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Spatial Disorientation in Gondola Centrifuges Predicted by the Form of Motion as a Whole in 3-D

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Abstract

INTRODUCTION—During a coordinated turn, subjects can misperceive tilts. Subjects accelerating in tilting-gondola centrifuges without external visual reference underestimate the roll angle, and underestimate more when backward-facing than when forward-facing. In addition, during centrifuge deceleration, the perception of pitch can include tumble while paradoxically maintaining a fixed perceived pitch angle. The goal of the present research was to test two competing hypotheses: (1) that components of motion are perceived relatively independently and then combined to form a three-dimensional perception, and (2) that perception is governed by familiarity of motions as a whole in three dimensions, with components depending more strongly on the overall shape of the motion.

METHODS—Published experimental data were used from existing tilting-gondola centrifuge studies. The two hypotheses were implemented formally in computer models, and centrifuge acceleration and deceleration were simulated.

RESULTS—The second, whole-motion oriented, hypothesis better predicted subjects' perceptions, including the forward-backward asymmetry and the paradoxical tumble upon deceleration. Important was the predominant stimulus at the beginning of the motion as well as the familiarity of centripetal acceleration.

CONCLUSION—Three-dimensional perception is better predicted by taking into account familiarity with the form of three-dimensional motion.

Keywords

models; self-motion; tilt; perception; vestibular; spatial disorientation

INTRODUCTION

Spatial disorientation can occur during complex motions and in altered gravitational environments, especially in the absence of vision [9]. Prediction of human perception and misperception of self-motion is facilitated by performing experimental studies in controlled settings, by identifying underlying principles of self-motion perception, and by testing hypotheses through the use of modeling. One particularly salient experimental motion is that in a centrifuge with a gondola that tilts to keep the subject's body axis aligned in roll with the sum of the centripetal and gravitational forces, as occurs for a pilot during a coordinated turn. This motion is experimentally feasible and yet complex enough to include changes in both linear and angular accelerations, as detected by the vestibular system of the inner ear and by other force receptors throughout the body.

Experimental research has determined that perceptions during the acceleration and deceleration stages of centrifuge runs carry certain asymmetries, not all of which have been explained. Most studied have been the roll and pitch components of perceived motion. When a subject is positioned forward-facing tangentially in the direction of motion, the typical perception during centrifuge acceleration without external visual reference is of forward motion with roll tilt along with slight pitch-up tilt [11,21,22,24-26]. When a subject is positioned backward-facing, the perceived roll tilt during acceleration is significantly smaller in magnitude than when forward-facing [24], while the perceived pitch may be similar to that when forward-facing [26] or may be weaker or reversed in direction [11]. During deceleration of the centrifuge, the perceived roll tilt is negligible regardless of whether the subject is forward-facing or backward-facing [24], while the perceived pitch is substantial and often paradoxical with ongoing tumble concurrent with a fixed pitch orientation [11]. It is worth noting that throughout both the centrifuge acceleration and deceleration, the body axis remains aligned in roll and nearly in pitch with the total linear acceleration stimulus, termed the gravito-inertial acceleration (GIA). The GIA is aligned with the total force on the body, and is defined as the sum of the linear acceleration vector and an earth-upward vector of magnitude that of gravity, two vectors that cannot be distinguished by the sensors.

Research has been sparse toward modeling these perceptions to help explain them. One current mystery is the forward-backward difference in perceived roll tilt during centrifuge acceleration. Forward-backward differences in perceived roll tilt are not addressed in existing models including an analysis of the stimulus [13], a model of perceived roll tilt with “canal suppression” [8], a model combining linear and angular acceleration in subjective vertical for a gondola centrifuge [2], and models for fixed-carriage centrifuges with upright subjects [4, 8,12,14,17,19,20,27]. Hypothesized has been the role of experience and learning effects [24]. For acceleration and deceleration in a tilting-gondola centrifuge, the three-dimensional stimulus has been analyzed with all degrees of freedom including linear-angular interactions [13], which showed that the three-dimensional stimulus carries an asymmetry that can explain the acceleration-deceleration differences in pitch perception. The paradoxical pitch perception, however, was not modeled, nor was the roll perception specifically studied.

The goal of the present research was to identify a minimal set of principles that could explain the known results for perception during acceleration and deceleration in a tilting-gondola centrifuge, and to implement and test these principles in a predictive model. The foundation of the approach consisted of the concepts of experience and familiarity, which have long been known to be factors in perception [3]. Two hypotheses were tested by comparing a Componentwise Model and a Whole-Motion Model.

The Componentwise Model is essentially the core of many existing three-dimensional models of self-motion perception, which implements the principle that each component—angular, linear, tilt—of perception tends toward the most familiar state. In particular, for tilt, the GIA tends to be used in perception as the indicator of vertical, and in the absence of ongoing acceleration, the perceptions of rotation and translation tend toward zero. These properties of the independent components of perception are well-established (reviewed in [9]), and can be viewed as tendencies toward the most familiar “motion” of stationarity in a fixed gravitational field.

The Whole-Motion Model also uses a perceptual preference for familiar motions, but implements this principle at a three-dimensional, whole-motion level. The goal was to follow the guiding principle of Occam's Razor, to favor the simplest explanation possible. For centrifuge acceleration, familiarity was implemented by using three main ideas: forward or backward motion continues forward or backward (not sideways) in the absence of sudden new accelerations, forward motion is more familiar than backward motion, and centripetal

acceleration is familiar when traveling through a curve. For centrifuge deceleration as well, implemented was the idea that the beginning of the motion sets the stage for the rest of the motion; the angular stimulus is the more relevant aspect for deceleration, as indicated by subject reports [11] and analysis of the stimulus, which includes greater initial angular stimulus than during acceleration (details in Methods). Specifically implemented, therefore, was the idea that rotation about a standard axis continues about that axis. In addition, a capability was included to allow angular velocity and angular tilt to dissociate.

The aim was to test and compare the Componentwise Model and the Whole-Motion Model. Each represents a set of hypotheses about self-motion perception, allowing tests of the two different sets of hypotheses in comparison with subjective perception during acceleration and deceleration in a tilting-gondola centrifuge.

METHODS

Experimental Data

Published experimental data [8,11,15,23-25] were used for comparison with the two hypotheses/models. For centrifuge acceleration, the investigation focused on roll tilt because experimental reports were more consistent than for pitch tilt. For centrifuge deceleration, the investigation focused on the more predominant pitch perception, and included roll tilt results as well.

For centrifuge acceleration, typical forward-facing and backward-facing subject reports show perceived roll tilt of magnitude less than that of the actual roll tilt. Tribukait and Eiken [24] reported that in a 9.1 m radius centrifuge which accelerated subjects until they were tilted in roll by 60° (with a GIA of 2g), the subjective visual horizontal, as indicated by adjusting a luminous line to the perceived horizontal, was tilted in roll at the end of the acceleration by $20.9^{\circ} \pm 8.4^{\circ}$ when forward-facing, and $6.9^{\circ} \pm 10.5^{\circ}$ when backward-facing. The centrifuge acceleration magnitude was $7.8^{\circ}/s^2$, which brought the centrifuge up to speed in 10s.

The present investigation analogously considered a 9.1 m radius centrifuge accelerating counterclockwise at $7.8^{\circ}/s^2$ for 10s. For centrifuge acceleration, the focus in modeling was on the portion of the run in which the centrifuge was accelerating rather than the constant-velocity portion after the acceleration. The goal was to investigate the forward-backward difference in perceived roll tilt. The difference, rather than the exact values of perceived roll tilt, was the focus, because variation has been found in experimental results, as explained next.

Other studies included centrifuge accelerations up to a GIA of magnitude between 1.1g and 4.5g, and gave similar results, though included only the forward-facing orientation. Tribukait and Eiken [25] reported that in a 7.25 m radius centrifuge which accelerated forward-facing subjects to 1.1g, 1.7g, 2.5g, or 4.5g (with corresponding roll tilt of 25°, 54°, 66°, or 77°), the subjective visual horizontal at the end of the acceleration showed gains of 0.65, 0.45, 0.41, and 0.40, respectively, relative to the actual roll tilt. Subjects' heads were approximately 20 cm above the axis of tilt, and the centrifuge acceleration magnitudes were all $15^{\circ}/s^2$. Additional research [23] has shown that in a tilting-gondola centrifuge, the subjective head transversal plane, as indicated by adjusting a luminous line “horizontally” with the perceived head transversal plane (i.e. parallel with the interaural axis), displayed substantial tilt relative to the actual head transversal plane. This result is significant because “perceived head tilt” could potentially be defined as the difference in angle between the subjective visual horizontal and the *perceived* head transversal plane. In that case, perceived head tilt could be as much as 1½ to 2 times as great as if measured by only the subjective visual horizontal (relative to the actual head transversal plane). Glasauer [8] reported that in a 10 m radius centrifuge which accelerated forward-facing subjects to 2g with a roll tilt of 60°, the subjective vertical, as indicated by

continuously adjusting a luminous line to the perceived vertical, tilted a maximum of $6.67^\circ \pm 8.32^\circ$. Subjects' heads were approximately 0.5 m above the axis of tilt, and the centrifuge acceleration took just a few seconds.

For centrifuge decelerations, typical perceptions are of tumbling or substantial pitch tilt in the direction of motion (i.e. pitch forward when forward-facing and pitch backward when backward-facing). Guedry et al. [11,15] reported that in a 6.1 m (20 ft) radius centrifuge decelerating from a GIA of 2g or 3g (corresponding to roll tilt of 60° or 70.5°), subjects perceived pitch or tumble, sometimes in a paradoxical fashion. In particular, subjects often reported remaining in a certain pitch orientation such as 90° pitch forward while still continuing to tumble forward. Deceleration magnitudes of $3.3^\circ/\text{s}^2$ and $6.4^\circ/\text{s}^2$ were used. Tribukait and Eiken [24] reported results on roll tilt perception in a 9.1 m radius centrifuge decelerating from a GIA of 2g (corresponding to roll tilt of 60°). After the 10s of deceleration at $7.8^\circ/\text{s}^2$, perceived roll tilt was generally around zero, with no consistent trend in direction, regardless of whether the subject was forward-facing or backward-facing.

For the investigation of centrifuge deceleration, the present research used the same parameters as for centrifuge acceleration: 9.1 m radius, $7.8^\circ/\text{s}^2$ for 10s from a velocity of $78^\circ/\text{s}$, corresponding to 60° roll tilt with GIA magnitude 2g.

Hypotheses/Models

Two sets of hypotheses were tested by developing two models: the Componentwise Model and the Whole-Motion Model. The inputs to both models were angular acceleration and the GIA, while the outputs were angular and linear velocity, 3-D position, and 3-D orientation including heading. Variables and computations were in a coordinate system aligned with the head. At any given time, this system was considered to be instantaneously fixed relative to the Earth to allow computation of nonzero velocities (as in [12,13]).

The Componentwise Model implemented the hypothesis that each component—angular, linear, tilt—of perception is generated relatively independently, as explained below, and then combined to form a three-dimensional motion (Fig 1A). Specifically, the Componentwise Model used a principle of familiarity for each component of motion, as is typically done in perception modeling, as follows. Simulated perceived angular velocity was governed in the standard way by angular acceleration, but with a simultaneous tendency to decay. For tilt, perceived orientation was governed by both the angular velocity and the GIA; perceived orientation changed according to tilt angular velocity but also tended toward aligning the subjective vertical with the GIA. Perceived linear velocity was governed by the deduced linear acceleration as the difference between the GIA and the perceived gravity vector, but with a simultaneous tendency to decay. This method of deducing the linear acceleration as the difference between the GIA and the perceived gravity vector is termed GIF-resolution (GIF being “gravito-inertial force”) and has been demonstrated experimentally [1,17,18]; GIF-resolution was also used in the Whole-Motion Model as explained in the next paragraph. For parameters, the time constant of decay for perceived angular velocity was initially set at $\tau_a=20\text{s}$, based upon experimental data [10]. Time constants for the linear (τ_l) and tilt (τ_t) tendencies were then fit to the experimental data on roll tilt for forward-facing acceleration. The resulting model was then tested for robustness with variations of the angular time constant. Once the parameters were set, the model was tested on backward-facing acceleration, to determine how well the Componentwise Model could predict backward-facing roll-tilt data. Additional testing was done by allowing the linear-forward and linear-backward time constants to be different, to parallel the hypotheses of the Whole-Motion Model.

The Whole-Motion Model implemented the hypothesis that perception is generated by a process that includes familiarity of motion as a whole (Fig 1B). Unlike the Componentwise

Model, which treated all directions of stimuli equivalently, the Whole-Motion Model took into account the predominant stimuli at the beginning of the motion and treated other components relative to the general form of motion, as explained here for centrifuge acceleration and deceleration. For acceleration in the centrifuge, the predominant linear acceleration was forward or backward, so simulated perceived velocity was computed from the forward or backward linear acceleration. Just as in the Componentwise Model, a time constant of decay, τ_l , was used for perceived linear velocity, and was fit to the experimental data. The hypothesis stated that forward motion is more familiar than backward motion, so a shorter time constant of decay was used for backward linear velocity than for forward linear velocity. These time constant values were the only difference between the forward-facing and backward-facing conditions in the model. For both directions, perceived angular velocity about the perceived Earth-vertical axis was governed by the projection of the stimulus' angular acceleration vector onto the perceived Earth vertical, with a simultaneous tendency to decay with a time constant of $\tau_a=20s$ just as in the Componentwise Model. Additional testing was also performed for robustness with variations of this angular velocity time constant. The Whole-Motion Model also understood centripetal acceleration, as explained next.

During centrifuge acceleration, simulated perceived roll tilt was the portion of the GIA roll not attributed to centripetal acceleration. Because centripetal acceleration is typically experienced with magnitude equal to angular times linear velocity (equivalent to angular velocity squared times radius), the model's "expected" radial acceleration and therefore expected roll of the GIA was computed as perceived angular times linear velocity. The difference between actual and expected GIA roll was interpreted to be subject roll. In the gondola, the GIA did not roll relative to the subject ($\phi_{ROLL}=0$ in Fig. 1B), so the amount of perceived roll of the subject was given by the expected roll of the GIA. For example, if the angular and linear velocities were veridically perceived, then the continual roll alignment of the GIA with the body would match the everyday experience of tilting into the curve with the centripetal acceleration, and the Whole-Motion Model would report roll tilt equaling the actual roll tilt. Pitch tilt was similarly computed as the difference between the actual forward linear acceleration stimulus and the expected forward linear acceleration stimulus as determined by the rate of change of perceived velocity ($d\mathbf{v}/dt$ in Fig. 1B). Finally, Earth-vertical velocity was set to zero as the most familiar motion, though future experimental research may allow further analysis of perceived vertical motion during acceleration.

For centrifuge deceleration, note that the angular stimulus is greater at the beginning than for centrifuge acceleration. Although Earth-vertical angular acceleration is equal, the initial tilt velocity of the gondola is greater for deceleration (because tilt is related to the square of the angular velocity), as is the cross-coupled acceleration, equal to the cross product of the Earth-vertical-axis angular velocity and the gondola-tilt angular velocity. This cross-coupled vector arises in rotating reference frames, and has been described in terms of fluid motion in the semicircular canals [16]. In sum, the three-dimensional angular stimulus at the beginning is greater for deceleration.

The Whole-Motion Model for centrifuge deceleration (not shown in Fig. 1B) depended upon further investigation of the stimulus to determine the three-dimensional shape of the motion, including the initial directions that would be associated with the stimulus alone, and is discussed under Results. Briefly, the predominant stimulus is pitch angular acceleration but with a conflicting, relatively constant, body-vertical GIA. Therefore, simulated perceived angular velocity was governed by pitch angular acceleration alone in the Whole-Motion Model, and orientation was governed by a tendency to keep the perceived vertical aligned with the GIA while also being influenced by the pitch angular velocity. Essentially, the angular velocity tried to pull the orientation toward greater tilt, but the GIA tried to pull the orientation toward upright. If the angular velocities of the two directions of pull were equal in magnitude, then the

orientation did not change; otherwise, the orientation changed in the direction of greater pull. This was implemented formally as explained below. Another version of the Whole-Motion Model was tested by including not just pitch in the computation of angular velocity but both pitch and roll, these being the two strongest among the three axes of angular acceleration through the first several seconds of deceleration. For both versions of the Whole-Motion Model for deceleration, the implementation used the same equations as the Componentwise Model (Fig. 1A) but used only the pitch (for the first version) or only the pitch and roll (for the second version) angular acceleration for the angular input. A tilt time constant of $\tau_t=1s$ was used for the tendency to remain aligned with the GIA, and a short linear time constant of $\tau_l=0.1s$ was used to represent the fact that linear motion may be superceded by the angular stimulus. For deceleration, only forward-facing motion was simulated because significant forward-facing/backward-facing differences upon deceleration have not been reported experimentally.

Software and Hardware

Simulations were performed in Matlab (The Mathworks, Natick, Massachusetts, USA) using custom-written code. For simulating perception during centrifuge acceleration, initial conditions were set to match the subjective perception of upright and stationary. For simulating perception during centrifuge deceleration, initial conditions were set to match the subjective perception of stationary with no roll tilt during constant velocity; two initial conditions of pitch were tested: upright, as well as pitch back 22° based upon data on visually perceived eye level during constant velocity [26]. Input to the models were the GIA and the angular acceleration, including those of tilt and coriolis cross-coupling [16] in three dimensions, that would be encountered by a subject upon $7.8^\circ/s^2$ counterclockwise acceleration or deceleration at 9.1 m radius for 10s. For differential equations, the Runge-Kutta 45 algorithm was used. All software was tested using veridical initial conditions along with time constants of infinity, which resulted in successful simulations of veridical perception. Matlab was run in Mac OS X on Mac Pro, MacBook Pro, and Power Mac G5 computers.

RESULTS

Componentwise Model: Acceleration

For forward-facing acceleration in a centrifuge, the Componentwise Model could fit the experimental data for perceived roll tilt. A roll tilt of 21° was obtained at the end of the forward-facing acceleration (Fig. 2A), matching experimental data of $20.9^\circ \pm 8.4^\circ$ [24], with time constants of $\tau_a=20s$ for angular, $\tau_l=5s$ for linear, and $\tau_t=0.8s$ for tilt. The value of the linear time constant turned out not to affect the outcome. The time constant for tilt was unsurprisingly the crucial parameter for predicted perceived roll tilt, so robustness was tested by varying the other time constants, for angular and linear velocity. Varying the angular time constant between 15s and 25s and the linear time constant between 1s and 10s produced perceived roll tilt between 18° and 22° , confirming the robustness of the fit, given the variability of the data.

For backward-facing acceleration, the resulting Componentwise Model was then tested by varying the linear time constant, τ_l , representing the hypothesis that the backward-linear time constant is shorter than the forward-linear time constant because forward motion is more familiar than backward motion. A roll tilt of 21° was obtained at the end of the backward-facing acceleration (Fig. 2A), identical to that for forward-facing acceleration, and not matching experimental data of $6.9^\circ \pm 10.5^\circ$ [24]. The predicted perceived roll tilt remained at 21° regardless of the linear time constant in the range 1s to 10s.

Though published experimental work does not include quantitative three-dimensional reports of subjective motion, the models are designed to provide three-dimensional output as well, described here briefly for comparison with future experimental results. The Componentwise

Model gave sideways curved motion (Fig. 2C) beginning forward then sliding into a sideways, outward-facing motion at an increasing radius. Backward pitch increased up to 38° at the end of the acceleration (Fig. 2A). The three-dimensional output during backward-facing acceleration was analogous, following a similar path but inward-facing (not shown), and forward pitch increased up to 38° .

Whole-Motion Model: Acceleration

For forward-facing acceleration in a centrifuge, the Whole-Motion Model could fit the experimental data for perceived roll tilt. A roll tilt of 21° was obtained at the end of the forward-facing acceleration (Fig. 3A), matching experimental data of $20.9^\circ \pm 8.4^\circ$ [24], with time constants of $\tau_a=20s$ for angular and $\tau_l=4.6s$ for linear. A separate time constant was not necessary for tilt because tilt was determined by the interpretation of centripetal acceleration, as described in Methods under the Whole-Motion Model portion of Hypotheses/Models. Robustness of the fit was confirmed by varying the angular time constant between 15s and 25s, which gave roll tilt in the range 19° to 22° .

For backward-facing acceleration, the resulting Whole-Motion Model was then tested by shortening the linear time constant, representing the lesser familiarity of backward motion compared to forward motion. A roll tilt of 7° was obtained at the end of the backward-facing acceleration (Fig. 3A), matching experimental data of $6.9^\circ \pm 10.5^\circ$ [24], with backward-linear time constant $\tau_l=1.7s$ as compared to the forward-linear time constant of $\tau_l=4.6s$.

The main result was the forward-facing/backward-facing difference. The Whole-Motion Model could predict a forward-facing/backward-facing difference in perceived roll tilt, while the Componentwise Model could not. It is worth noting that the exact values of the time constants are considered less important than the underlying ability to predict the asymmetry.

The three-dimensional output of the Whole-Motion Model gave forward motion around a curve when forward-facing (Fig. 3B) and backward motion around a smaller radius curve when backward-facing (Fig. 3C). For forward-facing acceleration, backward pitch increased up to 7° at the end of the acceleration (Fig. 3A), as compared to 38° for the Componentwise Model. For backward-facing acceleration, forward pitch also increased up to 7° at the end of the acceleration.

Componentwise Model: Deceleration

For centrifuge deceleration, the Componentwise Model could simulate the forward change in pitch perception during forward-facing deceleration, but not the lack of roll tilt reported experimentally [24]. Specifically, the Componentwise Model predicted a perceived roll tilt of 24° at the end of deceleration.

Whole-Motion Model: Deceleration

First, the stimulus to the subject was analyzed (Fig. 4A&B) to determine the predominant type of input at the beginning of the deceleration (as in [13]). This input necessarily included all three degrees of freedom of angular: centrifuge rotation about an Earth-vertical axis, gondola tilt about an Earth-horizontal axis, and cross-coupling giving stimulus about the orthogonal Earth-horizontal axis [16] as described in the note about angular stimulus in Methods, Hypotheses/Models. The result was that pitch overshadowed both yaw and roll, especially for the first half of the deceleration. For pitch and yaw, for example, the projected axis of rotation—based upon the stimulus alone—stayed within 10° of the pitch axis for more than 6s (Fig. 4B) of the 10s deceleration.

The Whole-Motion Model used this predominant pitch angular acceleration as input for angular motion; a second version was also tested by including both pitch and roll angular acceleration. As described under Methods, perceived orientation was computed by a competition between the angular velocity (pitch for the first version of the model, pitch and roll for the second) and the tendency to perceive vertical as aligned with the GIA. Simultaneously, perceived angular velocity was computed from the angular acceleration input, with a time constant of decay $\tau_a=20s$.

Simulations of the Whole-Motion Model gave results matching experimental reports, regardless of whether roll was included along with pitch as input, and regardless of whether the initial condition was upright or pitch back 22° . The forward pitch angle leveled out close to 60° , while the pitch velocity increased and remained significantly positive even while subjective pitch angle paradoxically remained nearly constant (Fig. 4C). The asymptotic pitch angle was the same regardless of the perceived pitch angle, 0° or 22° pitch back, preceding the centrifuge deceleration. Further testing with variations of the tilt time constant, τ_t , showed that other angles of forward pitch, $>60^\circ$ and $<60^\circ$, were easily modeled by the Whole-Motion Model. For example, $\tau_t=1.65s$ gave final pitch angle 90° , as compared to 60° with the originally-tested time constant value of $\tau_t=1s$.

The perceived roll remained below 10° and returned to near 0° by the end of the deceleration, even when full roll angular acceleration input was included in the model (Fig. 4C). The final roll angle depended slightly upon the perceived orientation preceding the centrifuge deceleration: Initial conditions of pitch back 0° and 22° gave roll angle $+1^\circ$ and -2° , respectively (positive being rightward). The perceived roll stayed unsurprisingly at 0° in the version of the model with only pitch as angular input (not shown).

The three-dimensional output of position and orientation from the Whole-Motion Model gave pitch-forward motion beginning with earth-upward motion followed by forward translation (Fig. 4D).

DISCUSSION

Principles of familiarity in self-motion perception are shown here to be able to explain forward-facing/backward-facing differences in roll-tilt perception during centrifuge acceleration as well as paradoxical pitch perception during centrifuge deceleration in a tilting-gondola centrifuge. These phenomena had not been explained previously by existing three-dimensional models of perception, which rely upon combining separate tendencies of angular, linear, and tilt components. The current “whole-motion” approach was implemented by developing a Whole-Motion Model comprising the hypothesis that perception is governed, at least in part, by familiarity of certain types of three-dimensional motion as a whole. The model implemented the ideas that (1) motion that begins with forward or backward linear stimulus typically continues forward or backward in the absence of sudden new sideways linear stimuli, (2) forward motion is more familiar than backward motion, (3) centripetal acceleration is familiar, and (4) motion dominated by angular acceleration about a standard axis (e.g. pitch) at the beginning of the motion continues about that axis. (Ideas (1-3) apply to centrifuge acceleration as shown in Fig. 1B, and (4) applies to centrifuge deceleration as described in Methods). Tested for comparison was a Componentwise Model (Fig. 1A) representing the core of typical existing three-dimensional perception and eye-movement models.

Centrifuge Acceleration

Why does the Whole-Motion Model succeed in predicting perceived roll tilt that is greater when forward-facing than when backward-facing? After all, the Whole-Motion Model is identical for forward-facing and backward-facing motion except for the value of one parameter,

the time constant of decay for linear velocity. This is a linear time constant, not a tilt time constant. Therefore, the roll-tilt difference would not immediately be expected and is consequently an emergent property of the model.

Further analysis can explain why a difference in perceived roll tilt could arise from a difference in familiarity between forward and backward motion. The key is the principle that the nervous system is accustomed to centripetal acceleration during everyday maneuvers. During forward acceleration in a centrifuge, if the forward and angular velocities are veridically perceived (or are perceived with long time constants of decay), then the continual roll alignment of the GIA with the body matches the everyday experience of tilting into a curve, as is common in running and bicycling as well as in maneuvers such as coordinated turns in aircraft. Therefore, the subject reports roll tilt. On the other hand, during backward acceleration in a centrifuge, if the perception of backward velocity decays quickly, then the perceived motion around a curve is consequently at a smaller perceived radius. The continual roll alignment of the GIA with the body again matches the everyday experience of tilting into a curve, but since the perceived linear velocity is small, only a small amount of tilt is necessary in everyday experience. Therefore, that small amount of roll tilt is perceived. In summary, the backward-facing subject perceives less roll tilt than the forward-facing subject.

The situation is slightly more complicated because perceived linear and angular velocity both decay, causing the amount of perceived roll tilt to change over time. Nevertheless, simulations of the Whole-Motion Model, which implements the above hypotheses, confirm the asymmetry and the changes in predicted perceived roll tilt (Fig. 3).

If this new model succeeds in capturing the forward-facing/backward-facing differences in roll tilt, then why doesn't the Componentwise Model capture those differences? Even with different forward-versus-backward linear time constants, τ_l , the Componentwise Model does not capture the roll-tilt differences. The reason is that the Componentwise Model is based upon familiarity of the individual components of motion rather than familiarity of motion as a whole. The Componentwise Model computes roll tilt only from angular tilt acceleration and roll tilt of the GIA, not taking into account any roll consequences of forward-backward motion, so no forward-facing/backward-facing differences can arise in the prediction of perceived roll tilt. Also, why does the Componentwise Model predict a perception of sideways motion? The reason is that the Componentwise Model does not recognize centripetal acceleration, and interprets the interaural acceleration as being associated with roll and *linear velocity* instead of roll and centripetal acceleration.

Centrifuge Deceleration

The whole-motion approach gives a possible explanation for the paradoxical perception of continuing tumble with constant pitch orientation during centrifuge deceleration. The ideas behind this approach are not all novel, but have been implemented and tested with computer simulations here. Because the stimuli to the body during deceleration are much different from those during acceleration, the Whole-Motion Model for deceleration was developed to focus on the deceleration's predominant stimuli: the angular stimuli. Implemented for deceleration here was the idea that the constantly body-vertical GIA suppresses a change in perceived pitch orientation [11], despite an ongoing pitch angular acceleration. Additionally implemented was the principle that a predominantly pitch stimulus for the first portion of motion (Fig. 4B) is interpreted as meaning that the angular motion is in pitch, not in yaw. This parallels the principle during acceleration that predominant forward or backward linear acceleration is interpreted as meaning that the linear motion is forward or backward, not sideways. The resulting Whole-Motion Model succeeds in capturing the paradoxical pitch perception and little perceived roll tilt, even when roll acceleration input is included (Fig. 4C), whereas the Componentwise Model

predicts substantial roll tilt because it does not take into account the initial predominance of the pitch stimulus over the yaw stimulus.

Comparison with Other Models

A previous study [13] investigated the full three-dimensional stimulus during tilting-gondola centrifuge runs in order to help identify which perceptual phenomena arise from the stimulus itself and which arise from properties peculiar to the nervous system. The three-dimensional model implemented the underlying laws of physics, and showed that the tumbling sensation during deceleration could be explained directly by the stimulus, but that the paradoxical perception could not. In addition, forward-facing/backward-facing differences in roll tilt could not arise from the stimulus itself.

A model by Glasauer [8] predicted the amount of perceived roll tilt during acceleration in centrifuges with both fixed cabins and free cabins (tilting gondolas). However, the model predicted zero perceived roll tilt in the tilting-gondola centrifuge, consistent with experimental data that showed only a trend in subjective roll tilt, but not a statistically significant amount under the given conditions. The relevant computations in the model were essentially equivalent to those in the Componentwise Model here, except that a test was added to prevent perceived roll tilt from moving in a direction inconsistent with the GIA tilt. In more recent data [21-25] and with different centrifuge parameters, perceived roll tilt has been found to move in a direction inconsistent with the GIA tilt, i.e. in the direction not predicted by the model. In any case, that model's goal was not to predict forward-facing/backward-facing differences in roll tilt; linear velocity, whether sideways or not, was not reported.

Other three-dimensional models have focused on other types of motion, including centrifuge runs with a fixed carriage [4,8,12,14,17,19,20,27], so direct comparison of models for a tilting gondola is not possible. However, a typical approach has at its foundation the same ideas that are implemented here in the Componentwise Model (Fig. 1A): perceived angular velocity arises from angular acceleration but decays, perceived linear velocity arises from linear acceleration but decays, and change in perceived vertical arises from tilt velocity but vertical is drawn also toward the GIA. Implementation of the GIF-resolution hypothesis may differ, e.g. by an additional step through an explicit internal model (e.g. [19]), but such additional loops or modified implementations usually only change the gain of a component rather than changing the overall form of the output. Another factor present in some models (e.g. as diagrammed in a proposed model of perception in a tilting-gondola centrifuge [2]) is an explicit low-pass filter for perceived tilt and/or an explicit high-pass filter for perceived translation. The Componentwise Model implicitly performs low-pass and high-pass filtering by way of the first-order differential equations.

Another type of model is a Bayesian model, whose development also centers around the concept of familiarity, in the form of “prior probability distributions” representing the fact that certain states are more likely than other states. A Bayesian model [14] has been used for fixed-carriage centrifuges, off-vertical axis rotation and related motions. This Bayesian model successfully predicts a number of experimental results by explicitly implementing the ideas that lack of rotation is most probable in the absence of angular acceleration and that sustained linear translation has a low probability. These same ideas are used in the present Componentwise and Whole-Motion Models; this Bayesian model is most like the Componentwise model in its “componentwise” use of probability distributions. However, whereas deterministic models such as those in the current paper use deterministic differential equations to represent the tendency toward the familiar, Bayesian models use probability distributions and thus give a range of output. A deterministic model's output typically follows values near the mean of a Bayesian model's output.

Centrifuges with Fixed Carriage

Forward-facing/backward-facing roll-tilt differences have also been reported in centrifuges with a fixed carriage [5,6]. During fixed-carriage centrifuge acceleration, subjects report faster roll tilt when backward facing than when forward facing, exactly the opposite of that reported in a tilting-gondola centrifuge. Despite this apparent discrepancy, there is a commonality: When forward-facing, subjects' perceptions are more veridical than when backward-facing. In a tilting-gondola centrifuge, forward-facing subjects more accurately report the actual roll tilt; in a fixed-carriage centrifuge, forward-facing subjects more accurately report the lack of roll tilt. Just as for perception in a tilting-gondola centrifuge, perception in a fixed-carriage centrifuge can be modeled by implementing the hypothesis that forward motion is more familiar, and therefore more accurately perceived during centrifuge acceleration, than backward motion (unpublished observations).

Further Research

The Whole-Motion Model, which implements the hypotheses of familiarity, makes predictions about all of the components of perceived motion, as well as the three-dimensional shape of the perceived motion. For example, pitch-back tilt is predicted during centrifuge acceleration, and pitch-forward tilt during deceleration. The magnitude of the predicted pitch tilt, on the order of 7° , is much smaller than is predicted from the Componentwise Model, on the order of 38° . Although experimental work has been conducted on perception of pitch by way of visually perceived eye level [26], the results are more variable than for roll, so pitch was not analyzed further here. However, the Whole-Motion Model's output more closely matches the relatively small pitch tilt reported immediately after acceleration.

Longer-term perceptions could also be studied. Experimental data on roll tilt have also been obtained for several minutes after the end of the centrifuge acceleration or deceleration [22, 23,25]. The results show "position storage" in which perceived roll tilt remains nonzero for a much longer time than would be predicted by decay time constants in the range of tens of seconds. The present paper concentrated on the centrifuge acceleration and deceleration, but the whole-motion approach could potentially be used to test hypotheses about longer-term perceptions.

The present work focuses on perceptual principles that the nervous system is presumably capable of implementing. However, it is not known what method the nervous system uses for the complex computations. It is well-known that a neural network can simulate any multivariable function. In addition, certain properties of the sensors are well-known; for example, after angular acceleration, the semicircular canal afferent firing rates return toward zero with a time constant on the order of ten seconds or less [7]. Further research on the nervous system's processes for perception can complement the practical ability to predict perception, as investigated in the present work.

Conclusions

Spatial disorientation often occurs during complex maneuvers. Prediction of misperception of self-motion in a centrifuge is shown here to be facilitated by a whole-motion approach. Three-dimensional perceived self-motion is unlikely to be a simple combination of individual components. Instead, perception may be governed by principles of familiarity of the three-dimensional motion as a whole, including familiarity of linear-angular combinations such as centripetal acceleration during rotation.

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Figure 1.

The two models. All vectors are in three dimensions and specified in coordinates aligned with the head (see text). (A) Componentwise Model. Inputs are angular acceleration and GIA. From angular acceleration, angular velocity is computed with decay time constant τ_a . From the angular velocity and the GIA, orientation is computed by the laws of physics (using a cross product) from the angular velocity but modified by a tendency with time constant τ_t toward vertical being aligned with the GIA. Perceived orientation is described by earth-upward vector $\mathbf{g}$ and by earth-horizontal vectors $\mathbf{i}$ and $\mathbf{j}$ representing fixed orthogonal compass directions, all specified in head coordinates in order to give their directions relative to the head. From the GIA and $\mathbf{g}$, linear velocity is computed with a decay time constant of τ_l , and position is

computed from linear velocity. Variables are as listed in the figure. (B) Whole-Motion Model. Inputs are angular acceleration and GIA. From the perceived earth-vertical component of angular acceleration, angular velocity (earth-vertical) is computed with decay time constant τ_a . From the angular velocity, heading (angle θ_h relative to a fixed compass direction) is computed. From the forward/backward perceived earth-horizontal component of the GIA (not necessarily equaling the noseward A_x if the head is pitched), linear velocity (forward or backward) is computed with decay time constant τ_l . This time constant is different for forward and backward motion, as explained in the text. Position is computed from linear velocity. From the angular and linear velocities, an expected centripetal acceleration and thus expected roll tilt of the GIA is computed and compared with the actual roll tilt of the GIA in order to determine the roll tilt angle, θ_r . The pitch angle θ_p is computed from the portion of the forward/backward GIA not used for linear acceleration, i.e. from the time-constant portion of the linear velocity differential equation.

Figure 2.

Componentwise Model results for centrifuge acceleration. (A) Time course of predicted perceived roll and pitch for the 10s of centrifuge acceleration, for both forward-facing and backward-facing orientations, which gave the same results. Negative roll is toward the centrifuge axis, and negative pitch is away from the direction of motion. The dotted line shows actual roll of the subject. Experimental means for roll are also shown at the endpoint of acceleration for forward-facing (FF) and backward-facing (BF) orientations. (B) Polyhedral "head" used for display of three-dimensional position and orientation in Figures 23 and 4. (C) Three-dimensional predicted perceived motion—top view—during forward-facing acceleration, shown in freeze-frame format with a polyhedral head every 1s, starting at (0,0).

On the last polyhedron (upper right) the right face is slightly visible because of 21° roll tilt to the left, matching the graph in part (A). The motion is described in the text.

Figure 3.

Whole-Motion Model results for centrifuge acceleration. (A) Time course of predicted perceived roll and pitch for the 10s of centrifuge acceleration, for both forward-facing (FF) and backward-facing (BF) orientations. Negative roll is toward the centrifuge axis, and negative pitch is away from the direction of motion. The dotted line shows actual roll of the subject. Experimental means for roll are also shown at the endpoint of the acceleration. (B) Three-dimensional predicted perceived motion during forward-facing acceleration, displayed using the same conventions as in Fig. 2C. (C) Three-dimensional predicted perceived motion during backward-facing acceleration, displayed using the same conventions as in Fig. 2C. The motions are described in the text.

Figure 4.

Deceleration in a counterclockwise-rotating centrifuge. (A) The stimulus: Angular velocity components computed from the three-dimensional angular acceleration. Positive roll is rightward, positive pitch is forward, and positive yaw is leftward. (B) Axis of the angular velocity resulting from the stimulus, for the first six seconds, back view relative to the head. The head is shown upright simply for clarity to indicate the angular stimulus relative to the head, and because the subject begins the deceleration with a perception of no roll tilt. Arrow lengths represent the *order* in which the axes occur, with the longest vector first to highlight the initial stimulus the most. Angles from horizontal are listed. (C) Predicted perceived roll and pitch, which is paradoxical, as described in the text. The starting point for this graph was 22° perceived pitch back (during centrifuge constant velocity). The graph starting with 0° pitch back (not shown) had pitch curves almost identical to these after the first two seconds. This graph was generated from the version of the model that included both pitch and roll input; the version of the model with only pitch input gave a very similar graph but with roll angle remaining zero. Positive roll is rightward, and positive pitch is forward. (D) Three-dimensional predicted perceived motion (including position and orientation) during deceleration, as viewed from the right side of the subject, displayed using the same conventions as in Fig. 2C. The

starting point for this graph was 22° perceived pitch back. The three-dimensional display with starting orientation 0° pitch back was similar (not shown).