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Sensory Conflict Compared in Microgravity, Artificial Gravity, Motion Sickness, and Vestibular Disorders

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Abstract

Perceptual disturbances and motion sickness are often attributed to sensory conflict. We investigated several conditions: head movements in microgravity, periodic motions in 1-g, and locomotion with vestibular disorders. In every case, linear vectors such as linear and gravitational acceleration are crucial factors, as previously found for head movements in artificial gravity, and thus the importance of measuring linear vectors emerges as a common theme. By modeling the sensory conflict between the vestibular and somatosensory systems, we computed a measure of linear conflict known as the “Stretch Factor.” We hypothesized that the motions with the greatest Stretch Factor would be the most provocative motions.

RESULTS—For head movements in microgravity, the Stretch Factor can explain why fast movements are more provocative than slow movements, and why pitch movements are more provocative than yaw movements. For off-vertical-axis rotation (OVAR) in 1-g, the Stretch Factor predicts that the most provocative frequency is higher than that for vertical linear oscillation (VLO). For example, the same sensor dynamics can predict a most provocative frequency around 0.2 Hz for VLO but 0.3 Hz for OVAR, solving a mystery of this experimentally observed discrepancy. Finally, we determined that certain sensory conflict perceptions reported by vestibular patients could be explained via mathematical simulation.

Keywords

perception; microgravity; modeling; OVAR; motion sickness

1. Introduction

Sensory conflict is thought to play a major role in perceptual disturbances and motion sickness [22, 47, 48, 52]. However, even with a sensory-conflict explanation, a number of perceptual and motion sickness phenomena still lurk at the edges of our understanding. Some of these phenomena occur in microgravity, in 1-g with periodic motion, and in vestibular disorders. Is there a common theme?

Space motion sickness, or “space adaptation syndrome,” occurs in microgravity. Unpleasant motion-sickness-like symptoms typically arise soon after entering microgravity, especially upon movement of the head [20, 49], and illusory sensations have also been reported [38]. It has been observed that head movements in the pitch direction are most likely to cause sickness symptoms [20, 49], and that faster head movements seem to be more disturbing [20]. The obvious question is whether pitch movements and faster movements cause more sensory conflict than others. For example, if two movements have the same amplitude, is there any reason to think that the faster movement should cause greater sensory conflict?

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Measures of conflict have been applied previously in microgravity. Three-dimensional modeling computations derived a “Twist Factor” (for angular motion) and a “Stretch Factor” (for linear motion) to quantify conflict during vestibular coriolis cross-coupled stimulation, in both 1-g and 0-g [24–26]. When two pieces of information—for example, from two different sensors—are in apparent conflict, the Twist Factor measures the discrepancy between the angular components of the two motions and/or orientations that would correspond to the different pieces of information, while the Stretch Factor measures the discrepancy between the linear components. These measures provided an explanation for a mysterious experimental observation: while cross-coupled stimulation—produced by turning or tilting the head during whole-body rotation about a different axis—has been found quite disturbing on Earth [20, 22, 41], subjects in 0-g are surprisingly immune to symptoms [18, 19, 35]. Classically, this motion sickness is explained by angular components of motion [20, 22], but the angular components are the same in 1-g and 0-g. The new analysis, using Twist and Stretch Factors, demonstrated that the magnitude of the Stretch Factor during cross-coupled stimulation, computed using full three-dimensional modeling with linear-angular interaction, is the measure that differentiates between 1-g and 0-g, and implies much greater conflict in 1-g. In addition, the Stretch Factor predicted asymmetries that have been observed in 1-g for different directions of head rotation [24, 26], as well as differences between accelerating and decelerating conditions [25].

Linear components of motion are also involved in another mystery which concerns vertical linear oscillation (VLO) versus off-vertical axis rotation (OVAR). Both are periodic motions that cause motion sickness, and it is well known that the degree of disturbance depends on frequency. However, one puzzling piece of information that has not been explained is the fact that the most disturbing frequency in VLO differs from that in OVAR. VLO is said to be most provocative around 0.2 Hz [1, 40, 46], as discussed in Methods below. OVAR, on the other hand, has been found most provocative around 0.3 Hz [12, 45]: As explained further in Methods below, tests across many frequencies found motion sickness greatest at intermediate frequencies 0.25 Hz and 0.33 Hz in one experiment [45], and in another experiment with frequencies including 0.25 Hz, 0.29 Hz and 0.33 Hz, the peak was found to be at 0.29 Hz [12]. In brief, the most provocative frequency for OVAR, around 0.3 Hz, is higher than that for VLO, around 0.2 Hz.

Just as linear vectors are relevant for microgravity, VLO and OVAR, they also appear in illusory motions perceived by vestibular patients. Prominent are perceptions of “walking on pillows” and “stepping into a hole” [55]. Both of these indicate a perception of illusory vertical motion in the vertical oscillation of walking. In a study [55] of patients with Ménière’s Disease (MD), benign paroxysmal positional vertigo (BPPV), and unilateral peripheral vestibular impairment (UPVI), 21% of patients reported perceptions of “walking on pillows,” and 46% of patients reported perceptions of “stepping into a hole.” More specifically, “walking on pillows” was reported by 20% of patients with MD, 16% with BPPV, and 30% with UPVI. “Stepping into a hole” was reported by 33% with MD, 48% with BPPV, and 65% with UPVI. Although the mechanisms behind these sensations are undoubtedly complicated, a rudimentary analysis may be possible, providing a window into understanding these perceptual phenomena.

The goal of the present research was to find common ground across different sensory environments. Modeling was performed for motions selected from microgravity, 1-g, and with vestibular disorders. First, pitch head movements in microgravity were modeled in comparison with yaw head movements, and a range of speeds was tested. The Stretch Factor was computed to compare between conditions and with experimental observations. Second, VLO and OVAR were modeled across a range of frequencies. The hypothesis tested was that sensory conflict produced by sensor dynamics could predict the experimentally

observed differences in provocative motion frequencies. Third, simulations were performed to model locomotion with altered vestibular gain but accurate somatosensory information. Toward the goal of a first-pass explanation, the aim here was to determine whether consideration of the linear components was sufficient to simulate the sensation of “walking on pillows” and “stepping into a hole.” In all cases, the sensory systems that most directly detect acceleration, e.g. the vestibular and somatosensory systems, were considered the focus. Although other senses such as vision can be a factor in motion sickness, the role of vision was not specifically investigated here; in fact, VLO and OVAR are typically performed in the dark.

2. Methods

2.1. Standard Model

Known properties of perception were used, creating a “Standard Model” mirroring established features of perception. Specifically, angular acceleration is known to lead to perception of rotation, while an earth-horizontal component of rotation gives perception of tilt, and the component of gravito-inertial acceleration (GIA) not aligned with perceived vertical leads to perception of linear motion. That resolution of the GIA (or GIF, gravito-inertial force) has been termed the GIF-resolution hypothesis, and has been demonstrated experimentally [5, 42–44]. All of the above are in accordance with the laws of physics. In addition, perception has certain tendencies; for instance, the perceived vertical moves toward alignment with the GIA. Meanwhile, perceived angular and linear velocities exhibit “velocity storage” to sustain them, but decay in the absence of acceleration. These tendencies can be modeled in many ways such as by parametrized feedback loops, differential equations with time constants, priors in Bayesian modeling, outcomes of Kalman filtering, etc. [6, 7, 9, 13, 23, 25, 34, 37, 39, 43, 50, 53, 58], but give the same first-order tendencies matching experimental data. For clarity, we chose to model via differential equations so that time constants could be most directly compared with experimental data.

Equations comprising the Standard Model were as follows:

Perceived angular velocity, ω , arises from angular acceleration, α , and decays with time constant τ_A . We therefore modeled perceived angular velocity in head-based coordinates by

$$\frac{d\omega}{dt} = \alpha - \frac{\omega}{\tau_A}.$$

Using a unit vector $\mathbf{k}$ to represent the perceived Earth-vertical direction in head coordinates, $\mathbf{k}$ changes according to perceived angular velocity. Additionally, the direction of the GIA influences the vector $\mathbf{k}$:

$$\frac{d\mathbf{k}}{dt} = \mathbf{k} \times \left(\omega + \frac{\theta}{\tau_T} \right)$$

where θ is the rotation vector from the GIA to $\mathbf{k}$ using the right-hand rule, and τ_T is the time constant governing the tendency to perceive the GIA as vertical. Analogous equations were used for the other two spatial directions as given by orthogonal unit vectors $\mathbf{i}$ and $\mathbf{j}$ in head coordinates, representing perceived Earth-horizontal compass directions:

$$\begin{aligned}\frac{d\mathbf{i}}{dt} &= \mathbf{i} \times \left(\boldsymbol{\omega} + \frac{\boldsymbol{\theta}}{\tau_T} \right) \\ \frac{d\mathbf{j}}{dt} &= \mathbf{j} \times \left(\boldsymbol{\omega} + \frac{\boldsymbol{\theta}}{\tau_T} \right)\end{aligned}$$

It is worth noting that this form with derivatives and cross products takes care of the noncommutativity of rotation. Perceived linear velocity, $\mathbf{v}$, arises from the portion of the GIA not attributed to gravity and decays with time constant τ_L . The simplest equation for $\mathbf{v}$ is in Earth-based coordinates:

$$\frac{d\mathbf{v}}{dt} = \mathbf{A} - \mathbf{g} - \frac{\mathbf{v}}{\tau_L}$$

where $\mathbf{A}$ is the GIA, and $\mathbf{g}$ is a vector in the perceived Earth-upward direction representing the portion of the GIA attributed to a “pseudo-acceleration” upward due to the presence of gravity. (The conversion between Earth- and head-based coordinates is the straightforward linear transformation.) Finally, perceived translation is represented by perceived position, $\mathbf{r}$, having derivative perceived velocity, since any first-order translational dynamics are already encompassed in τ_L above:

$$\frac{d\mathbf{r}}{dt} = \mathbf{v}.$$

2.2. Application #1: Head Movements in Microgravity

This study investigated pitch as compared to yaw head movements in a 0-g environment, and compared head movements of different speeds. Published observations from microgravity were used for comparison with the modeling results. These observations indicated that pitch movements are much more provocative than yaw movements [20, 49], even during short periods of 0-g in parabolic flight [36]. In addition, faster movements are more provocative [20].

We used the Standard Model and computed a measure of sensory conflict for 30° pitch and yaw movements and for average speeds from 10°/s to 90°/s. The base case was no movement, in which a subject also perceives no movement. From a modeling perspective, the subject was therefore considered to be adapted to the head-vertical component of acceleration; i.e. the absence of head-vertical acceleration did not indicate falling as it does in 1-g. However, upon head movement about a head-horizontal axis, the absence of an “expected” acceleration of gravity in a head-horizontal direction was considered to cause a conflict. We modeled this conflict using the Stretch Factor:

Stretch Factor: Given two different computed trajectories of motion, the Stretch Factor is the accumulated difference between the trajectories in three dimensions. Technically, the Stretch Factor is computed by calculating the length of the path given by the difference between the trajectories parametrized over time.

The Stretch Factor is a measure of linear conflict, as opposed to a measure of angular conflict. The corresponding angular conflict, such as the analogous Twist Factor [24–26], is zero for the current movements because the conflict-causing component, gravity and its absence, is linear, not angular.

To calculate the Stretch Factor for head movements in 0-g, one computed trajectory of the head was as given by neck proprioception, i.e. was the actual head movement, and the other computed trajectory was as modeled by the Standard Model with gravity considered only in the head-horizontal direction, as explained above. The movement distances were 30° and had half-sine velocity profiles with average speeds from 10°/s to 90°/s (e.g. the 30°/s movement lasted 1 second). The Stretch Factor was computed over 3 seconds in all cases to facilitate appropriate comparison. In this way, the movement distance was controlled because in all cases, the head had reached and stopped at a 30° angle by the 3-second point. For pitch, the “neck length”, as implemented by positioning the axis of tilt below the vestibular system, has been shown to have little effect on Stretch Factor [25], so a single value of 0.15 m was used here. The use of time constants or their exact values has also been shown to have negligible effect on relative values of Stretch Factors when comparing conditions [25], so the simulations were performed with the time-constant terms dropping out of the equations because the 3 s time frame is so short. Testing was also performed with typical time constants on the order of seconds and shorter to confirm that relative values of Stretch Factors were unaffected.

For comparison, two other sets of simulations and computations were performed. One considered subjects to be partially adapted to 0-g, by using a 50% adaptation level accomplished by setting the head-horizontal g-level in the Standard Model to 0.5 g. The other, to test robustness of the results, was for 45° instead of 30° head movements.

2.3. Application #2: Vertical Linear Oscillation and OVAR

We investigated the possible effects of the dynamics of sensory systems on VLO and OVAR for frequencies in the range 0.05 Hz to 1.25 Hz. The equations are explained in detail below, taking into account the fact that VLO is a linear motion aligned with the GIA so only the linear velocity and acceleration come into play, whereas OVAR has a GIA that rotates relative to the subject so tilt also comes into play; e.g. θ in the Standard Model is zero during VLO but nonzero during OVAR. Computations for OVAR primarily used a tilt angle of 20°, but were also tested at 30°. For each condition, the Stretch Factor was computed as a measure of sensory conflict. The conflict measured was between sensory systems that were considered to have different dynamics, as quantified by time constants. The study used time constants in the range 0.1 s to 3.1 s, as described below in the explanation of modeling.

Because experimental data on motion sickness are important for assessing the modeling results, we first summarize the experimental data. Studies show the most provocative frequency for VLO to be around 0.2 Hz, and the most provocative frequency for OVAR to be approximately 0.3 Hz. For VLO, a comprehensive study [40] showed a peak at 0.17 Hz upon a curve fit to data across frequencies from 0.083 Hz to 0.7 Hz and across rms accelerations from 0.0278g to 0.555g, although 0.25 Hz was more provocative than 0.167 Hz whenever tested at the same rms acceleration, at both 0.111g and 0.222g. One often-cited experiment [46] showed that the frequency 0.167 Hz was more provocative than the frequencies 0.083 Hz and 0.333 Hz. An earlier study [1] with periodic vertical oscillation generated by constant-velocity stretches alternating with constant-acceleration turn-arounds used the finer range of frequencies, 0.22 Hz, 0.27 Hz, 0.37 Hz, 0.53 Hz, and determined that 0.27 Hz was the most provocative based upon a measure involving basic motion sickness ratings of 0, 1 and 2. In summary, the most provocative frequency for VLO is considered to be around 0.2 Hz. For OVAR, on the other hand, experimental studies show the most provocative frequency to be greater. At 10° tilt, frequencies of 0.042, 0.083, 0.17, 0.25, 0.33, 0.41, 0.50, 0.67 and 0.75 Hz (2.5, 5, 10, 15, 20, 25, 30, 40 and 45 rpm) were tested, and time-to-mild-severity of motion sickness was found to be quickest for the two frequencies 0.25 Hz and 0.33 Hz [45]. For OVAR at 30° tilt, frequencies of 0.17, 0.25, 0.29, 0.33, 0.42 and 0.50 Hz (60, 90, 105, 120, 150 and 180°/s) were tested, and time-to-moderate-severity

of motion sickness was quickest at 0.29 Hz, verified as statistically significant compared to all other frequencies tested. In particular, 0.29 Hz was more provocative than 0.25 Hz and 0.33 Hz. Another experiment measured motion sickness sensitivity by a ratio of motion sickness score to the number of revolutions rather than the amount of time [10], so those results are not directly comparable to the VLO and other OVAR data. In short, the most provocative frequency for OVAR has been found to be around 0.3 Hz.

For modeling, the range of time constants was based upon available data. Perception of linear velocity is known to decay with time constants in a range of seconds or less [54]. The respective contributions of different sensory systems into that time constant are unknown, but sensory afferents are known to carry a variety of dynamics. Somatosensory receptors include rapidly adapting [31, 33] and slowly adapting [32, 33] mechanoreceptors; for example, afferents such as Merkel cell units have been found with a dominant time constant around 0.6 s [29], while a model of spike timing has reflected the variety of dynamics among mechanoreceptors [30]. Vestibular afferents also carry a range of time constants, and their dynamics are associated with their regularity of discharge, categorized as regular or irregular [14, 15]. Although a difference in time constants would not produce a noticeable conflict during isolated motions as occur in everyday life, a difference could cause a sustained conflict during ongoing oscillatory motion. For the present modeling, two different sensory systems are considered to have two different time constants, each within the range 0.1 s to 3.1 s.

The equations for the model are analogous to those previously developed for sinusoidal motion [27, 28]. The variables:

w = frequency of periodic motion, rad/s

A = amplitude of linear acceleration, m/s^2

$a(t)$ = linear acceleration, m/s^2

τ_1 = linear velocity time constant for one sensor, s

τ_2 = linear velocity time constant for second sensor, s

τ_T = tilt time constant, s

g = amplitude of gravitational acceleration = 9.81 m/s^2

$u(t)$ = function for perceived linear velocity before calibration, m/s

$v(t)$ = perceived linear velocity, m/s

S_{OVAR} = Stretch Factor during OVAR, m

S_{VLO} = Stretch Factor during VLO, m.

For VLO with vertical linear acceleration given by

$$a(t) = A \sin wt$$

the function for perceived linear velocity, before calibration, using first-order time constant τ_1 is governed by the differential equation

$$\frac{du(t)}{dt} = a(t) - \frac{u}{\tau_1}$$

which results in

$$u(t) = \frac{A\tau_1}{\sqrt{1+\tau_1^2 w^2}} \sin\left(wt - \tan^{-1}(\tau_1 w)\right)$$

as the linear velocity estimate by one sensor, before calibration. Calibration is then necessary in order to compare sensors. To calibrate, we include a gain on the hypothetical sensor's signal in an appropriate way that depends upon the sensor's dynamics. For example, a sensor with a short time constant gives a small "raw" velocity estimate, so the gain must be set higher to give an appropriate final linear velocity estimate. The exact value of the gain is determined by a step acceleration, where the steady-state raw velocity signal according to the differential equation turns out to be proportional to the first-order time constant. Therefore, the gain is set equal to the reciprocal of the time constant. In other words, the perceived linear velocity as indicated by the sensor is modeled by

$$v(t) = \frac{1}{\tau_1} u(t).$$

The difference between sensors is then obtained as the difference between two such equations for $v(t)$ using different time constants, τ_1 and τ_2 . The amplitude of the difference can be computed using standard trigonometric sum identities (e.g. [27] Appendix B) yielding the Stretch Factor:

$$S_{vLO} = A \left(\frac{1}{1+\tau_1^2 w^2} + \frac{1}{1+\tau_2^2 w^2} - \frac{2}{((1+\tau_1^2 w^2)(1+\tau_2^2 w^2))^{1/2}} \cos\left(\tan^{-1}(\tau_2 w) - \tan^{-1}(\tau_1 w)\right) \right)^{1/2}.$$

Technically, this Stretch Factor has units of length, by assuming a unit conversion of 1 m/(m/s). This conversion is performed because the Stretch Factor over any fixed period of time is proportional to the velocity. The result could be scaled to cover any fixed period of time, but since the goal is to treat lengths of time equivalently across conditions, any such scaling is immaterial to the results.

For OVAR, the GIA vector moves periodically in a conical manner. Because of the tendency to perceive the GIA as vertical, perceived tilt also follows a cone [11, 21, 56, 57]. The amplitude of perceived linear acceleration is given as the difference between the GIA and the perceived vertical according to the perceptual understanding of the laws of physics (i.e., the GIF-resolution hypothesis). The resulting equation for each component of perceived linear translation has been computed previously [28], from which the perceived linear velocity is the derivative (simply multiplying by w), along with additional calibration as above, which divides out the linear time constant:

$$v(t) = \frac{Ag\tau_r w}{\sqrt{1+\tau_1^2 w^2} \sqrt{1+g^2 \tau_r^2 w^2}} \cos\left(wt - \tan^{-1}(\tau_1 w) - \tan^{-1}(g\tau_r w)\right).$$

The difference between sensors is again obtained by subtracting two such equations with different time constants, with amplitude of the difference computed by standard

trigonometric sum identities (e.g. [27] Appendix B). Using shorthand $c_1 = 1 + \tau_1^2 w^2$, $c_2 = 1 + \tau_2^2 w^2$, and $c_3 = 1 + g^2 \tau_T^2 w^2$, the result is

$$S_{OVAR} = Ag\tau_T w \left(\frac{1}{c_1 c_3} + \frac{1}{c_2 c_3} - \frac{2}{(c_1 c_2)^{1/2} c_3} \cos \left(\tan^{-1}(\tau_2 w) - \tan^{-1}(\tau_1 w) \right) \right)^{1/2}$$

where the Stretch Factor S_{OVAR} uses the same convention as S_{VLO} for unit conversion.

2.4. Application #3: Vestibular Patients

Locomotion was simulated using kinematic data from healthy subjects but with alterations in the simulated vestibular gain for the linear accelerations. The goal was to produce a visual representation of the motion that a subject might perceive, to compare with the descriptions of “walking on pillows” or “stepping into a hole” [55].

Published experimental data on healthy locomotion [51] were used for the simulations. Initial stick figures were based upon Fig. 1A in Pozzo et al. 1990 [51], using markers at the following locations: lower border of the eye socket, meatus of the ear, neck at C7, hip (tubercle of the iliac crest), knee, ankle, and lateral 5th metatarsal. Next, the scale was tuned more precisely according to the numerical data on step length [51]. From the one-sided data, simulated locomotion was assumed symmetric by assigning to the right side of the body the analogous—offset by one-half step cycle—positions of the markers. Throughout the step cycle, “central body” positions were calculated between eye sockets, ears, neck, and hips by averaging the values from the left and right sides. The head trajectory was then more carefully placed based upon the numerically reported data, at 7.5cm vertical excursion with a sinusoidal profile [51], and the simulated markers at the head and neck were adjusted accordingly. Finally, “feet” were simulated by adding points to form right triangles. In the simulations, each foot’s contact with the ground was highlighted in pictures by a short piece of floor in contact with the foot, indicating the time and position of somatosensory input.

Simulations with altered vestibular gain aimed to produce figures that illustrate possible perceptions of body and floor motion. For these simulations, we used two example vestibular gains, 0.5 and 1.5, for the linear acceleration. Low gain is often associated with vestibular disorders [17], while high gain has sometimes been observed in Ménière’s Disease [16]. However, it is important to note that for historical and practical reasons, these clinical observations are associated with the angular vestibulo-ocular reflex and therefore give data on the response to angular stimuli. On the other hand, simulations of locomotion involve the response to linear stimuli. Thus, we adjust linear gain in the present simulations. In effect, the simulations propose a new hypothesis about vestibular gain that extends the available data to include responses for which experimental data are not yet available.

The gains were applied to the model by reducing or increasing the perceived linear acceleration, and therefore, the amplitude of perceived vertical head motion. Proprioceptive information was modeled as accurate, so the rest of the body was modeled as positioned and oriented correctly relative to the head. In addition, somatosensory information from the foot was modeled as accurate, so the floor was displayed touching the foot during the part of the step cycle in which the foot was perceived in contact with the floor. Because the head, and therefore body and foot, trajectory was altered, the floor-contact times could occur in such a way that the part of the floor contacting the foot was out of alignment with the actual floor position.

Again, these simulations were meant to give a simple possible explanation for the perceptual phenomenon, even though more sophisticated factors could be added later. We used data from healthy locomotion to generate the simulations, although vestibular patients may have other variations of trajectories during locomotion. The simulations were designed in such a way that the concepts introduced in this healthy-trajectory version would apply to other trajectories as well.

3. Results

3.1. Application #1: Head Movements in Microgravity

The Stretch Factor was found to be zero for all yaw head movements, but nonzero for all pitch head movements. This result was expected, because yaw head movements do not change the head-vertical direction.

The tests at different velocities gave the more notable results. The results were that faster head movements had greater Stretch Factors at the 3-second mark, even though the total distance and time were the same as for slower head movements (Fig. 1A). In other words, the Stretch Factor was greatest if the head moved quickly and then stayed at a 30° angle until the 3-second mark, as opposed to if the head moved more slowly, taking the full 3 seconds to tilt 30°. This result—greater Stretch Factor at the 3-second mark after faster 30° movements—also held for partial adaption to 0-g (Fig. 1A). A test with 45° instead of 30° tilt gave the same shapes of curves (not shown). For additional analysis, the Stretch Factor's increase over time was plotted for different movement speeds (Fig. 1B). As a result, it became clear that the faster movement generated the greater Stretch Factor both because it tilted the head to greater conflict-causing angles sooner, and because it then kept the head at the greatest angle (30°).

3.2. Application #2: Vertical Linear Oscillation and OVAR

Stretch Factors for VLO and OVAR were found to depend substantially on the values of the time constants used. The Stretch Factor arose from a discrepancy between two signals with different time constants (Fig. 2A). Regardless of the values of the time constants, however, the patterns of Stretch Factor over frequency and between VLO and OVAR were consistent throughout.

First, the Stretch Factor curve for both VLO and OVAR was always hill-shaped. In other words, the Stretch Factor peaked at an intermediate frequency (Fig. 2B). In addition, graphs of Stretch Factor were virtually identical for OVAR at 20° tilt and 30° tilt; all figures here are generated from the 20° tilt condition. Some of the peaks for VLO and OVAR corresponded to the experimentally-observed peaks of motion sickness around 0.2 Hz to 0.3 Hz, as discussed below, potentially giving insight into the values of time constants existing in the sensory processing within perception and motion-sickness pathways.

Second, the peak frequency for OVAR was always higher than that for VLO (Fig. 2B). The peak frequency for OVAR was found to be in a range around 1.5 times that for VLO (Fig. 3), depending upon the values of the linear time constants, when using a tilt time constant of $\tau_T = 0.1$ s. Toward comparison with the 1.5 frequency ratio found experimentally for motion sickness, certain pairs were especially noted: for example, linear time constant pairs (0.1s, 2.0s), (0.3s, 1.8s), (0.7s, 1.6s), etc. are combinations that give a ratio 1.5 OVAR-to-VLO (Fig. 3). In addition, short tilt time constants were found to give the largest OVAR-to-VLO ratios, with $\tau_T = 0.05$ s producing even larger ratios often above 2, whereas larger tilt time constants were found to give smaller ratios, with $\tau_T = 1$ s producing ratios below 1.1.

Additional investigation identified peaks in Stretch Factor around 0.2 Hz for VLO and 0.3 Hz for OVAR with selected values of the time constants (Fig. 4A). A particularly successful pair of values, 0.6 s and 1.1 s, for the linear time constants is in the range found experimentally (discussed in Methods), with 0.6 s matching that found in a somatosensory receptor [29]. The Stretch Factor resulted from the difference between responses corresponding to the two different time constants (Fig. 4B).

3.3. Application #3: Vestibular Patients

Simulations of locomotion resulted in two animations, representing 0.5 and 1.5 gain of sensed linear acceleration at the head, as described in Methods. For 0.5 gain (Fig. 5), the floor was perceived to be at its highest point when the foot first contacted the floor, then the floor was perceived to dip and rise again during the stance phase. For 1.5 gain (Fig. 6), the floor was perceived to be at its lowest point when the foot first contacted the floor, then the floor was perceived to rise and dip again during the stance phase.

4. Discussion

The linear component is the most relevant for certain motions, but its importance can be obscured by the complexity of the motion. Three-dimensional modeling can sort out the complexity and elucidate the implications of effects such as reduced gravity, discrepancies in sensory dynamics, and changes in vestibular gain. Modeling is used in the present research toward the classic scientific goal of finding common explanations across a variety of conditions, in this case for microgravity, artificial gravity, periodic motion, and vestibular disorders. For microgravity, the most striking finding was that a fast movement followed by remaining stationary generated the greatest Stretch Factor, while a slow movement that spanned the entire time period generated the smallest Stretch Factor. This result was meaningful because the motions had exactly the same length of time, distance, and endpoint, so the only difference was in the profile of the velocity. The result was consistent with subjective observations on motion sickness [20], providing a possible explanation for the observed phenomena. This result also added evidence for the utility of the Stretch Factor in microgravity, used previously to explain the lack of motion sickness during head movements while rotating in 0-g and to make predictions for artificial gravity [24–26]. For vestibular disorders and the perceptions of “walking on pillows” or “stepping into a hole”, the present simulations (Fig. 5 and 6) give a picture of the type of phenomena that occur with vestibular disorders, displaying through modeling the most basic version of somatosensory effects that could arise from changes in vestibular gain.

4.1. Vertical Linear Oscillation and OVAR

For VLO and OVAR, the results from the model were consistent with experimental data. In both cases, the Stretch Factor was found to peak at an intermediate frequency, and in all cases, the peak was at a higher frequency for OVAR than for VLO. This was true regardless of the sensory time constants, while slight variations in time constants could explain individual differences in motion sickness peaks.

Bos and Bles [8] had also modeled VLO and found a peak at an intermediate frequency, so the relationship between the models is worth discussing. In the Bos and Bles model, the sensory conflict is between the “sensed” and the “subjective” vertical motion. The sensed vertical motion is the same as that of one sensor in the present research, i.e. based upon a first-order time constant. The subjective vertical motion, however, is not from another sensor like that used in the present research, but is based upon additional processing of the original sensor signal. Interestingly, even though these two modeling studies’ second signals—subjective vertical versus second sensor—are conceptually different, the effects are quite

similar because the processing to produce the subjective vertical essentially lengthens the time constant, similar to having a second sensor with a longer time constant. The nervous system could use the methods of either or both models. It is already known that the nervous system makes use of differences between sensor dynamics: temporal and spatial response differences between individual otolith afferents have long been hypothesized to accomplish spatiotemporal convergence [2–4]. Above all, the consistent result between the Bos and Bles model and the present model confirms that sensory dynamics can produce conflicts that match experimental results on motion sickness. Bos and Bles also took the quantitative results a step further, determining a transfer function between the level of conflict and the motion sickness incidence (MSI) in order to more precisely model and explain motion sickness at non-peak levels across frequencies and acceleration amplitudes. In the present research, the goal was to determine the peak frequency for comparison with OVAR so additional processing was not performed, and the drop-off at non-peak frequencies (Figs. 2B and 4) was not intended to show the exact rate at which motion sickness dropped, but rather the direction up-or-down with frequency.

The present research instead compared VLO with OVAR, tackling a new question. Although a provocative frequency around 0.167 Hz or 0.2 Hz is typically mentioned as a “general” rule, experience and data show that OVAR actually has a most provocative frequency closer to 0.3 Hz (as discussed in Methods). Through direct application of known properties of perception, including computations involving linear-angular interactions, the model turned out to predict the patterns across frequency that have been found experimentally. These results thereby give a possible explanation for the higher frequencies of provocativeness for OVAR as compared to VLO. Upon further analysis, the quantitative modeling results can be translated into a summary as follows: VLO and OVAR can both cause a conflict in dynamics during oscillation (Fig. 2A), and a higher peak frequency is found if the time constants are shorter (Fig. 2B). Although the time constants are the same for VLO and OVAR, OVAR also includes GIF-resolution in order to resolve the acceleration signal into tilt and translation; perceived tilt lags the GIA, causing perceived translation to lead the GIA (consistent with the phase lead shown by horizontal eye movements during OVAR [57]). This phase lead of translation over the GIA increases the phase lead already produced by the time constant dynamics (Fig. 2A), and an increase of the phase lead has an effect similar to shortening the time constants. In summary, OVAR’s tilt with respect to gravity effectively shortens the linear time constants and thereby raises the frequency at which sensory conflict peaks.

4.2. Experimental Questions Raised

One of the purposes of modeling is to fine-tune experimental questions and to raise new questions. Accordingly, the present results introduce several ideas for VLO versus OVAR, for vestibular patients, and for microgravity.

For VLO versus OVAR, the results lead to additional tentative deductions that are worth further investigation. For example, certain pairs of linear time constants give the experimentally observed OVAR-to-VLO peak frequency ratio of 1.5 (Fig. 3), while other pairs do not. This result may indicate which sensors and/or time constants arising from processing are involved in the pathways relevant to motion sickness. Time constants of 0.6 s and 1.1 s give results consistent with experimental observations on motion sickness (Fig. 4A), raising the question of whether or which sensors, afferents, and/or higher-order neurons carry those time constants, and perhaps giving clues to shared pathways between motion sickness, perception, and/or reflexes. Meanwhile, the tilt time constant was found here to be quite short (0.1 s or less), consistent with the fact that perceived motion during OVAR is roughly in phase with the motion [57], but shorter than the time constant value on the order of seconds deduced previously using the amplitude of perceived tilt during horizontal

oscillation while upright [9]. This observation raises questions about the nervous system's treatment of periodic motions, whether periodic motions are treated differently from non-periodic motions, and at what level the differential processing might occur. Nonstandard perception of periodic motion has already been shown for OVAR: the additional hypothesis that perceived translation is linked in phase to perceived tilt was found necessary in order to explain the conical shape of perceived motion [28].

In addition, differences between subjects' frequencies of sensitivity to motion sickness may be explained by variability in sensor or processing dynamics (Fig. 2B). It is possible that inter-individual variability in peak frequency is related to variability in measurable time constants such as for the linear vestibulo-ocular reflex.

Other sensory systems and additional characteristics of sensory dynamics can also be studied in the context of motion sickness. The visual system is one such system, but even with acceleration detection alone, higher-order or nonlinear dynamics may play a role in sensory conflict.

For microgravity, the results give a foundation from which to compare any future data on the provocativeness of head movements. One mystery that has not been solved is why pitch head movements are more provocative than roll head movements, at least during the 0-g period of parabolic flight [36]. The current model distinguishes only between movements about head-vertical and head-horizontal axes.

For vestibular disorders, the results recommend specific questions about the perceptions of "walking on pillows" and "stepping into a hole". Although subjective perception may not be as precise as the model (Figs. 5 and 6), questions arise. For instance, does the floor seem to be pressed down in the middle of the stance phase? Does the floor seem to rise in the middle of the stance phase? Does the floor feel too high or too low when the foot first contacts it? Does the floor simply rise and fall, or does it also tilt? The answers to these questions can lead to further understanding of sensory processing and the relationship between senses. In addition, the answers will allow tuning of the model to better fit the sensation. As always, subjective differences are expected, with the model available to highlight those differences.

4.3. Conclusion

Linear vectors and linear-angular interaction warrant even further investigation as research progresses, both for the present conditions and for a wider range of motions. In addition, subjective variability may form one key to understanding sensory processing, with data on specific individuals becoming ever more valuable. With these data, the experimental-modeling interaction can continue to tackle the numerous mysteries of perception, elucidating similarities and differences between conditions, and providing insight into seemingly complex phenomena.

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Figure 1.

Stretch Factor, as a measure of sensory conflict, for head tilts in microgravity. (A) Stretch Factor at the 3-second mark. Partial adaptation to 0-g produces less conflict, and faster head movements produce greater total conflict by the 3-second mark, even though the head's path and final position of 30° tilt is the same in all cases. (B) The accumulating Stretch Factor up to the 3-second mark, comparing fast and slow movements. The faster movement, at 30°/s, stopped at the 1-second mark with the head tilted 30°. The Stretch Factor continued to increase because of the absence of an expected component of head-horizontal gravity while tilted.

Figure 2.

(A) Example oscillation showing a discrepancy between signals with different dynamics. Vertical linear oscillation at 0.2 Hz is modeled as a function of time, along with the translation estimates from two hypothetical sensors that have linear velocity time constants 0.6 s and 1.0 s. The oscillation keeps the sensor signals dissonant. (B) Stretch Factor curves as a function of frequency for a variety of linear time constant pairs. For each of VLO and OVAR, four curves are shown, with peaks from left to right corresponding to linear time constant pairs (1.8s, 2.0s), (0.6s, 1.0s), (0.1s, 2.0s), and (0.1s, 0.4s). The tilt time constant is 0.1 s throughout. A normalized Stretch Factor is shown, because pure Stretch Factor depends upon the length of time considered, which is immaterial for comparison between oscillatory motions. The Stretch Factor reaches its maximum at an intermediate frequency in all cases, and the peak for OVAR is always at a higher frequency than the peak for VLO.

Comparison of Peak Frequencies OVAR-to-VLO

Figure 3.

Multiple by which the Stretch Factor's peak frequency for OVAR exceeds the peak frequency for VLO. The peak frequency for OVAR is greater than that for VLO, as indicated by ratios greater than one, regardless of the values of the linear time constants. For time constants $\tau_1 = 0.4, 0.6, 0.8$, etc. up to 2.0 s as shown by the set of curves, and τ_2 from 0.1 to 3.1 s as shown along the horizontal axis, the OVAR- to-VLO ratio of peak frequencies ranges from 1.1 to 2.1 . This figure uses tilt time constant 0.1 s. Open circles indicate singularities where the two linear time constants are equal, thus producing no sensory conflict and zero Stretch Factor for both OVAR and VLO.

Figure 4.

(A) Stretch Factor as a function of frequency for a set of time constants that yields results consistent with experimental observations on motion sickness. The linear time constants are $\tau_1 = 0.6$ s and $\tau_2 = 1.1$ s, and the tilt time constant is $\tau_T = 0.07$ s. (B) Amplitude and phase of linear velocity as indicated by the two different linear sensors with time constants $\tau_1 = 0.6$ s and $\tau_2 = 1.1$ s, which lead to the Stretch Factor above. Amplitude during VLO (thin curves) and OVAR (thick curves) is shown in the top panel, and phase is shown in the bottom panel.

Figure 5.

Simulation of perception during walking if vertical head motion is perceived with low gain of 0.5. Shown is one-half of a step cycle with frames equally spaced in time. The time sequence is displayed left-to-right starting with the top row and progressing through the three rows. The other half of the step cycle would look identical. The first frame corresponds to the time when the head is at mid-height of its cycle, moving downward. Circled pieces show when the perceived height of the floor is inaccurate. The figure shows that as a foot reaches forward and contacts the floor, the perceived height of the floor moves above the actual height, then begins to move downward and reaches a low point as the other foot passes by the stance foot, and finally rises again as the other foot begins to reach forward.

Figure 6.

Simulation of perception during walking if vertical head motion is perceived with high gain of 1.5. Shown is one-half of a step cycle, with circled pieces showing when the perceived height of the floor is inaccurate, following the same conventions as in Fig. 5. The figure shows that as a foot reaches forward and contacts the floor, the perceived height of the floor moves below the actual height, then begins to move upward and reaches a high point as the other foot passes by the stance foot, and finally falls again as the other foot begins to reach forward.