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Modelling Three Dimensional Vestibular Responses During Complex Motion Stimulation

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INTRODUCTION

Complex motion stimuli provide a unique and powerful method to stretch the limited range of sensory stimulation we normally experience and to decouple those sensory inputs which normally correlate with one another during normal movements. By examining the responses induced by complex stimuli, the characteristics of the underlying neural processing (from sensor to response) can be examined more thoroughly, since the system is no longer in its accustomed range. Therefore, it is possible to distinguish different information processing mechanisms, which may be indistinguishable for natural stimuli.

"Reflexive" eye movement responses are one commonly studied vestibular response[1] to motion stimuli, but perceptual correlates of the stimuli are also elicited by motion. (As the term *correlate* suggests, the perceptions experienced by a subject during and after motion can be related to physical properties of the stimulus such as position, velocity and acceleration.) A quantification of some of the perceptual correlates has been made possible by psychophysical

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[1] The phrase *vestibular responses* can be misleading, since all motion stimuli affecting the vestibular sense organs also affect other sensory systems, such as the visual or somatosensory systems or the recently reported trunk graviceptors (Mittelstaedt 1992,1995). Thus, *vestibular* responses to motion stimuli are almost never purely vestibular and the responses are usually more accurately categorised by the physical stimulus than by any specific sensory system. Nonetheless, because the dynamics associated with the peripheral vestibular system are well known and the vestibular system plays such a large role in spatial orientation responses, both models presented in this paper focus primarily on the contributions of the vestibular system.

methods; self-orientation with respect to gravity, thresholds of motion perception and perception of self-position are possibly the most successful measures related to motion stimulation.

In the following, we will focus on modelling the responses induced by *inertial* stimuli (i.e., stimulation by angular and/or linear acceleration, including gravitational acceleration without any non-inertial *positional* information such as visual or auditory cues which could be used to determine self-position or self-velocity in space). Both authors have presented models for vestibular responses during and following complex motion stimuli. One of the models (Glasauer, 1992a,b, 1993) concentrated on human spatial orientation relative to gravity, based on psychophysical measurements of the visual vertical. The other was developed to help understand complex three-dimensional eye movement responses (Merfeld, 1990, 1995b; Merfeld *et al*., 1993) but was later extended to include perceived orientation relative to gravity (Merfeld, 1995a).

These independent models share several common conceptual ideas and postulate the existence of similar intermediate stages of information processing. One reason for these similarities is common roots : the approach of cybernetic analysis in conjunction with estimation theory. Moreover, both models are formulated in Cartesian co-ordinates, as suggested by the structure of the vestibular system, and describe the flow of information in the central nervous system (CNS) using mostly linear elements like filters, integrators and summing junctions but also include some non-linear operators.

Another common issue is the importance of gravity as both a sensory input and an internal estimate. Gravity, long known to influence spatial orientation, has turned out to have a pervasive influence on the VOR as well. For example, in Merfeld's model of the VOR, the estimate of gravity is an essential prerequisite to compute other motion estimates such as angular velocity and linear acceleration. Similarly, other models have also explicitly included the influence of gravitational cues on the VOR (Hain, 1986; Raphan and Sturm, 1991).

As a conceptual basis, the principle of an *internal model* will be applied (see Fig. 1). An internal model (not to be confused with the overall model) is an integral component of estimation techniques like observer theory and optimal estimation theory (i.e., Kalman filters), but internal models also have a long history in psychophysics (e.g., efference copy and correlation storage are essential components of an internal model). The purpose of internal models is to estimate external variables (like gravity, acceleration, velocity etc.) by mimicking the physical relationships between those variables and the sensory systems and thereby predicting their time-course from incomplete, noisy, and/or inaccurate sensory information.

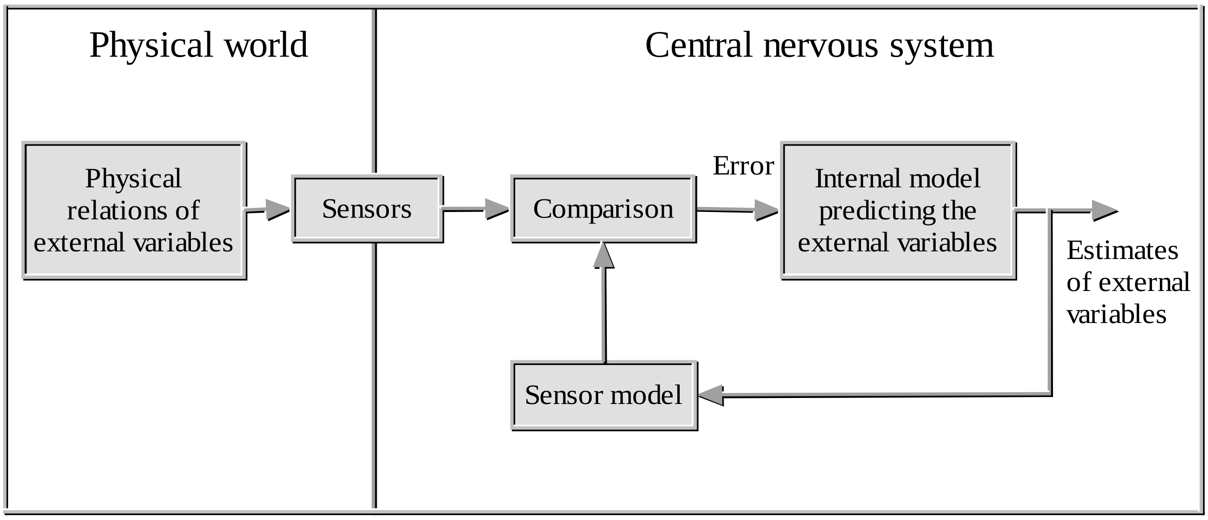

Figure 1 Principle outline of the internal model concept applied for the estimation of external physical variables like acceleration, velocity and position.

Rather than presenting a fully developed model structure, which is done elsewhere (Glasauer, 1992a, 1993; Merfeld, 1990, 1995a, 1995b; Merfeld *et al*., 1993), we will try to identify those information processing elements that are necessary to explain the experimental results which connect the sensory stimulation (input) to the physiological responses (output).

To illustrate the necessity of the different model elements, experimental evidence for them is supplied by a few examples. Much of the experimental data are well known, and have been re-examined by the authors in either humans or monkeys. The comparison of responses to 1) eccentric rotation around an earth-vertical axis and 2) roll-tilt around an earth-horizontal axis turns out to well illustrate most of the hypotheses and, therefore, will be discussed in the following sections.

PROBLEMS FACING THE NERVOUS SYSTEM

The input during inertial stimulation consists of angular acceleration, detected mainly by the semicircular canals, and linear acceleration, measured by all physiological linear accelerometers, including the otolith organs. From a technical point of view, the vestibular system is an inertial sensor system measuring the necessary 6 degrees of freedom.

Nevertheless, several problems arise when one tries to use the sensor output to compute position and orientation in space:

1) As stated by various researchers, the otoliths alone are not sufficient to distinguish between gravity and linear acceleration. This physical fact, called the Equivalence Principle, is a problem faced by the otoliths (or any other linear accelerometer). This problem is commonly referred to as gravito-inertial force (GIF) resolution.
2) Since the input to any graviceptor is acceleration, a double-integration is necessary to determine translational position in space. (This problem will not be further discussed in this paper.)
3) Physiological sensors are not perfect. For example, the afferent firing rate of the semicircular canals show characteristics of a high-pass filter with respect to angular velocity. (Hence, the well-known decay of the VOR and subjective sensations of rotation during constant-velocity rotation.)
4) Correct implementation of rotational kinematics require a three dimensional angular velocity to orientation integration, which is not simply a temporal integration of angular velocity. (Quaternion integration is one common way to achieve this integration, e.g. Tweed *et al*. 1994.)

All of these problems must be considered by the CNS when attempting to process ambiguous motion cues. One primary reason we have chosen to model these responses is because there are a large number of potential mechanisms by which the nervous system could try to solve the problems listed above. Modelling helps reduce the number of potential mechanisms that are consistent with the experimental evidence to a more manageable number.

How is the problem of gravito-inertial force (GIF) resolution solved in the CNS ?

As discussed above, the responses of a single linear accelerometer to translatory and gravitational acceleration are equivalent and therefore are not distinguishable by measurement. The otoliths can only measure the vector sum of both. The following equation describes this fact:

$$\underline{f} = \underline{a} + \underline{g} \qquad \text{(Eq. 1)}$$

where f denotes the total linear acceleration measured by the otoliths, which is composed of gravitational acceleration ($\underline{g}$) and other linear accelerations ($\underline{a}$) such as centrifugal

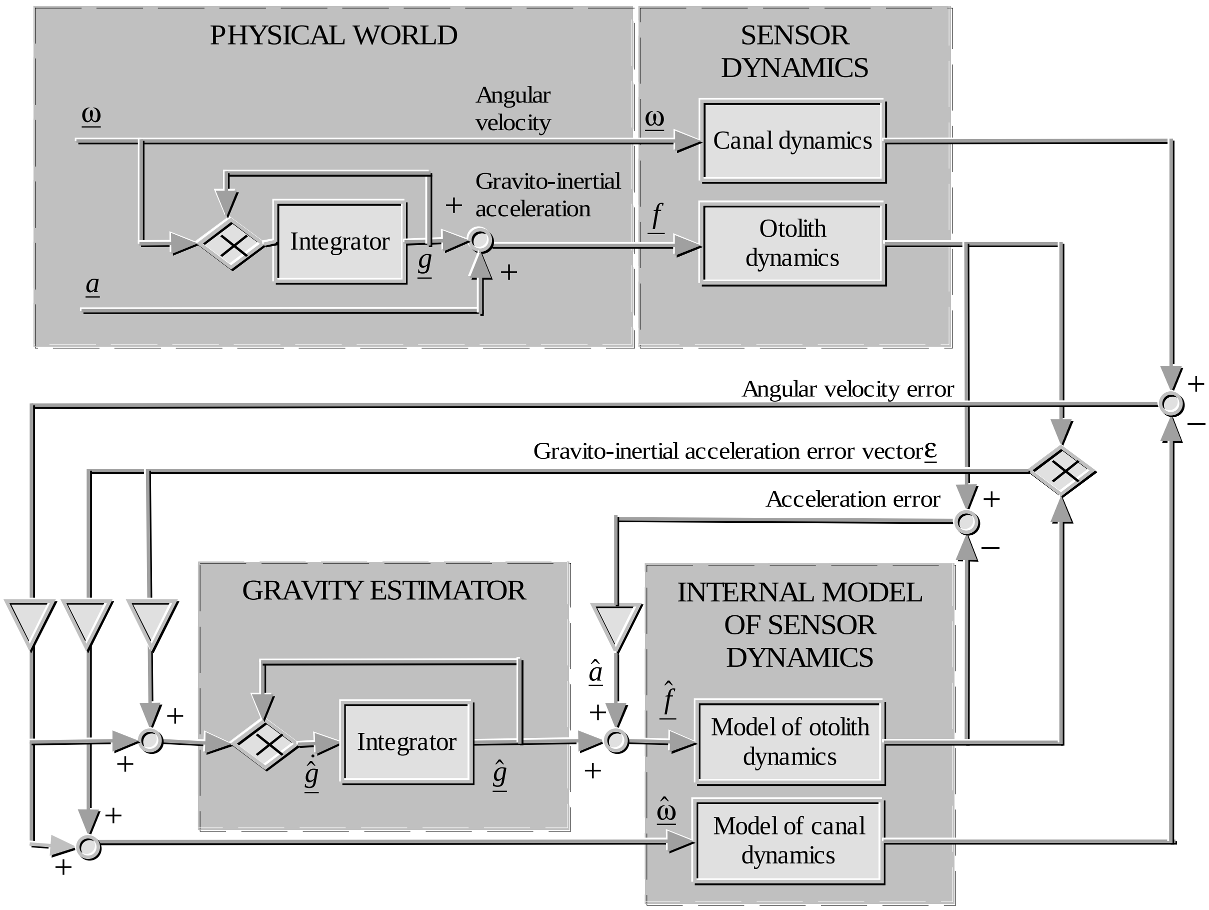

Figure 2 Outline of the three-dimensional model of Merfeld. The structure has been slightly modified for better understanding and comparison with Fig 3. The physical inputs, angular velocity and gravito-inertial acceleration, are processed by the sensor dynamics, then compared to internal estimates either by subtraction or by a means of a vector product (×). After scaling by gain factors (triangles), the error vectors are fed into the estimation process which contains internal models of sensor dynamics and physics. For explanation of symbols, see text.

acceleration or translatory acceleration (see Figs. 2 and 3, summation in *Physical world*). Therefore, the problem of GIF resolution has to be solved using other information. Here, the concept of the internal model is useful. The general idea of the internal model states that the outputs of the internal model are compared to the sensory inputs, the error of the model is then used by means of some sort of feedback to adjust the estimates of the internal model. With this concept in mind, we can first look at the physical relationship between the inertial inputs, and then suppose that those physical relationships are "known" to the CNS and implemented as precisely as necessary to mimic the physics.

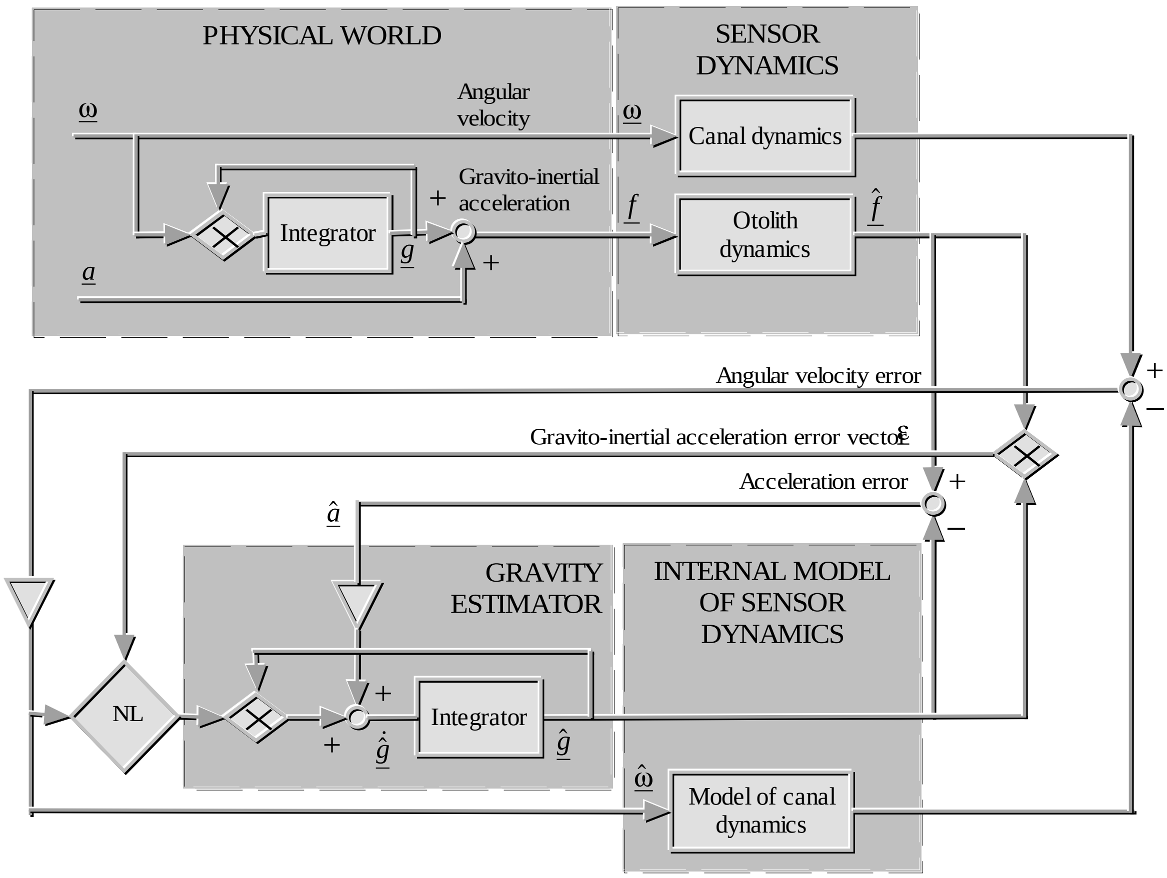

Figure 3 Outline of the three-dimensional model of Glasauer. The structure has been modified for better understanding and comparison with Fig 2. Similar to Merfeld's model, the sensory afferents are compared to internal estimates either by subtraction or by a means of a vector product (×), the resulting error vectors are fed into the estimation process. The model of canal dynamics, not explicitly formulated in Glasauer (1992a,b), is shown for better comparison. Note the differences in computation of the internal estimates of gravity $\underline{\hat{g}}$ and angular velocity $\underline{\hat{\omega}}$, and the similarities in computing the internal estimate of translatory acceleration $\underline{\hat{a}}$ and the gravito-inertial acceleration error vector $\underline{\varepsilon}$. For further explanation of symbols, see text.

Specifically, we hypothesize that the physical relationships between gravity, translational acceleration and gravito-inertial force are known by the CNS. The CNS then implements a representation of these physical relations using its internal estimates of the various quantities. Specifically, the nervous system implements a representation of the physical relationship as shown:

$$\underline{\hat{f}} = \underline{\hat{a}} + \underline{\hat{g}} \qquad \text{(Eq. 2)}$$

where $\underline{\hat{f}}$ is the estimate of the total acceleration (the otolithic afferents are a good estimate already), $\underline{\hat{g}}$ is the current estimate of gravity, and $\underline{\hat{a}}$ is the current estimate of translatory acceleration.

Similarly, the gravitational acceleration and the angular velocity of a body are physically related by the following vectorial differential equation :

$$\underline{\dot{g}} = \underline{g} \times \underline{\omega} \qquad \text{(Eq. 3)}$$

where $\times$ denotes the vector cross product, $\underline{g}$ is the gravitational acceleration and $\underline{\omega}$ the angular velocity of the body (see Figs. 2 and 3, cross-product in *physical world*). The equation describes the fact that during a body rotation around the body-fixed axis $\underline{\omega}$, the gravity vector is rotated in the opposite direction with respect to the body by the angular velocity -ω in a head-fixed coordinate system.

Note that Merfeld (Merfeld *et al.* 1993) originally implemented a quaternion integrator to perform these 3-D integration calculations, but both Merfeld and Glasauer now use the cross-product calculation to functionally replace the 3D integrator: the angular velocity vector $\underline{\omega}$ is not simply integrated over time to derive the new direction of gravity, one has to integrate over the vector product of gravity and angular velocity. This purely physical relationship (Eq. 3) is now hypothesized to be used by the CNS to determine an estimate of gravitational acceleration $\underline{\hat{g}}$:

$$\underline{\dot{\hat{g}}} = \underline{\hat{g}} \times \underline{\hat{\omega}} \qquad \text{(Eq. 4)}$$

Here, $\underline{\hat{\omega}}$ is not the physical angular velocity, but again an internal estimate (in the simplest case the canal afferents). Assuming that the magnitude of gravity remains constant, Eq. 4 can provide a continuous estimate of gravity for any sensory input. (This estimate will usually be inaccurate when the sensory cues are ambiguous or for sub-threshold stimuli.) The blocks *Estimation of Gravity* in Fig 2 and Fig 3 are both realizations of Eq. 4.

Once the magnitude and direction of gravity are estimated, subtracting the current estimate of gravity ($\underline{\hat{g}}$) from the total acceleration ($\underline{f}$) measured by the otoliths ($\underline{\hat{f}}$) yields translatory acceleration ($\underline{\hat{a}}$):

$$\underline{\hat{a}} = \underline{\hat{f}} - \underline{\hat{g}} \qquad \text{(Eq. 5)}$$

This yields *a* solution to the gravito-inertial force resolution problem (see also Fig 2 and 3).

However, this solution is not always correct. For example, problems arise because of the high-pass filter characteristics of the semicircular canals. The fluid mechanics of the semicircular canals implement an integration (from angular acceleration to angular velocity) over a frequency range between roughly 0.01 and 1.0 Hz. At frequencies below roughly 0.01 Hz, the canals act like high-pass filters. Therefore, a step of rotational velocity input results in a exponentially decaying response. Thus, low-frequency rotations quickly lead to a canal firing rate that is the same as the resting firing rate (i.e., firing rate measured with no angular velocity). If the rotation is about a tilted axis, i.e. off-vertical axis rotation (OVAR), the GIF resolution mechanism described above would fail to correctly estimate the direction of gravity, since the estimate of angular velocity ($\underline{\hat{\omega}}$), shown in Eq. 4 to influence the central estimate of gravity, is incorrect.

How to overcome the high-pass characteristics of the semicircular canals ?

One of the first models of otolith-canal interaction (Mayne 1974) suggested a simple solution to this problem. Rely on the semicircular canal afferents only at high frequencies, a range where the canals provide accurate angular velocity responses. At low frequencies, derive the central estimate of gravity ($\underline{\hat{g}}$) by low-pass filtering the otolith measurements of gravito-inertial force. Thus, similar to the synergy of OKN (opto-kinetic nystagmus) and VOR (vestibulo-ocular reflex) proposed by Robinson (1977), the insufficiency of the canals for the low frequency range can be replaced by an input from a different sensory system, here the otolith organs. However, Mayne's model was limited to just 2 dimensions[2].

Other solutions have also been proposed. For example, Merfeld suggested that, instead of lowpass filtering the cues from the otoliths, the difference between actual otolith output and estimated otolith output be used to rotate the estimated gravity vector in the correct direction. Another (Glasauer, 1992) suggested a non-linear pre-processing of the canal

[2] The 3D-generalisation of Mayne's 2D model, as proposed earlier (Mittelstaedt et al. 1989, Glasauer 1992a), can then be written as :

$$\dot{\underline{\hat{g}}} = \underline{\hat{g}} \times \underline{\hat{\omega}} + (\underline{\hat{f}} - \underline{\hat{g}})/\tau$$

where τ is the time constant of the proposed lowpass filter (See Fig 3, block *Estimation of Gravity*). It can even be shown (Glasauer 1992a) that the 3D generalisation of Mayne's approach can be interpreted as a linear optimal filter (in the sense of Kalman filtering theory) with respect to the otolith input, if the canal afferents reflect the true angular velocity . However, as explained above, the latter is not the case.

afferents (see Fig 3, block *NL*) which switches off implausible canal signals by comparing them to an error vector $\underline{\varepsilon}$ (see below), thereby providing an estimate of angular velocity which is closer to the required "true" angular velocity vector.

Interestingly, although the approaches are somewhat different, both postulate that the CNS calculates a cross-product error $\underline{\varepsilon}$ arising from a comparison between the measured and expected linear acceleration (see Fig 2 and 3, *gravito-inertial acceleration error vector*). It can be shown (see Appendix) that the error in our models differs only by a gain factor, but is otherwise based on the same computation. In Glasauer (1992a, 1993), this error is mathematically represented as:

$$\underline{\varepsilon} = \underline{\hat{f}} \times \underline{\hat{g}} \qquad \text{(Eq. 6)}$$

This gravito-inertial acceleration error vector is sensitive to the angle between the measured acceleration vector $\underline{\hat{f}}$ and the estimate of gravity $\underline{\hat{g}}$, being zero if both are collinear. It is perpendicular to both and can therefore be interpreted as angular velocity vector which can rotate the estimated gravity vector $\underline{\hat{g}}$ towards the measured vector $\underline{\hat{f}}$. But it also can be used to detect whether the actual angular velocity estimate $\underline{\hat{\omega}}$ points in the same direction as $\underline{\varepsilon}$ by means of a dot product $\underline{\hat{\omega}} \circ \underline{\varepsilon}$ (see Fig 3, implemented in block *NL*). If this dot product is positive, the rotation accomplished by Eq. 4 will indeed lead to an estimate $\underline{\hat{g}}$ of gravity which lies close to what is measured by the otoliths.

Unfortunately, this postulated internal variable is not easy to detect by neuro-physiological measurements, since during rotation it usually will coincide with the angular velocity measured by the canals. During sinusoidal linear acceleration, where it should also be present as a sinusoid, it can easily be confounded with the direct responses to the sinusoidal linear acceleration. One method of detecting this signal would indeed be eccentric rotation around an earth horizontal axis, as explained below.

EXPERIMENTAL TESTS FOR THE MODELS

Experimental evidence for the principles and structures described above can be demonstrated using complex inertial stimuli. One compelling example remains the comparison between the responses to lateral tilt stimulation and eccentric rotation about an earth-vertical axis. This comparison, first done for the subjective vertical (Stockwell &

Guedry 1970) then for eye movements (Merfeld & Young, 1995), shows quite clearly that an internal estimate of gravity must be represented in the CNS. In both test conditions, tilt and centrifugation, the direction of the measured linear acceleration vector changes by a controlled amount. During tilt, the angular velocity causing the tilt is perpendicular to gravity. During eccentric rotation, the angular velocity is parallel to gravity, and, therefore (see Eqs. 3 and 4), can not directly influence its direction.

The experimental results have shown that the perceived subjective vertical changes rapidly (nearly veridically) during tilt, but tilts slowly towards alignment with gravito-inertial force during centrifugation (Stockwell & Guedry, 1970). The authors concluded that the semicircular canals must influence the perception of vertical, since the subjective vertical changes rapidly when rotational cues from the vertical semicircular canals confirm the rotational tilt but slowly when confirming cues from the vertical canals are not available during centrifugation.

VOR measurements appear consistent with the perceptual findings discussed above. (A brief explanation follows, see Merfeld & Young (1995) for a more complete description.) No linear VOR was observed in squirrel monkeys during rapid tilts, while a significant linear VOR response was always observed during centrifugation. Since we hypothesized that the estimate of translatory linear acceleration is the difference between the otolith measurement of gravito-inertial force and the central estimate of gravity (Eq. 5), the central estimate of acceleration should be small (and little or no linear VOR should be evident) when the difference between gravity and the central estimate of gravity is small. Therefore, since the subjective indications of the vertical during rapid tilts did not differ from the true gravitational vertical, little or no linear VOR would be expected. However, when the difference between measured inertial force and the central estimate of gravity is large, as demonstrated by the transient difference between the subjective indications of the vertical and the gravito-inertial force measured by the otolith organs during centrifugation, the central estimate of translatory acceleration and, hence, the linear VOR might be large. The presence of a linear VOR component during centrifugation has been observed experimentally (Merfeld & Young, 1995) and confirmed by modeling predictions (Merfeld, 1995b).

More importantly, the comparison supports the notion of an internal representation of gravity: If the internal representation of gravity (i.e. of the subjective vertical) did not exist, these results would not be possible. To explain this, one has to reconsider the physical inputs during the centrifugation. After the centrifuge reaches its final speed, all linear acceleration inputs, including those of the otoliths, have reached a constant level. Nevertheless, the perception of roll tilt changes gradually. Therefore, an internal variable representing the perceived direction of gravity must exist; its time course can be assessed by measuring the subjective vertical.

Another result of measuring the subjective vertical during eccentric rotation was long ignored: the striking difference in the result between onset of motion and deceleration to a stop (see Graybiel & Clark, 1965, Glasauer, 1992/1993). While the subjective vertical slowly moves towards the resultant acceleration during motion onset, it briskly, and nearly veridically, comes back to upright after the rotation has stopped.

How can one explain this finding in the framework of the models depicted above? The answer has two parts, one supporting the concept of an internal model, the other strongly suggesting the existence of the gravito-inertial acceleration error vector $\underline{\varepsilon}$ (see Eq. 6). First, the most evident reason for the difference lies in the different initial conditions. While the canal afferents show the same pattern during start and stop (the only difference is the direction of the canal cue), the direction of the resultant linear acceleration vector, and, even more importantly, the direction of the internal representation of gravity is parallel to the angular velocity at the onset of motion, but is tilted away from alignment with angular deceleration during the stop. Indeed, according to Eq. 4 a tilted internal gravity vector will be rotated by the angular velocity vector, thus leading to a fast change of the subjective vertical during deceleration, but no change at the onset of motion, as found experimentally.

However, if the canal afferents themselves would be used in Eq. 4, the internal gravity vector would pivot around the subject’s body axis on a cone-like path for more than 30 seconds (due to the dynamics of the canal information processing). The subject would feel such a pivoting motion as a change in body position from left ear down to forward pitch to right ear down to backward pitch, etc. But this sensation is not reported by subjects exposed to this motion stimuli.

The gravito-inertial acceleration error vector ($\underline{\varepsilon}$), proposed above, is needed by both models to influence the internal estimate of angular velocity (see Fig 2 and 3) and thereby allow rapid changes in the internal estimate of the gravity vector as long as this change decreases the error vector. The rapid change happens up to the instant when the subjective vertical aligns with the rotation sensed by the semicircular canals, which, in turn, aligns with the otolith cue (i.e., with the true gravity vector).

Let us examine more closely the role of this error signal in both the tilt experiment and the eccentric rotation experiment. During tilt, the internal estimate of gravity and the total acceleration measured by the otoliths (gravity plus inertial acceleration) are almost equal; therefore the error $\underline{\varepsilon}$ remains close to zero and has little or no influence on the estimate of gravity. During onset of centrifugation, the change of direction of the gravito-inertial acceleration is only slowly reproduced by the internal estimates, as reflected by the subjective vertical. More importantly, gravito-inertial acceleration as measured by the otoliths and the internal estimate of gravity transiently point in different directions. Therefore, the gravito-inertial acceleration error has a large magnitude (see Eq. 6), which decays with a time constant similar to that of the change in the subjective vertical, and reaches zero as soon as the subjective vertical realigns with the gravito-inertial acceleration. During offset of centrifugation, the error $\underline{\varepsilon}$ and the angular velocity estimate are first perpendicular to each other which, in both models, leads to a fast change of the subjective vertical. However, as soon as the measured and estimated gravity vectors are aligned, further change is suppressed by the error vector.

Several other well-defined models of three-dimensional spatial orientation (e.g. Mayne 1974, Borah *et al*. 1988, Droulez & Darlot 1989), that do not include such an error term, have so far failed to reproduce these eccentric rotation experimental results.

The eccentric rotation experiment is not the only one that can be explained by and thus supports the modeling hypotheses described above. Other complex motion stimuli like perception of spatial orientation in a pivoting centrifuge cabin (Guedry *et al.* 1992, Glasauer 1992a, 1993), the perception of tilt during a “catapult-launch” experiment (Cohen *et al.* 1973), and eye movement responses during OVAR (Harris, 1987; Harris & Barnes, 1987; Merfeld, 1995a; Merfeld *et al*., 1993) have been successfully simulated.

SUMMARY

This comparison of our two recent models of spatial orientation revealed several common features which are hypothesized by the authors to have neuronal correlates in the CNS. Both models postulate, on the basis of very few assumptions, that the processing of linear and rotational acceleration information in the CNS mimics closely the physical laws of movement in a gravitational environment. The percepts of orientation and position in space are supposed to be based on internal estimates of the corresponding physical variables like gravity, translatory acceleration, and angular velocity. Inaccuracies which arise from sensor characteristics and imperfect neural processing are reduced by including error signals which are used to correct the internal estimates. One crucial signal for successful simulations turned out to be the gravito-inertial acceleration error which, in both models, serves as a corrective for the angular velocity required to compute the direction of gravito-inertial force.

The internal variables and the structure of the information processing are theoretical constructs that are actually hypothesized to exist in the CNS. Their neuronal implementation has yet to be uncovered. All of the common features of the models turn out to be well motivated by experiments utilizing complex motion stimuli, which proved to be a powerful method to decouple the inertial sensory cues that are correlated under normal conditions. Further experimentation and revalidation of the models will be necessary to improve the performance of the models and enable even better predictions about the underlying neuronal mechanisms.

Appendix

In Glasauer's model, the gravito-inertial acceleration error vector $\underline{\varepsilon}$ is explicitly formulated in Eq. 6 as:

$$\underline{\varepsilon} = \underline{\hat{f}} \times \underline{\hat{g}} \qquad \text{(Eq. A1)}$$

Merfeld's model, however, appears to use a different error vector (which will be shown to be mathematically *similar*):

$$\underline{\varepsilon}_M = \frac{\underline{\alpha} \times \underline{\hat{\alpha}}}{|\underline{\alpha}| \cdot |\underline{\hat{\alpha}}|} \qquad \text{(Eq. A2)}$$

where $\underline{\hat{\alpha}}$ is the internal estimate of $\underline{\alpha}$, the otolith afferents. Note that $\underline{\alpha} = \underline{\hat{f}}$, if the otolith transfer function is set equal in both models (which is possible without changing the results). Evidently, the direction of $\underline{\varepsilon}_M$ only depends on the direction of $\underline{\alpha} \times \underline{\hat{\alpha}}$. It can be shown that in Merfeld's model $\underline{\hat{\alpha}}$ is computed by :

$$\underline{\hat{\alpha}} = \frac{\underline{\hat{g}}_M + k_a \cdot \underline{\alpha}}{1 + k_a} \qquad \text{(Eq.A3)}$$

where k_a is the acceleration feedback gain and $\underline{\hat{g}}_M$ the current estimate of gravity in Merfeld's model.. Inserting this in $\underline{\alpha} \times \underline{\hat{\alpha}}$ gives :

$$\underline{\alpha} \times \underline{\hat{\alpha}} = \underline{\alpha} \times \frac{\underline{\hat{g}}_M + k_a \cdot \underline{\alpha}}{1 + k_a} = (\underline{\alpha} \times \underline{\hat{g}}_M + k_a \cdot \underline{\alpha} \times \underline{\alpha}) \frac{1}{1 + k_a} = \frac{\underline{\alpha} \times \underline{\hat{g}}_M}{1 + k_a} \qquad \text{(Eq. A4)}$$

since $\underline{\alpha} \times \underline{\alpha} = 0$. Inserting Eq. A4 and A1 in Eq. A2 shows that both gravito-inertial acceleration error vectors have the same direction and are only different by a normative gain factor:

$$\underline{\varepsilon}_M = \frac{\underline{\alpha} \times \underline{\hat{g}}_M}{|\underline{\alpha}| \cdot |\underline{\hat{\alpha}}| \cdot (1 + k_a)} = \underline{\varepsilon} \cdot \frac{1}{|\underline{\alpha}| \cdot |\underline{\hat{g}}_M + k_a \cdot \underline{\alpha}|} \qquad \text{(Eq. A5)}$$

However, this equation is only true if $\underline{\hat{g}}_M = \underline{\hat{g}}$, which is the true for the static case and other conditions like during and after short duration tilts. But since the internal estimates of gravity can be somewhat different in the two models, differences in the error vector *can* be found depending on the model parameters and the motion stimuli.

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