Otolith Signal Processing and Motion Sickness

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The otolith organs register the resultant gravito–inertial force (GIF), consisting of the vector sum of all linear accelerations acting on the head, including gravity. In many cases, a low-pass filter is appropriate to characterize the neural processing by which the subjective vertical (SV) is constructed from the GIF. The time constant of this low-pass filter is generally assumed to be about 20 s, based on measurements of the oculogravic illusion during centrifugation.[1] In contrast with this, we recently observed a much shorter time constant when we measured the somatogravic illusion in a centrifuge.[2] Five subjects were asked to continuously align a tactile rod with the direction of the perceived vertical, while the centrifuge (with an arm of 5.6 m) was accelerated with 10 deg/s^2 up to a constant level of 0.5 G. The group's mean time constant by which the rod was lined up with the GIF amounted only to 5 s. What then is the best value to represent the time constant of the neural filtering of the otolith signals? Here, we will provide an argument in favor of the shorter time constant, based on model simulations predicting motion sickness during linear oscillations along the vertical longitudinal axis (heave motion).

The model is based on the idea that motion sickness generally occurs when a correct sense of gravity is compromised by the motion stimulus: subjects only develop motion sickness when their SV is at stake.[3] Taking this role of the SV into account, the sensory rearrangement theory of Reason and Brand[4] can be refined to: "Motion sickness arises when the sensed vertical as determined on the basis of integrated information from the the eyes, the vestibular system, and the non-vestibular proprioceptors is at variance with the expected vertical as predicted on the basis of previous experience."

To operationalize this so-called "Subjective Vertical conflict theory" we extended the mathematical model of Oman[5] on motion sickness. The essence of the extended model is shown in FIGURE 1. The gravity vector (or sensed vertical, $\mathbf{v}_{sens}$) is explicitely determined from the total set of sensory information, including linear and angular motion information from the otoliths and the semicircular canals, as well as orientation information from the visual system. In the simple case of one-dimensional heave motion, the model only requires low-pass filtering of the otolith signals. Analogous to Oman's original model, an internal model has been implemented to obtain an optimal estimate of the gravity vector, or expected vertical ($\mathbf{v}_{exp}$). Because the internal model uses the same low-pass filter as the sensory path, $\mathbf{v}_{exp}$ will generally be the same as $\mathbf{v}_{sens}$ during normal locomotion. During external motion, however, the two vectors may differ because the motion will be input to the sensory path, but not to the internal model.[3] According to the SV-conflict theory, it is the difference, or conflict, between $\mathbf{v}_{exp}$ and $\mathbf{v}_{sens}$ that correlates with motion sickness. It

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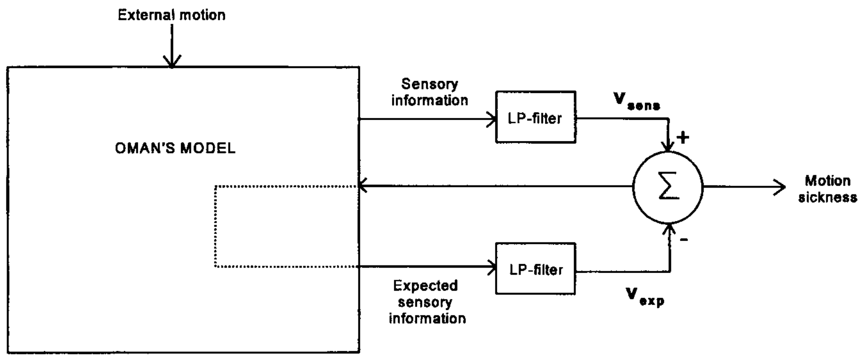
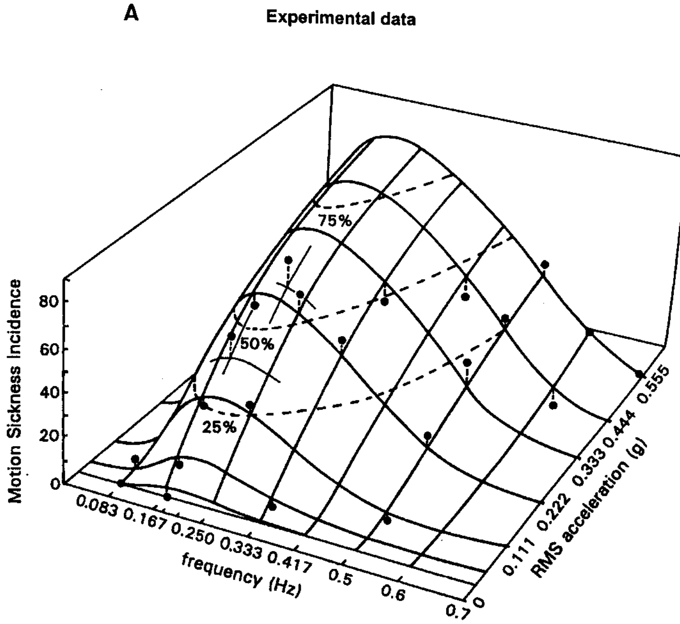


FIGURE 1. Schematic representation of the subjective vertical conflict model. The model of Oman[5] has been extended by modules to calculate the sensed vertical (v_{sens}) from the sensory information (*upper path*). In the case of linear motion (*upright*), the neural processing of the otolith signals can be appropriately simulated by a low-pass filter. In parallel, the same calculations are performed in an internal model (*lower path*) to derive the *expected* vertical (v_{exp}) from the *expected* sensory information. The difference (or conflict vector) between v_{sens} and v_{exp} is assumed to correlate with motion sickness. This conflict vector is also used for feedback into the internal model in order to update v_{exp} (indicated by the *dotted line*).

is interesting to note that v_{exp} can be updated by feedback of the conflict vector into the internal model, which, in the case of linear motion, may induce an extra time lag, since it places the low-pass filter of the internal model in series with the low-pass filter of the sensory path. As a result, the conflict vector can be expected to reach a maximum at a certain stimulus frequency, which is primarily determined by the time constant of the low-pass filter, and to a lesser extent by the weighting of the internal feedback.

We used the time constant of 5 s to simulate the conflict vector for oscillatory heave motion for frequencies up to 1 Hz. The results were compared with a study of O'Hanlon and McCauley,[6] who investigated the motion sickness incidence (MSI) in more than 500 subjects during pure heave motion. Their data showed a maximum of the MSI around a frequency of 0.16 Hz. To make the model's output directly comparable with MSI, the conflict vector was scaled into a predicted MSI value by means of a nonlinear normalization Hill-function, followed by a second-order leaky integrator accounting for accumulation in time. The upper limit of MSI was set to 80% in accordance to the results of O'Hanlon and McCauley. FIGURE 2 shows that the predicted MSI curve closely resembles the experimental data, and most importantly, the predicted maximum of MSI coincides with the observed maximum. It should be emphasized again that the location of this maximum is not affected by the amplitude scaling afterwards. It depends predominantly on the difference between v_{exp} and v_{sens}, and to a smaller degree on the internal feedback weighting.

In conclusion, using a time constant of 5 s the maximum MSI predicted by the model is in agreement with data from the literature. Thus it seems that the time constant for the determination of the SV from the otolith signals is shorter than suggested by the time course of the oculogravic illusion. The time constant of 5 s should not be considered too precise, since the model's output can be fine-tuned by manipulating the feedback weighting. It is our impression, however, that the data of O'Hanlon and McCauley can be simulated even better when using a time constant of *less* than 5 s. A value of 20 s is clearly too high for the SV-conflict model. It remains unclear why the time constant differs so much between the oculogravic and the somatogravic illusion, especially because the measurements discussed here were performed under approximately the same conditions.[1,2] Presumably, the difference is inherent in the different sensorimotor functions tested.



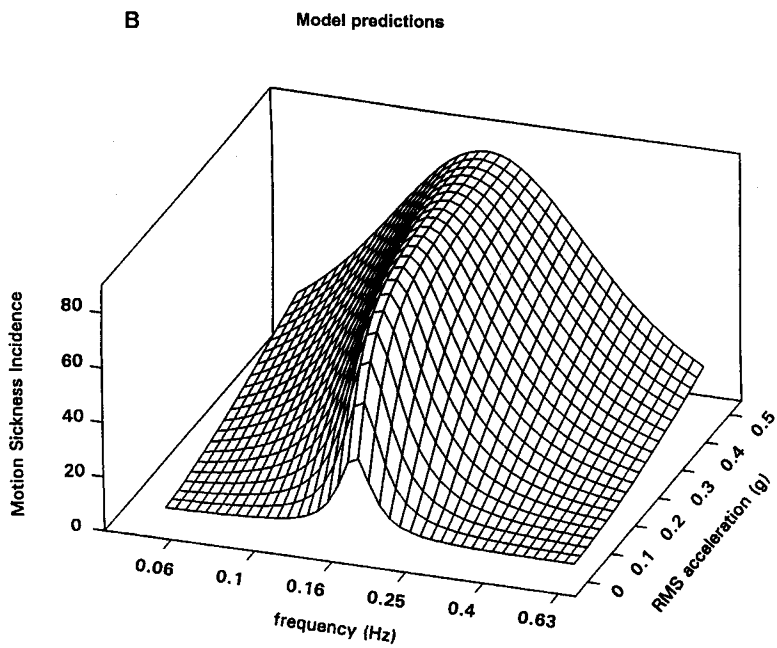


FIGURE 2. Comparison between experimental and predicted data on the motion sickness incidence (MSI) for heave motion. (**A**) Curve-fitted experimental data (adapted from O'Hanlon and McCauley[6]); (**B**) the model predictions. MSI is plotted as a function of the frequency and the amplitude of vertical oscillation. Both curves show a maximum at 0.16 Hz.

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