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Asymmetries and three-dimensional features of vestibular cross-coupled stimuli illuminated through modeling

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Abstract

Head movements during sustained rotation can cause angular cross-coupling which leads to tumbling illusions. Even though angular vectors predict equal magnitude illusions for head movements in opposite directions, the magnitudes of the illusions are often surprisingly asymmetric, such as during leftward versus rightward yaw while horizontal in a centrifuge. This paper presents a comprehensive investigation of the angular-linear stimulus combinations from eight different published papers in which asymmetries were found. Interactions between all angular and linear vectors, including gravity, are taken into account to model the three-dimensional consequences of the stimuli. Three main results followed. First, for every pair of head yaw movements, an asymmetry was found in the stimulus itself when considered in a fully three-dimensional manner, and the direction of the asymmetry matched the subjectively reported magnitude asymmetry. Second, for pitch and roll head movements for which motion sickness was measured, the stimulus was found symmetric in every case except one, and motion sickness generally aligned with other factors such as the existence of a head rest. Third, three-dimensional modeling predicted subjective inconsistency in the direction of perceived rotation when linear and angular components were oppositely-directed, and predicted surplus illusory rotation in the direction of head movement.

Keywords

Self-motion perception; modeling; centrifugation; coriolis cross-coupling; artificial gravity

1. Introduction

Head turns can cause disorientation and motion sickness when performed in a rotating environment [2, 4, 21]. This disorientation may be explained by the cross-coupling of angular velocity vectors: The angular velocity of the reference frame and the angular velocity of the head form a cross product that gives an angular acceleration orthogonal to both rotations. Indeed, subjects usually report illusory rotation about the axis of the angular acceleration.

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Mysterious, however, are recently-discovered asymmetries. A supine subject with head at the center of a clockwise-rotating centrifuge, for example, typically reports greater intensity of tumbling when turning the head in yaw to the left than to the right [6, 33]. This is mysterious because cross-coupling predicts equal intensity of illusory motion. These experimental results are well-established, and further asymmetries have also been found for various combinations of head-turn direction, head orientation, and body orientation on the centrifuge [6, 16, 18–20, 29, 33]. In all cases, the asymmetries identified are not predicted by angular cross-coupling alone.

For the left-right asymmetry while supine [6, 33], further analysis uncovered a possible explanation in the stimulus itself: Even when left and right yaw movements are perfect mirror images of each other, the ensuing three-dimensional physics consequences of the stimuli are not equal in magnitude [7, 9]. The difference stems from the fact that the cross-coupling directions differ in relation to the centrifuge axis, causing different linear-angular interactions. The consequence is that the laws of physics predict a greater misperception of motion for leftward (i.e. counterclockwise as viewed from the top of the head) head turns than for rightward head turns when supine in a clockwise-rotating centrifuge [7, 9]. Analogous methods have been used successfully to explain and predict other perceptual differences as well, such as for accelerating versus constant on-axis rotation [8], and for cross-coupling in 1-g versus 0-g [8, 9].

Additional subjective asymmetries have been found under other experimental conditions. In the centrifuge, besides the original four movements—nose-up to right-ear-down (NUP-to-RED), nose-up to left-ear-down (NUP-to-LED), LED-to-NUP, and RED-to-NUP—while supine [6, 16, 18–20, 29, 33], more recent experiments by Young and colleagues have tested NUP-to-RED and RED-to-NUP movements while lying on the right side [18], four movements—nose-down to right-ear-up (NDN-to-REU), nose-down to left-ear-up (NDN-to-LEU), REU-to-NDN, and LEU-to-NDN—while prone [19], as well as supine conditions with the centrifuge rotating counterclockwise instead of clockwise [19]. These combinations allowed consideration of different hypotheses. Included were hypotheses that the intensity of illusory motion is greater upon head turns in the following directions: to nose-up, counterclockwise, taking place in the left quadrant, ending with the head aligned with the body, ending with the nose pointed toward the direction of centrifuge rotation, and/or such that the cross-coupled vector is rotation head-upward away from the bed. This last hypothesis, termed the “perceived danger” hypothesis [19], was ultimately the only one in the list consistent with existing data, although not tested was the “three-dimensional stimulus” hypothesis that had been consistent with the original left-right asymmetry. Meanwhile, experiments by other groups have shown perceptual asymmetries not explained by angular cross-coupling alone and for which the induced angular acceleration is neither toward nor away from a bed. These include pitch head movements while sitting upright both on- and off-axis [31], roll head movements while upright on-axis [1], and pitch head movements while supine [6].

A three-dimensional analysis is now apropos for the additional experimental conditions listed above. Toward this new study, it is worth mentioning a few relevant results that have arisen since the original left-right analysis. One is that subjective tumbling intensity is

nonlinearly related to angular velocity [Fig. 2 in ref. 29] as predicted by physics due to linear-angular interaction [Fig. 9 in ref. 8], a nonlinearity that holds regardless of whether the angular velocities are of the centrifuge [8] or the head (confirmed though follow-up testing). In addition, perceptions of angular and linear motion affect each other in centrifuges [10, 12] and during off-vertical axis rotation [13]. In other words, there is evidence that a subject's perception of angular motion may be affected by the *linear* stimulus, and vice versa.

This paper has two main goals, both accomplished through investigation of the three-dimensional physics of the stimulus. The first goal is to test the Three-Dimensional Stimulus hypothesis about asymmetries: that the stimulus itself is asymmetric when considered in a three-dimensional manner, and that asymmetries in subject reports align with asymmetries of the stimulus in a variety of conditions with subjects lying on their side, supine and prone, as well as for experimental conditions that include pitch and roll head movements. The other goal is to compare combinations of stimulus components—linear versus angular as well as head versus body—with subject reports. For example: Does perceived rotation correspond with not just angular stimuli but also with *linear* components of the three-dimensional stimulus? Another question, relevant because the head and body are not always aligned: Is perceived rotation influenced by the orientation of the stimulus relative to the body in contrast to that relative to the head? Although answers to these two latter questions might be only partial with the current experimental data, the results can lay the foundation for further investigation.

2. Methods

2.1. Experimental data

The experimental data were those published in a number of peer-reviewed papers, summarized here. Although the papers also contained additional results and sometimes additional measures, only those pertaining to the present study are included. General notes: All conditions were without vision available, and all supine, prone and side-lying subjects were positioned with the head at or near the axis of centrifuge rotation, with body oriented radially on the centrifuge. Abbreviations:

NUP = nose up

RED = right ear down

LED = left ear down

NDN= nose down

REU = right ear up

LEU = left ear up

When head movements were less than 90°, “up” and “down” were not necessarily vertical when the head was turned. For yaw head movements (while supine, prone or lying on right side), the subjective measure of “intensity/magnitude” is used in the current paper because it was tested in all of the experiments. For pitch and roll movements (while supine or upright),

the subjective measure of motion sickness is used, because it was the common measure between experiments. All head movements were actively generated by the subjects, and except in cases indicated below, subjects were instructed and/or trained to perform head movements in 1 second. Indicated below for each experiment are subject orientation, body rotation direction clockwise (CW) or counterclockwise (CCW) and speed, head movement angle if outside the range 60° – 90° , head support if different in different positions, additional notes if necessary, and then results, including which movements gave greater magnitude subjective measures.

Hecht et al. [6]: Supine, CW $138^{\circ}/s$. Head rested on a flat cushion in all positions except pitch-forward. Results: For magnitude of illusory tilt during yaw movements, the greatest asymmetry was that counterclockwise (RED-to-NUP, NUP-to-LED) movements gave greater magnitude illusory tilt than clockwise (LED-to-NUP, NUP-to-RED) movements; also significant was that RED/LED-to-NUP gave greater magnitude than NUP-to-RED/LED. For motion sickness during pitch movements, pitch-forward movements gave greater motion sickness than pitch-back to flat. For direction of illusory motion, the percentages of subject reports were measured in the following three directions: cross-coupling direction (i.e. direction of angular acceleration determined by the cross product of centrifuge and head angular velocities), opposite cross-coupling direction, and neither direction. Subjective roll during head yaw was 60% in cross-coupling direction, 13% opposite, and 27% neither. Subjective pitch during head yaw was 76% in cross-coupling direction, 13% opposite, and 11% neither. Subjective roll during head pitch was 53% in cross-coupling direction, 0% opposite, and 47% neither. For illusory versus active motion, illusory motion was greater than the active head movement in 40% of the pitch movements, and 11% of the yaw movements.

Mast et al. [18]: Supine or lying on right side, CW $138^{\circ}/s$. Results: In both of the conditions supine and lying on right side, RED-to-NUP movements gave greater magnitude illusory motion than NUP-to-RED.

Meliga et al. [20]: Supine, CW $138^{\circ}/s$. Results: RED-to-NUP movements gave greater intensity illusory sensations than NUP-to-RED.

Jarchow and Young [16]: Supine, CW at 3, 5, 8.5, 14 and 23 rpm (23 rpm = $138^{\circ}/s$), head movement 30° , 60° and 90° . Results: RED-to-NUP movements gave greater intensity tumbling sensations, perceived body tilt and motion sickness than NUP-to-RED.

Sheehan et al. [29]: Supine, CW 19 rpm with head velocities ranging $6^{\circ}/s$ to $75^{\circ}/s$, and CW 23 rpm with head velocity $60^{\circ}/s$. Results: RED-to-NUP movements gave greater perceived tumbling intensity and perceived body tilt than NUP-to-RED.

Mateus et al. [19]: Supine CW, supine CCW, prone CW, all $138^{\circ}/s$. Results: For the supine CW condition, counterclockwise (RED-to-NUP, NUP-to-LED) movements gave greater intensity tumbling sensations than clockwise (LED-to-NUP, NUP-to-RED). For the supine CCW condition, clockwise (LED-to-NUP, NUP-to-RED) movements gave greater intensity tumbling sensations than counterclockwise (RED-to-NUP, NUP-to-LED). For the prone CW

condition, counterclockwise (REU-to-NDN, NDN-to-LEU) movements gave greater intensity tumbling sensations than clockwise (LEU-to-NDN, NDN-to-REU).

Woodman and Griffin [31]: Upright on-axis or off-axis 0.75m facing outward, CW 10 rpm (60°/s). Duration of head movement was not reported. Head pitch backward and forward, between position with Frankfort plane horizontal (approximately 30° pitched forward from upright) and upright. When upright, back of head was against a flat vertical headrest. Results: For both of the conditions on-axis and off-axis, pitch-forward movements gave greater motion sickness than pitch-back movements.

Dai et al. [1]: Upright on-axis, CW and CCW 138°/s. Head roll 45°. Results: The “Opposing upright” conditions (RED-to-upright while CW, LED-to-upright while CCW) gave greater motion sickness than all three other conditions: “Opposing lateral” (upright-to-RED while CCW, upright-to-LED while CW), “Corresponding upright” (RED-to-upright while CCW, LED-to-upright while CW), and “Corresponding lateral” (upright-to-RED while CW, upright-to-LED while CCW).

2.2. Physics and modeling

For each experimental condition, the unique three-dimensional consequences of the stimulus were computed as explained here. First, an essential fact: given an initial condition (i.e. an initial perception), and the ensuing linear and angular accelerations in all three dimensions, there is a unique three-dimensional motion that matches those accelerations. Here, the initial (perceived) condition before each head movement was considered to be stationary with the gravito-inertial acceleration (GIA) being vertical, as is standard based upon well-known properties of perception. The accelerations were then given by the experimental conditions (elaborated below). The ensuing associated unique motion was computed for a brief period of time, long enough to determine whether there were effective differences between the three-dimensional stimuli. A time length of 1.5 seconds was used, long enough to cover a 1-second head movement, plus extra to capture the nature of the ensuing motion. This short time frame was chosen to focus on the physics consequences of the stimulus itself; although longer-duration computations could incorporate perceptual time constants of angular and linear velocity as well as tilt, the focus here was on the three-dimensional stimulus. Time lengths of 2 and 3 seconds were also tested but they gave the same results.

The accelerations used were those arising from stimuli stated in the experimental papers, with all head movements considered to take place in 1 second. For conditions lying horizontal on a centrifuge, a centrifuge rotation speed of 138°/s was used, and head yaw movements of 30°, 60° and 90° were tested, as well as 90° pitch. For upright, one set of tests was for 60°/s clockwise rotation on-axis and at radius 0.75 m facing outward, each with 30° pitch forward as well as returning upright. The other set of tests was for 138°/s rotation on-axis and at radius 0.75 m oriented so that roll was outward, both CW and CCW, with 45° rightward and leftward roll as well as returning upright. Roll movement at radius 0.75 m during rotation of 138°/s had not been tested experimentally, but was included to complete the range of parameters tested.

For computational purposes, a few assumptions had to be made. For pitch and roll, a head-movement radius of 0.15m was used, meaning that the head moved in such a way that the vestibular system was 0.15m from the head rotation axis. Radii of 0m and 0.25m were subsequently tested, with the finding that all results were robust within this range. In addition, all head movements were considered to have a sinusoidal velocity profile; previous experience has shown that the exact profile is immaterial for comparisons like these, as long as the same profile is used for all movements being compared. For conditions in which the subject was horizontal with head at the axis of the centrifuge, research on perception was used to inform the choice of radius considered for centripetal acceleration detection. It is well known that a horizontal subject rotating on a centrifuge does not detect linear acceleration simply at the head [15, 22–26, 30]. Instead, for a subject with legs extended, the “center” of centripetal acceleration detection has been found to be caudal to the vestibular system, anywhere from 30 cm [24] to 59 cm [26] depending on the method of measurement. The computations in the present paper used 50 cm. The value 30 cm was tested as well, determining that all asymmetries and patterns were the same as for 50 cm.

The subject-based coordinate system had

$$(x, y, z) = (\text{noseward}, \text{leftward}, \text{head-upward}),$$

with rotations using the righthand rule. The parameters explained above for each condition completely determine all accelerations, including gravity, centripetal acceleration, coriolis acceleration in the cases of pitch and roll, cross-coupling acceleration, and the head movements’ own angular and linear accelerations within the rotating reference frame. An example is given by the supine NUP-to-RED 90° condition: First, during the head movement, the head angle in radians at time t seconds is

$$q = (45\pi/180)(1 - \cos(\pi t)).$$

Derivatives give angular velocity, w , and angular acceleration, a . Three-dimensional linear acceleration A in subject coordinates is the sum of those due to gravity and centripetal acceleration, i.e. in m/s^2 ,

$$A = (g \cos(q), g \sin(q), 0) + (0, 0, (138\pi/180)^2 (0.5)),$$

where $g = 9.81 \text{ m/s}^2$. Also, the cross-coupled angular acceleration at time t is the cross product of the centrifuge angular velocity,

$$(-(138\pi/180)\cos(q), -(138\pi/180)\sin(q), 0),$$

and the head angular velocity,

$$(0, 0, -w).$$

Therefore, the three-dimensional angular acceleration $\mathbf{a}$, which is the sum of those due to head turn and cross-coupling, is

$$\mathbf{a} = (0, 0, -a) + ((138\pi/180)\sin(q)w, (138\pi/180)\cos(q)w, 0).$$

For other conditions on the centrifuge or chair, calculations for the accelerations were analogous. For pitch and roll head movements, additional linear accelerations due to head rotation at a radius were added, with the following magnitudes: tangential = $0.15a$, centripetal = $0.15w^2$, and coriolis = $2Wv$, where W was the centrifuge or chair angular velocity, and v was the radial linear velocity of the head, which is a function of time such as $0.15w\cos(q)$ for upright pitch and roll. Radial head movement also continuously affected the radius for calculation of centripetal acceleration from the centrifuge/chair rotation, a straightforward calculation in most cases. However, for the supine pitch condition, an assumption had to be made about whether or how the radius of the “center” of centripetal acceleration detection changed. Because no data exist, the full range of possibilities was tested by testing both with the location remaining the same within the body, and with the location remaining 50 cm caudal to the vestibular system. The difference in results was negligible, and the results presented here were from the latter; in other words, for pitch conditions the centripetal acceleration was $(138\pi/180)^2(0.5 + 0.15(1 - \cos(q)))$.

For each condition, the stimulus—i.e. the set of accelerations $\mathbf{A}$ and $\mathbf{a}$ —was used to compute the associated unique motion starting from the initial (perceived) condition of stationary with vertical aligned with the GIA. Computations were performed in MATLAB (The MathWorks, Inc., Natick, Massachusetts). The motion began at the origin of an Earth-fixed rectangular coordinate system, with orientation specified in subject-based coordinates by keeping track of the Earth’s $\mathbf{i}$, $\mathbf{j}$ and $\mathbf{k}$ vectors (Earth x -, y - and z -directed unit vectors), in which the Earth’s z direction was vertical and x direction was the horizontal direction closest to the subject-based x direction in the initial condition. The computations were those of physics: Position was the integral of linear velocity, where linear velocity was the integral of $\mathbf{A} - \mathbf{g}$ which is the translational acceleration portion of the GIA with $\mathbf{g}$ being the vertically-directed vector of magnitude 9.81 m/s^2 . The orientation computation used the angular velocity vector $\mathbf{w}$, which was the integral of $\mathbf{a}$, and the fact that the derivatives of $\mathbf{i}$, $\mathbf{j}$ and $\mathbf{k}$ equal the respective cross products $\mathbf{i} \times \mathbf{w}$, $\mathbf{j} \times \mathbf{w}$ and $\mathbf{k} \times \mathbf{w}$.

2.3. Testing the Three-Dimensional Stimulus hypothesis about asymmetries

The first hypothesis was that the three-dimensional stimuli are asymmetric in the same way that subject reports were asymmetric in the experiments. In other words, the illusory motions that would be predicted purely by the laws of physics from the various stimuli have the same asymmetries as those of subject reports.

To test for asymmetries in the three-dimensional stimuli, the stimuli were compared in the relevant pairs, e.g. leftward versus rightward head yaw with the same acceleration magnitudes. To perform this comparison quantitatively, the associated three-dimensional unique motion was computed for each stimulus, and the motions' Stretch Factors were compared: The Stretch Factor is a quantitative measure that is essentially the distance that the motion progresses over a specified period of time, in this case 1.5 s. The active portion of the head movement is subtracted in order to focus on the illusory portion, so the Stretch Factor can be considered a measure of predicted illusory motion. Technically, the Stretch Factor is the arc length of the difference, at the head, between the unique motion calculated above and the active head movement relative to the body [7–9, 11]. (Actually, the active portion of head movement was negligible here compared to the illusory portion, so the computation could have simply used the total distance.) The Stretch Factor was chosen because it gives a way to identify three-dimensional differences in complex cases where the angular components are known to have the same magnitude.

To test the Three-Dimensional Stimulus hypothesis, for each pair of experimental conditions the asymmetries in subject reports were compared with asymmetries in Stretch Factor. For completeness, subject reports were also compared with four of the most promising previous hypotheses about which movement would give greater subjective intensity: To Head Straight in which the head moves into alignment with the body, Tumble Forward in which the cross-coupled vector is in the pitch-forward direction (and which coincidentally occurs whenever a supine or prone subject oriented radially on a centrifuge with head near the axis turns the nose to point opposite the direction of centrifuge motion), Tumble Head-Up in which the cross-coupled vector is rotation head-upward away from the bed (also termed the “perceived danger” hypothesis [19]), and To Nose-Up in which the nose ends in an upward-pointing orientation relative to the Earth. An exception for upright pitch and roll motions was that To Nose-Up did not apply, and therefore that hypothesis about greater subjective intensity was replaced with a more relevant possibility, End Head Free in which the head ended in a position free from external restraint such as a head rest.

2.4. Testing combinations of stimulus components

The second hypothesis was that perceived rotation is related to both angular and linear components of the three-dimensional stimulus, rather than just the angular components. This hypothesis was tested for the two types of head movements where experimental results were available [6], both while supine: yaw (NUP-to-RED, RED-to-NUP, NUP-to-LED, LED-to-NUP) and pitch (pitch-forward, pitch-back). For each, the following components of the stimulus' associated three-dimensional motion were computed: head angular velocity, head orientation, head linear velocity, body angular velocity, body orientation, and body linear velocity (for which body location was considered to be the center of centripetal acceleration detection). Orientation was specified by its three components; e.g. pitch orientation was the angle of rotation about the y -axis that the naso-occipital (x) axis differed from horizontal. This information was used to test the hypothesis in two ways.

The first test focused on the cross-coupling direction, and compared the directions of subjects' perceived motion with the different categories of stimulus (head/body and angular/

linear) for the three components with data in *Experimental data*: roll during head yaw, pitch during head yaw, and roll during head pitch. Tested was whether the percentages of subject reports in the direction of cross-coupling most closely matched the head angular velocity stimulus, or whether they better matched a combination of head and body, and/or angular and linear velocity stimuli. The combinations of stimuli tested were “head – angular”, “head & body – angular”, “head – angular & linear”, and “head & body – angular & linear”. For example, for roll during head yaw, calculated for the combination “head & body – angular & linear” was the percentage of stimuli in the (roll) direction of cross-coupling over all yaw movements, i.e. the percent of the 16 possible (4×4) in which a stimulus (head angular, head linear, body angular, body linear) was in the roll direction of cross-coupling in a yaw movement (NUP-to-RED, RED-to-NUP, NUP-to-LED, LED-to-NUP). For linear stimuli, rightward and leftward linear velocities were considered as being in the same direction as rightward and leftward roll, respectively, and similarly for forward and backward linear velocities and pitch, based upon evidence of linear-angular perceptual alignment [13].

The second test focused on subject reports of extra illusory motion in the direction of active head movement. The angular and orientation computations above were used in combination with modeling from *Physics and modeling* in order to determine whether subject reports could stem from the three-dimensional stimulus itself.

3. Results

3.1. Asymmetries

For yaw head turns during centrifuge rotation, asymmetries were discovered in all cases (Fig. 1A). The Stretch Factor depended only upon the relationship between head-turn direction and centrifuge direction, not on the orientation of the head or body, so the following terminology was used:

“Corresponding Yaw” was clockwise (i.e. in the rightward direction regardless of initial orientation) during clockwise centrifuge rotation, or counterclockwise during counterclockwise centrifuge rotation.

“Opposing Yaw” was clockwise during counterclockwise centrifuge rotation, or vice versa.

To understand the reason for the asymmetry, the excursion of the GIA was graphed (Fig. 1B) for a clockwise-rotating centrifuge comparing NUP-to-RED(Corresponding) and NUP-to-LED (Opposing). The GIA relative to the subjective vertical determines the Stretch Factor, because their difference gives linear acceleration leading to the trajectory (Fig. 2).

As shown in Table 1 which compares hypotheses for yaw movements, all conditions with greater magnitude three-dimensional stimulus—i.e. greater Stretch—were exactly those in which subjects reported greater magnitude/intensity of illusory motion or tumbling. Therefore, the Three-Dimensional Stimulus hypothesis is consistent with the experimental results. Interestingly, all of the conditions with greater magnitude stimulus also had cross-coupled vector head-upward away from the bed, so the Tumble Head-Up hypothesis is also consistent with the experimental data.

For pitch and roll, the finding of an asymmetry depended on the parameters (Fig. 1A). Most conditions showed negligible asymmetry, but for supine orientation in a centrifuge, pitch backward had substantially greater Stretch Factor than pitch forward (trajectories in Fig. 3). The combination that was included to complete the parameter space, 0.75m off-axis with 45° roll movement at 138°/s rotation, showed a small asymmetry.

As shown in Table 2 which compares hypotheses for pitch and roll movements, the factor most associated with subject reports of motion sickness was whether the head ended free or at a head rest. The Stretch Factor was found to be symmetric for the upright conditions, so the Three-Dimensional Stimulus hypothesis was not testable with those conditions. The Stretch Factor was found to be asymmetric for the supine condition, but in the opposite direction from subject reports of motion sickness. Therefore, at first glance the Three-Dimensional Stimulus hypothesis seemed inconsistent with the subject reports. However, subject reports of *intensity* were not asymmetric in this study [6], and were consistent with the Stretch Factor, i.e. with the Three-Dimensional Stimulus hypothesis. In conclusion, the results confirmed what is already known about motion sickness, that differences in subject reports can arise not only from differences in the three-dimensional acceleration stimulus, but also other factors such as head restraint [17, 27, 28].

3.2. Angular, linear and orientation stimuli

For the cross-coupling direction, computations of the stimulus components (Figs. 4 and 5) gave percentages in the direction of cross-coupling (Fig. 6). The only computational ambiguity arose in the linear stimuli for roll during pitch movement (ROLL row in Fig. 5) where the curves reverse direction within the time frame; each of head and body linear components was counted as 25% in the direction of cross-coupling, based upon the graphs.

The result of this test was that the percentages of subject reports in the direction of cross-coupling showed a pattern most reflected by a combination of all four categories of stimulus—head angular, head linear, body angular, and body linear—rather than by head alone or angular alone (Fig. 6).

An additional observation: Movements in the right quadrant, NUP-to-RED versus RED-to-NUP, had a greater asymmetry than movements in the left quadrant, NUP-to-LED versus LED-to-NUP (Fig. 4). Most strikingly, for RED-to-NUP, all three axes were found to have every angular and linear component for both head and body directed in the same direction (Column 2 in Fig. 4). The right quadrant happens to be that most studied experimentally [6, 16, 18–20, 29, 33].

For extra illusory motion in the direction of active head movement, the modeling results were compatible with experimental findings of this surplus illusory motion. Whereas neither yaw nor pitch head movements have obvious angular velocity stimuli that explain extra illusory motion, in both cases the orientation results *do* predict additional perceived motion (YAW row in Fig. 4, PITCH row in Fig. 5). Specifically, the NUP-to-RED and NUP-to-LED motions were face-down at the 1.5 second mark (Fig. 2), far exceeding the 90° head movement. Further investigation of the numerical data showed that the yaw orientations at the end of the 90° active head turns were already 138° rightward, and past 180° leftward, for

the NUP-to-RED and NUP-to-LED movements, respectively. The supine pitch-forward motion was roughly face-down at the 1.5 second mark (Fig. 3), almost 90° past that expected from active head movement, and the numerical data showed that the orientation was already 68° pitch forward at the end of the active head movement toward upright (0°). The pitch-backward movement was more complicated (Fig. 3), with the head roughly upside down at the 1.5 second mark; the numerical data showed that the pitch orientation was already almost upside down, at -176° pitch, at the end of the active head movement toward head-supine (-90° orientation).

For pitch movements, linear components were also computable: Linear velocities of both the head and body were in the direction of active pitch during forward pitch movement, but oppositely directed during backward pitch movement (PITCH row in Fig. 5). In other words, the linear velocity was forward in both cases.

4. Discussion

The three-dimensional physics of the stimulus is shown here to be consistent with features of subjects' perception of motion during cross-coupled movements. First, subjective asymmetries during leftward versus rightward head turns match the asymmetries in the three-dimensional linear-angular interaction, supporting the Three-Dimensional Stimulus hypothesis about asymmetries. Second, subjects' consistency of perceived tumbling in the cross-coupling direction better matches a combination of angular and linear stimuli than just the angular stimulus. Third, subject reports of extra illusory motion in the active head movement direction can be explained by the three-dimensional physics, which predict greater rotation than just the active head rotation.

4.1. Asymmetries

For subjects lying horizontal in a centrifuge, the current hypothesis of a three-dimensional stimulus asymmetry was demonstrated to be supported in all cases. Meanwhile, another hypothesis also consistent with these subject reports is the Tumble Head-Up hypothesis (introduced in [19], under the name "perceived danger" hypothesis) that cross-coupled rotation head-upward away from the bed gives greater perceived tumbling. An intriguing coincidence is that the three-dimensional stimulus explanation and the tumbling direction explanation are in agreement in every case studied experimentally; it is possible that both factors contribute to the perceptual asymmetries that have been observed so far. However, these two hypotheses are different, the Three-Dimensional Stimulus hypothesis relating to magnitude and the Tumble Head-Up hypothesis relating to direction, and there exist motions for which the two hypotheses would give opposite predictions. This is discussed further in *4.4. Questions raised* below.

Meanwhile, the two hypotheses may work in concert. For example, the Tumble Head-Up hypothesis does not initially seem to apply to pitch head movements while supine in a centrifuge, but modeling the stimulus in three dimensions (Fig. 3) shows head-upward body motion during pitch-forward head movement, and head-downward body motion during pitch-backward head movement. Motion sickness (Table 2) is then found to be consistent

with the Tumble Head-Up hypothesis when used through this modeling with the Three-Dimensional Stimulus hypothesis.

4.2. Direction of perceived motion

The three-dimensional physics also give a possible explanation for subject reports of illusory motion opposite the direction of cross-coupling. In particular, certain components of the stimulus are directed opposite the angular cross-coupled vector (Figs. 4 and 5). This result shows that reports of oppositely-directed motion, or of confusion [3, 32], do not require more complicated physiological explanations such as ones involving efference copy or motor commands, but could be explained solely by the fact that the three-dimensional acceleration stimulus includes oppositely-directed components.

4.3. Real-world environments

While the present research focused on head movements during rotation at a constant velocity, real-world head movements can occur during rotation at different velocities as well as non-constant velocity, and with different rates and amounts of head movement. Nevertheless, based upon previous research there is reason to believe that the present results have implications for a range of motion environments.

Different constant velocities of rotation, for example, have been studied both experimentally and with physics analysis. The subjective intensity of the illusion is known to correlate with the rotation velocity [5, 14], and asymmetries exist across a range of head-turn velocities [29]. Analysis with the present three-dimensional physics approach has been used to study a range of constant velocities [8, 9], confirming that the stimulus magnitude varies with velocity, as measured both by traditional angular calculations and also by the Stretch Factor as used in the present paper. Asymmetries were also found in the three-dimensional stimulus using this approach, and the degree of asymmetry was found to depend on the rotation speed and centrifuge radius [9]. Further calculations using the present paper's centrifuge radius and head-turn profile show different amounts of asymmetry at various rotation speeds as discussed below in *4.4 Questions raised*. In other words, the results of the present paper should hold across a range of rotation velocities.

Non-constant velocities of rotation are especially intriguing. They have also been studied both experimentally and with physics analysis, at least for on-axis rotation. During upright on-axis whole-body rotation, the illusory effects upon head movement have been found greatest during decelerating rotation, and smallest during accelerating rotation [4]. A three-dimensional physics analysis was performed on these conditions [8], confirming that the stimulus magnitude is greatest during decelerating rotation and smallest during accelerating rotation, as measured by the Stretch Factor. In that study, as in the present research, the full three-dimensional modeling turned out to be crucial because an analysis of angular vectors alone does not predict acceleration-deceleration differences. Instead, the stimulus differences are apparent only through analysis of the full three-dimensional linear-angular interaction and by taking into account initial conditions.

Not studied so far, either experimentally or with a three-dimensional physics-stimulus analysis, is non-constant velocity of rotation with a view toward possible asymmetries of the

type in the present paper. Although the basic comparisons between acceleration and deceleration have been made, the research has not yet addressed possible asymmetries in intensity of illusory motion comparing left/right, clockwise/counterclockwise, nose-up, etc. The present results suggest further research on this topic, as well as expanding the range of combinations of head-turn velocities and distances.

4.4. Questions raised

One role of modeling is to clarify questions on the experimental side. An example is that of non-constant velocity as discussed in the preceding section, 4.3. *Real-world environments*. Another obvious question is which hypothesis—the Tumble Head-Up (i.e. perceived danger [19]) hypothesis or the current Three-Dimensional Stimulus hypothesis—would be most supported in conditions that could distinguish the two hypotheses. One such condition would be supine with *feet* at the axis of a clockwise-rotating centrifuge, for example with the subject's center of linear acceleration detection 50 cm from the centrifuge axis while the centrifuge rotates at 138°/s. Slower rotation speeds give smaller asymmetries in the physical stimulus and therefore more difficult comparison of the hypotheses; nevertheless further computation, for future reference, showed that for a 90° head yaw movement in 1 second, centrifuge rotations of 3, 5, 8.5, 14, and 23 rpm gave Stretch asymmetries of 1.09-to-1, 1.15-to-1, 1.26-to-1, 1.43-to-1, and 1.65-to-1, respectively.

Another question is to what extent linear stimuli affect rotation perception, and vice versa, in self-motion perception in general. The present research suggests that perceived rotation direction may be more consistent when the angular and linear consequences of the stimuli are aligned. However, data are currently sparse.

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Fig. 1.

(A) Differences between stimuli, based upon three-dimensional physics, for pairs of head movements that are mirror images of each other within the rotating reference frame. As explained in the text, the Stretch Factor is a quantitative measure of the three-dimensional consequences of the physics of the stimulus. Yaw movements were performed while lying horizontal on a centrifuge, and most pitch and roll movements were performed while upright, as further described in the text. (B) Excursion of the GIA vector over 1.5 s in a clockwise-rotating centrifuge, showing the difference between NUP-to-RED (Corresponding Yaw) and NUP-to-LED (Opposing Yaw). Compass directions are given for purposes of

display, with “north” being the initial direction of the feet. Both GIA vectors begin in the subjective vertical direction, and the excursion of each is shown by an arrow every 0.15 s and by a trace of the excursion of the tip. The NUP-to-RED GIA moves south, west and downward, while the NUP-to-LED GIA moves north, east and even further downward. This larger discrepancy in NUP-to-LED between GIA and subjective upward is the main cause of the greater Stretch Factor (and greater “conflict”) during NUP-to-LED than NUP-to-RED.

Fig. 2.

Three-dimensional freeze-frame depiction of the consequences of linear and angular stimuli while supine in a clockwise-rotating centrifuge during NUP-to-RED (Corresponding Yaw) and NUP-to-LED (Opposing Yaw). For each, a subject is displayed every 0.15 s for 1.5 s. The NUP-to-RED subject begins almost supine but tilted somewhat head-up to align the subjective vertical with the GIA, and then tumbles backward with a twist. At 1.5 s, the subject is right-side-down with head turned rightward to face earth-downward, as indicated in the SIDE VIEW with the subject's "head" wearing a cap with bill pointing head-forward (and earth-downward). The NUP-to-LED subject begins almost supine and tumbles forward with a twist. At 1.5 s, the subject has tilted past left-side-down with head turned leftward.

Fig. 3.

Three-dimensional freeze-frame depiction of the consequences of linear and angular stimuli during pitch-forward and pitch-backward head movements while supine in a clockwise-rotating centrifuge, using the same conventions as in Fig. 2. The pitch-forward subject begins almost supine but tilted somewhat head-up to align the subjective vertical with the GIA, and then undergoes a rightward yaw-like movement. At 1.5 s, the subject's body is roughly upright with the head faced earth-downward in a 90° pitch forward position. The pitch-backward subject begins almost supine and undergoes a leftward yaw-like movement. At 1.5 s, the subject is almost upside-down.

Fig. 4.

Components of the three-dimensional consequences of the stimulus for yaw head movements while supine in a clockwise-rotating centrifuge. Each column shows a particular head movement, labeled at the top of the column. Each row shows one axis of rotation, labeled at left, and the roll and pitch graphs show the corresponding linear motion, labeled at right. Indicated in the legend are the head angular velocity, body angular velocity, head rate of change of orientation, body rate of change of orientation, head linear velocity, and body linear velocity. Rates of change of orientation are shown only during periods when the axis is within 45° of horizontal, i.e. when orientation about the axis is most meaningful. The

arrow within each plot indicates the direction of cross-coupling, which is the direction of illusory rotation predicted by angular-only analysis.

Fig. 5.
Components of the three-dimensional consequences of the stimulus for pitch head movements while supine in a clockwise-rotating centrifuge, with the same conventions as in Fig. 4.

Fig. 6.

Percentages of subject reports and three-dimensionally predicted (with linear-angular interaction) components in the direction of angular cross-coupling during head movements while supine in a centrifuge. The three sets of bars are for roll perception during yaw movements, pitch perception during yaw movements, and roll perception during pitch movements, respectively. The first bar in each set shows the percentage of experimental subject reports of rotation in the direction of cross-coupling. The subsequent four bars show the percentages of three-dimensionally predicted components in the direction of cross-coupling, over all such head movements, with each bar comprising the indicated combination of components: head angular velocity (always 100% in the direction of cross-coupling), head and body angular velocities, head angular and linear velocities, and head and body angular and linear velocities. Of the various combinations of components predicted three-dimensionally, the best match with experimental results occurs with both head and body, and with both angular and linear, components included.

Asymmetries within yaw movement pairs: five hypotheses compared to experimental results on the primary asymmetry in subjective magnitude/intensity

Table 1

Condition	Movement pair	Three-D Stimulus (Greater Stretch)	Previous hypotheses				Exp'l results:	
			To Head Straight	Tumble Forward	Tumble Head-Up	To Nose-Up	Greater magnitude/intensity	
[6,16,18–20,29]:								
supine CW	NUP-to-RED	no	no	no	no	no	no	
	RED-to-NUP	YES	YES	YES	YES	YES		
[6]:								
supine CW	NUP-to-LED	YES	no	YES	YES	no	YES	
	LED-to-NUP	no	YES	no	no	YES	no	
[19]:								
supine CCW	NUP-to-RED	YES	no	YES	YES	no	YES	
	RED-to-NUP	no	YES	no	no	YES	no	
supine CCW	NUP-to-LED	no	no	no	no	no	no	
	LED-to-NUP	YES	YES	YES	YES	YES	YES	
prone CW	NDN-to-REU	no	no	YES	no	–	no	
	REU-to-NDN	YES	YES	no	YES	–	YES	
prone CW	NDN-to-LEU	YES	no	no	YES	–	YES	
	LEU-to-NDN	no	YES	YES	no	–	no	
[18]:								
on right CW	NUP-to-RED	no	YES	no	no	no	no	
	RED-to-NUP	YES	no	no	YES	YES	YES	

Table 2

Asymmetries within pitch and roll movement pairs: five hypotheses compared to experimental results on the asymmetry in subjective motion sickness

Condition	Movement pair	Three-D Stimulus (Greater Stretch)	Previous hypotheses				Exp'l results:	
			To Head Straight	Tumble Forward	Tumble Head-Up	End Head Free	Greater motion sickness	
[31]:								
on-axis CW	pitch back	(equal)	YES	(equal)	–	no	no	
	pitch forward	(equal)	no	(equal)	–	YES	YES	
off-axis CW	pitch back	(equal)	YES	(equal)	–	no	no	
	pitch forward	(equal)	no	(equal)	–	YES	YES	
[1]:								
on-axis CW	upright-to-RED *	(equal)	no	no	–	(equal)	no	
	RED-to-upright *	(equal)	YES	YES	–	(equal)	YES **	
on-axis CW	upright-to-LED *	(equal)	no	YES	–	(equal)	no	
	LED-to-upright *	(equal)	YES	no	–	(equal)	no	
[6]:								
supine CW	pitch forward	no	no	(equal)	(equal)	YES	YES	
	pitch back	YES	YES	(equal)	(equal)	no	no	

* Each movement was also performed during CCW rotation, and the corresponding movements were grouped in the analysis (CCW upright-to-LED with CW upright-to-RED, etc.).

** Instead of an asymmetric pair, there was one set of movements with greater motion sickness than the other three.