Adaptive Changes in the Perception of Fast and Slow Movement at Different Head Positions

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BACKGROUND: This paper examines the subjective sense of orientation during asymmetric body rotations in normal subjects.

METHODS: Self-motion perception was investigated in 10 healthy individuals during asymmetric whole-body rotation with different head orientations. Both on-vertical axis and off-vertical axis rotations were employed. Subjects tracked a remembered earth-fixed visual target while rotating in the dark for four cycles of asymmetric rotation (two half-sinusoidal cycles of the same amplitude, but of different duration).

RESULTS: The rotations induced a bias in the perception of velocity (more pronounced with fast than with slow motion). At the end of rotation, a marked target position error (TPE) was present. For the on-vertical axis rotations, the TPE was no different if the rotations were performed with a 30° nose-down, a 60° nose-up, or a 90° side-down head tilt. With off-vertical axis rotations, the simultaneous activation of the semicircular canals and otolithic receptors produced a significant increase of TPE for all head positions.

DISCUSSIONS: This difference between on-vertical and off-vertical axis rotation was probably partly due to the vestibular transfer function and partly due to different adaptation to the speed of rotation. Such a phenomenon might be generated in different components of the vestibular system. The adaptive process enhancing the perception of dynamic movement around the vertical axis is not related to the specific semicircular canals that are activated; the addition of an otolithic component results in a significant increase of the TPE.

KEYWORDS: whole-body rotation, asymmetric stimulation, motion perception, vestibular adaptation, spatial orientation.

The information originating from the vestibular receptors elicits not only ocular and postural reflexes, but also contributes to the perception of body movements. The phenomenon of self-motion perception has been investigated and compared with the vestibulo-ocular reflex (VOR),[3,15,26] even in response to long-term habituation.[4,7,27] In general, the VOR and motion perception responses show several similarities, and both responses tend to diminish when consistent repetitive stimulus patterns (natural or galvanic stimulation) are delivered. However, the response attenuation following persistent stimulation has been recently challenged with the application of an asymmetric rotation,[16,20,21] which consisted of two half-sinusoidal cycles of the same amplitude, but different duration, featuring a fast (FHC) and a slow half cycle (SHC). In fact, in contrast with the VOR, self-motion perception due to slow movements is progressively reduced while that due to fast movements remains stable or even increases.[21] Therefore, the final outcome is a shift of the sense of orientation in the direction of the fast component. This does not occur for the VOR,[21] in which the slow responses tend to increase, while the fast ones decrease. It has been demonstrated that this perceptual bias was partly due to the dynamic characteristics of the vestibular system, and also due to an additional adaptive mechanism that prolonged its high dynamic sensitivity.[16,20,21] It has been suggested that such enhancement of motion perception toward the faster body rotation could be a useful tool for focusing our attention on the predicted future direction.[21]

Up to now, the evidence of such a phenomenon has been observed only in response to horizontal canal stimulation (on-vertical axis rotation at 30° nose-down head pitch)[21]. The influence of vertical canals and otoliths on such adaptive signal elaboration still needs to be investigated, given its importance in understanding how motion perception varies under different angular and linear accelerations.

Such a finding might be of major interest in aviation medicine, given the asymmetric accelerations that characterize the flight environment. Moreover, the lack of a correct sense of orientation plays a crucial role in the genesis of flight mishaps and is often identified as one of the main contributing factors.[10,23] Previous data indicated that linear vertical oscillations are the most represented stimuli for vestibular sensors during a typical long-haul flight mission.[14] Such finding emphasizes the role of those vestibular receptors sensing linear vertical accelerations (i.e., the aircrew's z-axis), where an additional rotation in the pitch and roll axes has also been observed to facilitate the onset of spatial disorientation and motion sickness.[6,28] Therefore, to separately analyze the behavior of the three semicircular canals and that of the otoliths during asymmetric rotation, we investigated the responses of normal subjects while rotating with different head positions during on- and off-vertical axis stimulation.

METHODS

Subjects and Equipment

Following written informed consent, 10 healthy civilian volunteers (personnel from Perugia University) ages 20–35 yr (8 men and 2 women, mean age 25.8 yr) participated in the study. Such an age range corresponds to the one observed in most operational pilots in the Italian Air Force. The experimental protocol was in accordance with the Declaration of Helsinki (1964) and was approved by the Ethical Committee of the University of Perugia.

Subjects were seated on a computer-controlled yaw rotating chair in a completely darkened and acoustically isolated cabin of 150 cm radius (**Fig. 1A**). A headphone was worn by the subjects in order to exclude possible bias due to the low-intensity acoustic noise generated by the chair rotation. The head was fastened to a holder by a belt fixed to the chair. The body was also fastened to the chair to prevent any movement. Subjects placed one hand on their chests and the other hand on the pointer joystick used for reproducing the self-motion perception. In addition, an adaptable plaster collar was used for maintaining a constant head/body angle. For the on-vertical axis rotations, the axis of rotation was through the subject's head-centered axis. For the off-vertical rotations, the subject's head-centered axis was 1 m away from the axis of chair rotation.

Procedure

For asymmetric horizontal rotation (yaw rotation), the stimulation consisted of four continuous asymmetric cycles delivered to examine the short-term effects of asymmetric rotation on the perceptual responses. The stimulus asymmetry consisted of two half-sinusoidal cycles of the same amplitude, but different duration, featuring an FHC and an SHC (**Fig. 1B**). An 80% time-asymmetry was used for a frequency of 0.15 Hz. This level of asymmetry was computed by considering the time interval (6.6 s) of the entire rotation cycle at 0.15 Hz, so that the FHC lasted 1.3 s (20% of total) and the SHC 5.3 s (residual 80%). Considering such parameters, the FHC frequency of rotation was ~0.38 Hz, while that of the SHC was ~0.09 Hz. This level of asymmetry was proved to be the best for eliciting the adaptive effects.[21] The cycles were initiated from the center toward one side of the yaw rotating chair and back to the center (from 0 to ±40°). Both directions of chair rotation were delivered, so that fast rotation was directed right- or leftward, up-, or downward depending on the head position relative to the rotation axis.

A psychophysical tracking procedure to assess self-motion perception was used.[19,25] Subjects were asked to manually rotate a pointer in the opposite direction of the body movement, reproducing in this way the self-motion perception. The pointer was connected with a precision potentiometer and pivoted on a chair-fixed support, located on the right side about 25 cm ahead of the body axis (Fig. 1A). The instantaneous position of the pointer (a joystick) measured the perceived body position in space.[19,25] Before being enrolled in the experiment, subjects were given practice sessions in the dark, consisting of body motion tracking during both symmetric and asymmetric rotations. During the experimental sessions, the responses to asymmetric stimulation were considered accurate when the tracking response to the first cycle reproduced the stimulus profile in amplitude, phase, and shape. In our previous experience,[21] we found that the error most frequently altering the amplitude of the perceptual responses was due to the discontinuity of the manual tracking, which was reflected in the tracking profile. Therefore, the similarity between the tracking and the stimulus shape was an important factor for evaluating the accuracy of the perceptual responses, and played a crucial role in the preliminary training phase. All subjects reported that this procedure was simple and intuitive.

The motion signals from the pointer and the chair were recorded with a PC, for off-line computing the position of the pointer with respect to the platform (Fig. 1B). The analogic waveforms were converted into digital values for processing by a 12-bit A/D card (Labview, National Instruments, Austin, TX) at a sampling rate of 500 Hz per channel. We evaluated the mismatch between the perceived positions indicated by the pointer and the body position in space at the end of the four rotation cycles.

During asymmetric rotation, subjects perceived the fast hemicycle more vividly than the slow hemicycle.[21] Thus, at the end of each session, the pointer was rotated in the direction of the slow hemicycle (Fig. 1B). The final position assumed by the pointer compared with the real body position was called tracking position error (TPE) (Fig. 1B) and resulted from the algebraic sum of each single cycle error during the four-cycle rotation.[21]
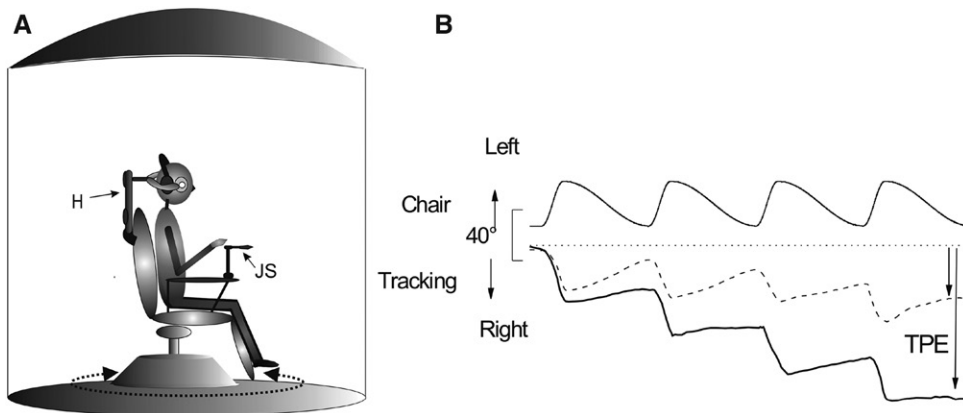
Fig. 1. A) Schematic drawing of the experimental setting. Acoustically isolated cabin and rotating chair: H: head holder, JS: joystick. B) Motion perception tracking in response to four asymmetric cycles. Traces above: chair asymmetric rotation. Traces below: motion tracking during rotation (dashed line: on-vertical axis rotation; entire line: off-vertical axis rotation). Stimulus during the FHC was to the left side and during the SHC was to the right. TPE (arrows) is noted after on-vertical axis and off-vertical axis rotations.

All subjects underwent six different protocols for examining the TPE. They were seated on the yaw rotatory chair with three different starting head positions and two different vertical rotation axes. Thus, in three subsequent experimental sessions, the subject's head was placed in different positions, so as to produce a response to yaw, pitch, and roll stimuli, as shown in **Fig. 2** for on-vertical axis rotation:

1) 30° nose-down pitch for activating the horizontal semicircular canals (Fig. 2A);
2) 90° (right or left) side-down tilted for activating the "pitch-like" vertical semicircular canals with the head maintained in pitched 30° nose-down (Fig. 2B);
3) 60° nose-up pitch for activating the "roll-like" vertical semicircular canals (Fig. 2C).

The vertical axis of rotation was head centered for activating only the semicircular canals. Before each test, subjects were repositioned on the rotating platform to maintain vertical rotation in the center of the vestibular apparatus to avoid linear acceleration components during rotation (for the on-vertical rotation axis). In addition, 1 m off-vertical axis rotations were delivered at all different head positions reported above for activating the semicircular canals by angular acceleration and the otolithic receptors by linear acceleration (off-vertical rotation axis) (**Fig. 3**).

During on-vertical rotation the otoliths of the two labyrinths are mildly activated in opposite directions and their signals are consequently cancelled, presumably within the vestibular nuclei. On the contrary, during off-vertical rotation the same linear component bilaterally acts on the otoliths, so that their output becomes part of the final response. In our case, two linear accelerations were acting on the otolithic receptors: the centrifugal and the tangential acceleration. Therefore, both these components were taken into account in the analysis of motion perception during rotation in the horizontal plane.

A fast rotation either to the right or to the left was applied to each subject, and no evident differences in the TPE were detected in response to stimuli of opposite FHC in all experimental conditions, as in the case of on-vertical rotation. Therefore, we indifferently used the TPE obtained from left or right rotation.

The different protocols were administered in randomized sessions and separated by at least 1-d intervals, to avoid any carry-over effects. Each subject was tested four times for each protocol and the mean value for each subject was recorded for statistical analysis.

Statistical Analysis

All mean values are followed by the standard deviation (SD). Repeated-measures ANOVA (two-way) was used for multiple comparisons. When the main effects or interactions were significant, post hoc analysis was made with the Bonferroni test. The level of significance was set at $P < 0.05$ for both ANOVA and post hoc comparisons. Prior to ANOVA, Levene's test assessed the homogeneity of the variances. The estimated statistical power calculated on the base of the size effect (0.4), the significance level ($P < 0.05$), the sample size ($N = 10$), and the applied test (repeated-measure two-way ANOVA) was 0.83.

RESULTS

In all subjects the four cycles of asymmetric on-vertical axis rotation, with 30° nose-down head pitch for horizontal canal activation, were delivered with the FHC to one side and the SHC in the opposite direction (Fig. 1B). The amplitude of FHC sensed component increased cycle by cycle, reaching a total amplitude of 110 ± 13° (vs. a total of 160° resulting from the four half-cycles of fast chair rotation).

On the contrary, the SHC tracking response progressively decreased cycle by cycle and after two to three cycles, the subjects did not perceive any more rotation. The total amplitude obtained from the SHC response was, therefore, only 52 ± 6°.

Because of these discrepancies between responses to different stimulus velocities, a final TPE of 58 ± 8° toward the FHC side was detected at the end of the four cycles (i.e., 110 − 52°) (**Table I**). Each subject showed a fairly constant TPE when tested in the four testing sessions with an intrasubject variability of less than ±5°. All these data were consistent with those reported in previous studies.[16,21]

In the same subjects four cycles of asymmetric on-vertical axis stimulation, with 90° (right or left side) down tilt ("pitch-like" stimulus) and 60° nose-up pitch ("roll-like" stimulus) for vertical canal activation, were delivered at different head positions (Fig. 2). In all these conditions, FHC responses increased
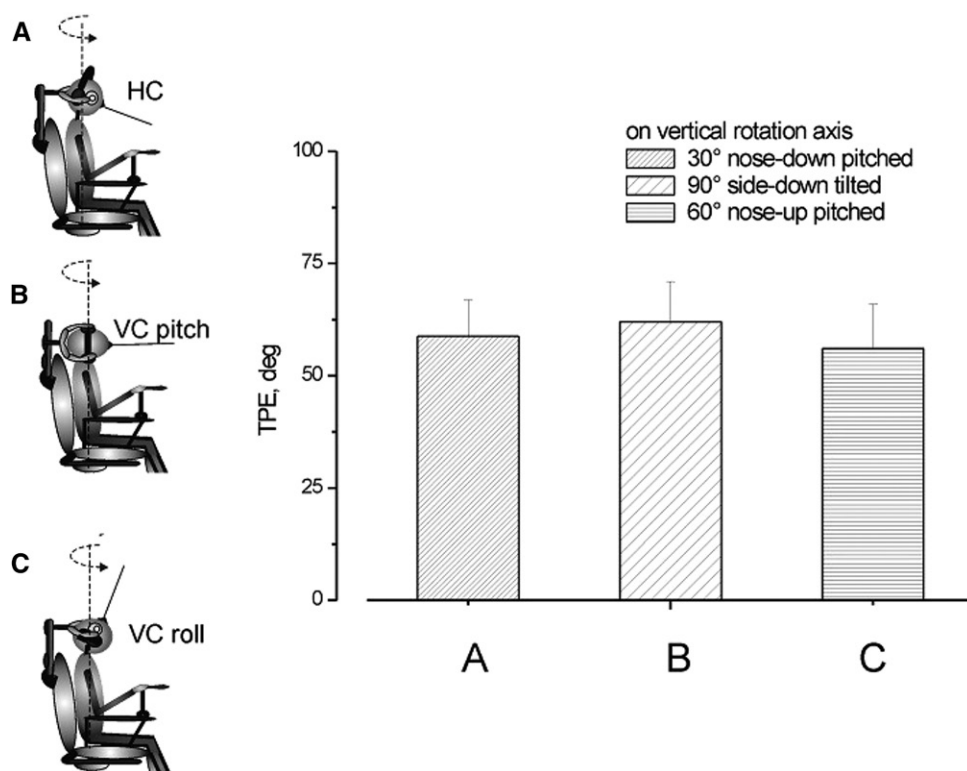
Fig. 2. Schematic drawing of the experimental setting for on-vertical axis asymmetric rotation at different head positions: A) 30° nose-down pitch for horizontal canal activation; B) 90° side-down tilt for pitch-like canal activation; C) 60° nose-up pitch for roll-like vertical canal activation. Vertical dashed line: rotation axis. The A, B, and C columns of the graph report the TPE mean and SD of 10 subjects observed after a 4-cycle asymmetric on-vertical axis rotation in the A, B, and C conditions, respectively.

and SHC responses progressively decreased during asymmetric rotation, inducing a final TPE of $56 \pm 10°$ for the 90° side down tilt ($114 \pm 12°$ of cumulative FHC response vs. $58 \pm 7°$ of SHC response), and $62 \pm 9°$ for the 60° nose-up head pitch ($112 \pm 15°$ of cumulative FHC response vs. $50 \pm 5°$ of SHC response) (Table I). These values were not significantly different from those observed during the 30° nose-down head pitch (i.e., $58 \pm 8°$). The statistical findings were (post hoc Bonferroni): 60° nose-up pitch vs. 30° nose-down pitch: $P = 0.5$; 90° side-down tilt vs. 30° nose-down pitch: $P = 0.2$.

In the same subjects, four cycles of asymmetric stimulation were delivered at different head positions also during off-vertical axis rotation, for simultaneous stimulation of the otoliths and semicircular canals (Fig. 3). Asymmetric rotations with the same head positions used for on-vertical axis rotations were tested. The TPE was significantly greater than that observed after semicircular canal activation alone (Table I, last row). The TPE statistical comparison (ANOVA) between on-vertical and off-vertical rotation was: $F(1,18)$: 698.43, $P < 0.002$.

The TPE values obtained after off-vertical axis rotations were not statistically different between the three head positions (post hoc Bonferroni): 60° nose-up ($121.9 \pm 10°$ of TPE) vs. 30° nose-down ($122.4 \pm 8°$ of TPE): $P = 0.3$; 90° (right or left) side-down ($131.1 \pm 14°$ of TPE) vs. 30° nose-down: $P = 0.2$; and 60° nose-up vs. 90° (right or left) side-down: $P = 0.7$. The statistical comparison (ANOVA) between head positions during off-vertical rotation was: $F(2,36)$: 0.7, $P = 0.12$; the interaction between rotation axis and head position was: $F(2,36)$: 1.3, $P = 0.09$.

DISCUSSION

Our study confirmed the unexpected finding of an altered motion perception during horizontal canal activation due to an asymmetric rotatory input around the on-vertical axis, and extended this a finding to the responses obtained from a similar activation of the vertical canals. The asymmetric rotation induces an error in sensing actual body rotation so that the final perceived body position is significantly shifted in the direction of the fast component of the stimulus (FHC). The reduced perception of slow rotation along with the substantially correct perception of fast rotation is responsible for this final orientation shift. This is not due to the sole functional characteristic of the canal receptors, but also to an adaptive process that progressively reinforces the perception of fast movements and minimizes that of slow ones.[9,21]

Such a finding is associated with a VOR adaptive mechanism, acting in the opposite direction, and thus resulting in progressively more symmetric oculomotor responses. This confirms the general rule that the VOR tends to be symmetric in response to asymmetric or unbalanced peripheral inputs.[21]

In this study, the same perceptual error was detected when the vertical canals were activated in response to both "roll-like" and "pitch-like" rotation. This suggests that the dynamic tendency to enhance fast vs. slow movement perception is a general property of the vestibular system, regardless of the type of receptor and circuitry involved. In fact, a TPE of similar amplitude was found for all the semicircular canals. Therefore, due to the similarity existing between each canal responsiveness to angular acceleration as well as in their time constant for cupula and central integrator, we can conclude that the adaptive process observed in this study is also present in the vertical canal central circuitry.

Moreover, when the stimulation is extended to the otolith receptors, as in the case of off-vertical axis rotation, this adaptive process is further enhanced, as shown by the TPE increase. This significant positional error is due to the simultaneous activation of semicircular canals and otoliths induced by the addition of a linear acceleration component. However, we do not
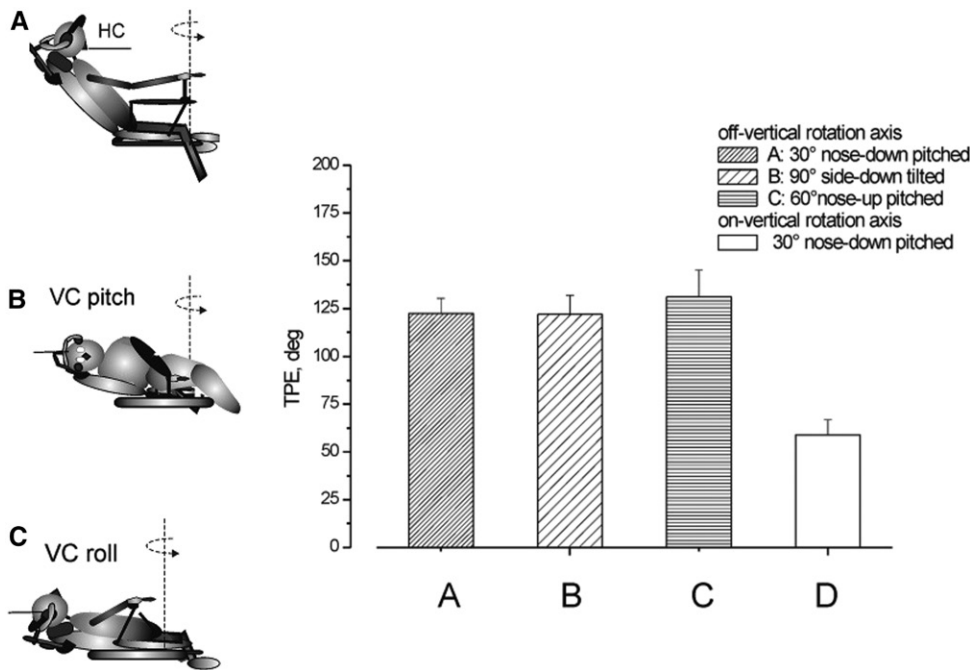
Fig. 3. Schematic drawing of the experimental setting for off-vertical axis asymmetric rotation at different head positions for simultaneous canal and otolith activation, according to the same head orientation criteria of Fig. 2: A) 30° nose-down pitch; B) 90° side-down tilt; C) 60° nose-up pitch. Vertical dashed line: off-vertical rotation axis. The graph reports the TPE mean and SD of 10 subjects observed after 4-cycle asymmetric off-vertical axis rotation with different head positions. The A, B, and C columns refer to the head position in off-vertical axis rotation as shown in the A, B, and C head positions shown by the schematic drawing, respectively. For comparison, the D column reports the TPE observed during "on-vertical axis rotation (30° nose-down pitch)."

perception of body orientation and movement is elaborated, such as the hippocampus, the posterior parietal cortex, or the parieto-insular vestibular cortex.[5,13,24] However, the vestibular nuclei, where synaptic plastic events have been reported in vitro following repetitive electrical stimulation, might also be involved.[11,17] In fact, such an electrical activation of vestibular afferent fibers, using a stimulus pattern resembling asymmetric rotation, induced a long-term increase of the response in the ventral part of the medial vestibular nuclei and a long-term decrease in its dorsal part. These different responses of in vitro vestibular neurons can be at the base of the difference between perceptual (e.g., TPE) and reflex effects (e.g., VOR), that was observed following an asymmetric stimulation.[21] Moreover, since all our data were obtained with a rotation about the vertical axis, these adaptive changes could take place downstream, in the vestibular pathway, where a common information on horizontal movements can be shared.

From a functional point of view, the shift of self-motion perception in the direction of the faster body movement suggests an expansion of the dynamic resolution of the vestibular system, which may be adequate to better perceive (as by a contrast-enhancing mechanism) the velocity of body rotation during fast movements, and to better extract the information relevant to the 'impending' straight-ahead, as during progression along curvilinear trajectories.[8,12] Conversely, the decreased sensitivity to slow movements may not necessarily be a functional deficit, as other sensory modalities, such as vision and proprioception, may easily replace the reduction of vestibular low-frequency responses and provide adequate feedback.[2,16,22]

In aviation, these findings can contribute to further understanding the physiological behavior of vestibular sensors under those asymmetrically changing orientation cues observed during standard in-flight conditions. This might be of particular importance during lack of sufficient visual information from the external environment (e.g., nighttime operations, flying in clouds or over featureless terrain). In these cases, an exaggerated sense of position (marked error in the representation of target position leading to distorted location of the initial straight-ahead) could be detrimental in certain phases of flight that involve curvilinear motion, and this factor would potentially play an additional role in spatial disorientation. Efforts to provide correct information on actual aircraft position and motion are clearly needed. This goal can be reached by

know whether the otoliths just facilitate the canals' adaptive process, or if they induce per se an additional bias in motion perception. Due to the direction of linear acceleration forces, in this last case the tangential component would probably play a major role with respect to the centrifugal one.

In any case, this is in contrast to the static information on head position provided by the otoliths, which theoretically should counteract the position error induced by the velocity bias. To enhance the perceptive error, otolithic activation should further increase the response to rapid rotation and decrease that to slow rotation. Therefore, this confirms that the perceptive responses to linear translation undergo a central high-pass filtering process,[1] in contrast with the low-pass filtering property observed in the case of long-lasting gravity modulation.[2,18] The current study did not investigate whether this effect can be extended to all possible axes of rotation, although the two different test conditions adopted for linear stimuli led to similar results.

The neural site of this adaptive mechanism might be a high-order process, involving regions of the brain where the

Table I. Comparison of TPE (in degrees) After a Four-Cycle Asymmetric Rotation at Different Static Head Positions, Activating the Horizontal or Vertical Semicircular Canals Through On- and Off-Vertical Axis Rotation (*N* = 10).

	H CANALS	V CANALS (ROLL-LIKE)	V CANALS (PITCH-LIKE)
On-vertical rotation	58.8 ± 8	62 ± 9	56 ± 10
Off-vertical rotation	122.4 ± 8	121.9 ± 10	131.1 ± 14

continuous training, which should include situation dependent scenarios related to specific vestibular illusions as those reported in this study. The final aim is to enhance the aircrew's awareness of spatial orientation with the use of ground-based and in-flight training courses, along with the development of orientation tools to be introduced inside the cockpit as part of the flight control systems.[23] In conclusion, the present study has identified a new type of adaptive mechanism acting on self-motion perception, potentially focusing our attention on the future direction of body movement by enhancing the perception related to the more intense body rotation.

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REFERENCES

1. Angelaki DE, Bush GA, Perachio AA. Two-dimensional spatiotemporal coding of linear acceleration in vestibular nuclei neurons. J Neurosci. 1993; 13(4):1403–1417.
2. Barmack NH, Nastos MA, Pettorossi VE. The horizontal and vertical cervico-ocular reflexes of the rabbit. Brain Res. 1981; 224(2):264–278.
3. Bertolini G, Ramat S, Laurens J, Bockisch CJ, Marti S, et al. Velocity storage contribution to vestibular self-motion perception in healthy human subjects. J Neurophysiol. 2011; 105(1):209–223.
4. Brandt T, Dichgans J, Büchele W. Motion habituation: inverted self-motion perception. Exp Brain Res. 1974; 21(4):337–352.
5. Brandt T, Dieterich M. The vestibular cortex. Its locations, functions, and disorders. Ann N Y Acad Sci. 1999; 871:293–312.
6. Cheung B. Non-visual spatial orientation mechaninsms. In: Previc FH, Ercoline WR. Spatial disorientation in aviation. Progress in astronautica & aeronautics. Reston (VA): AIAA; 2004. Vol. 203:37–94.
7. Clément G, Tilikete C, Courjon JH. Retention of habituation of vestibulo-ocular reflex and sensation of rotation in humans. Exp Brain Res. 2008; 190(3):307–315.
8. Courtine G, Schieppati M. Human walking along a curved path. I. Body trajectory, segment orientation and the effect of vision. Eur J Neurosci. 2003; 18:177–190.
9. Fernandez C, Goldberg JM. Physiology of the peripheral neurons innervating semicircular canals of the squirrel monkey. II. Response to sinusoidal stimulation and dynamics of the peripheral vestibular system. J Neurophysiol. 1971; 34(4):661–675.
10. Gibb R, Ercoline WR, Scharff L. Spatial disorientation: decades of pilot fatalities. Aviat Space Environ Med. 2011; 82(7):717–724.
11. Grassi S, Della Torre G, Capocchi G, Zampolini M, Pettorossi VE. The role of GABA in NMDA-dependent long term depression (LTD) of rat medial vestibular nuclei. Brain Res. 1995; 699(2):183–191.
12. Grasso R, Glasauer S, Takei Y, Berthoz A. The predictive brain: anticipatory control of head direction for the steering of locomotion. Neuroreport. 1996; 7(6):1170–1174.
13. Lopez C, Blanke O. The thalamocortical vestibular system in animals and humans. Brain Res Rev. 2011; 67(1–2):119–146.
14. Lucertini M, Autore A, Covioli J, Biselli R, D'Amelio R. Motion sickness prediction in aeromedical evacuation of patients with Ebola. Aerosp Med Hum Perform. 2016; 87(1):71–74.
15. Mergner T, Siebold C, Schweigart G, Becker W. Human perception of horizontal trunk and head rotation in space during vestibular and neck stimulation. Exp Brain Res. 1991; 85(2):389–404.
16. Panichi R, Botti FM, Ferraresi A, Faralli M, Kyriakareli A, et al. Self-motion perception and vestibulo-ocular reflex during whole body yaw rotation in standing subjects: The role of head position and neck proprioception. Hum Mov Sci. 2011; 30(2):314–332.
17. Pettorossi VE, Dieni CV, Scarduzio M, Grassi S. Long-term potentiation of synaptic response and intrinsic excitability in neurons of the rat medial vestibular nuclei. Neuroscience. 2011; 187:1–14.
18. Pettorossi VE, Errico P, Santarelli RM. Contribution of the maculo-ocular reflex to gaze stability in the rabbit. Exp Brain Res. 1991; 83(2):366–374.
19. Pettorossi VE, Panichi R, Bambagioni D, Grassi S, Botti FM. Contribution of eye position to movement perception. Acta Otolaryngol. 2004; 124(4):471–474.
20. Pettorossi VE, Panichi R, Botti FM, Biscarini A, Filippi GM, Schieppati M. Long-lasting effects of neck muscle vibration and contraction on self-motion perception of vestibular origin. Clin Neurophysiol. 2015; 126(10):1886–1900.
21. Pettorossi VE, Panichi R, Botti FM, Kyriakareli A, Ferraresi A, et al. Prolonged asymmetric vestibular stimulation induces opposite, long-term effects on self-motion perception and ocular responses. J Physiol. 2013; 591(7):1907–1920.
22. Pettorossi VE, Schieppati M. Neck proprioception shapes body orientation and perception of motion. Front Hum Neurosci. 2014; 8:895.
23. Research and Technology Organization (RTO). Spatial disorientation training—demonstration and avoidance. Neuilly-sur-Seine (France): NATO RTO; Oct. 2008. RTO-TR-HFM-118.
24. Sharp PE, Blair HT, Etkin D, Tzanetos DB. Influences of vestibular and visual motion information on the spatial firing patterns of hippocampal place cells. J Neurosci. 1995; 15(1, Pt. 1):173–189.
25. Siegle JH, Campos JL, Mohler BJ, Loomis JM, Bülthoff HH. Measurement of instantaneous perceived self-motion using continuous pointing. Exp Brain Res. 2009; 195(3):429–444.
26. Sinha N, Zaher N, Shaikh AG, Lasker AG, Zee DS, Tarnutzer AA. Perception of self motion during and after passive rotation of the body around an earth-vertical axis. Prog Brain Res. 2008; 171:277–281.
27. St George RJ, Day BL, Fitzpatrick RC. Adaptation of vestibular signals for self-motion perception. J Physiol. 2011; 589(Pt. 4):843–853.
28. Wertheim AH, Bos JE, Bles W. Contribution of roll and pitch to seasickness. Brain Res Bull. 1998; 47(5):517–524.