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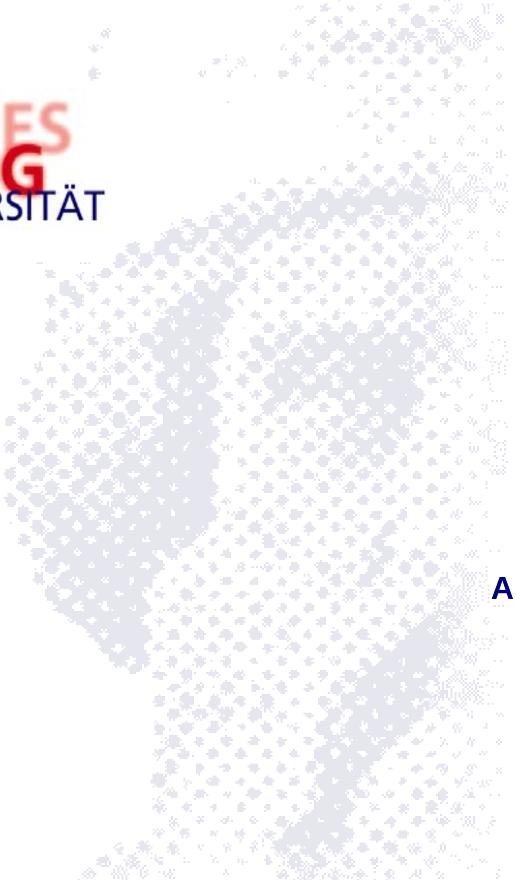

Psychologisches Institut
Allgemeine Experimentelle Psychologie
Staudingerweg 9
55128 Mainz
Telefon +49 6131 39-22481
Fax +49 6131 39-22480
Internet www.psych.uni-mainz.de/

Dipl.-Biol. Esther Brendel
Prof. Dr. Heiko Hecht
M.A. Heiko Brendel

Vestibular Expertise – A Combination of Increased Vestibular Sensitivity and Perceptual Countermeasures?

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Contents

Abstract

People adapt to environments that pose a particular challenge to the vestibular system, such as high-performance air craft, gymnastics, or artificial gravity. We explored 2 measures, namely gaze-holding ability and the subjective autokinetic effect to assess adaptive changes in vestibular experts, such as pilots and gymnasts. Novices and experts were exposed to rotations around a body-vertical axis for 30 seconds while fixating a head-stationary target. Then eye-movements and subjective magnitude ratings of the ensuing autokinetic effect were recorded in the dark. This short-term rotation affected experts more severely than novices with respect to their gaze-holding accuracy. At the same time, experts appeared to compensate the vestibular upset much better as witnessed by smaller subjective after-effects of rotation. Implications for a concept of vestibular expertise are discussed.

Keywords

gaze-holding, horizontal short-term rotation, vestibular adaptation, autokinetic effect

Vestibular Expertise – A Combination of Increased Vestibular Sensitivity and Perceptual Countermeasures?

We would like to convince the reader that a concept of vestibular expertise is helpful when trying to understand the sensory response to repeated vestibular conflict. Unlike in other domains of expertise, training that involves body rotations has aversive side-effects. An increase in vestibular sensitivity is functional for some aspects of the particular skills of a gymnast or a pilot whereas it is dysfunctional in others. That is, the gymnast should profit from a higher sensitivity of his vestibular system enabling him to balance more accurately than average people. At the same time such increased sensitivity may cause an undesired increase of illusory motion sensations, which could lead to more body sway or even vertigo as the result of a sequence of pirouettes. To understand how the functional and potentially dysfunctional aspects come to bear we tested novices and experts with a gaze-holding task, which was chosen to reflect vestibular sensitivity, and with a perceptual task, which was chosen to reflect a later processing stage. We first detail the concept of vestibular expertise and then report an experiment conducted with pilots and gymnasts on the one hand and untrained control subjects on the other hand.

We take the concept of vestibular expertise to be critical when it comes to unusual environments, such as microgravity or rotating environments. These pose a special challenge for the vestibular system and all aspects of sensorimotor coordination which incorporate vestibular information (Reschke et al., 1998). Typically, illusory sensations, reflexive eye-movements, and motion sickness occur (Young, Sienko, Lyne, Hecht, & Natapoff, 2003). Fortunately, adaptation to the new environment takes place. In astronauts, for instance, the microgravity environment entails adapation of perception, spatial orientation, and motor calibration, which is complete within three to four days (Parker, 1991). For rotating environments on the ground, Lackner and DiZio (2003) hold that the human motor system can fully adapt provided the appropriate adaptation paradigm is employed. A largely unanswered question is how well humans can maintain an adaptive state to more than one environment at the same time. Intermittent centrifugation, for example, may be a method of choice to keep astronauts healthy in space (Burton, 1988, 1994). However, changing from stationary microgravity to the spinning environment of artificial gravity every day requires quick and efficient change of adaptive states. Adaptation tends to be context specific (Shelhamer & Zee, 2003), however, little is known about the adaptive changes that ensue when experts are repeatedly subjected to two different environments. We hypothesize that the response to a brief period of centrifugation should differ systematically between novices and such experts.

The current paper focuses on vestibular aftereffects of angular acceleration on gaze-holding performance in the time window before an adaptive state is reached and after the post-rotatory nystagmus (non-compensatory vestibulo-ocular reflex (VOR)) has largely subsided. By focusing on this time window, we hoped to gain insight into the factors that contribute to sensory adaptation. For lack of published data on such aftereffects, the nature of our experiments was exploratory. We chose gaze-holding as our measure of vestibular function and – most importantly – we hypothesized that vestibular expertise, that is long-term exposure to unusual vestibular stimulation, mediates the effects of brief body rotations on gaze-holding performance. We surmised that gymnasts and pilots have acquired such expertise and that a look at their gaze-holding patterns might be revealing.

Methods

Design and Hypotheses

Pilot experiments suggested that a brief, passive 30-second body rotation around a vertical axis (yaw-axis) constitutes sufficient vestibular stimulation to interfere with a gaze-holding task administered 30 seconds afterwards. More general after-effects of vestibular stimulation have thus far not been explored within the context of vestibular expertise. Given the novelty of our research question, we have collected a number of measures that could reveal such effects if present. We pursued three main goals. First, we sought to establish that short-term rotation indeed has a negative effect on subsequent gaze-holding accuracy, even after the decay of post-rotatory nystagmus (PRN) and optokinetic after-nystagmus (OKAN). Second, expert performance should reveal whether vestibular expertise reduces the effect. Finally, eye-movements should be compared to the autokinetic effect. A between-groups design was chosen to compare the performance of subjects with vestibular training, namely pilots and gymnasts, to a control group.

Subjects

Subjects were recruited by advertisements on campus and from airfields around the city of Mainz. 71 subjects volunteered, the first 20 were used for piloting purposes. The other 51 were included in the experiment. As the gaze holding eye-movements were generally very small (withing 2 degrees of visual angle) artifacts resulting from blinks, or other noise were fairly likely. We decided to exclude all participants from analysis from whom more than ten percent of the gaze positions had not been successfully registered by the eye-tracker. Therefore only 24 subjects were included in data analysis.

We will discuss problems arising from the exclusion of the other subjects along with the interpretation of our results.

The expert group consisted of 15 subjects (9 male, mean age 33 years, SD of 15 years) who were private pilots (of gliders, motor gliders, ultralights, and airplanes with a maximum weight of one ton) and gymnasts (including trampoline jumpers, ballet dancers, and other athletes) with at least two years of experience in their respective vestibular training and with at least half an hour training per week. The control group consisted of nine subjects (4 male, mean age 31 years, SD of 14 years) who did not have any particular vestibular training exceeding that acquired in common sports like mountain-biking or ball-sports. None of the subjects reported any disease or anomaly of the vestibular system.

Subjects were kept naïve with respect to specific hypotheses but were familiarized with the setup and the procedure before they gave their informed consent. Subjects were also instructed to report any symptoms of motion sickness during the rotation and to abort the experiment if they preferred to do so. No subject chose to abandon the experiment. The measurements were taken in a dark room at the Johannes Gutenberg-University Mainz and in a comparable room at the airfield of Oppenheim (four of the experts).

Experimental Setup and Procedure

The setup of the experiment is illustrated in Figure 1. The procedure and the paradigm were varied in several pilot studies to maximize the effect of short-term vestibular stimulation on eye-movements while at the same time ensuring that PRN and OKAN had subsided to levels no longer detectable by our instruments. Figure 2 illustrates the timeline of the experiment applied in the main study, including the measuring points for eye-movement recordings. Gaze-holding performance was measured before vestibular stimulation, after vestibular stimulation, and after a resting period of five minutes.

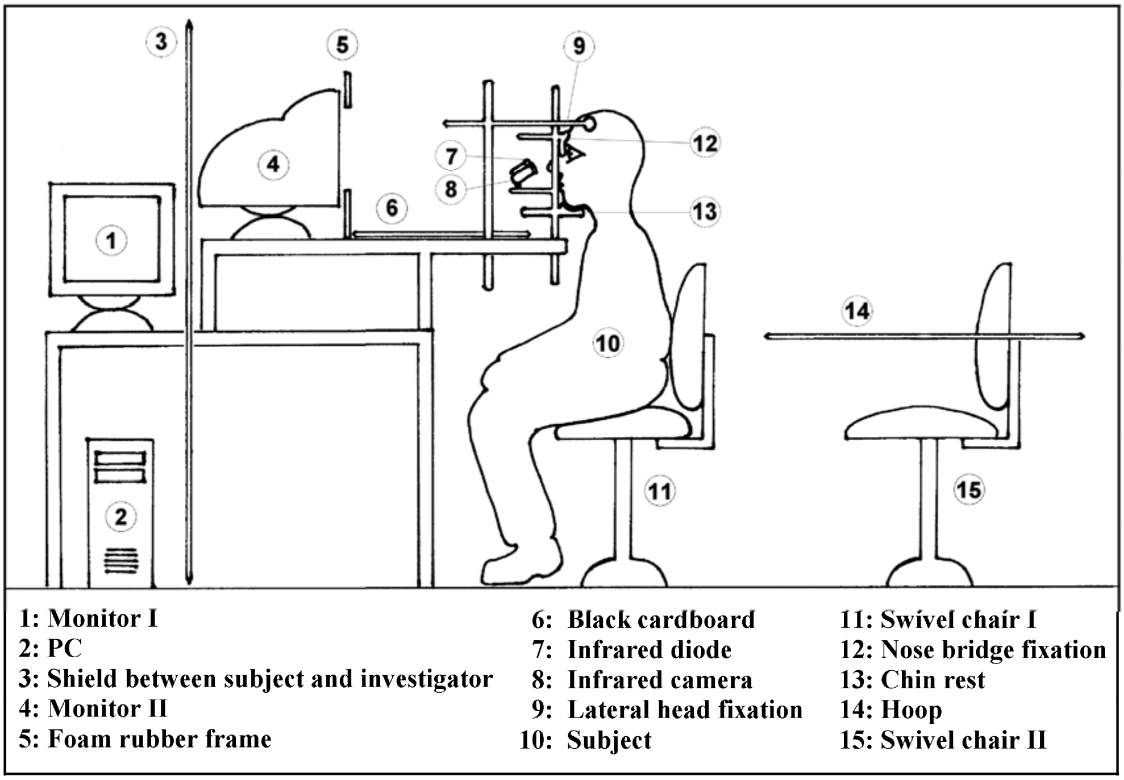
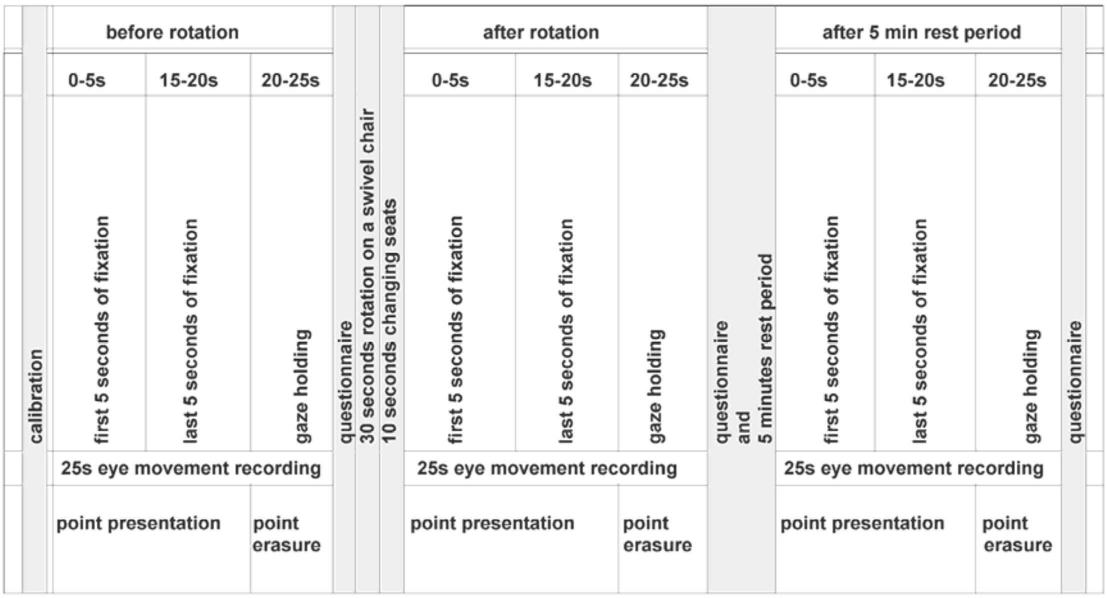


Figure 1. Schematic drawing of the experimental setup.



	before rotation						after rotation				after 5 min rest period			
	0-5s	15-20s	20-25s				0-5s	15-20s	20-25s		0-5s	15-20s	20-25s	
calibration	first 5 seconds of fixation	last 5 seconds of fixation	gaze holding	questionnaire	30 seconds rotation on a swivel chair	10 seconds changing seats	first 5 seconds of fixation	last 5 seconds of fixation	gaze holding	questionnaire and 5 minutes rest period	first 5 seconds of fixation	last 5 seconds of fixation	gaze holding	questionnaire
	25s eye movement recording						25s eye movement recording				25s eye movement recording			
	point presentation		point erasure				point presentation		point erasure		point presentation		point erasure	

Figure 2. Timeline of the main experiment.

Eye-movements were recorded in darkness by an infrared camera to avoid suppression of vestibularly induced eye-movements by visual periphery. Subjects were instructed to fix their gaze on a white dot on the screen for twenty seconds, and after deletion of the target to fixate the place where it had been for ten more seconds.

All subjects were told that the target presented on the screen was not actually moving, despite the frequent strong impression to the contrary. They were asked to estimate the maximum perceived target movement in centimeters. For that purpose, a grid was presented on the screen directly after the gaze-holding task was completed and before the lights were turned on. Then, subjects were given a questionnaire to report their estimates and to answer questions about vertigo, motion sickness, etc.

Before the second measurement, subjects were rotated for 30 seconds in the lit room while they were instructed to fixate their thumb held in front of them. As far as possible, subjects were not to react to the rotation. The rotational velocity of 180° per second was approximated by a mechanical metronome providing the rhythm in which the investigator had to grip the next quarter of the hoop attached to the swivel chair. The interval between rotation and the gaze-holding task was 30 seconds. First, subjects had to stand up and change seats after the rotation, then the room was darkened and the 20-second fixation task as well as the 10-second gaze-holding task followed.

Data processing and statistical analysis

ViewPoint EyeTracker® PC-60 Software from Arrington Research was used for data registration. The position of gaze was calculated using the vector between the pupil's centre and the corneal reflex (pupil-glint-vector) – a method reported to be quite resistant to small head movements (Joos, Rötting, & Velichkovsky, 2003; Teiwes, 1991). Recalibration of the eye-movement recording device immediately after rotation would have been too time-consuming. Thus, we computed eye-movement variability with respect to the centroid of the distribution of gaze positions for each recording: The mean of the x-coordinates and y-coordinates of all gaze positions during the last five seconds of the fixation task served as coordinates of the centroid. The average horizontal distance of the gaze positions from this centroid was calculated for the first five seconds of the gaze-holding task in the dark for each subject (eye-movement recordings). In addition, the horizontal component of the autokinetic effect during the fixation task was derived from the questionnaire ratings (autokinetic effect ratings).

Statistical analyses were carried out using SPSS 15.0.1 for Windows. Both of the above described measures, the eye-movement recordings and the autokinetic effect ratings were converted into degrees of visual angle to make them directly comparable and to use them as one combined dependent variable in a repeated-measures analysis of variance with the three-leveled factor *rotation* (before rotation, after rotation, after five minutes of rest), the two-leveled factor *measurement* (eye-movement recordings, autokinetic effect ratings), and the between-groups factor *expertise* (experts, novices). Similar analyses were performed with eye-movement recordings from other measuring points during the fixation task and with vertical eye-movements. In addition, separate repeated-measures analyses of variance were calculated for experts and novices to resolve the nature of the interactions found in the main analysis. Values of $p < 0.05$ were considered to indicate statistical significance.

Results

Eye-Movement Data

Figure 3 shows exemplary eye-movement plots. No clear PRN or OKAN was detected in the eye-movement recordings. Note, that head and eye-movements during the rotation were not allowed. During the pilot phase, those subjects who did not fixate their thumb during rotation and remained in their seats did show evidence of PRN. PRN was also found in those pilot trials where the fixation task preceding the gaze-holding task was shorter (see Figure 4). Thus, it appears that some form of velocity storage dumping had occurred in our experimental subject.

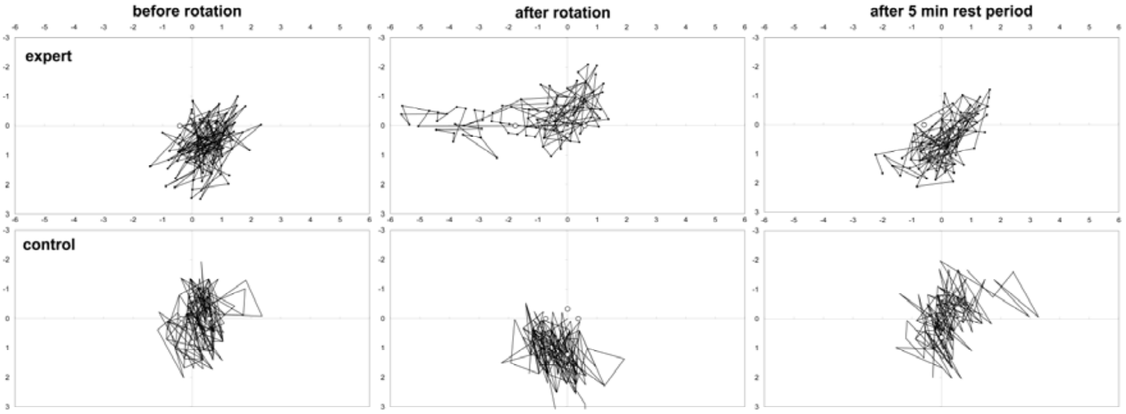


Figure 3. Exemplary eye-movement plots in degrees of visual angle showing the gaze positions during the first five seconds of the gaze-holding task. The white dots indicate the average distance of the gaze positions from the centroid (which was calculated from gaze positions registered during the preceding fixation task) in the respective direction.

As Figure 5 illustrates, the rotation had a significant effect on horizontal eye-movements only during the free gaze-holding task (see main findings below). None of the other measuring points of the procedure showed a significant main effect of rotation, neither did eye movements in the vertical direction at any measuring point.

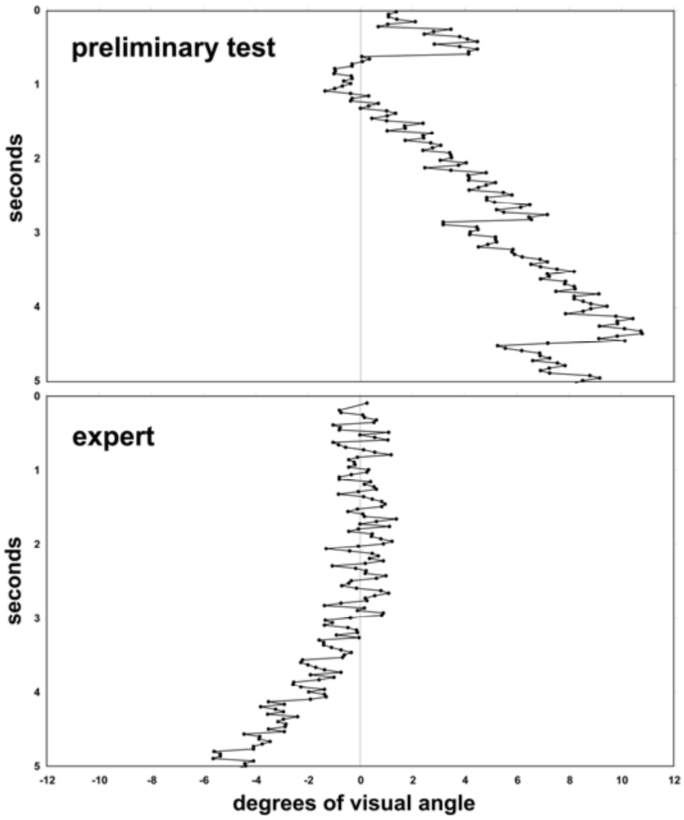


Figure 4. Exemplary horizontal gaze positions during gaze-holding in a preliminary test (showing PRN) and in the main study (showing a drift but no clear PRN). The complete horizontal and vertical gaze positions of this main study's expert are shown in Figure 3.

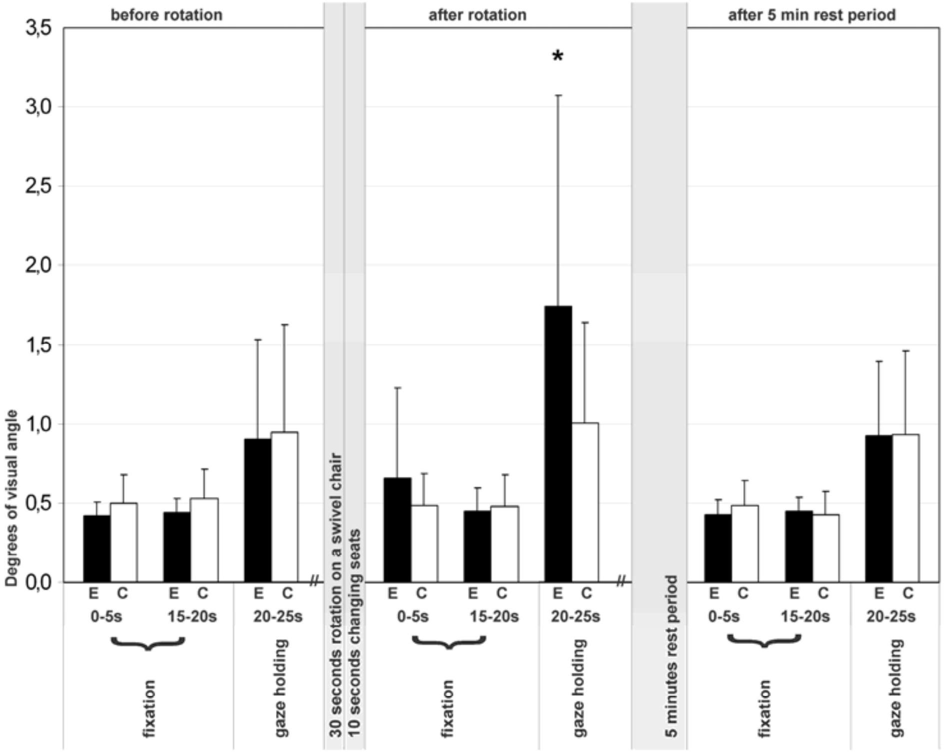


Figure 5. Gaze-holding variability as measured by the extent of horizontal eye-movements for experts (E) and for the novices of the control group (C). Error bars indicate standard error of the mean. The asterisk indicates a significant effect of *rotation* at $p < 0.05$.

Main Findings

The repeated-measures analysis of variance described above yielded a significant main effect of *rotation* on horizontal eye-movements and autokinetic effect ratings during the gaze-holding task ($F_{2,44}$ = 12.38, p = 0.001, Huynh-Feldt corrected, epsilon = 0.56) indicating that for all subjects the horizontal eye-movements were significantly wider after rotation (M = 1.46 degrees of visual angle, SD = 1.16) than before rotation (M = 0.92, SD = 0.63) or after five minutes of rest (M = 0.93, SD = 0.48). Accordingly, the autokinetic effect ratings were significantly greater after rotation (M = 3.79 degrees of visual angle, SD = 5.36) than before rotation (M = 0.19, SD = 0.49) or after five minutes of rest (M = 0.45, SD = 1.09). After rotation, more than half of the subjects in both groups perceived the fixation target as moving horizontally, whereas before rotation and after five minutes of rest that frequency was around twenty percent.

The main effect of *measurement* and the between-groups effect of *expertise* were both non-significant. However, there was a significant interaction of the factors *measurement* and *rotation* ($F_{1,22}$ = 12,22, p = 0.001, Huynh-Feldt corrected, epsilon = 0.56) as well as a three-way interaction of the factors *measurement, rotation,* and *expertise* ($F_{1,22}$ = 5.40, p = 0.023, Huynh-Feldt corrected, epsilon = 0.56), indicating that while rotation had little effect on the eye-movements in the control group, it affected their autokinetic effect. In contrast, rotation upset the experts' eye-movements; while the autokinetic effect was less pronounced than in the control group (see Figure 6).

Significance markings in Figure 6 are based on separate analyses of eye-movement recordings and autokinetic effect ratings for each group: *Rotation* had a significant negative effect on gaze-holding accuracy in experts ($F_{2,28}$ = 5.98, p = 0.017, Huynh-Feldt corrected, epsilon = 0.69) but not in the control group ($F_{2,16}$ = 0.06, p = 0.934, Huynh-Feldt corrected, epsilon = 0.92). In experts, the average horizontal distance of the gaze positions from the centroid was significantly greater after rotation (M = 1.74 degrees of visual angle, SD = 1.33) than before rotation (M = 0.90, SD = 0.63) or after five minutes of rest (M = 0.93, SD = 0.47). In the control group, the horizontal eye-movements showed no significant differences before rotation (M = 0.95, SD = 0.68), after rotation (M = 1.00, SD = 0.64) and after five minutes of rest (M = 0.93, SD = 0.53).

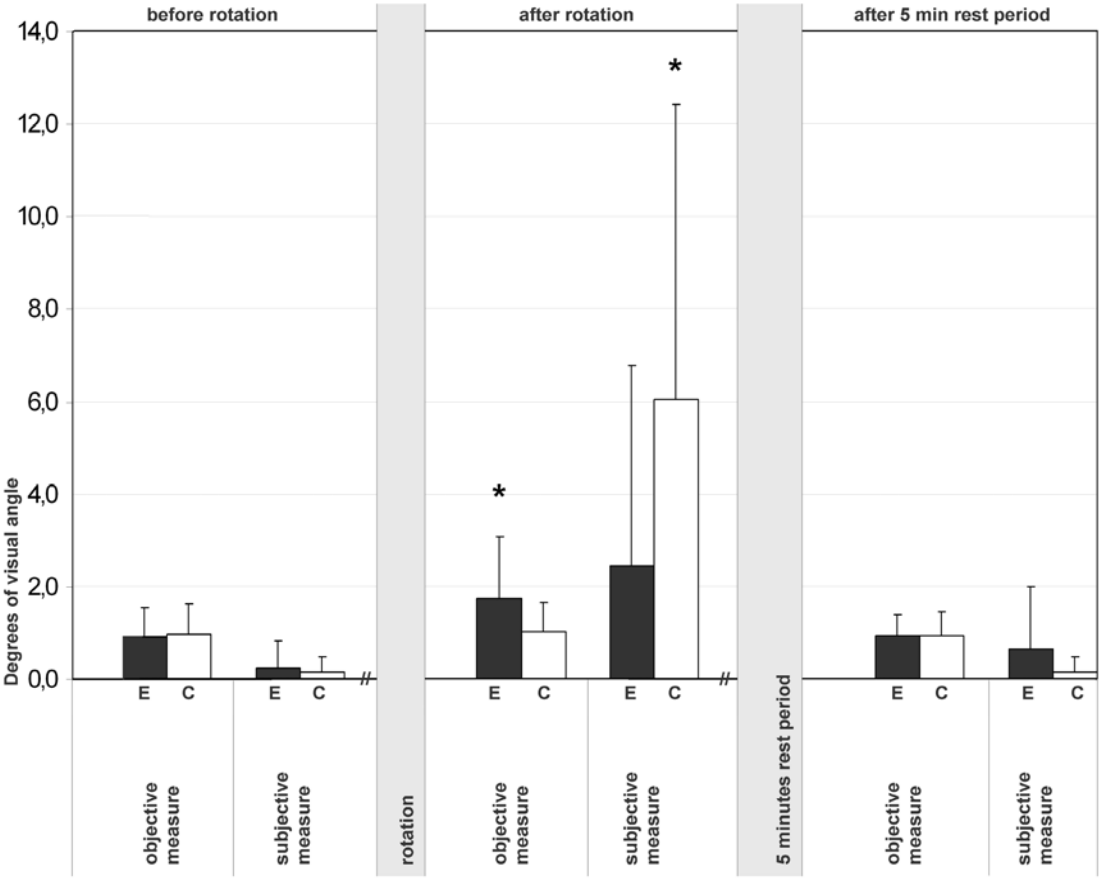


Figure 6. Gaze-holding variability and size of the autokinetic effect plotted for experts (E) and the control group (C). The asterisk indicates a significant effect of *rotation* at $p < 0.05$.

Figure 6 further illustrates an increased strength of the horizontal autokinetic effect after rotation in experts (before rotation: M = 0.22 degrees of visual angle, SD = 0.58, after rotation: M = 2.43, SD = 4.33, after five minutes of rest: M = 0.64, SD = 1.35) but this effect failed to reach significance ($F_{2,28} = 3.00$, p = 0.098, Huynh-Feldt corrected, epsilon = 0.58). In contrast, the autokinetic effect ratings of the control group were significantly increased after rotation ($F_{2,16} = 7.90$, p = 0.023, Huynh-Feldt corrected, epsilon = 0.50, before rotation: M = 0.15, SD = 0.30, after rotation: M = 6.05, SD = 6.36, after five minutes of rest: M = 0.15, SD = 0.30).

Questionnaire Results

Experts had significantly more years of experience than novices (minimum = 2, M = 13.7, SD = 11.3, $t_{21} = 2.68$, p = 0.014, two-sided) but not more hours of training per week devoted to their respective sports (minimum = 0.5, M = 4.2, SD = 4.0, $t_{20} = 1.83$, p = 0.083, two-sided). There were no significant differences between experts and controls regarding age, sex and visual defects. Vertigo after rotation tended to be less marked in experts than in the control group. The use of any conscious technique against vertigo was reported equally often. However, significantly more subjects of the control group (66.7 percent) reported continuing symptoms of motion sickness (13.3 percent, $t_{22} = 2.48$, p = 0.022, two-sided). Pilots reported a reduction of motion sickness sensitivity with growing expertise while gymnasts reported a slight increase. Subjective visual dominance did not differ between experts and controls, and it was correlated positively with the magnitude of the autokinetic effect (Spearman’s nonparametric correlation test: r = 0.478, p = 0.018, two-sided), but not with gaze-holding accuracy.

Discussion

Gaze-Holding Performance and Autokinetic Effect

Short-term rotation had a negative effect on gaze-holding accuracy. A 30-second yaw body rotation with fixation of a head-stationary target, followed by a 30-second pause during which observers reseated themselves and fixated a target, caused an increase in gaze-holding variability in the dark. This increase was measured after the typical post-rotatory nystagmus had subsided below measurable size. Post-rotational eye-movements during gaze-holding were particularly affected with respect to their horizontal variability, which was to be expected since observers had received rotation around the yaw axis.

Comparing gymnasts and pilots to the control group revealed a significant impact of rotation on the expert's gaze-holding accuracy while the effect on untrained subjects failed to reach significance. This indicates that novices were merely less sensitive, vestibularly speaking. The effect of rotation appeared to be similar in nature but more variable and smaller such that it failed to reach significance.

Independence of eye movements and motion sensations have been reported before for VOR adaptation and illusory sensations (Meliga, Hecht, Young, & Mast, 2005; Young et al., 2003). The autokinetic effect may reflect the processed vestibular signal after its integration with visual information. In both groups, the autokinetic effect was stronger after rotation. However, in experts this increase was non-significant and considerably smaller than in the control group. This is all the more remarkable since the gaze-holding accuracy of the experts had suffered more than that of the control group.

Our findings are based on 24 subjects whose eye-movement data passed our quite strict criterion of data quality (a maximum of ten percent of the positions of gaze was allowed not to be successfully recorded by the eye-tracker). If we relax this criterion and allow more cases for analysis, even though the data may not be reliable, the general tendencies of the results remain the same. However, the interaction of the factors *measurement* and *rotation* as well as the three-way interaction of the factors *measurement*, *rotation*, and *expertise* fail to reach significance in these analyses. The same happens if we just include all 49 cases with any eye-movement data available (there were two cases in which the eye-tracker registered no data at all in the interesting time window). It seems that the effects we found are rather robust. However, a replication of this study with a more reliable eye-movement tracking system with a higher resolution would be desirable.

In our study pilots and gymnasts exhibited a greater vestibular sensitivity, and at the same time they reacted more adequately to the upset caused by the brief 30-second rotation. It appears that with vestibular expertise the sensorimotor system learns to compensate for its enhanced sensitivity. This compensation is available to the perceptual visual system but not to the oculomotor system. The training of gymnasts and pilots typically calls for a down-weighting or deliberate discounting of proprioceptive cues (Berwanger, 1996; Zehl & Kratzer, 2000), which lends support to the compensation interpretation. Accordingly, subjects who gave themselves a higher subjective visual dominance rating experienced a stronger autokinetic effect in our study. However, no significant difference in subjective visual dominance was found between experts and the control group.

In the questionnaire, no correlation was found between the effect of rotation on the target's perception and the total time of training or flying. The compensation mechanism mentioned above may develop early in training. A related idea has been suggested by Ahn (2003) and Lee et al. (2004). All our subjects were told in advance that the fixation target was stationary. Since predictive mechanisms play a role in oculomotor control (Han et al., 2005), we might have received even more extreme results had we not told our subjects. A strengthened influence of such predictive mechanisms in experts could be one possible component of their sensorimotor compensation mechanism.

Velocity Storage or Beyond?

In our preliminary tests, a free gaze-holding task without visual feedback followed each fixation task, during which visual suppression of PRN or OKAN was no longer possible. It became apparent that visually suppressed nystagmus resurfaces when the interval between the end of rotation and the eye-movement recording was twenty seconds or less, even though considerable active movement of the subject – including movements of the head – and full-field earth-stationary visual stimulation had taken place. Both have been reported to rapidly decrease the duration of velocity storage, which is responsible for OKAN and PRN (Benson, 1974, p. 294; Lafortune, Ireland, & Jell, 1990; Leigh & Zee, 1999, p. 36). Otherwise, time constants of five to almost 50 seconds have been reported for OKAN (Leigh & Zee, 1999, p. 47). We additionally applied visual fixation of a head-stationary target during rotation, which suppresses immediate VOR (Waespe & Henn, 1987, p. 109) and reduces the charging of the velocity storage mechanism. We also lengthened the interval between rotation and eye-movement recording to 30 seconds by increasing the duration of the fixation task to twenty seconds. In effect, no further PRN or OKAN could be detected with our equipment during the following free gaze-holding task (see Figure 4). We cannot rule out with certainty, however, that some higher-level aspect of velocity storage may be responsible for the gaze-holding effects that we found. After all, velocity storage is an important function for the visual system and may even serve to estimate the head position relative to gravity (Green & Angelaki, 2003). Thus, this neural integrator may be implemented at several levels of the sensorimotor system.

Vestibular Expertise

All subjects in the expert group had at least two years of training in their respective fields. Their total hours of experience lay well within the range resulting in adaptive VOR changes, as for instance reported for fighter pilots by Lee et al. (2004). These authors found no correlation between the amount of experience and the effect of rotation on the eye-movements. The same is true for studies by Ahn (2003). The results presented here are in agreement with Lee et al. (2004) who found that rotation had a larger effect on oculomotor functioning in pilots compared to non-pilots. Our gymnasts seemed to be affected in the same manner. The gaze-holding task thus appears to reflect a general aspect of vestibular expertise that is very different, in a way more down-stream, than what can be measured by immediate PRN. Such studies typically found that expertise decreases the effect of rotation on PRN, for instance in ballet dancers and gymnasts compared to untrained subjects (Osterhammel et al., 1968, as cited in Ahn et al., 2000; Rossberg, 1971). Thus, the mechanism which produces the post-rotational effect measured in this study seems to be qualitatively different from the velocity storage mechanism responsible for producing PRN and OKAN. Moreover, both mechanisms are influenced differently by vestibular training. Before drawing this conclusion, however, a study with trained and untrained subjects should simultaneously investigate both the PRN and gaze-holding combined with other cortical after-effects of rotation.

The vestibular expertise acquired by our subjects seemed to be limited to sensorimotor functioning. We found no significant correlations between the effects of rotation on eye-movements or the autokinetic effect and other factors such as age, sex, alertness, current general health, stress, a full stomach, the dominant eye, visual defects, or the sensation of vertigo produced by the swivel chair. Similarly, Lee et al. (2004) found no relationship between VOR changes and age, height, and weight in their study with fighter pilots.

The finding that gymnasts, in contrast to pilots, did not report a decrease of motion sickness sensitivity as a function of expertise is consistent with the notion of vestibular sensitization due to training. However, it contradicts findings by Bouyer and Watt (1996) whose subjects showed a complete loss of motion sickness sensitivity after several days of training in torso rotation. Nevertheless, they found no change in the daily VOR gain habituation corresponding to the change in motion sickness sensitivity. Vestibular expertise acquired by pilots and gymnasts may be qualitatively different although they performed comparably in our study.

Conclusion

This study has shown that short-term rotation about an earth-vertical axis had a negative effect on gaze-holding performance even after the decay of PRN and OKAN. Experts with special vestibular training showed a decrease in gaze-holding accuracy, whereas compared to control subjects they experienced smaller increases in the autokinetic effect during post-rotational fixation and less sustained motion sickness symptoms. Note that the magnitude of the autokinetic effect by far exceeded the magnitude of the eye-movements with which it may be correlated. Thus, the effect implicates mechanisms beyond the VOR (for a recent review see Wade and Heller, 2003).

In sum, vestibular expertise appears to be a two-layered process that deserves further exploration. During the acquisition of such expertise the immediate vestibular afferents become more sensitive with training, and at the same time higher-order processes counteract or reduce those side effects that interfere with perceiving and acting. The time-course of this process and its consequences for the different aspects of visuomotor functioning remain to be explored.

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Author Note

Esther S. Brendel, Institute of Zoology, Department of Biology, Johannes Gutenberg-University of Mainz, Germany; Heiko Hecht, Department of General Experimental Psychology, Psychological Institute, Johannes Gutenberg-University of Mainz, Germany; Heiko Brendel, Institute of Anthropology, Department of Biology, Johannes Gutenberg-University of Mainz, Germany.

Esther S. Brendel is now at the Department of General Experimental Psychology, Psychological Institute, Johannes Gutenberg-University of Mainz, Germany; Heiko Brendel is now at the Department of History and Cultural Studies, Johannes Gutenberg-University of Mainz, Germany.

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Correspondence concerning this article should be addressed to Esther S. Brendel, Department of General Experimental Psychology, Psychological Institute, Johannes Gutenberg-Universität, Staudingerweg 9, D-55099 Mainz, Germany. E-mail: ebrendel@uni-mainz.de