. Note the steep decline in eigenvalues with rank order. Only the first 25 of 37 eigenvalues are shown.

the response of the subject was not only determined by the static body orientation at the time the response was made but depended also on the rotation that led to that position. This hysteresis phenomenon was present in both the spatial-perception data (mean value: 14.4 ± 19.6°, $P < 0.001$, Student's *t*-test) and the body-tilt estimates (mean value: 5.3 ± 9.1°, $P < 0.001$, Student's *t*-test).

The first principal component (P_1) gradually increases with roll angle up to ~140° and then decreases for still larger tilts. Note, however, that it has not declined to zero at the upside down position (plus or minus 180°). Accordingly, the main role of the P_1 component in the description is to account for differences in the size of the A effect. Its eigenvalue of 0.47 shows that this basis function accounts for 47% of the variance in $\gamma(\rho) - M(\rho)$. By contrast, the second component is clearly important for the characterization of response differences at the smaller tilt angles. It rises steeply to a maximum in the tilt range ~40–50° then declines again and ultimately reverses sign near 140°. The third component has less characteristic features and merely accounts for a modest 9% of the variance in the data.

DESCRIPTIVE MODEL. The next step is to use the set of principal components for the description of individual response curves (see *Eq. 1,* for the general idea). As noted earlier, a perfect description of each individual response requires all 37 principal components. However, such an exhaustive representation is undesirable for our purpose, which is to obtain a simplified description that nevertheless captures the main characteristic features of the response and separates them from the noisy variability. Fortunately a fairly good description of the individual response errors, $\gamma(\rho)$, satisfactory for the present purpose, could already be obtained by using only three principal components, according to

$$\gamma(\rho) = M(\rho) + a_1 \cdot P_1(\rho) + a_2 \cdot P_2(\rho) + a_3 \cdot P_3(\rho) + \epsilon(\rho) \qquad (2)$$

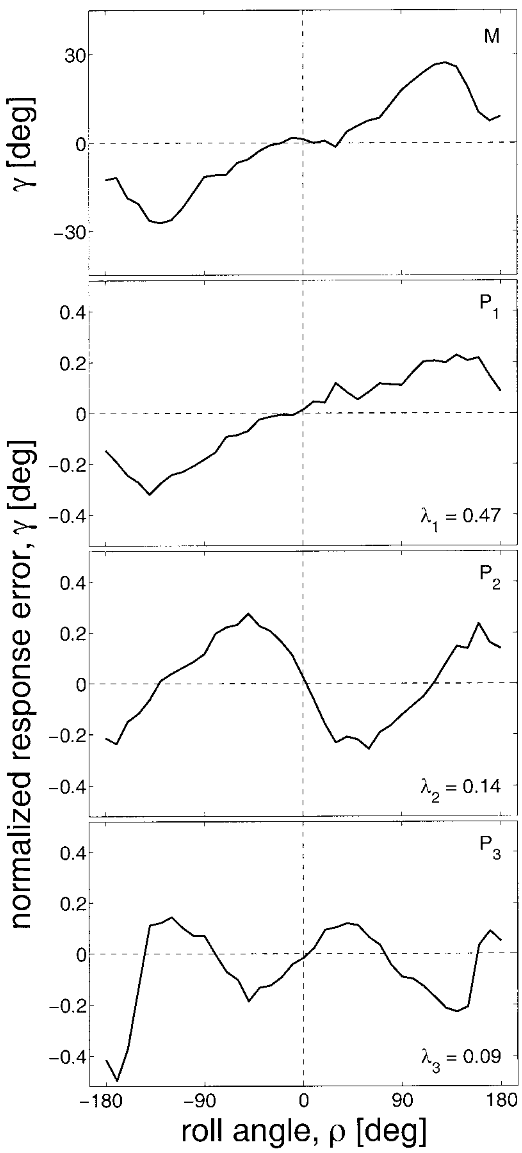

FIG. 4. Overall mean and first 3 principal components. The overall mean (*M*), first (P_1), second (P_2), and third (P_3) principal components with accompanying eigenvalues (λ), which were used to describe the individual response curves according to *Eq. 2.* See *Quantitative analysis of task performance* for further details.

where the noise term $\epsilon(\rho)$ represents the contribution of the remaining principal components $\{P_4, \ldots, P_{37}\}$. If the proposed descriptive model is valid, the contribution of the three principal components, expressed by three numbers (coefficients a_1, a_2, and a_3), describes the deviation of a given individual response $\gamma(\rho)$ from the overall mean. If this holds, these three parameters can characterize the salient aspects of the subject's behavior not just for a few selected tilt angles but for the entire range. Obviously this can only be an approximation and it is important to check first whether the model fit with the data is sufficiently good.

PERFORMANCE OF THREE-PARAMETER DESCRIPTIVE MODEL. The question to be faced now is whether the simple three-component model is already sufficient to capture the global features of the responses that were actually obtained in the different experiments. As illustrated in Fig. 5 for three subjects, it appears that the main differences in response characteristics from all three paradigms can be described quite well (mean $R^2 = 0.79$, range 0.42–0.97 for all sessions from all subjects). For example, in the small tilt range, *subject MS* showed a large E effect in the oculomotor vertical task in marked contrast to the A effect seen in the oculomotor horizontal experiment. These different features are well replicated in the fit ($R^2 = 0.93$). By contrast, the *bottom left panel* shows one of the poorest fits. There is no reason to blame the descriptive model: because systematic errors are so small in this case, the noisy scatter causes a small signal-to-noise ratio. Whenever the body-tilt estimates showed larger systematic errors (see *middle panel* in *bottom row,* for example), the R^2 value was accordingly better. Quantitative evidence that the descriptive model is indeed equally powerful in describing pointing results and body-tilt estimates is presented in the next section.

ROLE OF FIRST TWO PRINCIPAL COMPONENTS IN DESCRIPTION OF SYSTEMATIC ERRORS. We suggested earlier that the contribution of the first principal component is mainly related to the size of the A effect at large tilts, whereas the second component is important for the characterization of the systematic errors at small angles. To support this, Fig. 6 shows these relations for two tilt angles where the E and A effects were near their maximum (see Fig. 1). That both relations are linear is not surprising since each response is described as a linear combination of the overall mean and the principal-component contributions. Still, it is useful to see how the size of the E and A effect is related to the principal-component coefficients.

Apart from this, two features of the two relations are noteworthy. First, it appears that the relations are remarkably tight. The contribution of the first principal component (*right*) accounts for no less than 82% of the overall variability in A effect at the 130° tilt angle. The second component shows a less tight relation but still describes, by itself alone, 57% of the variability in E/A effects at 40°. Second, notice that the same relations hold equally well for pointing responses (○) and body-tilt estimates (□), showing that the description is applicable to both types of paradigm. Taken together, the plots in Fig. 6 underscore the descriptive power of the first two principal components, computed from the pooled data, to represent the responses in any type of experiment. Therefore our description of task- and paradigm-related differences in performance will concentrate on the P_1 and P_2 contributions found in each test.

Task and paradigm dependence of subject performance

While Fig. 5 is useful as an illustration of the fact that the linear regression on P_1, P_2, and P_3 can capture global features of individual response sets quite well, it is inadequate to summarize the task and paradigm dependencies. To illustrate these more concisely, the contributions of the first two principal components to the responses of all sessions are presented in Fig. 7, together with their confidence limits (see legend for computation). The key to Fig. 7 (*bottom right*) illustrates how taking combinations of the overall mean (*M*) and systematically varied contributions of the two basis functions, P_1 and P_2, can produce a variety of different response curves (see legend for further explanation). The coordinates of each session represent the corresponding coefficients a_1 and a_2 from *Eq. 2* so that the overall mean (*M* in Fig. 4) has coordinates (0,0). Using

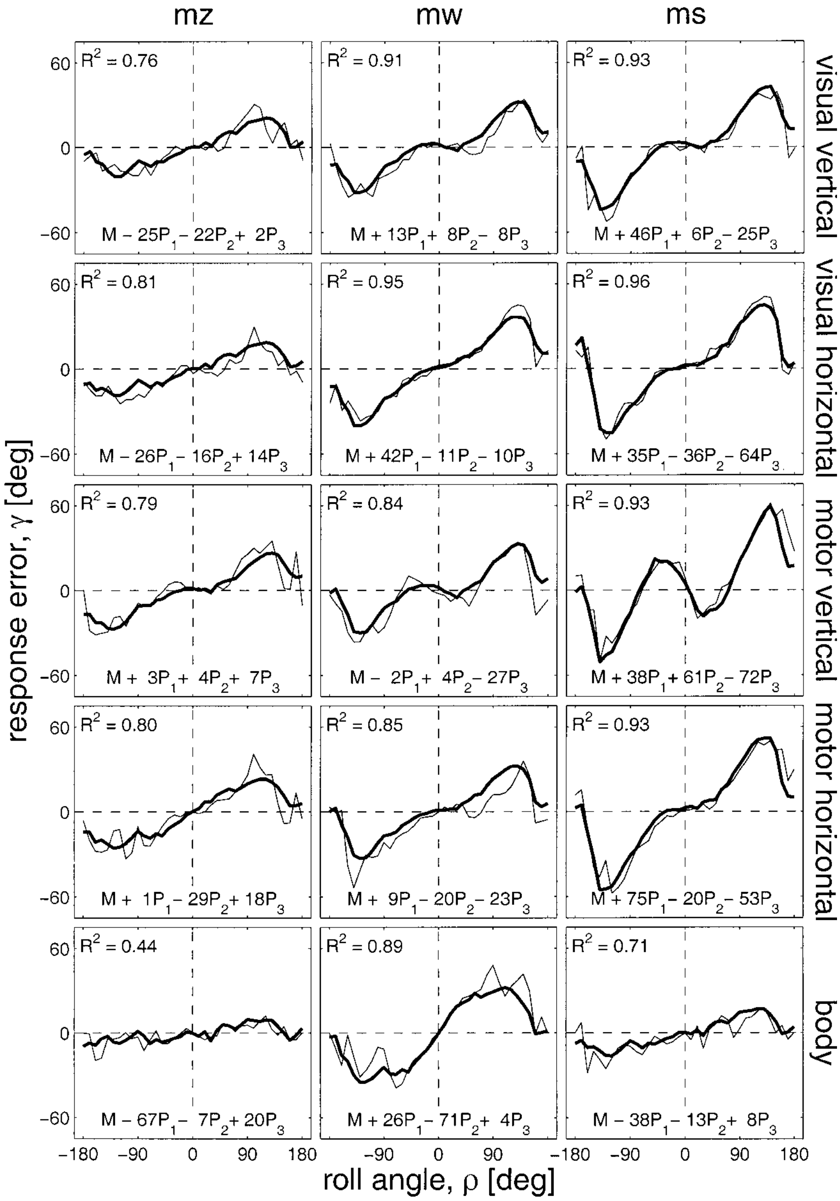

FIG. 5. Principal-component descriptions of response errors from 3 subjects. Principal-component descriptions (thick line) match the characteristic features of the individual responses (thin line) quite well including the striking differences in the size of E and A effects. Bottom line in each panel denotes that each fit curve reflects the sum of the overall mean (*M*) and a set of P_1–P_3 contributions weighted appropriately for each session. The body-tilt estimates, collected in the visual horizontal session, show large differences in a_1 and a_2 values.

this format, the horizontal (● and ■) and vertical (○ and □) pointing data are shown in Fig. 7, *top.* The scatter plots show that the variation in P_1 contributions, in different sessions, is roughly comparable for the visual and oculomotor paradigm, irrespective of task (horizontal and vertical). The picture in the body-tilt data (*bottom left*), showing a clear shift to negative P_1 values and a larger range, is significantly different from the pointing data ($P < 0.001$, Kolmogorov-Smirnov test).

The P_2 contributions of the oculomotor experiments show an almost complete separation depending on whether the task required earth-vertical or -horizontal settings. This difference is highly significant ($P < 0.001$, Kolmogorov-Smirnov test). In the visual data, the range of the P_2 contributions is more constrained. Although a tendency for a task-related shift can be discerned, similar to the oculomotor data, this difference does not reach statistical significance. These P_2 findings, in the visual and oculomotor task, reflect our earlier qualitative observations that there was a tendency toward strongly diminished A effects or even the emergence of E effects in the oculomotor-vertical data, which was much less obvious in the visual-vertical data (see Fig. 1).

The P_2 contributions in the body-orientation estimates span a wide range, almost comparable to the pooled oculomotor data (horizontal and vertical combined). This finding reflects the fact that the verbal data show considerable variation in the small tilt range showing a spectrum from clear A effects to clear E effects (see Fig. 1). Further inspection of the data did not show any clear correlation between P_3 contributions and task or paradigm (not shown).

Intersubject and intrasubject variability in pointing responses

If there was no intrasubject variability among the results of repeated sessions or intersubject differences, all points in Fig. 7 from a given type of experiment would cluster together within the uncertainty boundaries, but that is clearly not the case. Since the same experiment was repeated in some sub-

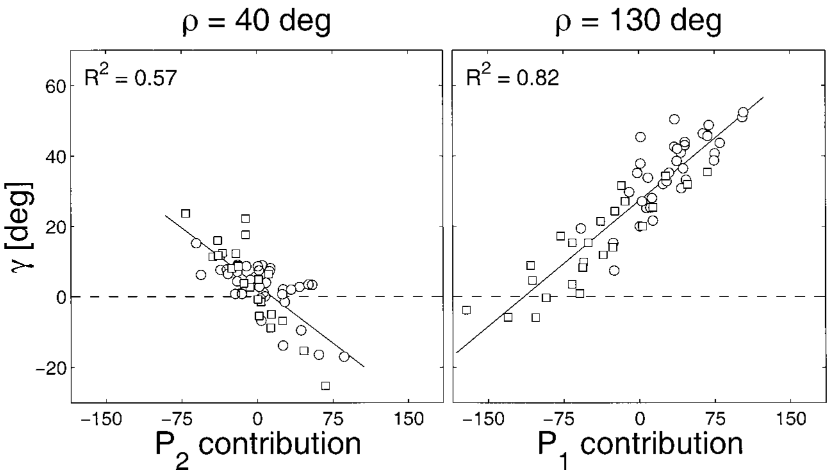

FIG. 6. Relation between principal-component contributions and response errors at 2 selected tilt angles. Response error at 40 and 130° roll angle as a function of the 2nd and 1st principal-component contributions (*left* and *right panels,* respectively). For each session, the response errors for pointing (○) and body-tilt paradigm (□) were determined by averaging the response error for corresponding clockwise and counterclockwise rotations. Positive errors indicate A effects while E effects are negative. Note that some body-orientation estimates showed an E effect even at 130° tilt, whereas at 40° tilt, E effects were present in both pointing and body-orientation estimates. The regression lines match the relation that can be predicted from the shape of the overall mean (*M*) and the principal component under consideration. R^2 values show that the relation is tight in both panels. Even though the P_1 contributes to the principal-component description for small tilt angles, as can be gathered from it shape (see Fig. 4), it is not a good indicator ($R^2 = 0.12$) for the 40° response error (not shown). Similarly, the P_2 is a poor descriptor at $\rho = 130$. Further details: slope in *left*: -0.22 ± 0.03; intercept 3.25 ± 0.79; $n = 60$; slope in *right*: 0.24 ± 0.01; intercept 27.18 ± 0.85; $n = 60$.

jects, we can give an impression of the day-to-day repeatability of the results. In Fig. 8 we show the results of four oculomotor experiments in *subject JG.* The oculomotor horizontal and vertical curves are shown in the *top panels.* If the experiments had been reproducible, the four session curves should only show noisy variations about their corresponding mean. Instead, there is a clear suggestion of systematic intrasubject differences from day to day.

Examples of such systematic changes, collected in sessions 3 and 4, are shown in Fig. 8, *middle* and *bottom rows,* together with their principal-component fits. As can be seen, the errors made by this subject were systematically larger in session 3. Note the similarity in a_1 values in both the horizontal and the vertical data of the same sessions. A quantitative summary of the results of all subjects that were tested more than once in any paradigm is given in Table 1. In a total of 18 session comparisons that could be made, the P_1 component was significantly different in 17 cases. The P_2 component was significantly different in 10 pairs.

The impression from Table 1 that the oculomotor response curves for the horizontal and vertical task show parallel changes in P_1 values from session to session led us to a further question. If there is a degree of covariation in the size of the A effect expressed by the horizontal and vertical data from one subject on different days, is this perhaps a reflection of a general trend in the data from all subjects? Figure 9, *left,* where we have plotted the a_1 values from the oculomotor horizontal data against those derived from the vertical data in the same session, confirms that there is a clear correlation ($r = 0.78$). The a_2 values showed no correlation ($r = -0.13$, *right*).

A similar question can be raised for the visual data. Is it true that subjects with a small or large a_1 value in the horizontal task show the same tendency in the vertical task? A complication that arises here is that these experiments were performed in separate sessions on different days. If a given subject has been tested several times, a decision is needed on how the comparison is to be made. Since any particular pairing would be as arbitrary as any other, we just took all possible pairings. No correlation could be found based on this analysis.

Relation between estimated body tilt and earth-centric orientation perception

There is evidence that the signals used for the estimation of body tilt are at least partially distinct from those participating in the subjective horizontal and vertical tasks (Anastasopoulos et al. 1997; Bisdorff et al. 1996; Mittelstaedt 1988). In support of this hypothesis, earlier tilt experiments concentrating on the range near 90° yielded no correlation between errors made in body-tilt estimates and those in subjective horizontal/vertical tasks by the same subjects (Mast and Jarchow 1996; Mittelstaedt 1988). Our results allow us to explore this issue based on data in the entire tilt range. As Fig. 10, *top left,* shows, the P_1 components for body-tilt estimates were consistently smaller than the corresponding component in the assigned pointing task (○ and ●: visual line; □ and ■: oculomotor) of the same session. Nevertheless there was a significant correlation that was weaker than when two pointing tasks (oculomotor horizontal and vertical) were compared (see Fig. 9). There was no correlation between a_2 values for body tilt and pointing (*top right*). Symbols ● and ■, representing data from a single subject (*JG*), show that the P_1 contribution in the verbal estimates exhibited considerable variations from session to session. By contrast, the P_2 component was more reproducible.

To further evaluate the relation between pointing and verbal responses, we also made a correlation analysis for each tilt angle. This was done separately for the reconstructed signals, using the descriptive model, and for the

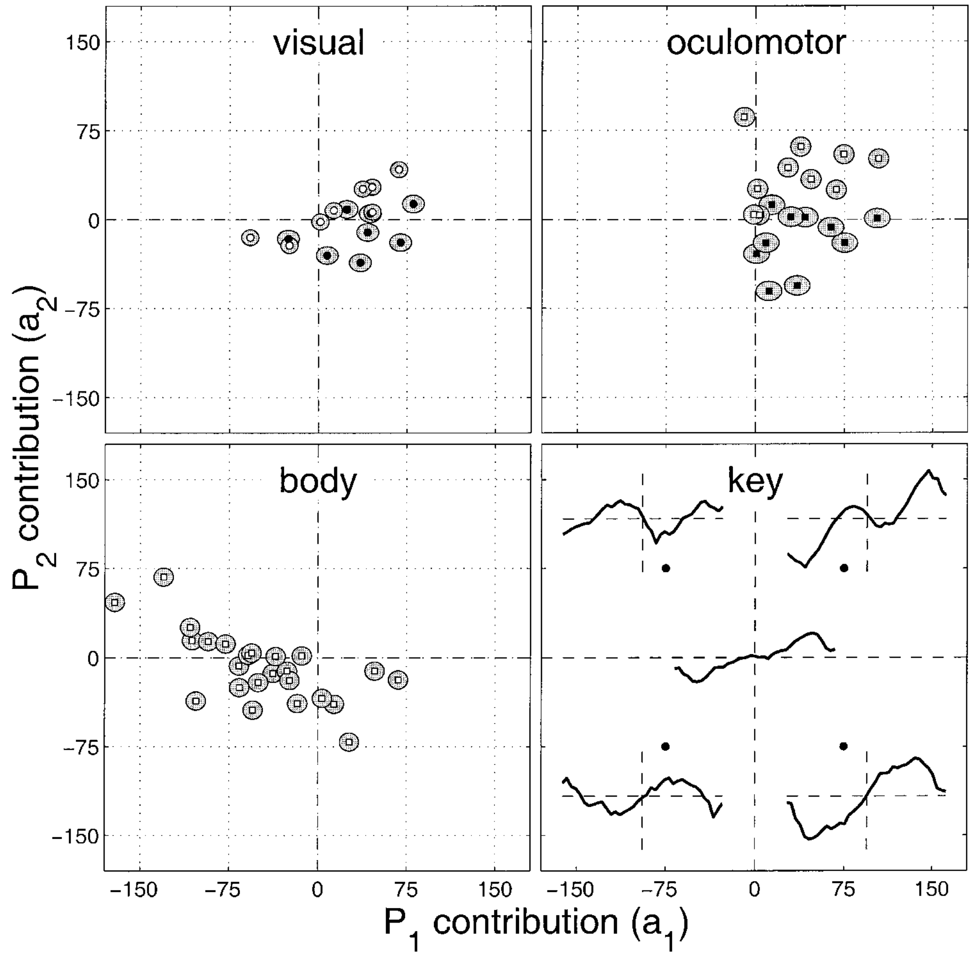

FIG. 7. Principal-component description of results in all 3 paradigms. *Bottom right*: (key) illustration by example how taking combinations of the overall mean (*M,* central curve) and the contributions of the 2 basis function P_1 and P_2, indicated by ● (±75), produces quite different response profiles (the 4 remaining curves). Note that the P_2 predominantly affects the appearance of the curve at small roll tilts. The P_1 component, by contrast, has only little effect on the response characterizations for small tilts and primarily affects the size of the A effect at larger tilts (see also Fig. 6). Scatter plots of best-fit P_1 and P_2 contributions for the description of pointing results (*top*) show that horizontality (■ and ●) and verticality (□ and ○) data end up in nearly separate clusters for the oculomotor experiments. The 4 pointing task-paradigm combinations show comparable P_1 contributions, whereas the body-tilt estimate P_1 distribution (*bottom left*) is broader and shifted toward the left. The shaded zone surrounding each symbol represents the statistical uncertainty in the coefficients, caused by the presence of noisy scatter. To keep this figure readable, the zones show only 1 SD of each coefficient. These zones have to be doubled in width, thus portraying 95% confidence limits, to determine what significance can be adhered to differences in a_1 and a_2 values among sessions. Two sessions can be considered to yield statistically different results when the corresponding points in Fig. 7 are separated by at least this margin. The computation of the confidence zones has its conceptual basis in the descriptive model, expressed in the form of *Eq. 2.* For a given session curve, the principal component coefficients a_1 and a_2 are fully determined, without any uncertainty. It is obvious however that, even if the subject was completely stable from session to session except for the presence of random noise, the latter would still cause the experimentally determined values to deviate from their theoretically expected value. If the noise is Gaussian and if its variance (σ^2) is known as a function of tilt angle, the resulting uncertainty in the coefficients can be computed analytically (Rice 1995, see p. 538). We will later discuss the tilt-dependent noise characteristics that were used in this computation (see *Tilt dependence of noisy scatter* and Fig. 11).

noisy scatter (*Eq. 2*). As Fig. 10, *bottom*, shows, there was a convincing correlation in signal values for tilt angles beyond 60°. By contrast, the correlation of the noisy scatter between pointing and verbal was much smaller and generally insignificant.

Tilt dependence of noisy scatter

The descriptive model that we have been using to describe the results assumes that the first three principal components characterize the signal and that the remaining components describe only noisy variations. The fit results obtained with the first three principal components (see Fig. 5) suggest that this is a reasonable approximation. By implication, analysis of the residue can provide an impression of the properties of the noise term in the model. Such a quantitative characterization of the noise is of interest for several reasons. First, the dependence of the noise variance on tilt angle is of theoretical interest as a constraint for modeling (see DISCUSSION). Second, one might surmise that the oculomotor paradigm might be corrupted by higher noise levels than the visual paradigm and it is of interest to check this possibility. Finally, the characterization of the

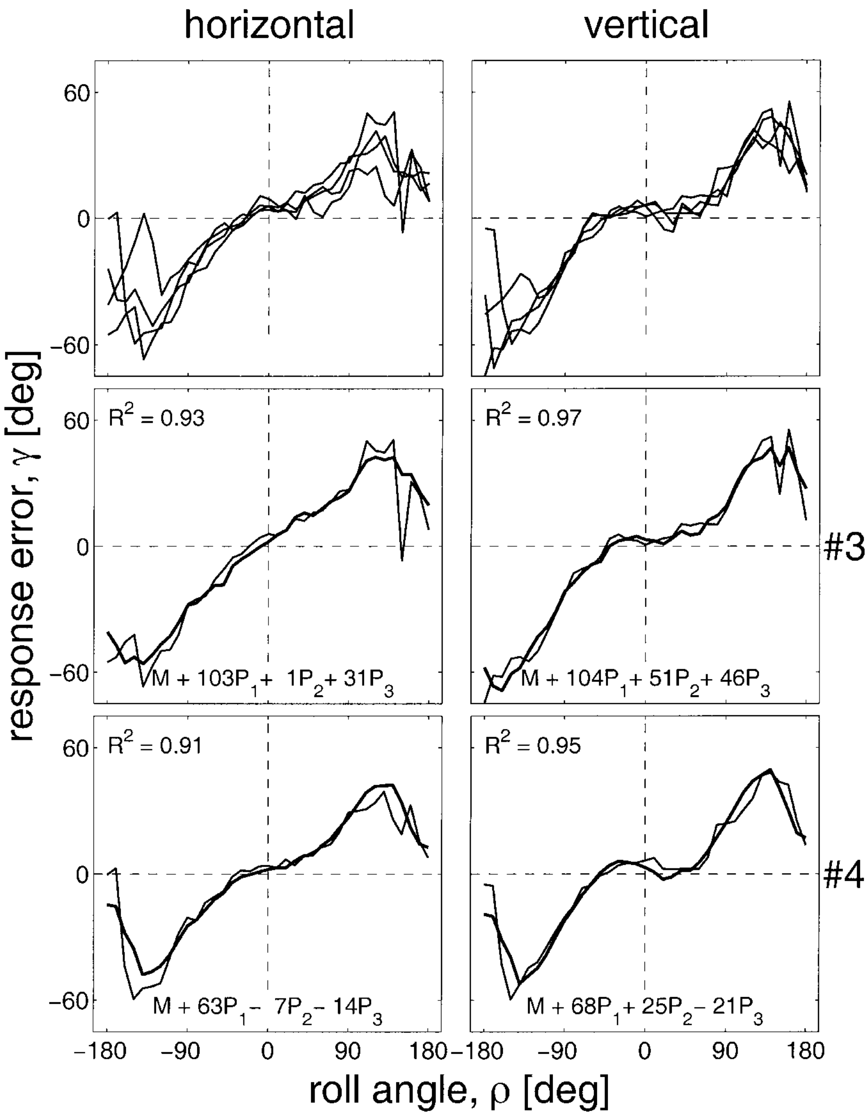

FIG. 8. Systematic day-to-day changes. *Top*: results from *subject JG* in 4 oculomotor sessions. Note that the shape of the horizontal curves differs from that of the vertical curves, in line with our earlier description. The day-to-day differences are considerable, especially for large tilt angles. To illustrate this, the horizontal and vertical oculomotor data from sessions 3 and 4 are shown in the *middle* and *bottom rows* as well as the accompanying principal-component descriptions. Note that there was a large difference in a_1 values between the 2 sessions and that the coefficients for horizontal and vertical in the same session were similar.

noisy scatter underlies our estimation of the coefficient confidence intervals shown in Fig. 7.

It may seem that the ideal procedure to test the descriptive model assumption that the residue, $\epsilon(\rho)$, is random noise, would be to repeat each type of experiment many times in each subject. In theory, such an extensive data set would permit one to check whether the residues conform to a Gaussian distribution centered at zero and would yield the tilt dependence of the noise amplitude in each subject. In practice, however, subjects showed also systematic changes in repeated sessions (see Figs. 9 and 10 and Table 1) so that the total scatter would reflect both systematic and random variations.

To sidestep this problem, we pooled the residue data from all available earth-centric pointing experiments to reconstruct the overall noise profile. As can be seen from the standard deviation (σ) of the pooled residues (Fig. 11, thick line, *top left*), the noise increased with tilt angle. It should be noticed that the curve is nearly symmetrical for positive and negative roll angles and that the increase is monotonic. It is interesting to recall, at this juncture, that the pattern of mean systematic errors shows a clearly different tilt dependence (Fig. 1). Accordingly, the random noise is not simply proportional to the mean level of systematic errors. If that was the case, the noise should have shown a marked decline beyond ~130°, in parallel with the diminishing size of the A effect in this range.

Figure 11, *top right*, shows that the noise profiles, obtained by pooling data from opposite directions of tilt and for horizontal and vertical task results, were quite similar for the visual and the oculomotor paradigm. In both cases we see a steep, monotonic increase in noise amplitude yielding the largest values when subjects were upside down.

The noise profiles, reconstructed so far, were obtained based on the assumption that the first three principal components capture all the systematic variability. While the bend in the λ-k curve in Fig. 3 seems compatible with the idea that the remaining components represent mainly noisy variations, there is no clear-cut boundary between signal and noise. Clearly if the higher-order components still reflect some systematic variability, we have overestimated the noise level.

To check for this possibility, we used an alternative procedure to reconstruct the noise profiles based on an independent assumption. In general, the response curves are roughly symmetrical, apart from scatter, for equal positive and negative tilts (see Fig. 1). In our second approach, we made the simplifying

TABLE 1. *Summary of the results from repeated experiments*

			Horizontal			Vertical		
Paradigm	Subject	Session	a_1	a_2	R^2	a_1	a_2	R^2
Visual	*JG*	1	7.3	−30.2	0.86	—	—	—
		2	69.4	−19.3	0.91	—	—	—
		3	—	—	—	1.5	−1.8	0.82
		4	—	—	—	68.0	42.3	0.96
	MW	1	80.2	13.4	0.91	—	—	—
		2	41.5	−10.6	0.95	—	—	—
		3	—	—	—	−57.7	−15.1	0.60
		4	—	—	—	12.8	7.8	0.91
Oculomotor	*JG*	1	13.6	12.4	0.81	46.5	33.9	0.95
		2	41.8	2.0	0.90	74.4	54.8	0.97
		3	102.8	1.0	0.93	103.9	51.2	0.97
		4	63.5	−6.6	0.91	68.0	25.1	0.95
	MS	1	35.1	−55.9	0.93	1.7	25.9	0.94
		2	75.2	−19.8	0.93	37.8	61.2	0.93

The principal component fit results of repeated pointing experiments. The R^2 value denotes the goodness of fit of the principal-component description. Clear differences in a_1 and a_2 values, beyond 95% confidence limits, were present between sessions of the same subject. From the 18 intrasubject comparisons that can be made, 17 yielded different P_1 contributions. The a_2 values were different in 10 session comparisons. Note that the P_1 contributions in oculomotor sessions showed comparable session-to-session changes in horizontal and vertical data.

assumption to regard all deviations from symmetry as due to noisy scatter. The results of this procedure are shown in the Fig. 11, *top left* (dashed line). Again we see a steep monotonic increase and an overall striking similarity with the earlier result. Apparently, the errors due to imperfections of the fit, that entered the result of our first reconstruction method, are small relative to the noisy scatter in the system.

The same analyses were also carried out on the available body-tilt estimates. It appears that the reconstructed noise profile is almost flat across most of the tilt range, which contrasts markedly with the pointing data. The plausibility of this result is again supported by the fact that the two methods to obtain the noise are in remarkable agreement. We conclude that, while body-tilt estimates tend to have smaller systematic errors (on average), the scatter in these responses is relatively large when compared with the pointing data.

DISCUSSION

Overview

RECAPITULATION OF OBJECTIVES AND MAIN RESULTS. This investigation has centered on the question of whether the brain has a common central representation of gravicentric signals that can be tapped by various systems involved in spatial orientation. The first objective was to clarify whether the main features of the subjective earth-reference frame in spatial perception would be similar when tested with the visual-line method or the oculomotor paradigm. In making this comparison, we concentrated on the question whether the two paradigms yield a similar pattern of systematic misalignment of the subjective earth-reference frame, as expressed in the A effect (tilt undercompensation). The second objective was to compare performance in the earth-centric perception tasks and the ability to estimate body tilt. We investigated earlier claims in the literature that the A effect, which is a very prominent phenomenon in external-space perception, is virtually absent in judgments of body tilt (Mast and Jarchow 1996; Mittelstaedt 1983).

To realize these objectives, we collected earth-centric direction judgments and body-tilt estimates across the entire tilt range. All experiments were carefully designed to create comparable conditions, were performed on the same subjects, and were analyzed in a way that allowed appropriate comparison of the data by using a principal-component analysis. Broadly speaking, without going into details for the moment, the results show: first, in many respects, the visual and the oculomotor

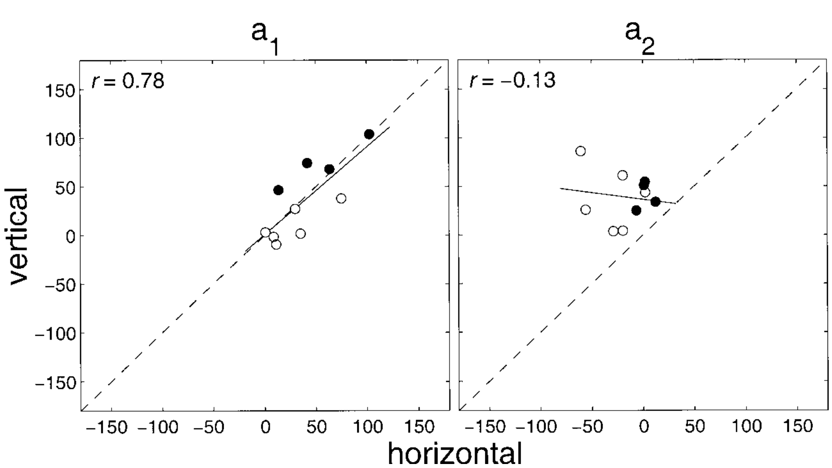

FIG. 9. Covariation between oculomotor horizontal and vertical responses. a_1 coefficients derived from the horizontal and vertical data obtained in the same session were strongly correlated ($r = 0.78$, $n = 10$, $P < 0.01$, *left*). No significant correlation was found between the a_2 values (*right*). ●, 4 oculomotor sessions from *subject JG* shown earlier in Fig. 8. In the visual-line data for horizontal and vertical, which were obtained in separate sessions, no such correlation was present.

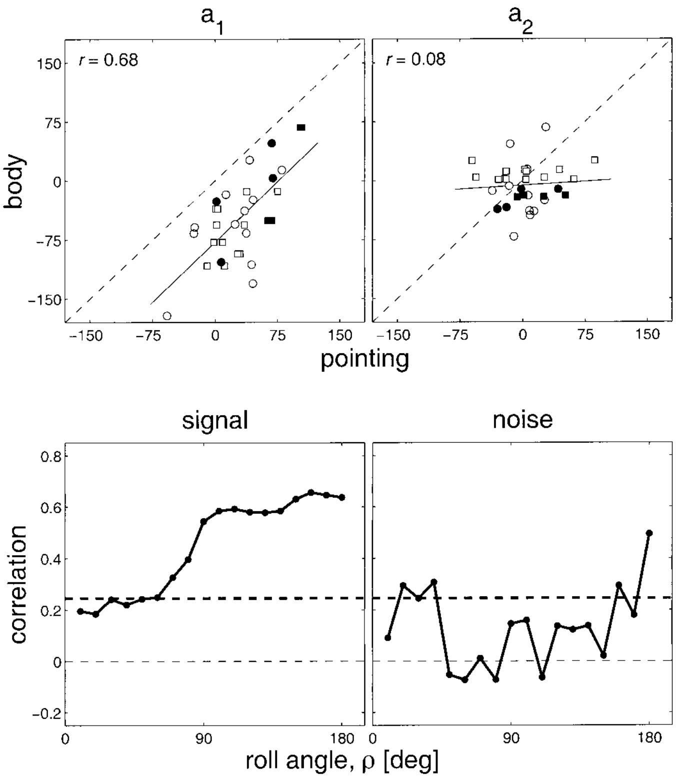

FIG. 10. Relation between pointing responses and body-tilt estimates. *Top*: covariation between pointing responses and body-tilt estimates. a_1 values of the pointing responses are correlated to the body-tilt estimates obtained in the same session ($r = 0.68$, $n = 32$, $P \ll 0.001$, *left*). Note that the P_1 contributions are systematically smaller in the body-tilt estimation paradigm. No relation was observed between the P_2 contributions (*right*). ○ and ●, visual-line results, oculomotor sessions are marked by ■ and □. ■ and ●, denoting the data from *subject JG,* illustrate that there were considerable variations in body-tilt errors from day to day. *Bottom*: correlation in systematic and random errors between pointing and body-tilt estimates. The correlation between the systematic errors, represented by the principal-component description, in pointing and body-tilt task was calculated for each tilt angle (*left*). A significant correlation emerges for roll tilts beyond 60°. A similar analysis on the residues, reflecting random variations, is shown in the *right panel*. Note that the correlation is smaller and mostly insignificant. Clockwise and counterclockwise tilts were pooled, yielding 64 data points for each tilt angle. Bold dashed line indicates the level where correlation reaches significance.

paradigm yielded essentially similar results and showed comparable noise characteristics. Second, although the body-tilt estimates showed much less tilt underestimation than the spatial-perception pointing responses, we obtained clear evidence for a substantial A effect in both tasks. To conclude this overview, the next two subsections will further elaborate these points by comparing our results with the work of others and discussing possible explanations.

SYSTEMATIC MISALIGNMENT OF THE SUBJECTIVE EARTH-REFERENCE FRAME AND THE SENSE OF SELF-POSITION. All earth-centric direction judgments showed large systematic errors at large tilt angles (A effect). This phenomenon, captured by our principal component analysis, was present in all four task-paradigm combinations without major differences (Figs. 1 and 12). Thus this effect is equally pronounced whether tested with a visual-line stimulus or with pointing saccades that were executed in complete darkness. The fact that also the reconstructed pattern of random errors was similar in the two paradigms is interesting (see Fig. 11). From an experimental point of view, it attests to the suitability of the oculomotor system as an alternative pointer.

The broad similarity of the oculomotor data with the visual-line data shows that the saccadic system has access to the result of the same or comparable neural computations. This finding lends support to the idea that there may be a central representation of gravicentric signals that is not tied uniquely to the availability of a visual stimulus and is also accessible for other purposes such as the control of eye movements. In a clear departure from more limited data in the literature, the body-tilt estimates showed that, in our experimental conditions, subjects had a marked tendency to underestimate their tilt. At the same time, it is equally obvious that these systematic errors were still much smaller than those in the earth-centric tasks (see Fig. 1) so that the underlying signal processing must be different.

IS THE SUBJECTIVE EARTH-REFERENCE FRAME DISTORTED? There have been several reports in the literature that horizontality and verticality estimates from tilted subjects have different error profiles, implying that they are not simply orthogonal. As Fig. 12 shows, however, the picture emerging from this earlier work is partly conflicting. The nonorthogonality found by Betts and Curthoys (1998) in visual-line experiments is small and opposite in sign compared with the oculomotor findings by Pettorossi et al. (1998) and Wood et al. (1998). In our experimental conditions, the oculomotor nonorthogonality was comparable in sign and magnitude to the results of the earlier two studies. The phenomenon was often less than convincing in the visual-line experiments, but its sign was identical to that in the oculomotor data.

Why this phenomenon was more pronounced in the oculo-

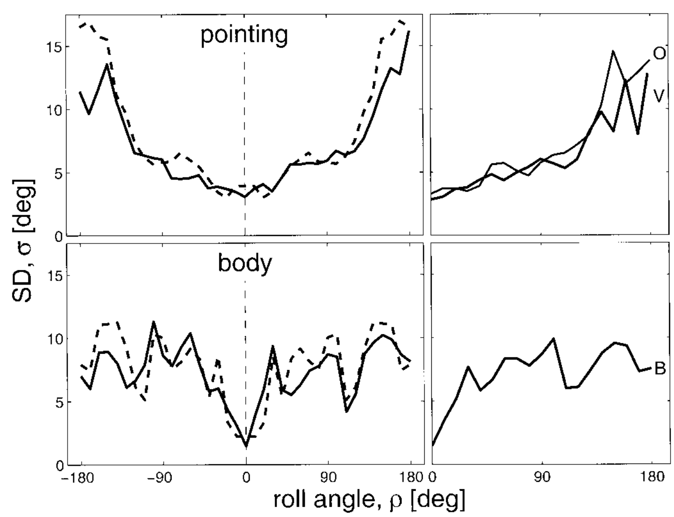

FIG. 11. Tilt dependence of noisy scatter. To obtain an estimate of the noisy response variations, we analyzed the residues [$\epsilon(\rho)$, *Eq. 2*] of the 3-parameter descriptive model, assuming that the systematic response properties are captured in the fit. The standard deviation (σ) of the pooled pointing residues (—, *top left*) shows that the noise increased monotonically with roll tilt. An alternative analysis to estimate the noise characteristics, which assumes symmetry, shows generally the same picture (- - -, *top*). The amplitude shown here equals the standard deviation of the difference between responses obtained by a clockwise and counterclockwise rotation, scaled by $1/\sqrt{2}$. Note that the visual and oculomotor paradigm yield similar noise profiles (pooled for left and right tilts, see *top right*). Similar analyses for body-orientation estimates show that the noise in this paradigm is characterized by a flat profile (*bottom*). These noise profiles were used in the estimation of the confidence limits of the coefficients in Fig. 7, as discussed earlier. O, oculomotor; V, visual; B, body.

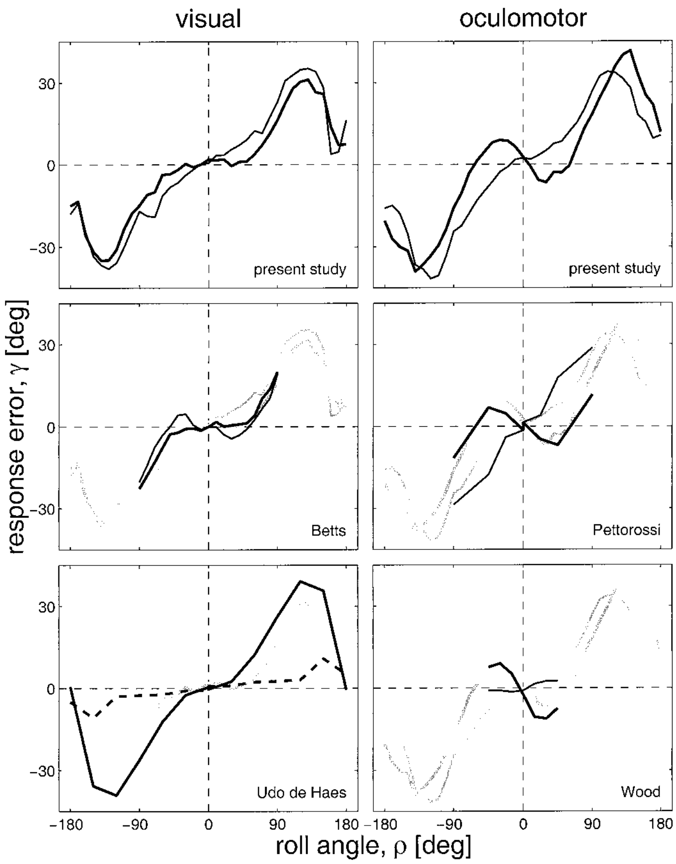

FIG. 12. Comparison of present results with the literature. *Top*: mean results of this paper for subjective vertical (thick line) and subjective horizontal (thin line) in each paradigm. Other panels show the mean response curves of visual (*left*) and oculomotor (*right*) paradigms of earlier studies (Betts and Curthoys 1998; Pettorossi et al. 1998; Udo de Haes 1970; Wood et al. 1998) together with our results (gray line). *Bottom left*: also shown is the tilt dependency of the canal-mediated effect (dashed line) described by Udo de Haes and Schöne (1970), scaled to match the mean hysteresis effect in our pointing data. Note that the 3 oculomotor studies show qualitatively similar differences between vertical and horizontal data in the small tilt range where comparison is possible. The visual data from our study show a similar non-orthogonality at a much reduced scale, in contrast with the Betts and Curthoys study where it appears to be reversed.

motor experiments remains unclear, but it is unlikely to reflect tilt-related errors in the oculomotor pointer itself since the distortion was not apparent when tilted subjects make saccades to visual targets (Shelhamer et al. 1992) nor when they make saccades in the dark aligned to their vertical or horizontal body axis (Pettorossi et al. 1998). Therefore we consider it more likely that the neural representation of external space subserving the earth-centric task is itself distorted and that this distortion is more pronounced in the oculomotor paradigm due to the absence of vision. In this connection, it is interesting that saccade endpoints to an array of remembered targets are spatially distorted (Gnadt et al. 1991). We suggest that generating an imagined target for the pointing saccades in the oculomotor paradigm may be subject to a similar effect.

Pettorossi et al. (1998) explained the nonorthogonal responses by suggesting that the percept of verticality is more primal, implying that the horizontality judgments are obtained more indirectly, causing larger errors. We found little support for this hypothesis since our data do not convey the impression that the verticality judgments are generally more accurate (see Fig. 12).

Importance of dynamic factors

As mentioned earlier, when subjects were brought to the same 180° roll-tilt position by rotations in opposite directions, always starting from the neutral upright position, the pointing responses were not identical but deviated in opposite directions (see Figs. 1 and 12). The body-tilt estimates showed a similar phenomenon at smaller scale. This finding clearly demonstrates that the final static tilt angle is not the only important variable and that dynamical factors determining how that position was reached are also relevant.

The work of Udo de Haes and Schöne (1970) suggests that a canal-otolith interaction effect may have contributed to this phenomenon. In their experiments, designed to investigate the role of the semicircular canals on the subjective vertical by using a provocative stimulus, subjects were rotated at a constant velocity of 60°/s for 1 min and then suddenly stopped at a specified tilt position. When the effects of preceding clockwise and counterclockwise rotations were compared for the same final tilt position, the subjective vertical appeared to deviate in the direction of the preceding rotation. In our experiments, this putative canal contribution would act to increase the A effect. Udo de Haes and Schöne (1970) found that the magnitude and the duration of this canal-mediated effect was not fixed but increased with the final roll angle where it was tested, with a peak at 150° (see Fig. 12, *bottom left*). At these large tilt angles, it slowly diminished in the course of several minutes.

These results from earlier work suggest that the role of the canals in our experiments would have been less if we had used a slower rotation velocity or had inserted a longer waiting period before taking measurements. However, there is evidence that very long waiting periods may bring other dynamic factors into play. Imposing long delays before measurements are taken, as in the study of Udo de Haes (1970), may cause an increased A effect because of adaptation in the somatosensory system (Schöne and Lechner-Steinleitner 1978; Wade 1970) or of otolith afferents (Fernandez and Goldberg 1976). Thus it may be impossible to achieve a steady-state situation because any choice of temporal parameters in the design of tilt experiments will yield its own set of contributing dynamic factors. The fact that most studies (including our own) used a constant-rotation velocity, rather than a constant-rotation duration, to bring the subject in the final tilted position further complicates the situation. The associated differences in the duration of tilt rotation between large and small tilts will cause different degrees of vestibular conflict. If one wishes to exclude canal influences, by using slow or even sub-threshold rotation velocities, followed by long waiting periods, adaptation in the somatosensory system and in the otoliths may become more severe. The same may hold if subjects are tested continually by slow incremental roll tilt without returning to the upright position after each measurement. Whatever the precise contribution of the dynamic factors discussed here, the main conclusions drawn in this paper stand apart from these issues since their effect in all experiments must have been similar.

Existing spatial-perception models

It has been suggested that the otoliths, the semicircular canals, the somatosensory system all play some role in the subjective vertical (for review, see Howard 1982, 1986). Since the otoliths respond to total linear acceleration, their raw signals cannot distinguish between gravity and translational accelerations. Recent work on reflexive eye movements suggests that the brain combines the information from the otoliths and the canals to differentiate between tilt and translation (Angelaki et al. 1999; Hess and Angelaki 1999; Merfeld et al. 1999; Snyder 1999). Theoretically the problem can be solved completely for conditions where the canal signals are veridical (see e.g., Angelaki et al. 1999). That it becomes more complex in the frequency range where this is not the case may have some relevance for our experiments (see *Attempted synthesis*).

The evidence that the canals are also involved in the perception of the vertical comes from the study of Udo de Haes and Schöne (1970) and from experiments using eccentric rotation about an earth-vertical axis (Stockwell and Guedry 1970). The latter authors observed that, whereas the subjective vertical changes rapidly after pure roll rotations, it tilts only slowly toward its final value during eccentric rotations where the information from the otoliths and the semicircular canals is conflicting. To explain this phenomenon, Glasauer (1992) proposed that the brain relies on an internal model that obtains an estimate of gravity by using canal and otolith signals in conjunction. This proposal shows clear similarities with a model describing reflexive eye movements during eccentric rotations (Glasauer and Merfeld 1997; Merfeld 1995).

These theories, however, are unable to explain the occurrence of systematic errors at large tilt angles as expressed in the A effect. In a quantitative model of earth-centric orientation perception during static tilt, which concentrates on the explanation of this phenomenon, Mittelstaedt (1983) uses signals from the otoliths to reconstruct body tilt in space and assigns an important role to an internal signal termed the idiotropic vector. At large tilts, the latter acts to bias the percept of verticality toward the subject's body axis, thereby accounting for the A effect. According to the model, it affects the computation of the subjective vertical without influencing the subjective estimate of body tilt. In support of this notion, earlier work on the perception of body orientation showed that human subjects are able to accurately position themselves horizontally, yet making large errors when asked to set a luminous line horizontal (Mast and Jarchow 1996) or vertical (Mittelstaedt 1983). In addition, work on the perception of body tilt in lying subjects (90° roll tilt) has suggested a role for truncal graviceptors and has provided evidence that this category of somatosensory signals does not affect the subjective vertical (Mittelstaedt 1988).

Recently, Eggert (1998) has proposed an interesting reinterpretation of the idiotropic vector which is mathematically fully compatible with Mittelstaedt's theory (Mittelstaedt 1999). His model, based on optimal communication theory, considers the problem facing the brain when it has to decide what is earth-vertical when depending on noisy input signals. The main idea is that, in this evaluation process, the brain relies partly on an assumption about the a priori probability that a particular tilt of the earth-vertical relative to the body may occur. This prior distribution is a tilt-dependent curve with a Gaussian shape, peaking at the long body-axis, indicating that alignment of the subjective vertical with the long body-axis is considered most likely. A narrow prior, which assigns a high probability to small differences between the subjective vertical and the longitudinal body-axis, improves the performance at small roll tilts at a price in the form of a large A effect at large body tilts. In the Mittelstaedt model, such subjects would have a large idiotropic vector.

Recently evidence has accumulated that somatosensory signals also may affect external-space perception and the sense of self-position. An intriguing finding is that subjects lacking these signals show almost no A effect in the subjective visual vertical when tilted in a horizontal position (Anastasopoulos et al. 1999; Yardley 1990). In a discussion on the percept of body verticality, Bisdorff et al. (1996) hypothesize that proprioceptive-contact cues play a major role in the detection of body tilt. In a recent review, Bronstein (1999) has suggested that proprioceptive signals may contribute to the systematic errors by adaptation in the somatosensory system. This view implies that prolonged tilts should lead to a larger A effect, as has indeed been found by Wade (1970) and by Schöne and Lechner-Steinleitner (1978).

Attempted synthesis

To clarify to what extent our experimental results can be understood by borrowing existing concepts, reviewed in the previous section, we shall now discuss the conceptual scheme in Fig. 13. This qualitative model contains proposals to account for the observed dynamic effects and to explain how the similarities and differences characterizing verbal and pointing responses may come about.

At the front end of the model, a vestibular estimate of the orientation of the head in space (H_v) is reconstructed at stage C by combining the tilt-related signals from the otoliths (α) and the head-velocity signal (ω) from the semicircular canals (see Angelaki et al. 1999; Glasauer and Merfeld 1997). The hysteresis effect in our data demonstrates that static final tilt position is not the only important variable. This means that a purely static model will be inadequate and that a dynamic process is involved. As suggested earlier (Stockwell and Guedry 1970; Udo de Haes and Schöne 1970), when the two vestibular input signals are in conflict, the internal estimate of head tilt in space gradually evolves from a compromise value to a final state reflecting the otolith signals. Apparently, this putative canal-mediated interaction effect had not fully subsided after the 24-s waiting period (cf. Udo de Haes and Schöne 1970), thereby causing a dynamic tilt-underestimation effect that underlies the hysteresis phenomenon. The finding that the systematic errors for earth-centric pointing and body-tilt sense were most strongly correlated at the upside-down position (see Fig. 10, *bottom left*) indicates that the strength of the hysteresis in the two tasks showed parallel variations in different sessions. In other words, subjects with a stronger hysteresis effect in pointing tasks also tended to have a more pronounced hysteresis effect in the body-tilt estimates obtained in the same session. On this basis, we propose that the dynamic effects in both types of task are due to the same canal-otolith interaction (stage C in Fig. 13). The idea that canal information may contribute to body-tilt perception has been discussed by Seidman et al. (1998).

Our data show convincingly that this canal-otolith interac-

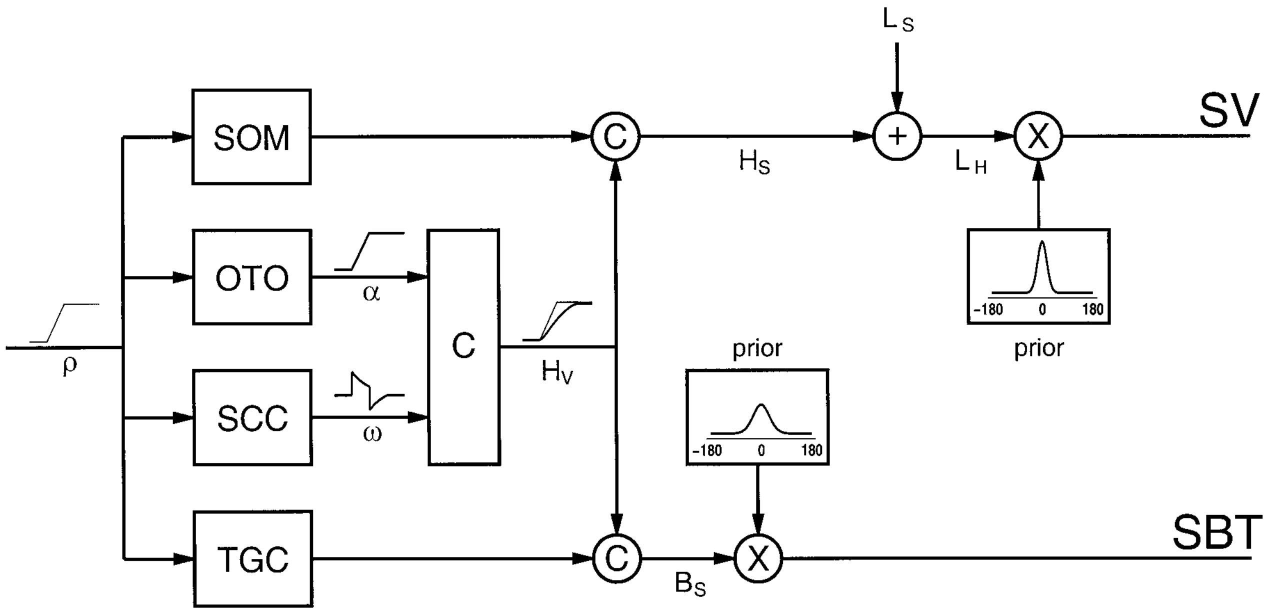

FIG. 13. Gravicentric signals for space perception and for the estimation of body tilt. The scheme illustrates the idea that various sensory inputs are used by the brain to obtain an internal representation of body orientation in space when the subject is rotated, at constant velocity, from an upright to a lateral tilt position (ρ). As discussed in the text, sensory signals provided by the otoliths (OTO), and the semicircular canals (SCC) are combined in stage C to yield a representation of head orientation in space (H_v). This vestibular signal serves as a common input for 2 parallel modules subserving spatial pointing (shown here for the subjective vertical, SV) and body-tilt perception (subjective body tilt, SBT), respectively. As shown, somatosensory inputs (SOM) further contribute to obtain the head in space signal (H_s) necessary for earth-centric pointing. Somatosensory signals involved in obtaining body-tilt estimates are denoted by the acronym TGC to emphasize the specific role of truncal graviceptors without excluding other somatosensory signals such as those yielding contact cues or proprioceptive information. To explain the joint occurrence of dynamic effects in the pointing responses and the verbal tilt-estimates (see Figs. 1 and 12), we propose that, due to adaptation in the canal signal (ω), conflicting information from the otolith afferents (α) and the canals causes a lag in H_v. That the canals can have such a dynamic effect on the subjective vertical has been suggested by Udo de Haes and Schöne (1970), who showed that the time course of this dynamic effect may far outlast the time constant of the canals, especially at the larger tilt angles. We assume that, as a consequence, H_v had not yet reached a steady state when our measurements were taken after the 24-s waiting period and that this has caused shared A effects in both pointing and verbal responses. Each module on the *right-hand side* relies on a computational strategy of the type proposed by Eggert (1998). Since the 2 priors operate on different signals and subserve different task requirements, their width may be different, as shown.

tion cannot have been the only source of systematic errors. This mechanism can only lead to tilt underestimation (A effect) and would be expected to make only a substantial contribution at the large tilt angles where canal adaptation must have been most pronounced. In fact, a considerable number of sessions clearly showed errors of the opposite sign (E effect) in the small tilt range, both in the earth-centric pointing and in the body-tilt responses. These cases can be recognized in Fig. 7 from their positive P_2 components which signify the presence of an E effect at 40 deg roll tilt (Fig. 6, *left*).

Further evidence for an additional source of systematic errors, in both pointing and verbal responses, comes from an analysis of the size and the tilt dependence of the response errors at the large tilt angles. Previous work on the subjective visual vertical by Udo de Haes (1970) still found a very considerable A effect, roughly comparable with our results (see Fig. 12), despite extreme precautions to prevent the expression of dynamic canal-mediated effects. On this basis one would expect that only a small part of the systematic errors in the pointing results at larger tilt angles is due to the canal-mediated effect so that there must have been an additional mechanism. Indeed, as Fig. 12 shows, the size and the tilt dependence of the response errors in the pointing experiments corresponds rather well with the error profile in the experiments from Udo de Haes (1970). To obtain a rough estimate of the contribution of the dynamic mechanism, we assumed that the magnitude of the canal-mediated effect in our experiments had a similar tilt-angle dependence as the one reconstructed by Udo de Haes and Schöne (1970), reproduced in Fig. 12, *bottom left.* We scaled the amplitude of this function so that its value at 180° matched the actual hysteresis effect in the data of that particular session and then determined the size of the A effect contributed by this mechanism at 130°. Based on this approximation, the actual A effect in the pointing data at 130° tilt was 21.9 ± 14.7° (mean ± SD) larger than the A effect ascribed to the assumed dynamic effect alone.

The fact that the average A effect in the body estimates near 130° was clearly much smaller than in the pointing data (see Figs. 1, 6, and 10) might lead one to believe that in this task only the dynamic canal-mediated effect played a role. We have already rejected this hypothesis on the basis of the occasional presence of E effects (see the preceding text), but analysis shows that it also fails to explain the A effects at large tilt angles. Using a similar comparison as explained above for the pointing data, we found that A effects at 130° were larger (6.8 ± 11.4°) than would be expected from the hysteresis effect in verbal estimates of the same session. So in summary, both the repeated occurrence of E effects at 40° and the analysis of the size of the errors at 130° clearly establish that there must have been an additional source of response bias in both pointing and verbal responses.

We will now try to provide a rational explanation for this bias, starting with the earth-centric perception results. At first sight, it is puzzling why the brain should contain a central mechanism responsible for considerable systematic errors. As explained earlier, Mittelstaedt (1983) tried to solve this paradox by proposing that in the presence of noise, reliance on an internal bias signal (the idiotropic vector) can reduce errors at small tilt angles at the expense of large systematic errors at the more rarely encountered large tilt angles. Another attractive feature of his model is that it can provide, at least in principle, an explanation of the occurrence of both A and E effects, as a direct consequence of the size of the bias signal without invoking separate mechanisms. With this in mind, we incorporated the idiotropic vector, embodied here by the Eggert prior distribution (see *Existing spatial-perception models*), as the major source of the systematic errors in pointing responses.

To illustrate the basic idea, without following the Eggert model in every detail, we refer to the *top right section* of the scheme, which explains its application to the visual vertical task. To compute the subjective vertical (SV), the brain needs information about head orientation in space (H_s), which, as often assumed, is obtained here by combining the vestibular signal H_v and somatosensory inputs (SOM). By subtracting H_s from the requested spatial judgment L_s, the brain computes the desired line orientation relative to the head (L_h). What makes the pointing task "spatial" is the requirement to have access to head in space information. Using the same signals and the same simple rules, the saccadic pointer can program a saccade in body coordinates.

The challenge facing the brain is that L_h is subject to fluctuations from trial to trial not only due to noise in the sensors but also as a result of errors in its central computation. The proposed solution entails that the brain evaluates the available L_h signal by taking into account its assumed trustworthiness as well as an estimate of which L_h values are most likely on an a priori basis (the prior). Pursuing overall optimal performance over many trials, at various tilts, this computational strategy (X) leads to improved performance at small tilts and large systematic errors at large tilts (Eggert 1998). Note that these systematic errors are superimposed on the canal-mediated effect. In the extreme case that L_h contains only noise, the brain fully relies on the prior which biases the response to the long body-axis. In the other extreme case that L_h is considered very reliable, the effect of the prior becomes negligible. In our experiments, the pointing responses must have been signal driven (L_h) with some biasing effect of the prior. As this explanation makes clear, a quantitative evaluation of the model would require assumptions about the width of the prior and the tilt-dependent noise characteristics in L_h.

Making specific assumptions concerning the origin of the gravity-related input, its noise characteristics, and the shape and width of the prior, the Eggert model can mimic the main features (E and A effects) of space-perception responses. Interestingly, the model even predicts the monotonic increase of the noisy scatter in pointing responses with tilt angle (see Fig. 11). We did not explore the model at the quantitative level so that it remains to be seen whether indeed the error profiles that we have recorded can be fitted by adjusting its parameters. We gained the impression that, when using the parameters in Eggert (1998), the model predicts too large E effects at small tilts. Also it has a rigid coupling between the size of the A effect at large angles and the size of the E/A effect at small tilts, whereas we saw a degree of independent variation (see Fig. 7).

If the notion of a prior is considered an acceptable explanation for part of the systematic errors in external-space perception, could a similar principle be at work in the body-tilt estimation paradigm? In self-positioning experiments, Mittelstaedt (1983) found only small systematic errors (see preceding text) and on this basis denied any role to the idiotropic in that task. Our data, obtained with a different paradigm (verbal report of subjective self-tilt rather than self-positioning), show very clearly that there are systematic errors that cannot be assigned to the canal-otolith interaction effect (see preceding text).

As illustrated in the *bottom right section* of the scheme, we therefore propose that our subjects may have also used an optimal computation strategy in the body-tilt task. In the scheme, the brain first computes a signal representing body orientation in space (B_s) by combining the vestibular signal H_v and signals from the truncal graviceptors (TGC). The prior in this system represents an a priori assumption about the probability that a particular body tilt will occur. Since upright positions are most common in daily life, the prior is tuned at zero tilt. Except for this difference in the neural signal to be evaluated, the line of reasoning and the effect of the prior on the occurrence of systematic errors are comparable to our earlier explanation (see preceding text). However, the question arises why these systematic errors were smaller than in the pointing task of the same session while still showing a degree of correlation across sessions (see Fig. 10). To account for the smaller self-tilt estimation errors at large tilts, we assume that the body-tilt prior is broader. But if reliance on a prior is part of a strategy to achieve optimal performance in the face of noisy input signals, why would the two systems rely on different a priori assumptions? The strategic element in this computation involves a cost-benefit evaluation where the cost of occasional large errors has to weighed against improved performance in more typical situations. Since the assessment of what constitutes overall optimal performance may well be different for the sense of self tilt and for external-space perception, the idea that the prior may be different in the two systems is perhaps not so strange as it appears at first sight.

Since the width of the priors is a major factor in determining the size of systematic errors at large tilts, we have to assume that this parameter may vary among subjects and even within the same subject on different days (see Fig. 8 and Table 1). Partly coupled prior variations in the two modules would help to explain why the A effect in the two tasks correlated at large tilts, adding to a similar effect of the hysteresis phenomenon. These two sources of the A effect are of little importance at small tilts where independent extra-vestibular signal sources (SOM and TGC) may have spoiled the correlation (see Fig. 10, *bottom left*).

Finally we have to address the question why earlier studies, requiring subjects to adopt a 90° tilt (Mast and Jarchow 1996; Mittelstaedt 1983) did not find large systematic errors. As explained earlier, the occurrence of large A effects is not only determined by the width of the prior but also by the estimated noise characteristics of the input signal on which the judgment is to be based. Comparison of our data with those of Mittelstaedt (1983) shows that our subjects had a much larger scatter in their responses at 90° tilt. It is possible that our use of a clock scale has forced subjects to make a transformation that yielded additional noisy fluctuations. The fact that we tested many different angles, whereas the earlier studies concentrated on a particular tilt angle, which may provide special and more reliable cues, may have worked in the same direction. Anyway, if signal B_s was more trustworthy in the earlier studies, the effect of the prior must have been more limited. In other words, whether or not the putative body-tilt prior is revealed may depend on how the system is tested. Therefore it would be useful to repeat the earlier self-positioning experiments at a large number of tilt angles.

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