

Vestibular Stimulus and Perceived Roll Tilt During Coordinated Turns in Aircraft and Gondola Centrifuge

Arne Tribukait; Adrian Ström; Eddie Bergsten; Ola Eiken

- BACKGROUND:** One disorienting movement pattern, common during flight, is the entering of a coordinated turn. While the otoliths persistently sense upright head position, the change in roll attitude constitutes a semicircular canal stimulus. This sensory conflict also arises during acceleration in a swing-out gondola centrifuge. From a vestibular viewpoint there are, however, certain differences between the two stimulus situations; the aim of the present study was to elucidate whether these differences are reflected in the perceived roll attitude.
- METHODS:** Eight nonpilots were tested in a centrifuge (four runs) and during flight (two turns). The subjective visual horizontal (SVH) was measured using an adjustable luminous line in darkness. The centrifuge was accelerated from stationary to 1.56 G (roll 50°) within 7 s; the duration of the G plateau was 5 min. With the aircraft, turns with approximately 1.4 G (45°) were entered within 15 s and lasted for 5 min. Tilt perception (TP) was defined as the ratio of SVH/real roll tilt; initial and final values were calculated for each centrifugation/turn.
- RESULTS:** In both systems there was a sensation of tilt that declined with time. The initial TP was (mean \pm SD): 0.40 \pm 0.27 (centrifuge) and 0.37 \pm 0.30 (flight). The final TP was 0.20 \pm 0.26 and 0.17 \pm 0.19, respectively. Both initial and final TP correlated between the two conditions.
- CONCLUSION:** The physical roll tilt is under-estimated to a similar degree in the centrifuge and aircraft. Also the correspondence at the individual level suggests that the vestibular dilemma of coordinated flight can be recreated in a lifelike manner using a gondola centrifuge.
- KEYWORDS:** sense of balance, spatial orientation, spatial disorientation, vestibular psychophysics.

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The present study concerns the vestibular stimulus pattern and the resulting sensation of roll tilt during the entering of a coordinated turn with an aircraft and during planetary acceleration in a swing-out gondola centrifuge. A coordinated turn constitutes a challenge to the sense of balance, since our sensory systems for linear acceleration and gravity, e.g., the otolith organs, cannot, according to the principle of equivalence, detect that the aircraft is tilted in roll. This vestibular dilemma had been recognized almost a century ago by the German ace Friedrich Noltenius.¹⁶ In a paper published in 1921, he related his own experiences of spatial illusions during flight to the recently discovered “sixth sense” or the “sense of space.” He had realized that the semicircular canals constitute a factor that can facilitate the maintenance of adequate spatial orientation during curved flight. Also, the Dutch pilot van Wulfften Palthe²⁹ was interested in the problem of coordinated flight. With a two-seated Spyker machine he asked subjects

with different degrees of flight experience to verbally judge, while blindfolded, the roll position during and after turns with a bank angle of 45–75° entered and exited in approximately 5 s. Besides noting the considerable proportion of erroneous judgments made by subjects who also had experience of flying, he reflected upon the high threshold for conscious perception of angular speed during flight compared to that on spinning

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chairs.²⁹ Tschermak and Schubert²⁵ used a visual indicator to measure the perceived roll tilt during coordinated turns with an aircraft; efforts were made to minimize other visual input than the luminous line. At 2 G (bank angle 60°), the single test subject (one of the authors) indicated a perceived tilt of approximately 10°. In spite of these pioneering experiments it appears that no systematic quantitative studies on the perceived horizontal plane have been performed during real flight.

It is often assumed that the entering of a coordinated turn can be simulated using a large swing-out gondola centrifuge.^{5,9} During centrifugation, the tangentially pivoted gondola is hanging in the direction of the resultant G vector. If the subject is seated upright and facing forward in the gondola, he or she will experience a gravito-inertial force vector that is persistently acting in the median plane of the head and body (Fig. 1). Thus, the graviceptive systems will not be capable of detecting that the subject is tilted with respect to the surface of the Earth.^{4,9} If the change in roll orientation occurs rapidly, however, it will constitute a stimulus to the semicircular canals, similar to that elicited by a lateral head tilting in the static 1-G environment.⁵

Considering stimuli to the semicircular canal system, it is often useful to distinguish between angular acceleration, angular velocity, and angular displacement. Physically, the flow

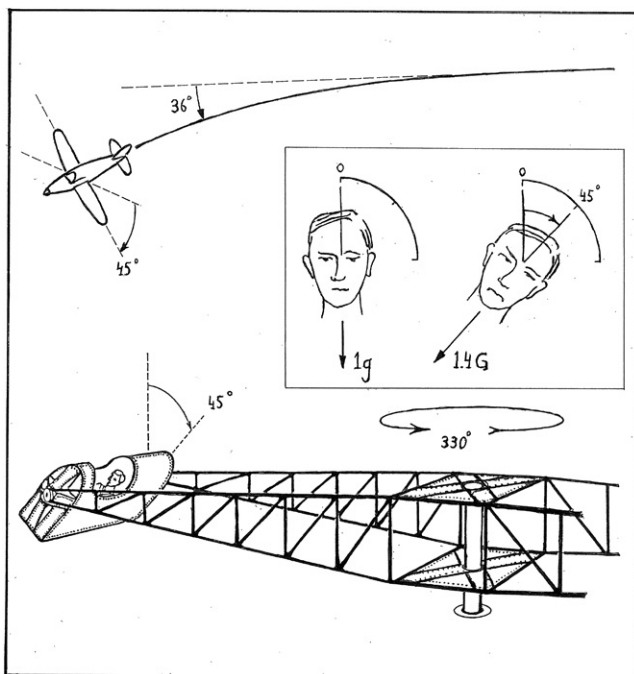


Fig. 1. The entering of a coordinated turn in an aircraft and its simulation in a gondola centrifuge. In both, the resultant of the Earth gravity force and the centrifugal force does not change direction with respect to the subject, while there is a roll change-in-position stimulus to the semicircular canals. Nevertheless, the small radius of the centrifuge implies that canal stimulation in yaw and pitch will be much greater during acceleration of the centrifuge than in an aircraft entering a turn. Consequently, in a centrifuge with $r = 7.25$ m, acceleration to 1.4 g within 10 s will entail 330° of planetary rotation. In contrast, if the entering of a 1.4-g turn with an aircraft traveling at 140 kn is performed within 10 s, the change in heading direction will be approximately 36°. In addition, whereas tangential speed can be kept constant in the aircraft, the simulated entering of a turn in the centrifuge is associated with a forward tangential acceleration.

of endolymph in the canal is caused by angular head acceleration. During short-lasting (“natural”) head turns, the deflection of the cupula and the firing rate in primary canal afferents corresponds to the angular velocity of the head, i.e., the canal functions as an acceleration-to-velocity integrator.³² In addition, at a central nervous level, angular-velocity information from the canals can be integrated over time to yield a measure of angular displacement (change in angular head orientation).^{1,8,11}

Perceived orientation of the body with respect to the Earth horizontal plane is a central component of spatial orientation.¹³ As regards the roll plane, this can be quantitatively studied using a visual indicator. The test subject is asked to adjust a luminous line, in otherwise complete darkness, so that it appears to be horizontal (or vertical). This measure of roll-plane spatial orientation is denoted the subjective visual horizontal (SVH)² or vertical (SVV).^{12,14} Healthy subjects, sitting upright in the static 1-G environment, rarely show deviations of the SVH or SVV greater than 2.5° from the true horizontal plane.^{2,3,19} Recording during static head and body tilt gives a measure of otolith function; in the ideal case, tilting the subject would not influence the adjustment of the line. In reality, there is, however, often a tendency to overcompensate for smaller head and body tilts, whereas larger tilts are undercompensated.^{15,27} Further, changes in head orientation with respect to gravity often generate redundant vestibular information; the brain receives input not only from the otolith organs, which sense the head’s orientation prior to and after the movement, but also from the semicircular canals, which respond to the movement per se. Consequently, the perceived head tilt angle will be greater if a change in roll head orientation is made rapidly than if tilting occurs with an angular velocity below the stimulus threshold of the canals.¹⁸ In addition, the effect of roll-plane canal stimulation on the SVV may be considerable if a period of roll rotation ends with the subject in a tilted²⁶ or upside-down²⁸ orientation.

Using a swing-out gondola centrifuge, we investigated how the SVH is influenced by different patterns of stimuli to the semicircular canals and otolith organs. Briefly, acceleration of the centrifuge from stationary to a predetermined G level induces a sensation of being tilted toward the center of the centrifuge. This is reflected in a tilt of the SVH with respect to the gravito-inertial horizontal of the gondola. In nonpilots these phenomena usually decline during constant angular velocity of the centrifuge. On average, the initial SVH tilt is approximately 30% of the roll inclination of the gondola; the time constant for exponential decline is often 1-2 min, reflecting a memory for canal information on angular displacements.^{20,22,23}

Conspicuously, when the subjects were seated facing backward in the gondola, the SVH tilt, induced by acceleration of the centrifuge, was substantially smaller.²¹ This finding suggests that the sensation of roll tilt is not simply related to the roll (angular-displacement) component of the canal stimulus, but that the yaw and pitch (angular-velocity) components also play a significant role. Whereas the roll component is of equal magnitude (but of opposite sign) when the subject is in the backward position, the stimulus pattern in yaw and pitch is very

different (and less familiar). Then, simplistically, there seem to be two possible explanations for the difference in perceived roll tilt angle between the forward and backward positions. Either the transition from yaw to near pitch-backward angular velocity, experienced during acceleration facing forward, supplements the roll angular-displacement stimulus, thereby contributing to the sensation of being tilted in roll, or the unfamiliar angular-velocity stimulus (i.e., transition from yaw to pitch-forward angular velocity) during acceleration in the backward position is confounding, interfering with the subject's ability to perceive the roll-plane component.

In this connection it is interesting to compare the stimulus pattern experienced by the test subject in the gondola of a centrifuge, accelerating from stationary, with that encountered by the pilot of an aircraft entering a coordinated turn. There are a few inescapable differences between these two situations. Firstly, the centrifuge has a fixed radius and increases the resultant G force (and the corresponding roll inclination of the gondola) via an increase in tangential speed, whereas the aircraft can maintain constant speed while changing the radius of its trajectory from infinity (during straight-ahead level flight) to a finite value. Secondly, whereas the radius of the centrifuge is typically less than 10 m, the trajectory of an aircraft, traveling at 250 km/h, will have a radius of nearly 500 m during a 1.4-G turn. The angular velocity of the turn (planetary rotation) will be $67^\circ \cdot \text{s}^{-1}$ in a centrifuge (with $r = 7.25$ m) but only $8.3^\circ \cdot \text{s}^{-1}$ in the aircraft. This means that the magnitude of the canal angular velocity stimulus is nearly an order of magnitude greater in the centrifuge than in the aircraft.

Again, considering the difference in perceived roll tilt (i.e., in the magnitude of the SVH tilt) between the forward and backward positions in the centrifuge, it can be hypothesized that the SVH tilt is dependent on two factors, one being the roll angular displacement of the gondola, the other being angular velocity stimuli in yaw and pitch. If the cause of the forward-backward asymmetry in roll tilt perception were the test subject's ability to interpret, while heading forward, the transition from yaw angular velocity to near-pitch (backward) angular velocity, then the measure of perceived roll tilt would be smaller during a real turn in an aircraft than during the simulated coordinated turn in the centrifuge (i.e., due to the fact that the angular velocity components in yaw and pitch are substantially lower in the aircraft than in the centrifuge). If, alternatively, the small SVH tilt after acceleration of the centrifuge with the subject heading backward were due to distraction by the unfamiliar pattern of canal stimulation in yaw and pitch, then the perceived roll tilt would be similar during a coordinated turn in the aircraft as during centrifugation with the subject in the forward position.

Hence, the primary aim of the present study was to investigate whether the perception of a given roll tilt angle is similar during a coordinated turn with an aircraft as after acceleration in a gondola centrifuge. A secondary aim was to compare the interindividual variability in the two situations and establish if testing in the centrifuge can reveal an individual's ability to sense the roll attitude during a coordinated turn with an aircraft.

METHODS

Subjects

Eight healthy subjects (two women and six men), ages 24-45 yr, were recruited for the study. As regards experience of coordinated turns, the subjects were not motorcycle drivers and they did not have any experience of maneuvering an aircraft. One of them (No. 4), however, had since childhood extensively practiced in various sports. All except No. 4 and No. 6 had earlier participated in similar experiments in a centrifuge. The subjects participated with their informed consent and were free to withdraw at any time during the experiment. The test procedures were in accordance with the declaration of Helsinki and were approved by the human ethics committee in Stockholm.

Equipment

The centrifuge experiments were performed in the swing-out gondola centrifuge at KTH in Solna, Sweden. The radius of this centrifuge is 7.25 m and its rotation is anticlockwise (as seen from above). The tangentially pivoted gondola deflects outwards in the direction of the resultant force vector (vectorial sum of the Earth gravity force and the centrifugal force; Fig. 1). Facing forward, the subject was fixed in a cockpit seat by means of safety belts. He or she was instructed to avoid head movements and to keep the back of the head against a head rest (a padded vertical groove). The gondola was equipped with video surveillance and the test subject could always communicate with the experimenter via a two-way intercom system. The subject's heart rate and rhythm were monitored continuously by means of electrocardiography.

The aircraft experiments were carried out in a 6-seated propeller aircraft (Piper Lance). The subject was seated in the right rear seat. The head rest was similar to that used in the centrifuge. The second-row seat in front of the subject had been replaced by a construction on which the device with the adjustable luminous line could be positioned at a straight-ahead eye-level position. On board there were, in addition to the pilot and test subject, the experimenter and a technician, managing the data collection. All wore headsets and could freely communicate with each other.

In front of the subject (at a straight-ahead eye-level position 55 cm from the subject's eyes) there was a line (75 mm long and 1.7 mm wide) of red light-emitting diodes. The line was mounted on the axle of a digital servo (DSR 1015, Thunder Tiger Corp., Taichung City, Taiwan). The axis of rotation coincided with the subject's naso-occipital (visual) axis. The servo was controlled by a microprocessor (Arduino UNO with a program in C). The subject used two push buttons on a remote control to adjust the line every time it was switched on, so that it appeared to be horizontal (i.e., corresponded with the subject's spontaneous imagination of the horizon of the external world). If the subject kept one of these buttons pressed, the rotation of the line was $11^\circ \cdot \text{s}^{-1}$; by briefly tapping the buttons the subject could adjust the orientation of the line in steps of 0.2° . When pleased with a setting the subject pressed a third button, which extinguished the line. The deviation of the line from the

gravitoinertial horizontal was then automatically recorded with an accuracy of 0.1° . The line was instantaneously offset $8\text{--}26^\circ$ (randomly), alternately clockwise and counterclockwise with respect to the subject's latest setting, and it was switched on again after a latency period of 1 s. The subjects were able to make 10–15 settings of the line per minute. Programming for the recording of data from the microprocessor was performed in LabView (National Instruments Corporation, Austin, TX) on a HP ProBook 6570b (Intel Core i5, 2.60 GHz) connected to the microprocessor via a network cable.

Complete darkness was attained in the following way: The subject wore a modified diver's mask. The glass of the mask had been removed. Via a light-proof flexible tube (diameter 20 cm), made of an external layer of reflecting plastic and aluminum foil and an internal layer of black velvet, the mask was connected to the device with the luminous line. The mask was equipped with light proof ventilation channels, permitting breathing through the nose. The subject was able to put on and remove the mask without assistance.

Procedure

The subject was instructed to imagine the horizon of the sea and to adjust the line so that it was parallel with this horizon. In case of any sensation of being tilted sideways, he or she should indicate the horizon in relation to which he or she felt tilted, not the transversal plane of their own head. The subject was encouraged to trust his or her own feelings rather than thinking and calculating.

The centrifuge was accelerated from stationary to 1.56 G. At 1.56 G the angular velocity of the centrifuge about its main axle is $72.7^\circ \cdot \text{s}^{-1}$ and the frontal plane (roll) inclination of the gondola is 50° . The angular acceleration of the centrifuge was $10.4^\circ \cdot \text{s}^{-2}$; i.e., the 1.56-G level was attained within 7 s. Thus, the mean frontal-plane angular velocity was well above the stimulus threshold for the semicircular canals. The recording time at 1.56 G was 5 min. To minimize the risk of motion sickness, deceleration of the centrifuge was performed at $1^\circ \cdot \text{s}^{-2}$.

Subjects were tested in the centrifuge both before and after the aircraft experiment. On each occasion the subject underwent two centrifuge runs. Exceptions were subject Nos. 4 and 6 (i.e., those who had no earlier experience of the test procedure); at the first test occasion, these subjects underwent one extra run in order to ascertain that the task had been properly understood. Pauses between runs were 5–10 min; during the pauses the gondola was opened and the light was turned on.

During the aircraft experiments the air speed was approximately 120 kn. The pilot aimed at entering, in a coordinated way, left turns with a bank of 50° within 10–15 s. Each subject underwent two such turns maintained for 5 min and preceded by at least 2 min of straight-ahead level flight. Recording of the SVH commenced approximately 1 min before entering the turn. The resultant G level in the head-to-foot direction (G_z), as well as the component acting in the lateral direction (G_y), was recorded at 5 Hz using a 3DM-GX3-45 Miniature GPS-Aided Inertial Navigation System (LORD MicroStrain®, Williston, VT). This device also provided a heading signal.

In the centrifuge experiments, an initial series of eight settings of the luminous line was performed prior to each run. During centrifugation, data collection commenced (i.e., the line was switched on) as soon as the 1.56-G level was attained. In the aircraft, recording commenced approximately 1 min before entering the turn and continued for approximately 1 min after exiting the turn.

Analysis

Tilt of the SVH to the right (right end of the line set down, from the subject's point of view) is denoted positive; tilt to the left is denoted negative. The 1-G value for the SVH was calculated as the mean of the settings made before acceleration of the centrifuge (or before beginning the turns with the aircraft). In the centrifuge experiments, time zero is defined as the point in time when the 1.56-G plateau was attained. For the flight experiments the points in time when the entering of the curve commenced, as well as when the entering was complete (corresponding to $t = 0$ in the centrifuge experiments), were established via scrutiny of the recording curves for G_z and heading direction.

For a given point in time, the roll tilt of the aircraft can be calculated as $\theta = \arccos(1/G_z)$, assuming that the G_y component is negligible. Since short-lasting variations in G_z are often not related to changes in roll tilt of the aircraft, the G_z recording was first filtered using a Savitzky-Golay filter with 100 side-points. From the heading signal the period of revolution (orbital time) was established for each turn. Based on the period of revolution and the mean value for G_z , the mean radius and tangential speed were estimated for each turn.

Because the roll-tilt angle cannot be kept perfectly stable in the aircraft and, as it turned out, the roll tilt was slightly smaller in the aircraft than in the centrifuge, we have, for each setting of the luminous line, calculated a relative measure, denoted tilt perception (TP), as the ratio between the SVH and the roll tilt of the aircraft at that point in time. This is based on the assumption that, within a limited range for G_z , the SVH tilt is approximately proportional to the physical roll tilt angle, as found in an earlier study.²² In order to calculate initial and final values for the relative roll TP, the following procedures were used. It is in the order of things that any major changes in the SVH tend to be most pronounced early during centrifugation (or during a coordinated turn). Therefore, the initial value has been established via linear curve fitting to the data points obtained during the first minute and extrapolation to $t = 0$, i.e., the point in time when the G plateau commenced (in the centrifuge) or the aircraft had entered the turn.

As to the final value of the SVH, we assumed that the SVH had stabilized after 3 min. This assumption is based on earlier findings that the time constant for exponential decay is approximately 60 s; after $3 \times$ the time constant, an exponentially decaying phenomenon approximates the baseline. Thus, the final value for tilt perception was calculated as the mean of the data points obtained during minutes 4 and 5. The reason for not using exponential curve fitting in the present study is the recent findings that many pilots, in contrast to nonpilots, do not show

an exponential decay²⁴ and that findings of a complementary study on pilots will be related to the present one. Using data from nonpilots, it has been checked that exponential curve fitting and the method chosen here produce very similar values of the initial and final SVH tilts.

To compare the two conditions with respect to initial and final TP, data were treated as follows: initial and final TP were established for each centrifuge run and aircraft turn. Then, for the individual, mean values were calculated for all centrifuge runs as well as for the aircraft turns. Differences between points in time (initial and final) and between centrifuge and aircraft were evaluated using repeated-measures analysis of variance (ANOVA) with two dependent factors, duplicates in time (initial and final), and duplicates in conditions (centrifuge and aircraft). Post hoc comparisons were done using Tukey's HSD test, explaining significant results from the ANOVA. For evaluating the correspondence between results obtained in the two conditions, linear regression analyses were performed for initial and final tilt perception.

RESULTS

One of the subjects (No. 6) interrupted the flight experiment after the first turn because of motion sickness. There was no such problem in the centrifuge. Subject No. 3 underwent an extra turn in the aircraft, since no 1-G data were obtained prior to the first turn. For two subjects (No. 3 and No. 8), the post-flight test in the centrifuge had to be cancelled for technical reasons.

With the aircraft it was not possible to perform the entering of turns with the same accuracy as in the centrifuge. As estimated using the recordings of heading direction and G_z , the entering of the turns was accomplished within 15.2 ± 5.8 s. The resulting G_z during the turns was 1.38 ± 0.03 G, corresponding to a roll tilt of $43.7 \pm 1.4^\circ$. The airspeed was 122 ± 11 kn (62.6 ± 5.4 m · s⁻¹) and the radius was 423 ± 77 m.

In the 1-G environment, prior to acceleration of the centrifuge or before entering turns with the aircraft, the SVH was close to the true gravitational horizontal. The group means (\pm SD) were $0.56 \pm 1.87^\circ$ (centrifuge before flight), $0.96 \pm 2.32^\circ$ (in aircraft), and $0.35 \pm 1.08^\circ$ (centrifuge after flight). In all cases, acceleration of the centrifuge induced a tilt of the SVH to the right (clockwise from the subject's point of view), corresponding to a sensation of head and body tilt to the left. In six of the subjects, this SVH tilt gradually decayed to near-zero during constant angular velocity of the centrifuge. In two of the subjects (Nos. 2 and 4), there was also, however, a considerable SVH tilt by the end of centrifugation. One of these subjects (No. 4) stated spontaneously and very clearly that she associated the sensation of increased weight during centrifugation with being in a coordinated turn, as she had experienced it also during downhill skiing and bicycling. Since the sensation of increased weight did not subside, the sensation of being tilted lasted during the entire 1.56-G plateau. Although she was aware of the fact that the increased gravity vector was acting in the head to

seat direction, and that she thus was gravitationally upright, she could not avoid imagining that she was in a persistent turn, leaning toward the center.

In the aircraft, the general pattern was similar to that found in the centrifuge. There were, however, two notable exceptions. During the first turn, Subject 2 showed a pronounced scattering in the data and, during the later 3 min, the SVH was tilted in the opposite direction, i.e., as would have been an appropriate response during a coordinated turn to the right. After the flight experiments, this subject also confirmed that he had got the impression that the first turn was to the right. The second exception was Subject 4. Judging from the data, she did not perceive precisely when the turns began. Thus, she seemed to anticipate the first turn, responding with a 20° SVH tilt before the turn had actually started. During the second turn, her response was, in contrast, delayed until the moment when G_z first reached 1.4 G. Disregarding this, she seemed to have a pronounced sensation of leftward tilt during each entire turn. Data from the first turn of Subject No. 2 and from the second of No. 4 will not be included in the statistical analyses.

Fig. 2A-D shows, for four of the subjects, recordings from one centrifuge run and one turn with the aircraft. The diagrams also show recordings of G_z and the calculated roll tilt of the aircraft. Individual values for initial and final TP are presented in **Table I**. The two-factor ANOVA revealed a significant difference between the initial and final TP [$F(1) = 20.7$, $P = 0.0026$]; Tukey's HSD tests showed that the difference was significant for the centrifuge data ($P = 0.004$) as well as for the data from the aircraft ($P = 0.005$). However, there was no significant difference between data obtained in the centrifuge and those obtained in the aircraft [$F(1) = 0.757$, $P = 0.41$]. For both the initial and final TP there was a correlation between the two test conditions (initial TP: $r = 0.83$, $P = 0.01$; final TP: $r = 0.88$; $P = 0.004$).

DISCUSSION

The present findings show that in spite of differences in the vestibular stimulus pattern the perceived roll tilt angle is of similar magnitude after entering a coordinated turn with an aircraft as after acceleration in a swing-out gondola centrifuge. In addition, there was a correlation between findings from the two test situations; individuals with a greater perceived tilt angle during centrifugation also tended to be less disoriented during turns with the aircraft.

The vestibular stimulus to a test subject during a centrifuge run has been mathematically characterized by others.⁵⁻⁷ Since there is no roll-tilt stimulus to the otoliths, the tilt of the SVH must be induced by semicircular canal stimulation. When the subject is in the forward position, the swing out of the gondola during acceleration is equivalent with a roll change in head position (as when tilting one's head toward the shoulder in the static 1-G environment). We earlier suggested that the SVH tilt recorded after acceleration of the centrifuge was caused by this roll angular-displacement canal stimulus, but that the roll tilt of the gondola is underestimated because of conflicting

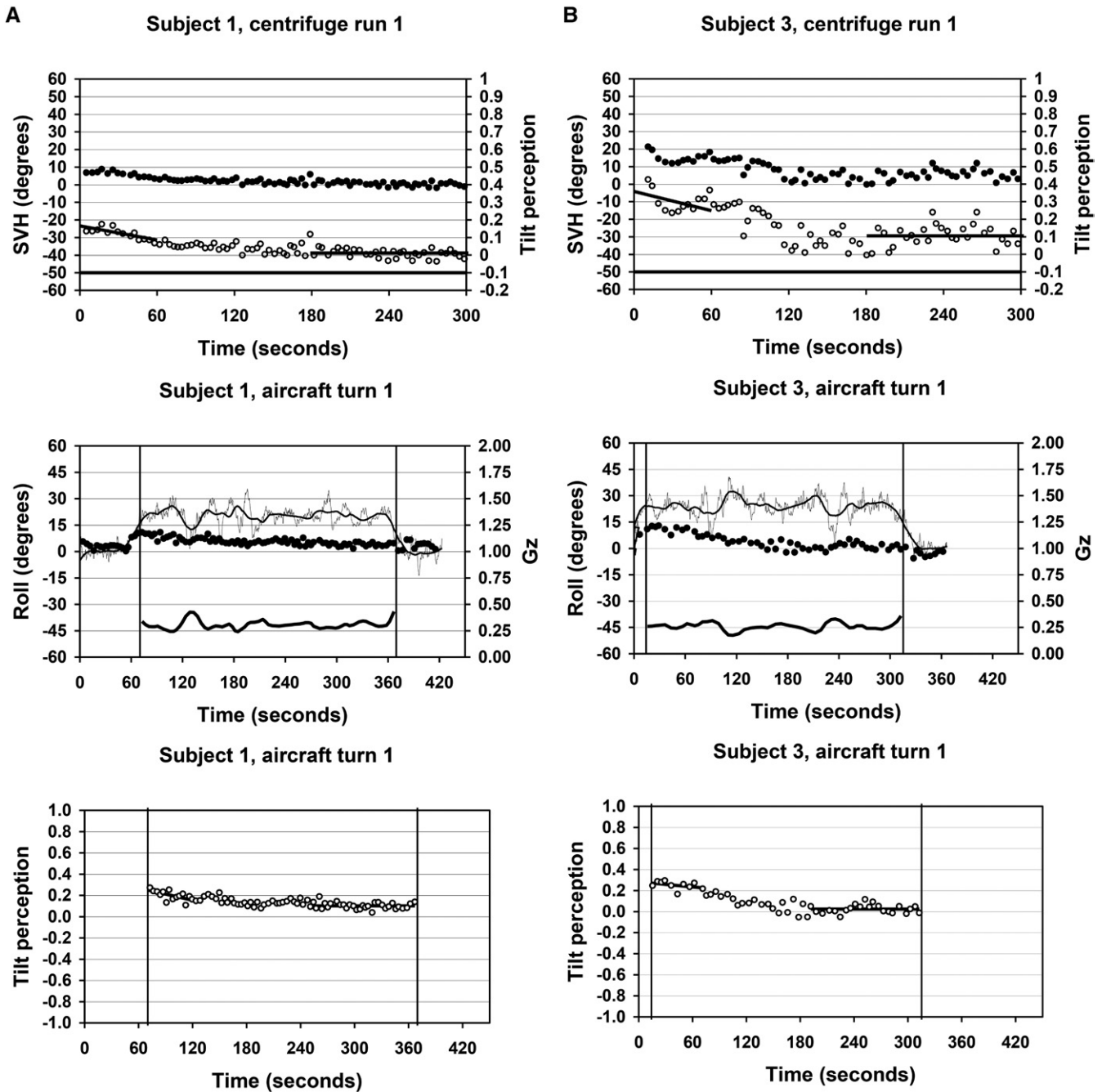


Fig. 2. Recordings from one centrifuge run and one turn with the aircraft for A) Subject 1, B) Subject 3, C) Subject 4, and D) Subject 5. Black symbols represent original settings of the luminous line (SVH). White symbols represent relative values of tilt perception, i.e., SVH divided by the tilt of the gondola or aircraft for a given point in time. The middle diagrams also show recordings of G_z (unfiltered: thin lines, filtered: bold lines) as well as the roll tilt of the aircraft (extra bold) calculated from the filtered G_z -curve.

graviceptive input. The subsequent finding that the perceived roll tilt is smaller when the subject is in the backward position (see Introduction), however, inspired us to hypothesize that the sensation of roll tilt after acceleration facing forward is dependent, to a considerable degree, also on the pattern of canal stimulation in yaw and pitch, i.e., the transition from yaw to pitch-backward angular velocity. If this hypothesis were correct, the perceived roll tilt of a subject facing forward would be smaller in a centrifuge with a larger radius; for a given roll

angular displacement the yaw and pitch angular velocity components will decrease with increasing radius.

An aircraft can be used as a centrifuge with a very large radius (although the beginning of a turn is not accompanied by any tangential acceleration). The differences in angular-velocity stimuli to a test subject during acceleration from stationary to 1.41 G in a swing-out gondola centrifuge ($r = 7.25$ m) and during the entering of a 1.41-G turn with an aircraft (traveling at 140 kn) are illustrated in Fig. 3. For a given roll-plane canal

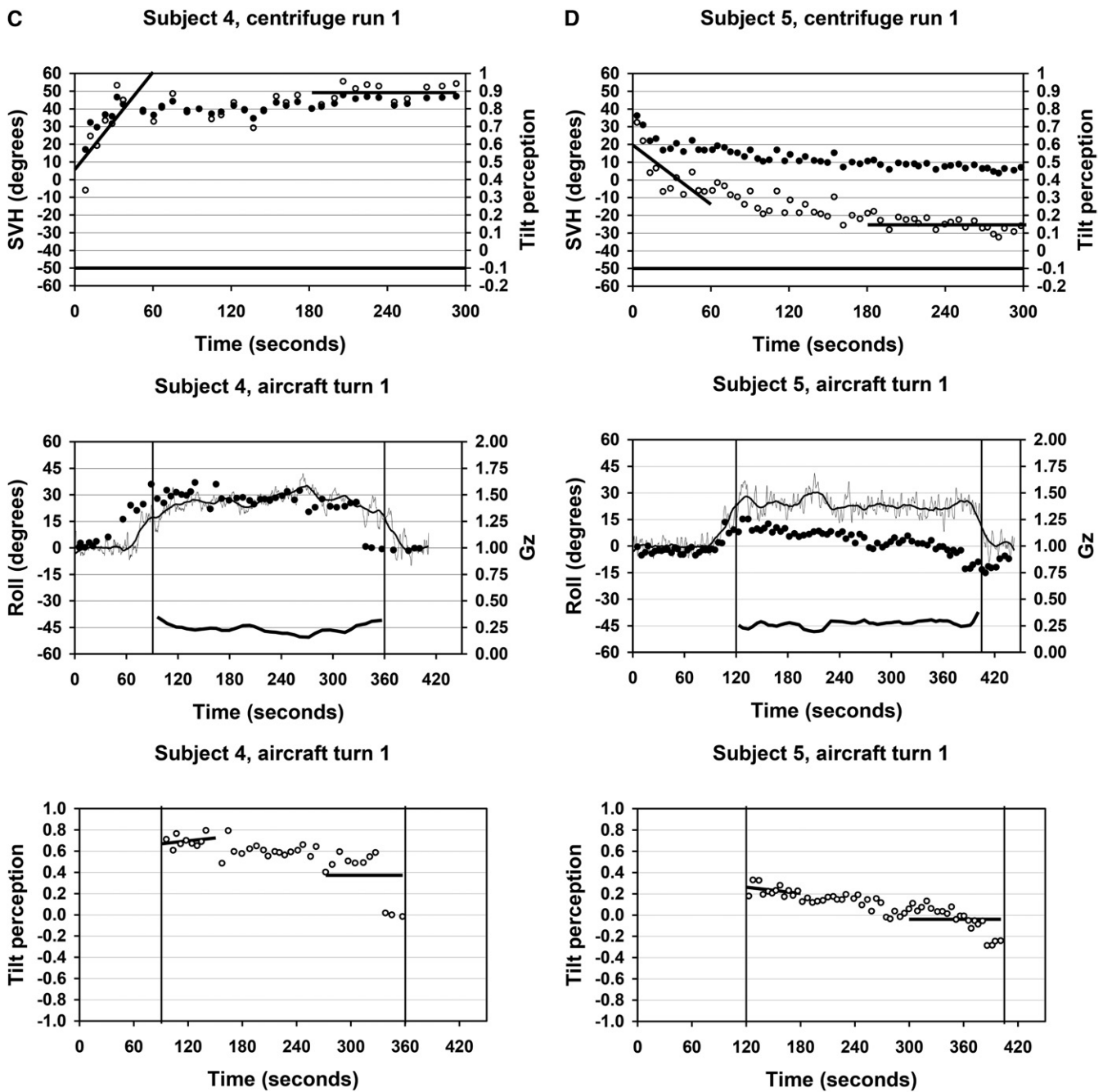


Fig. 2. *Continued.*

stimulus, the angular-velocity components in yaw and pitch are almost an order of magnitude greater in the centrifuge than in the aircraft. Thus, if the indicated roll (SVH tilt) in the centrifuge were mainly dependent on the yaw and pitch components, then the SVH tilt would have been negligible in the aircraft. As this was obviously not the case the hypothesis must be rejected. To complete the line of reasoning, it might nevertheless be speculated that the unfamiliar angular-velocity stimulus (transition from yaw to pitch-forward angular velocity) during acceleration in the backward position is confounding, interfering with the subject's ability to perceive the roll-plane component.

As to the significance of canal stimulation in yaw and pitch, it is reasonable to assume that a pitch-plane stimulus would not, in itself, cause any sensation of roll tilt in subjects with symmetric vestibular function. Yaw-plane rotation has been found to influence spatial orientation in roll; in an upright test subject centric rotation about an Earth-vertical axis induces a transient tilt of the SVV³¹ or SVH.³⁰ However, this effect is reversed if the head is tilted forward, suggesting it is mediated by the posterior vertical rather than by the horizontal semicircular canals.¹⁷ Merfeld *et al.*¹⁰ studied the effects of yaw-plane angular velocity on the sensation of roll tilt during eccentric rotation in a fixed-chair centrifuge. The perceived horizontal was measured using a visual

Table I. Tilt Perception in Centrifuge and Aircraft.

SUBJECT	INITIAL TILT PERCEPTION				FINAL TILT PERCEPTION			
	CENTRIFUGE	AIRCRAFT			CENTRIFUGE	AIRCRAFT		
		TURN 1	TURN 2	TURN 3		TURN 1	TURN 2	TURN 3
1	0.16	0.25	0.20		0.02	0.10	-0.01	
2	0.74	(0.16)	0.85		0.45	(-0.15)	0.49	
3	0.34	0.27	0.62	0.66	0.06	0.02	0.08	0.02
4	0.84	0.67	(-0.13)		0.74	0.37	(0.57)	
5	0.52	0.26	0.38		0.12	-0.04	-0.14	
6	0.22	-0.06			0.12	0.07		
7	0.22	0.34	0.24		0.07	0.11	0.09	
8	0.17	0.03	0.23		0.04	-0.03	0.09	
Mean	0.40		0.37		0.20		0.16	
Median	0.28		0.31		0.09		0.08	
1 SD	0.27		0.30		0.26		0.17	

Values are based on the ratio between the SVH and the actual tilt of the gondola/aircraft. As regards centrifuge data, each individual value is the mean for all runs undergone by the subject. Values within parentheses are not included in the group statistics. Subject No. 3 underwent an extra turn with the aircraft because no 1-G data were obtained prior to Turn 1. Subject No. 6 interrupted the flight experiment after Turn 1.

indicator or a somatosensory bar. Subjects were seated facing motion or back to motion. In both positions the perceived tilt lagged behind the physical tilt during acceleration of the chair.

Notably, the sensation of tilt developed more rapidly when the subject was seated back-to-motion (time constant approximately 15 s) than when he or she was facing motion (time constant approximately 30 s). During deceleration, however, the lag effect was very small for both positions. Such findings imply that the effects of a canal stimulus are not by necessity restricted to the plane of the stimulus and, in addition, that oppositely directed stimuli of equal magnitude can yield responses of different magnitude. Thus, the perceptual effects of a given stimulus are dependent also on other stimulus components. If this is not a “failure phenomenon,” it might suggest that certain patterns of vestibular stimuli are interpreted by the brain as meaningful wholes.

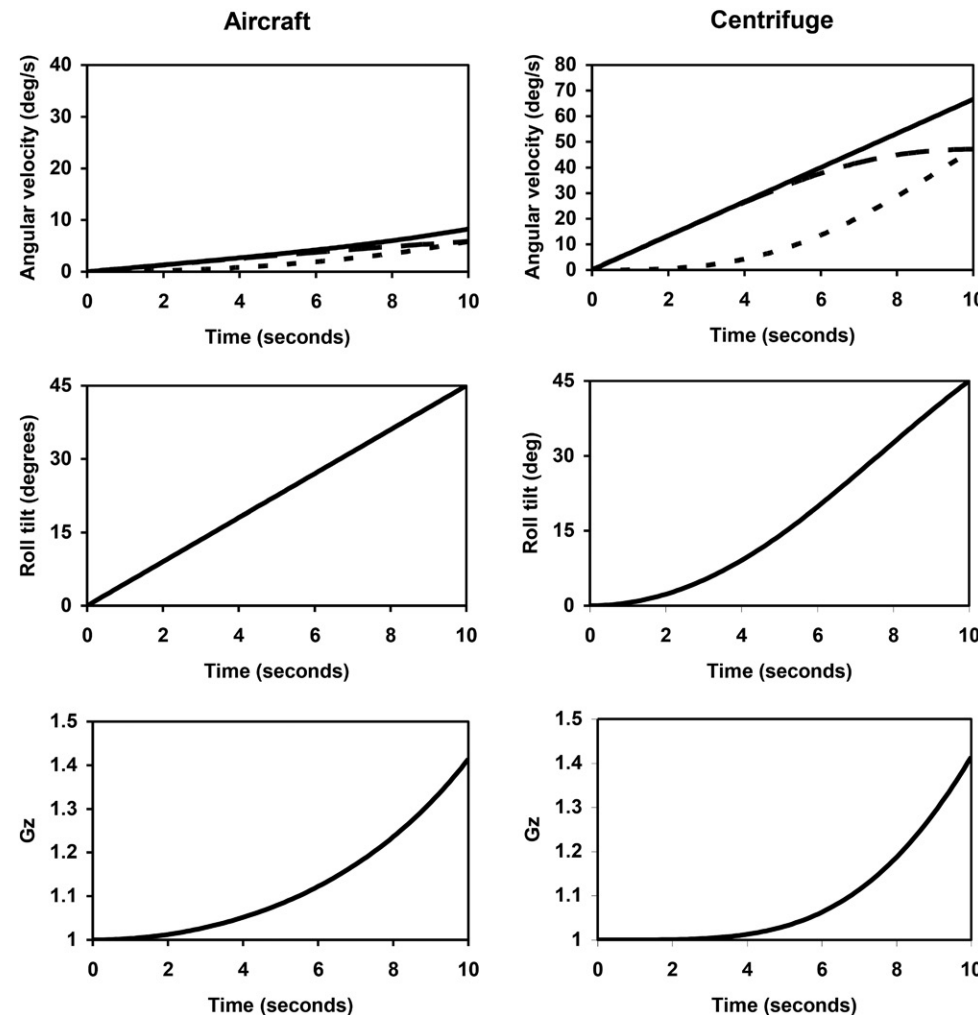


Fig. 3. Angular velocity stimuli, roll tilt, and G_z during the entering of a 1.4-g turn with an aircraft (left diagrams) and during acceleration in a gondola centrifuge (right diagrams). In the upper diagrams, planetary angular velocity is represented by continuous lines, the yaw-plane component by dashed lines, and the pitch-plane component by dotted lines. Note that the vertical scales of the upper diagrams are different.

The concept of familiarity of the stimulus pattern as a whole has been extensively discussed by Holly and Harmon.⁷ A basic assumption in their so-called “Whole-Motion Model” is that spatial orientation is governed to some extent by the familiarity of certain three-dimensional motion patterns. The model also involves the notion that the brain’s interpretation of complex vestibular stimuli tends to be determined by early cues. Three key ideas in the model are that 1) motion that begins with a forward or backward linear acceleration typically continues

forward or backward; 2) forward motion is more familiar than backward motion; and 3) the time constant for decay of perceived linear acceleration is greater for forward than for backward motion. The model is capable of explaining the difference in perceived roll tilt between the forward and backward position during gondola centrifugation.

In this connection it should be mentioned that one tangible early stimulus cue that occurs in the centrifuge but not in the aircraft is the forward tangential jerk at the beginning of acceleration. Although this jerk does not, in itself, provide any information regarding the direction of the coming turn, it will inevitably alert the subject. Within a fraction of a second after the jerk, the yaw-left angular velocity component exceeds the stimulus threshold of the semicircular canals. Thus, in the centrifuge, as opposed to the in aircraft, the subject will receive, via somatosensation and the sense of balance, an early and tangible indication that he or she is entering a left turn. If, as suggested by Holly and Harmon,⁷ such early cues are significant for the brain's interpretation of complex vestibular information, then the sensation of roll tilt would be smaller during a real coordinated turn with an aircraft than after acceleration in a gondola centrifuge. Another possibility, also in line with the Whole-Motion Model, could be a reduced precision in the settings with the line, i.e., the subject could indicate a similar degree of roll tilt in the aircraft, but be less confident in his or her indications. It should be noted, in addition, that in a small propeller aircraft, vibrations and turbulence-induced variations in the G vector also seem likely to impair the perception of subtle changes in attitude and heading.

There are reasons to comment on two individuals in the present study who differed from the others in showing a considerable SVH tilt by the end of the centrifugation periods. One of these responded consistently during all runs in the centrifuge, but during his first turn in the aircraft, the precision of the settings with the line was poor and, more remarkably, during the later 3 min, the SVH was tilted in the opposite direction, i.e., as would have been an appropriate response during a coordinated turn to the right. Afterwards, the subject confirmed that he had got the impression that the first turn was to the right. The other subject described very clearly in conjunction with the centrifuge experiments that she associated the persistent sensation of increased weight during the runs with being in a coordinated turn. In the aircraft, however, she did apparently not perceive precisely when the turns began. These observations support the notion, implicit in the Whole-Motion Model, that an early cue consisting of forward linear acceleration and a yaw-plane canal stimulus may determine the perception of complex movement patterns. They are also in line with verbal reports by experienced pilots that the feeling of increased weight may contribute to the sensation of roll tilt during a coordinated turn, although this feeling does not reveal whether the turn is to the left or right.

To summarize, whereas the direction of a coordinated turn, as well as the time point of its beginning, is likely to be more easily detected via the sense of balance and the somatosensory system in a swing-out gondola centrifuge than in an aircraft, it appears that the magnitude of the perceived roll tilt angle is, nevertheless, similar in the two systems. Considering merely the group means,

this correspondence suggests the possibility of using a centrifuge-based flight simulator to recreate, in a way that is convincing to the vestibular system, a movement pattern that is among the most basic during flight. In addition, the correlation in perceived roll-tilt angle between the two systems suggests that testing in a centrifuge can reveal individual characteristics in spatial orientation that are also of significance during real flight.

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REFERENCES

1. Clark BJ, Taube JS. Vestibular and attractor network basis of the head direction cell signal in subcortical circuits. *Front Neural Circuits*. 2012; 6:7.
2. Dai MJ, Curthoys IS, Halmagyi GM. Linear acceleration perception in the roll plane before and after unilateral vestibular neurectomy. *Exp Brain Res*. 1989; 77(2):315–328.
3. Friedmann G. The judgment of the visual vertical and horizontal with peripheral and central vestibular lesions. *Brain*. 1970; 93(2):313–328.
4. Glasauer S. Human spatial orientation during centrifuge experiments: nonlinear interaction of semicircular canals and otoliths. In: Krejčová H, Jerabek J, editors. *Proceedings of the XVIIth Barany Society Meeting, Prague 1992*. Uppsala (Sweden): Bárány Society; 1993:48–52.
5. Guedry FE, Oman CM. *Vestibular stimulation during a simple centrifuge run*. Pensacola (FL): NMARL; 1990.
6. Guedry FE, Rupert AH, McGrath BJ, Oman CM. The dynamics of spatial orientation during complex and changing linear and angular acceleration. *J Vestib Res*. 1992; 2(4):259–283.
7. Holly JE, Harmon KJ. Spatial disorientation in gondola centrifuges predicted by the form of motion as a whole in 3-D. *Aviat Space Environ Med*. 2009; 80(2):125–134.
8. Israël I, Bronstein AM, Kanayama R, Faldon M, Gresty MA. Visual and vestibular factors influencing vestibular “navigation”. *Exp Brain Res*. 1996; 112(3):411–419.
9. McGrath BJ, Guedry FE, Oman CM, Rupert AH. Vestibulo-ocular response of human subjects seated in a pivoting support system during 3Gz centrifuge stimulation. *J Vestib Res*. 1995; 5(5):331–347.
10. Merfeld DM, Zupan LH, Gifford CA. Neural processing of gravito-inertial cues in humans. II. Influence of the semicircular canals during eccentric rotation. *J Neurophysiol*. 2001; 85(4):1648–1660.
11. Mergner T, Rumberger A, Becker W. Is perceived angular displacement the time integral of perceived angular velocity? *Brain Res Bull*. 1996; 40(5-6):467–470; discussion 470–471.
12. Mittelstaedt H. A new solution to the problem of the subjective vertical. *Naturwissenschaften*. 1983; 70(6):272–281.
13. Mittelstaedt H. The role of the otoliths in the perception of the orientation of self and world to the vertical. *Zoologische Jahrbücher – Abteilung für allgemeine Zoologie und Physiologie der Tiere*. Jena: Gustav Fischer Verlag; 1991; 95:419–425.
14. Mittelstaedt H. New diagnostic tests for the functions of utricles and saccules and somatic graviceptors. *Acta Otolaryngol*. 1995; 115(Suppl. 520): 188–193.

15. Müller GE. Über das Aubertsche Phänomen. *Zeitschrift für Sinnesphysiologie*. 1916; 49:109–246.
16. Noltenius F. Raumbild und Fallgefühl im Fluge. *Eur Arch Otorhinolaryngol*. 1921; 108:107–26.
17. Pavlou M, Wijnberg N, Faldon ME, Bronstein AM. Effect of semicircular canal stimulation on the perception of the visual vertical. *J Neurophysiol*. 2003; 90(2):622–630.
18. Stockwell CW, Guedry FE. The effect of semicircular canal stimulation during tilting during subsequent perception of the visual vertical. *Acta Otolaryngol*. 1970; 70(3):170–175.
19. Tribukait A. Subjective visual horizontal in the upright posture and asymmetry in roll-tilt perception: Independent measures of vestibular function. *J Vestib Res*. 2006; 16(1-2):35–43.
20. Tribukait A, Eiken O. Perception of the head transversal plane and the subjective horizontal during gondola centrifugation. *Percept Psychophys*. 2005; 67(3):369–382.
21. Tribukait A, Eiken O. Semicircular canal contribution to the perception of roll tilt during gondola centrifugation. *Aviat Space Environ Med*. 2005; 76(10):940–946.
22. Tribukait A, Eiken O. Roll-tilt perception during gondola centrifugation: Influence of steady-state acceleration (G) level. *Aviat Space Environ Med*. 2006; 77(7):695–703.
23. Tribukait A, Eiken O. On the time course of short-term forgetting: a human experimental model for the sense of balance. *Cogn NeurDyn*. 2016; 10(1):7–22.
24. Tribukait A, Grönkvist M, Eiken O. The perception of roll tilt in pilots during a simulated coordinated turn in a gondola centrifuge. *Aviat Space Environ Med*. 2011; 82(5):523–530.
25. Tschermak A, Schubert G. Über Vertikalorientierung im Rotatorium und im Flugzeuge. *Pflugers Arch Gesamte Physiol Menschen Tiere*. 1931; 228(1):234–257.
26. Udo de Haes HA, Schöne H. Interaction between statolith organs and semicircular canals on apparent vertical and nystagmus. *Acta Otolaryngol*. 1970; 69(1):25–31.
27. Van Beuzekom AD, Medendorp WP, Van Gisbergen JAM. The subjective vertical and the sense of self orientation during active body tilt. *Vision Res*. 2001; 41(25–26):3229–3242.
28. von Holst E, Grisebach E. Einfluss des Bogengangsystems auf die “subjective Lotrechte” beim Menschen. *Naturwissenschaften*. 1951; 38(3):67–68.
29. van Wulfften Palthe PM. Function of the deeper sensibility and of the vestibular organs in flying. *Acta Otolaryngol*. 1922; 4(1):415–449.
30. Wade SW, Curthoys IS. The effect of ocular torsional position on perception of the roll tilt of visual stimuli. *Vision Res*. 1997; 37(8):1071–1078.
31. Wapner S, Werner H, Morant RB. Experiments on sensory-tonic field theory of perception: III. Effects of body rotation on the visual perception of verticality. *J Exp Psychol*. 1951; 42(5):351–357.
32. Young LR. Perception of the body in space: mechanisms. In: Geiger SR, editor. *Handbook of physiology III/1*. Bethesda (MD): American Physiological Society; 1984.