

Vestibulo-Ocular Responses, Visual Field Dependence, and Motion Sickness in Aerobatic Pilots

Olga Kuldavletova; Sebastian Tanguy; Pierre Denise; Gaëlle Quarck

- BACKGROUND:** Aerobatic flight is a challenge for the vestibular system, which is likely to lead to adaptive changes in the vestibular responses of pilots. We investigated whether aerobatic pilots, as individuals who experience intense vestibular stimulation, present modifications of the vestibulo-ocular reflex, motion sickness susceptibility and intensity, visual vertical estimation, and visual dependence as compared to normal volunteers.
- METHODS:** To evaluate vestibulo-ocular reflexes, eye movements were recorded with videonystagmography while subjects were rotated on a rotatory chair with the axis of rotation being vertical (canal-ocular reflex) or inclined to 17° (otolith-ocular reflex). Motion sickness was evaluated after the rotatory test using the Graybiel diagnostic criteria. General motion sickness susceptibility and visual field dependence were also evaluated.
- RESULTS:** Averaged data did not show significant difference in canal-ocular reflex and otolith ocular-reflex between groups. However, a significant asymmetry in otolith-driven ocular responses was found in pilots ($CW 0.50 \pm 1.21^\circ \cdot s^{-1}$ vs. $CCW 1.59 \pm 1.12^\circ \cdot s^{-1}$), though visual vertical estimation was not altered in pilots and both groups were found field independent. Pilots were generally less susceptible to motion sickness (MSSQ scores: 2.52 ± 5.59 vs. 13.5 ± 11.36) and less affected by the nauseogenic stimulation (Graybiel diagnostic criteria 3.36 ± 3.81 vs. 8.39 ± 7.01).
- DISCUSSION:** We did not observe the expected habituation in the group of aerobatic pilots. However, there was a significant asymmetry in the otolith-driven ocular responses in pilots, but not in the controls, which may result from the asymmetry in piloting protocols.
- KEYWORDS:** aerobatic pilots, vestibular system, vestibulo-ocular reflex, motion sickness.

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Vestibular processing in the central nervous system is adjusted during life by everyday movements. Unusual and unnatural passive stimuli cause the mismatch between the actual sensory input and an expected input formed based on previous experience. This sensory mismatch is the most commonly cited to be the cause of motion sickness.²³ Moreover, the same previously unusual stimulus applied repetitively can lead to adaptation and/or habituation that changes the responses and diminishes the risk of occurrence of motion sickness symptoms.

Vestibulo-ocular reflex (VOR) is the eye rotations that compensate for the movements of the head, serving to stabilize the gaze. The VOR can originate from both the semicircular canal system and the otolithic system and the two parts of the reflex are separate: the canal-ocular reflex (COR) and the otolith-ocular reflex (OOR).

VOR is plastic and can habituate under repetitive prolonged stimulus and is characterized by a bidirectional or unidirectional

decrease of response, which has been demonstrated by numerous studies employing habituation protocols.⁵ Habituation was demonstrated in sportsmen experiencing intensive vestibular stimulations (e.g., figure skaters, ballet dancers, gymnasts).²⁷ Adaptation can appear, for example, if one uses spectacles that magnify or miniaturize the visual scene, inducing adaptive increase or decrease in gain in the COR.²¹

Mental effort can also evoke modifications in COR gain: Jones et al.¹⁷ used a mental suppression paradigm to observe a decrease in COR gain after 3 h of training. Attention mechanisms

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and alertness are also crucial factors in regulating the COR; for example, mental arithmetic has been demonstrated to enhance COR gain.⁷

Only a few studies have dealt with the plasticity of the human OOR. The OOR was modified along with the COR after visual-vestibular mismatch habituation protocols.¹⁸ In the study on the OOR of figure skaters, the OOR amplitude of modulation was found to be lower than in the control group, and the bias corresponded more to the actual stimulus.²⁸

Aviation is a challenge to the vestibular system of an aviator. Such a strong stimulus is likely to drive the development of adaptive changes in the vestibular processing of pilots. Moreover, because there are different aviation kinds and purposes, the stimulus differs a lot in the total peak linear acceleration magnitude, rotatory stimulus, whether concentration is primarily on the instrument panel or on the environment, and other factors. This suggests that different types of pilots might be affected differently by their activity and the vestibular adaptive changes in aerobatic pilots might differ from those in civil passenger aviation, for example. Thus, while sportsmen usually demonstrate a decrease in the VOR time constant (TC) and gain which indicates habituation, the existing data from pilots is less clear.

The study of Fisher in 1919 reported the results of postrotatory nystagmus assessment studies in approximately 1500 veteran pilots and concluded that the duration of after-turning nystagmus in aviators is not affected by flying.¹³ In contrast, another study reported reduced COR among 100 Swedish Air Force pilots.³ It was mentioned, however, that the variability of results from the pilots was large. Interestingly, the author stated that the differences in vestibular responses were more pronounced in highly experienced pilots, while pilots with less flying experience did not differ from the controls. In addition, they reported that the nystagmus parameters often had a directional preponderance. It was also noted that the absence from flying for at least several months leads to normalization of the status. Unlike the previous findings, Schwarz and Henn²⁴ found that in military student pilots the time constant of the nystagmus response after vestibular stimulation was shorter (P less than 0.001; t -test), whereas the gain tended to be higher (P less than 0.025).²⁴ One more study demonstrated that during vestibular stimulation on a rotatory chair at a frequency range of 0.01 Hz–0.32 Hz there was little difference in fighter pilots and controls except for at the frequency of 0.16 Hz. In a consequent experiment they showed that after four successive velocity-step tests at 0.16 Hz there was little modification in the COR gain in pilots (0.64 ± 0.04 to 0.58 ± 0.032), while it significantly increased in nonpilots (0.59 ± 0.03 to 0.78 ± 0.06).¹ Lee investigated COR by slow harmonic acceleration in Korean Air Force pilots and found that for frequencies of 0.04–0.32 Hz the gain of the COR in pilots was significantly higher than that of the control subjects.¹⁹ A more recent study evaluated the function of all six semicircular canals in active fighter pilots (1000–3000 h of training) using the video head impulse test, and found the decrease in gain only in the left posterior canal.³⁰

The literature on aviators is very heterogeneous and provides contradictory results. Some studies report modifications in the vestibular reflexes of pilots, while some studies report no differences. Different studies reported the COR gain to increase and to decrease in comparison with control subjects. Most of the studies were assessing solely lateral semicircular canal function except for one.²⁹ However, no study was held on the otolithic response in pilots. Moreover, all the studies have been performed on military pilots. No vestibular studies have been held on aerobatic pilots.

Literature shows that motion sickness (MS) occurrence is likely to be linked with vestibular habituation. Shupak et al.,²⁵ in a study on sailor students, demonstrated simultaneous diminution of MS severity and diminution of VOR gain at 0.01 Hz after 6 mo of sailing. They conclude that VOR gain can serve as a physiological correlate helping to predict seasickness susceptibility. A more recent study by Clement used short-term vestibular training to assess short-term habituation.⁵ It demonstrated that after the training, MS and VOR peak velocity and time constant declined in all subjects. Another study showed that the time constant of COR was reduced due to the habituation protocol, which was in line with MS symptoms reduction.⁹ Most literature demonstrates a positive correlation between the TC of the VOR;^{22,25} however, there is also evidence for a negative correlation.¹² Both MS and VOR habituation were shown to involve the velocity storage mechanism.^{6,9,12}

Literature shows a decrease or a complete cessation of symptoms of MS in pilots after several sessions of training.²⁶ One study described three symptomatic peaks during aerobatic training that occurred in the first three flights, the seventh flight (on which there was an abrupt increase in aircraft acceleration), and the first three flights of the phase in which aerobatics was introduced.²⁹ For these pilots, every introduction of a new stimulus evoked MS, which then decreased with training.

Vestibular processing modifications can also affect the sense of self-orientation in space. It has been shown that prolonged exposure to altered conditions like microgravity leads to changes in the perceived orientation of vertical,¹⁶ as do the habituation protocols.⁵ Thus, adaptation of vestibular reflexes can be linked to perturbations in spatial orientation and rearrangements in visual-vestibular interactions. The rod-and-frame test (RFT), which serves to reveal perceptual strategy (visual field dependence-independence), is a tool that helps to assess the subjective vertical assessment and the influence of the visual field cues in this process. There is some evidence of a link between field independence and a greater susceptibility to simulator sickness,⁴ but the topic is debated.²⁰

The aim of the current study was to investigate whether aerobatic pilots, as individuals who experience an intense vestibular stimulation, present a modification of the vestibular function and MS susceptibility in comparison to normal volunteers. We hypothesized that aerobatic pilots might develop a vestibular adaptation to their activity and thus present altered VOR and visual vertical estimation and a lower MS susceptibility.

METHODS

Subjects

A total population of 31 subjects participated in the study. The population consisted of a group of pilots (11 subjects: 10 male, 1 female, age 30.3 ± 14.4 yr) and a control group (18 subjects: 16 male, 2 female, age 25.6 ± 11.3 yr). All the pilots were undergoing the same intensive course on aerobatic piloting in Caen, France, at the time of the study.

Subjects who did not finish the protocol on the rotatory chair due to motion sickness were excluded from analysis. Datasets for any test, when the data was absent, incomplete, or of bad quality, were excluded from the analysis. In particular, in the Motion Sickness Susceptibility Questionnaire (MSSQ),¹⁴ the data from one pilot and three control subjects are absent, COR recordings from one control subject and one pilot are also missing; for the OOR, Graybiel diagnostic criteria,¹⁵ and RFT² the datasets are complete.

All participants were clinically normal according to a screening battery that included a combined neurological and otological physical examination performed by an M.D., Ph.D. The ethics committee approved this study (N°: CCPPRBN 2004-03) and informed consent from all participants were obtained.

Materials

To assess visual-vestibular interactions (visual field dependency), RFT was applied using the original device and the original protocol.² The VOR was evaluated using a rotatory chair that can be tilted with respect to gravity. We used two protocols—Earth-vertical axis rotation (EVAR) and off-vertical axis rotation (OVAR) to stimulate the semicircular canals and otoliths accordingly. **Fig. 1** illustrates the protocols for both types of stimulation.

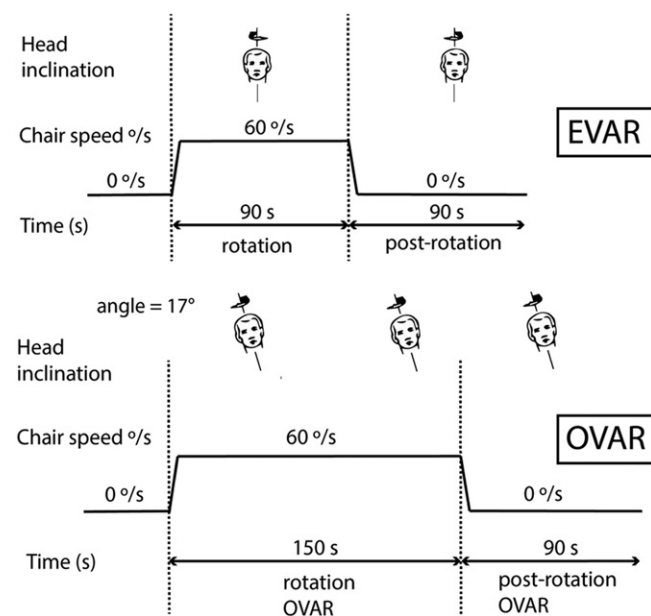


Fig. 1. The protocols for EVAR (above) and OVAR (below).

Eye movements induced by VOR for the left eye were recorded by a video oculograph (Chronos 3D, Chronos Vision, Berlin, Germany) sampled online at 100 Hz. Each experimental session started with a calibration, accomplished using sequentially illuminating LED.

The level of MS evoked by the rotatory chair stimulation was assessed with a diagnostic criteria proposed by Graybiel and colleagues.¹⁵ Apart from that, the self-reported childhood (part A) and current (part B) history of MS susceptibility in subjects was collected with the help of the MSSQ.¹⁴

Procedure

The visual field dependence test was held before the rotation session. Individuals who were unable to set the rod upright and instead set it tilted (more than 5°) were classified as “field-dependent.” Individuals who were able to ignore the misleading context of the frame, setting the rod upright, were classified as “field-independent.”

The Graybiel diagnostic criteria were applied after the EVAR and OVAR rotatory chair session. The nauseogenic part of the protocol are the two OVAR stimulation sequences. In the criteria, symptoms were divided in categories with varying symptom intensities. The subject could underline only one level of intensity per category. The subject also completed the MSSQ, reporting history of motion sickness susceptibility during childhood (before 12 yr) and adulthood (the last 10 yr). The participants sat upright on the rotatory chair with their head immobilized in the straight position. All stimulations were carried out in darkness with the participants’ eyes open.

The EVAR protocol for assessing COR consisted of two sequences with counterbalanced directions of rotation [clockwise (CW) and counterclockwise (CCW)]. The axis of rotation was vertical, the subjects were accelerated in 1 s to a velocity of rotation of $\pm 60^\circ \cdot s^{-1}$, and after 90 s of rotation, they were decelerated in 1 s. The ocular responses were recorded from the beginning of the rotation until 90 s after the stop.

Eye movement velocity was calculated digitally using the two-point central difference algorithm (50-ms step size).¹⁰ The saccadic eye movements were removed from the eye velocity signal and replaced by a linear interpolation, resulting in a slow phase velocity.¹⁰ Then it was manually verified and corrected as required.

For COR recordings, an exponential curve was fit on the slow phase velocity curve of the pre- and postrotatory eye movements. The variables studied were the peak phase velocity ($^\circ \cdot s^{-1}$) and time constant (TC, s) of the exponential decrease of the slow phase velocity curve.¹⁰

The protocol for the OOR assessment was also composed of two sequences identical except for the direction of rotation. OVAR started with an axis tilted at 17° to the Earth-vertical. Subjects were accelerated during 1 s to a constant velocity of rotation of $\pm 60^\circ \cdot s^{-1}$. Rotation continued for 150 s and then a subject was decelerated during 1 s. The stimulation parameters ($60^\circ \cdot s^{-1}$, 17° tilt) were chosen to induce a sufficient otolithic stimulation and a slight motion sickness.¹¹ For OOR recordings, the eye movements were analyzed when OOR was well established (60 s after the onset of movement).

The slow phase velocity curve of OOR nystagmus was modeled according to the formula:

$$\text{SPV}(t) = B + A \cos(2\pi/T + \phi)$$

with t as time (s); T as the period of rotation (6 s). Magnitudes B , A , and ϕ are the bias ($^{\circ} \cdot \text{s}^{-1}$), the amplitude of modulation ($^{\circ} \cdot \text{s}^{-1}$), and the phase ($^{\circ}$), respectively. The variables compared were bias and modulation. In the results, CW and CCW refer to the clockwise and counterclockwise directions of rotation, not of the eye movements.

Statistical Analysis

To perform the analysis and create graphs, we used SigmaStat 3.5 and SigmaPlot 10.0 (Systat Software, Inc., Slough, Berkshire, UK). Groups were compared with bilateral unpaired t -test; asymmetry was assessed with bilateral paired t -test. When the data was not normally distributed, the nonparametric analog of the t -test was used (Wilcoxon signed rank test for the paired data and Mann-Whitney rank sum test for the nonpaired data). The results are presented as mean \pm SD. The threshold of statistical significance was set at 0.05.

RESULTS

During EVAR the COR gain in pilots did not show significant difference from the control group [0.59 ± 0.11 vs. 0.61 ± 0.1 ; $t = 0.53$; 25 degrees of freedom (df); $P = 0.6$]. There was no significant difference ($t = -1.37$; df = 25; $P = 0.18$) detected in TC between the groups either (12.4 ± 1.9 s vs. 11.3 ± 2 s).

The amplitude of the OOR was not found to be different between groups ($1.54 \pm 1.15^{\circ} \cdot \text{s}^{-1}$ in pilots vs. $1.17 \pm 0.66^{\circ} \cdot \text{s}^{-1}$ in controls; $t = -1.12$; df = 27; $P = 0.27$). The bias along the horizontal axis had a tendency to be lower in pilots than in control subjects ($1.05 \pm 0.93^{\circ} \cdot \text{s}^{-1}$ vs. $1.8 \pm 1.2^{\circ} \cdot \text{s}^{-1}$), though not statistically significantly ($t = 1.77$; df = 27; $P = 0.09$).

However, the pilots presented asymmetric OOR bias, while the control subjects did not [CW vs. CCW: $0.50 \pm 1.21^{\circ} \cdot \text{s}^{-1}$ vs. $1.59 \pm 1.12^{\circ} \cdot \text{s}^{-1}$ ($t = -2.26$; df = 10; $P = 0.03$, paired t -test) in pilots and $1.89 \pm 1.82^{\circ} \cdot \text{s}^{-1}$ vs. $1.7 \pm 1.73^{\circ} \cdot \text{s}^{-1}$ ($Z = 0.46$; $N = 81$; $P = 0.67$, Wilcoxon signed rank test) in the control group; Fig. 2].

The unsigned mean error in subjective vertical, with respect to the real vertical, revealed the RFT was not different between groups ($1.66 \pm 1^{\circ}$ for control subjects vs. $1.7 \pm 1.17^{\circ}$ for pilots; $P = 0.89$, U statistic = 102.5; Mann-Whitney rank sum test). Both groups were field independent as the mean error was not more than the normal physiological value.

Self-reported history of MS susceptibility (MSSQ score) was found to be significantly less in pilots than the control group during the last 10 yr (2.52 ± 5.59 vs. 13.5 ± 11.36 ; $P = 0.003$, U statistic = 126.5; Mann-Whitney rank sum test) and before the age of 12 (5.85 ± 11.35 vs. 20.96 ± 15.26 ; $P = 0.02$, U statistic = 117; Mann-Whitney rank sum test); see Fig. 3. The symptoms score obtained with the Graybiel diagnostic criteria was also significantly different in the effect of the vestibular stimulation

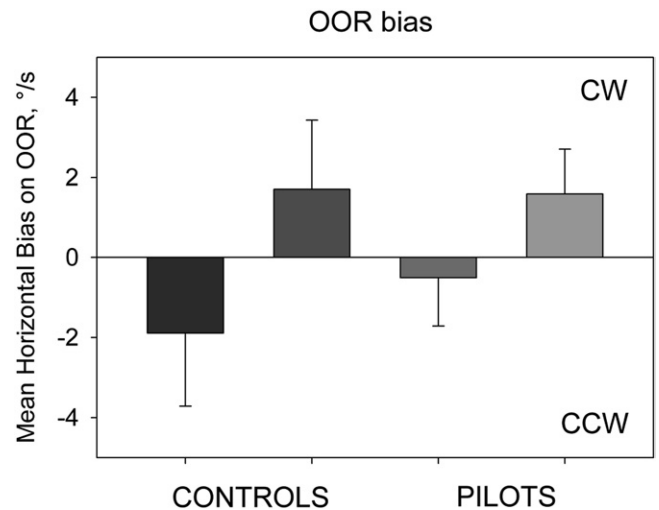


Fig. 2. Horizontal bias in the otolith response in Clockwise and Counterclockwise rotations in pilots and the control group.

of the study in the two groups (3.36 ± 3.81 vs. 8.39 ± 7.01 ; U statistic = 148; $P = 0.03$, Mann-Whitney rank sum test; Fig. 4).

DISCUSSION

The mean unsigned errors made by both groups in the rod and frame test did not differ statistically on average. The normal range of deviation from the real vertical without the field tilt influence is $0 \pm 2^{\circ}$.³¹ For both groups the mean error was less than 2° , which shows that the subjects are field independent. These results suggest that from the perspective of perception, no alteration is induced in pilots by their activity.

The pilots presented less history of susceptibility to MS than control participants. This finding is consistent with the data on other types of pilots and supports the observations of MS susceptibility habituation.^{26,29} However, it might be the result either of habituation, or of the fact that people who are less susceptible to motion sickness are more likely to choose aviation as an activity. The second explanation seems more likely, as long as the score of the part A of the MSSQ suggests that even in childhood MS experience in pilots was significantly less than in the control group. The rotatory chair stimulation was less nauseogenic for pilots than for control subjects (the score of 3.4 for pilots corresponds to slight-to-moderate malaise, while 8.4 is interpreted as a moderate-to-severe malaise¹⁵), which corresponds to the general susceptibility of the groups. It should be mentioned that the analysis of motion sickness of subjects in this study is limited. First, the choice of the stimulus intensity was made to be optimal between sufficient otolith stimulation and the low nauseogenicity. Therefore, due to the low nauseogenicity, the differences between groups might seem not as pronounced as they are in reality. Second, subjects who did not finish the protocol due to motion sickness were excluded from the analysis, which could influence the mean score. However, even with these limitations the difference is detectable.

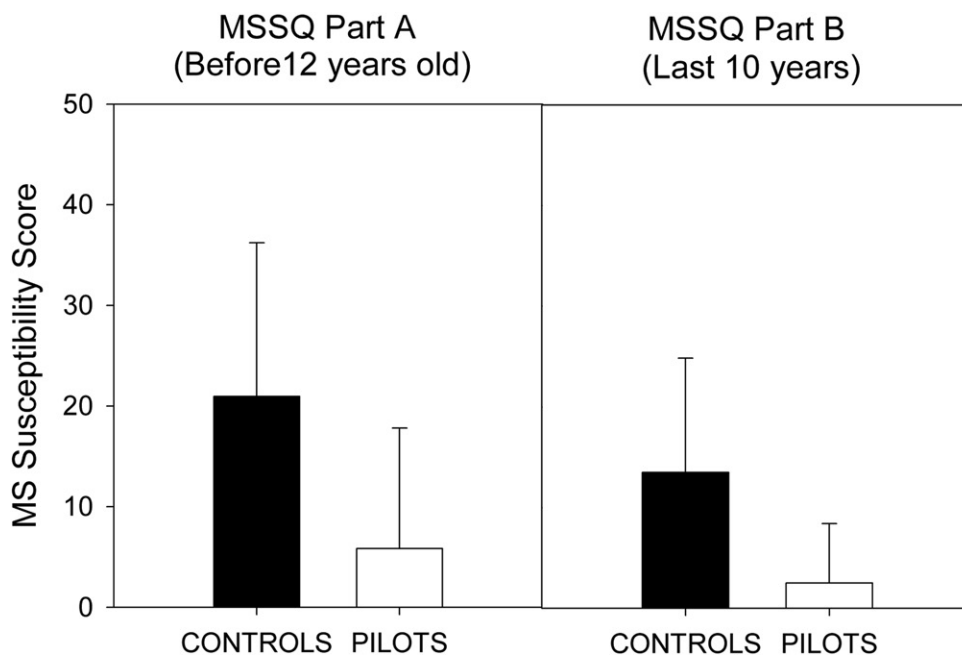


Fig. 3. Motion sickness susceptibility scores in childhood (Part A) and adulthood (Part B) in pilots and the control group.

Literature suggests that the habituation to MS is linked with the habituation of the COR^{9,25} as well as with a change in the subjective vertical,⁵ none of which was observed in the group of aerobatic pilots in this study. Indeed, contrary to what has been observed in sportsmen like figure skaters,²⁷ we did not find a

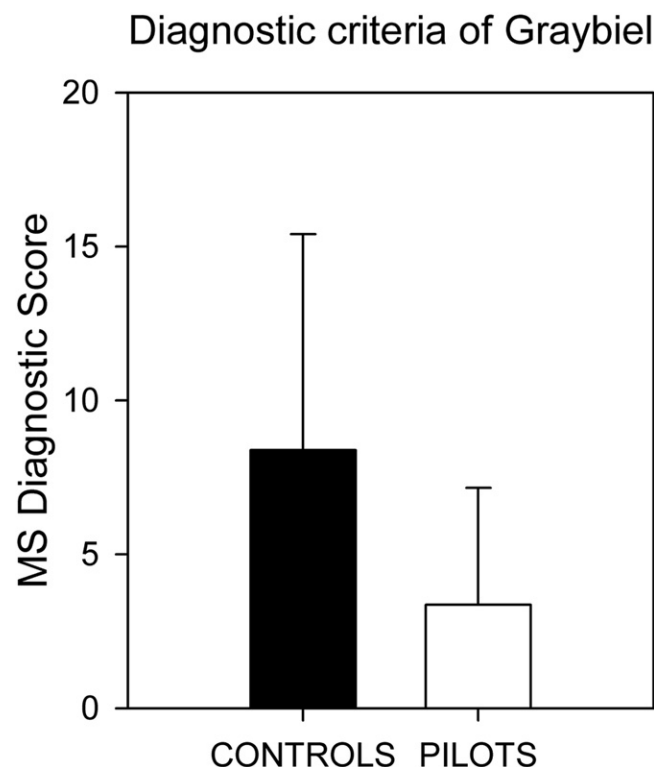


Fig. 4. Scores of the motion sickness diagnostic criteria of Graybiel in pilots and the control group.

significant change in pilots' canal function. Aerobatic pilots perform rotations differently than figure skaters or gymnasts. First, many rotations are performed with orientation changing with respect to gravity, which implies otolithic inputs together with canal inputs. This might be interpreted in the brain differently than a pure canal stimulation. Second, unlike figure skaters, who suppress their compensatory eye movements to perform the rotations better, pilots should have precise ocular compensations to better orient themselves in space and keep visual attention. This suggests active attention and usage of all the sensory cues that might help to build a robust representation of their position. Unlike many other pilots, the aerobatic

pilots dominantly concentrate not on the instrument panel, but on their perception of the environment and orientation in space, in particular by using visual information. It was shown in velocity step habituation in cats that visual suppression during the secondary nystagmus prevented the full development of habituation.⁸ This suggests that the aerobatic pilots are less likely to diminish the gain of the VOR.

The investigation of the otolithic system with the OVAR indeed revealed an alteration in otolith-ocular reflex in pilots. Comparing to control subjects, otolith-driven eye movements of pilots had a significant decrease in bias for the rightward head movements, while for the leftward it remained the same as observed in the control group. That is, pilots demonstrated a significant asymmetry in bias of the horizontal otolith-ocular response. The bias asymmetry suggests a unilateral habituation. This is surprising because this asymmetry could lead to spatial orientation alteration, which we do not observe indirectly, according to the results of the RFT test. Habituation is usually caused by repetitive stimulus. In this case it could possibly be explained by the directional preferences of the aerobatic maneuvers performance. According to anecdotal data from the pilots, this preference indeed takes place due not only to the subjective habits, but also to the construction of the vehicle that pilots use for their training and performances. Aerobatic aircrafts have propellers that rotate clockwise. This facilitates and accelerates leftward rotations. In addition, the cockpit is constructed in such a way that the stick is usually controlled with the right hand and is physically much easier to push leftwards. These constructive features explain the fact that, according to the anecdotal estimations by pilot instructors, more than two-thirds of rotations are performed leftwards. Such unequal and asymmetric conditions concerning leftward rotation could

have induced asymmetric habituation in the OOR of pilots. However, the results show the opposite. We could suggest that during intense stimulations, there are not only accelerations that should be taken into account, but also decelerations. It is likely that during aerobatic maneuvering, decelerating is even more abrupt. Therefore, it might be the termination of leftward maneuvers that contributes the most to the vestibular signaling.

However, the observed asymmetry remains unclear, suggesting the necessity of further research of otolithic function in pilots, and aerobatic pilots in particular. It should be noted that the design of airplanes can affect the vestibular system of pilots.

In summary, our study demonstrates that aerobatic pilots have a significant asymmetry in horizontal eye movements driven by otoliths, while the control subjects are symmetric. It might be the result of habituation to rapid decelerations during the maneuvers, which could possibly lead to disturbances in spatial orientation. However, pilots were equally successful in visual vertical estimation as control subjects and all subjects tested were field independent. We found no change in the ocular responses driven by the semicircular canals in the pilot group. Pilots were found to be less susceptible to motion sickness.

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REFERENCES

- Ahn SC. Short-term vestibular responses to repeated rotations in pilots. *Aviat Space Environ Med.* 2003; 74(3):285–287.
- Asch SE, Witkin HA. Studies in space orientation: I. Perception of the upright with displaced visual fields. *J Exp Psychol.* 1948; 38(3):325–337.
- Aschan G. Response to rotatory stimuli in fighter pilots. *Acta Otolaryngol Suppl.* 1954; 116:24–31.
- Barrett GV, Thornton CL. Relationship between perceptual style and simulator sickness. *J Appl Psychol.* 1968; 52(4):304–308.
- Clément G, Deguine O, Bourg M, Traon AP-L. Effects of vestibular training on motion sickness, nystagmus, and subjective vertical. *J Vestib Res.* 2007; 17(5–6):227–237.
- Cohen B, Dai M, Raphan T. The critical role of velocity storage in production of motion sickness. *Ann N Y Acad Sci.* 2003; 1004(1):359–376.
- Collins WE, Guedry FE. Arousal effects and nystagmus during prolonged constant angular acceleration. *Acta Otolaryngol.* 1962; 54(1–6):349–362.
- Courjon JH, Clément G, Schmid R. The influence of interstimulus interval on the development of vestibular habituation to repeated velocity steps. *Exp Brain Res.* 1985; 59(1):10–15.
- Dai M, Kunin M, Raphan T, Cohen B. The relation of motion sickness to the spatial-temporal properties of velocity storage. *Exp Brain Res.* 2003; 151(2):173–189.
- Denise P, Darlot C, Ignatiew-Charles P, Toupet M. Unilateral peripheral semicircular canal lesion and off-vertical axis rotation. *Acta Otolaryngol.* 1996; 116(3):361–367.
- Denise P, Etard O, Zupan L, Darlot C. Motion sickness during off-vertical axis rotation: prediction by a model of sensory interactions and correlation with other forms of motion sickness. *Neurosci Lett.* 1996; 203(3):183–186.
- DiZio P, Lackner JR. Motion sickness susceptibility in parabolic flight and velocity storage activity. *Aviat Space Environ Med.* 1991; 62(4):300–307.
- Fisher L, Babcock HL. The reliability of the nystagmus test. *J Am Med Assoc.* 1919; 72(11):779–782.
- Golding JF. Motion sickness susceptibility questionnaire revised and its relationship to other forms of sickness. *Brain Res Bull.* 1998; 47(5):507–516.
- Graybiel A, Wood CD, Miller EF, Cramer DB. Diagnostic criteria for grading the severity of acute motion sickness. *Aerosp Med.* 1968; 39:453–455.
- Harris LR, Jenkin M, Jenkin H, Zacher JE, Dyde RT. The effect of long-term exposure to microgravity on the perception of upright. *NPJ Microgravity.* 2017;3. [Accessed 19 March 2018]. Available from <http://www.nature.com/articles/s41526-016-0005-5>.
- Jones GM, Berthoz A, Segal B. Adaptive modification of the vestibulo-ocular reflex by mental effort in darkness. *Exp Brain Res.* 1984; 56(1):149–153.
- Koizuka I, Katsumi N, Hattori K, Okada T, Kato I. Effect of adaptive plasticity of linear vestibulo-ocular reflex upon angular vestibulo-ocular reflex. *Auris Nasus Larynx.* 2000; 27(2):89–93.
- Lee MY, Kim MS, Park BR. Adaptation of the horizontal vestibuloocular reflex in pilots. *Laryngoscope.* 2004; 114(5):897–902.
- Mirabile CS Jr, Glueck BC, Stroebel CF. Susceptibility to motion sickness and field dependence-independence as measured with the rod and frame test. *Neuropsychobiology.* 1976; 2(1):45–51.
- Paige GD, Sargent EW. Visually-induced adaptive plasticity in the human vestibulo-ocular reflex. *Exp Brain Res.* 1991; 84(1):25–34.
- Quarck G, Etard O, Darlot C, Denise P. Motion sickness susceptibility correlates with otolith- and canal-ocular reflexes. *Neuroreport.* 1998; 9(10):2253–2256.
- Reason JT. Motion sickness adaptation: a neural mismatch model. *J R Soc Med.* 1978; 71(11):819–829.
- Schwarz U, Henn V. Vestibular habituation in student pilots. *Aviat Space Environ Med.* 1989; 60:755–761.
- Shupak A, Kerem D, Gordon C, Spitzer O, Mendelowitz N, Melamed Y. Vestibulo-ocular reflex as a parameter of seasickness susceptibility. *Ann Otol Rhinol Laryngol.* 1990; 99(2):131–136.
- Syburra T, Huber S, Suter J. Motion sickness in pilot trainees: management to keep them flying. *Aviat Space Environ Med.* 2009; 80(10):887–889.
- Tanguy S, Quarck G, Etard O, Gauthier A, Denise P. Vestibulo-ocular reflex and motion sickness in figure skaters. *Eur J Appl Physiol.* 2008; 104(6):1031–1037.
- Tanguy SG, Quarck GM, Etard OM, Gauthier AF, Denise P. Are otolithic inputs interpreted better in figure skaters? *Neuroreport.* 2008; 19(5):565–568.
- Tucker GJ, Hand DJ, Godbey AL, Reinhardt RF. *Airsickness in student aviators.* Pensacola (FL, USA): Naval School of Aviation Medicine; 1965.
- Zuma e Maia FC, Mangabeira Albernaz PL, Cal R, Brusco TR, da Costa SS. Assessment of the vestibuloocular reflex in fighter pilots with the video head impulse test. *Acta Otolaryngol.* 2015; 135(7):681–684.
- Zwergal A, Rettinger N, Frenzel C, Dieterich M, Brandt T, Strupp M. A bucket of static vestibular function. *Neurology.* 2009; 72(19):1689–1692.