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Effects of age, viewing distance and target complexity on static ocular counterroll

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ABSTRACT

The ocular counterroll (OCR) reflex generates partially compensatory torsional eye movements during static head roll tilt. We assessed the influence of age, viewing distance and target complexity on the OCR across the age span (13–63 years; $n = 47$), by recording eye movements during head-on-body roll tilt ($0 \pm 40^\circ$ in 5° steps) while subjects viewed simple vs. complex targets at 0.33 and 1 m. We found that subjects ≥ 31 years had lower gains than those ≤ 30 years, but only for far targets. Consistent with prior reports, far targets elicited higher OCR gains than near targets, and target complexity had no effect on gains, suggesting that visual input is primarily used to maintain vergence during OCR.

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1. Introduction

In humans, when the head is tilted about the naso-occipital axis, a partially compensatory torsional eye movement occurs in the direction opposite the head tilt. This torsional vestibulo-ocular reflex (VOR), termed ocular counterroll (OCR), serves to stabilize retinal images in space during lateral head tilt. OCR is classified into two types: dynamic and static. Dynamic OCR is mediated by both the semicircular canals and otolith organs during active roll head movements (Groen, Bos, & de Graaf, 1999; Morrow & Sharpe, 1993; Schmid-Priscoveanu, Straumann, & Kori, 2000) and compensates for about 40–70% of dynamic head roll in humans (Bergamin & Straumann, 2001; Collewijn, Van der Steen, Ferman, & Jansen, 1985; Kori, Schmid-Priscoveanu, & Straumann, 2001; Morrow & Sharpe, 1993). Static OCR, on the other hand, is mediated by the otolith organs during sustained head tilt as a response to change in the vector of gravitational acceleration, and compensates for about 3–29% of static head roll amplitude in humans (Averbuch-Heller et al., 1997; Bockisch & Haslwanter, 2001; Collewijn et al., 1985; Hamasaki, Hasebe, & Ohtsuki, 2005; Kingma, Stegeman, & Vogels, 1997; Klier & Crawford, 1998; Kori et al., 2001; Lichtenberg, Young, & Arrott, 1982; Markham & Diamond, 2001; Ooi, Cornell, Curthoys, Burgess, & MacDougall, 2004; Schmid-Priscoveanu,

Straumann, Bohmer, & Obzina, 1999; Schworm, Ygge, Pansell, & Lennerstrand, 2002; Wong & Sharpe, 2005; Zingler, Kryvoshey, Schneider, Glasauer, Brandt, & Strupp, 2006). Static OCR arises mainly from stimulation of the utricles, although some argue that saccular (De Graaf, Bos, & Groen, 1996) and somatosensory (Krejcova, Highstein, & Cohen, 1971) inputs might also play a minor role.

The rotational and linear VOR are known to be influenced by age (Baloh, Enrietto, Jacobson, & Lin, 2001; Baloh, Jacobson, & Socotch, 1993; Brzezny, Glasauer, Bayer, Siebold, & Buttner, 2003; Demer, 1994; Paige, 1992; Peterka, Black, & Schoenhoff, 1990a, 1990b; Tian, Crane, Wiest, & Demer, 2002; Wall, Black, & Hunt, 1984), suggesting that both the canal-mediated and otolith-mediated VOR responses are susceptible to age-related degenerative changes in the peripheral and central vestibular system (Bergstrom, 1973; Brody, 1976; Engstrom, Bergstrom, & Rosenhall, 1974; Johnsson, 1971; Lopez, Honrubia, & Baloh, 1997; Richter, 1980; Rosenhall, 1973; Sloane, Baloh, & Honrubia, 1989; Torvik, Torp, & Lindboe, 1986). A previous study (Furman & Schor, 2003) on static OCR responses (which we refer to as OCR in the rest of this paper), however, did not demonstrate any changes in OCR gain in elderly (>65 years) subjects, as compared to young subjects (<30 years). We hypothesized that the effects of aging on OCR might be dependent on the testing condition, similar to the observation that lower rotational VOR gain in the elderly can only be detected at high head velocities and low frequencies of stimulation (Baloh et al., 1993; Paige, 1992). The first goal of this study was to investigate the influence of age on OCR responses under different testing conditions across the age span.

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Previous studies on static OCR using different methods have produced results that are variable and sometimes conflicting, with gain values ranging from 0.03 to 0.29 (Averbuch-Heller et al., 1997; Bockisch & Haslwanter, 2001; Collewijn et al., 1985; Hamasaki et al., 2005; Kingma et al., 1997; Klier & Crawford, 1998; Kori et al., 2001; Lichtenberg et al., 1982; Markham & Diamond, 2001; Ooi et al., 2004; Schmid-Priscoveanu et al., 1999; Schworm et al., 2002; Wong & Sharpe, 2005; Zingler et al., 2006). Some studies even challenged the presence of a static compensatory OCR (Jampel, 2002; Jampel & Shi, 2002). We hypothesized that these disparate observations might result from the use of visual targets with differing characteristics at different viewing distances, and generally small sample sizes (mean = 9; range = 2–19), which could be an issue when the reflex being measured exhibits relatively high inter-subject variability. The second goal of this study was to compare OCR responses during viewing of well-controlled targets (simple vs. complex) at different viewing distances (near vs. far) in a very large sample of normal subjects ($n = 47$).

2. Methods

2.1. Subjects

Forty-seven healthy subjects with normal vision (mean age: 33 ± 14 years; median age: 30 years; age range: 13–63 years; 32 females), without any vestibular, neurologic or eye diseases, participated in this study. The number of subjects by decade was 9 (10–20 years), 14 (21–30 years), 11 (31–40 years), 6 (41–50 years), 7 (51–60 years), and 1 (61–70 years). The research protocol was approved by the Research Ethics Board of the Hospital for Sick Children in Toronto and adhered to the tenets of the Declaration of Helsinki. Informed consent was obtained from all subjects.

2.2. Visual stimuli

Two earth-fixed wide-field visual stimuli were used: (1) a simple target consisting of a small (1.1°) central red fixation cross against a uniform gray background; and (2) a complex target consisting of the same fixation cross against a wide field grid pattern with black horizontal and vertical lines. Both the simple and complex targets subtended 42° horizontally and 28° vertically. For the simple target, the only structured portion visible within the field of view of the eye tracker mask (described below) was the fixation cross. For the complex target the grid pattern filled the area visible within the tracker mask field of view. Each stimulus was presented at far (1.0 m) and near (0.33 m) viewing distances. The simple and complex stimuli were scaled so that they subtended the same visual angle during far and near viewing conditions. All experiments were performed during binocular viewing.

2.3. Recording of eye movements

A commercially available infrared video-based system was used (3D-VOG, Senso Motoric Instruments GmbH, Teltow, Germany) to measure 3D eye movements (horizontal, vertical, and torsional). Eye positions were acquired for both eyes simultaneously by two miniature charge-coupled device (CCD) infrared-illuminated video cameras mounted on a pair of goggles. Three infrared LEDs at a wavelength of 920 nm and an intensity of $<1 \text{ mW/cm}^2$ illuminated each eye. The sampling frequency was 60 Hz for all three axes. The monochrome image was digitized with 256 gray levels (8-bit) for image processing. The spatial resolution of the system for ocular torsion was approximately 0.1° . Maximum deviation of torsion linearity was $\pm 1.4\%$ at a range of $\pm 20^\circ$ (Schworm et al., 2002). Trials in which horizontal or vertical eye movements exceeded $\pm 20^\circ$, and

portions of records containing blinks were excluded from further analysis.

Goggle slippage was prevented by coupling the goggles firmly to the subject's head using an elastic strap fitted tightly around the back of the head, as well as the use of a bite bar made of disposable balsa wood attached to the nasal bridge of the goggles.

2.4. Head roll tilt paradigms

During initial set-up, care was taken to adjust the height of the testing chair relative to the target for each subject in order to avoid any significant head pitch, and to ensure that gaze was in the qualitative straight-ahead direction. Before each experiment, a binocular horizontal and vertical calibration was performed using a fixation cross (visual angle = 1.1°) at nine locations: 0° , $\pm 10^\circ$ and $\pm 15^\circ$ horizontally and vertically. At the beginning of the experiment, the subject was instructed to maintain fixation on the target (simple or complex target) while sitting with the head in an upright position. This allowed us to obtain reference images of the iris of each eye for comparison with images taken subsequently at each head tilt position for the computation of torsion. After the reference images were obtained, the subject's head was tilted about the naso-occipital axis in 5° steps over a range of 40° toward either the right (clockwise, CW i.e., positive) or left shoulder (counterclockwise, CCW i.e., negative) and then back to the upright position, followed by the same stepwise head tilt in the other direction. The initial head tilt direction was randomized across conditions (simple vs. complex targets, far vs. near viewing) and across subjects. At each head tilt position, the head was held stationary for at least 15 s to allow the canal-mediated dynamic OCR to subside (the dynamic torsional time constant ≈ 6 s) (Hamasaki et al., 2005; Moore, Clement, Raphan, & Cohen, 2001). Head movements were controlled by placement of the experimenter's hands on each parietal area of the subject's skull. Head roll and pitch angles were monitored continuously using the read-out of the inertial sensor mounted on the eye tracker mask, which was displayed on the eye tracker monitor. Head position was typically maintained within $\pm 1^\circ$ of the desired final position. If the subject's head moved outside of this range during a trial, the trial was repeated for that position. The subject was instructed to maintain fixation on the target throughout the experiment. The total duration of one tilt series in one direction was approximately 5 min, and there were eight series in total.

2.5. Data analysis

Horizontal, vertical, and torsional eye positions for each eye were recorded in pixels, converted from pixels to degrees of eye rotation, and then exported. Positive directions for horizontal, vertical and torsional angles were defined as right, up, and clockwise, respectively, all from the subject's point of view. Horizontal and vertical eye positions were computed using a black-pupil technique, by calculating the geometric center of the lowest infrared reflection (i.e., center of pupil). Ocular torsion was computed by calculating the angular displacement of a user-defined iris segment selected from the reference image. This was achieved by measuring the luminance levels of this user-defined iris segment, which were then cross-correlated to that of the same iris segment for each consecutive video frame (every 16.67 ms) throughout the recording. The concordance between the user-defined iris segment and that of the same iris segment of each consecutive frame was computed and was termed "torsion quality", which could range between 0.0 (no concordance) and 1.0 (complete concordance). Although data with a torsion quality ≥ 0.3 are considered reliable by the manufacturer of the system, we included only data with torsion quality ≥ 0.8 in our analysis to ensure that we analyzed only the most ro-

bust torsional data. All eye movements were recorded in Fick coordinates, and “false torsion” associated with Fick geometry was calculated using the following formula:

$$T = T_{\text{Fick}} - [\text{atan}\{\tan(H_{\text{Fick}}/2) * \tan(V_{\text{Fick}}/2)\} * 2]$$

where T is false torsion, and T_{Fick} , H_{Fick} , and V_{Fick} are torsional, horizontal, and vertical eye positions measured in Fick coordinates, respectively.

For each subject, the head was tilted in the roll plane to the desired angle. Once the desired head position was attained, the head was held stationary for 15 s. While eye movements were recorded continuously throughout the experiment, we analyzed a 1 s epoch (constituting 60 samples at a sampling frequency of 60 Hz) of this continuous record at the end of each 15 s tilt period. This was to ensure that the dynamic VOR canal signal had decayed and the static torsional eye responses had stabilized. These values were then averaged across subjects to get a group mean response. To compare OCR responses across different conditions, changes in mean torsional eye position were plotted as a function of head position ($0 \pm 40^\circ$ in 5° steps) and five-parameter sigmoids were fitted. Mean OCR gains were calculated by computing the group means at each head tilt position, followed by performing a five parameter sigmoidal fit, and taking the derivative of the fitted function. The sigmoidal fits were excellent, with r^2 values consistently >0.99 .

To assess the effects of age (≥ 31 years vs. ≤ 30 years), target complexity (simple vs. complex), viewing distance (1 m vs. 0.33 m), and head tilt direction (CW vs. CCW), on OCR gains, differences were tested by analysis of variance (ANOVA) with age as a factor, and with target complexity, viewing distance, head tilt direction, and eye as repeated measures. Significance level was set at $p < 0.05$. Any significant differences were investigated further by post-hoc Tukey HSD tests. OCR responses did not differ between right vs. left eye; accordingly, we pooled the data from both eyes for all subsequent analyses.

3. Results

A representative tracing of the eye torsional position during step-wise counter-clockwise head tilt is shown in Fig. 1. Consistent with previous studies (Collewyn et al., 1985; Pansell, Schworm, & Ygge, 2003), following the initiation of a head tilt, a rapid torsional eye movement, that is a torsional peak (Pansell et al., 2003), occurred in the same direction as the head movement. This was followed by a few nystagmus beats that were superimposed on the

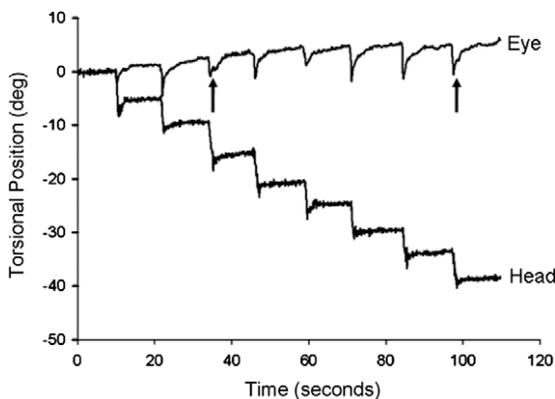


Fig. 1. Representative tracings of counter-clockwise head tilt (i.e., head roll toward the left shoulder) from 0° to -40° , and the corresponding partially compensatory torsional eye movements in a typical subject. Positive y-axis values = clockwise; negative y-axis values = counter-clockwise. Arrows indicate nystagmus beats that were superimposed on the torsional peak, with slow phases directed in the opposite direction to the head tilt.

torsional peak, with compensatory slow phases directed in the direction opposite to the head tilt. The eye then came to a partially compensatory torsional position after the head maintained a static tilt position for at least 15 s (Collewyn et al., 1985; Pansell et al., 2003).

All subjects exhibited partially compensatory OCR responses that varied with head-tilt angle. The relationship between head-tilt angle and torsional eye position across all subjects during far and near viewing is shown in Fig. 2. Over the head tilt range of 0° to about $\pm 15^\circ$, torsional eye position varied approximately linearly with head-tilt angle, however, as the head-tilt angle increased torsional eye responses became increasingly saturated. This response saturation was well-captured by five parameter sigmoidal fits, with $r^2 = 0.9997$ for far viewing and 0.9989 for near viewing.

The amplitude of torsional eye movements during far viewing was significantly higher than those during near viewing across all head-tilt angles (Fig. 2). Mean OCR gains (mean \pm SEM) were larger for far (-0.170 ± 0.007) than for near (-0.136 ± 0.006) viewing ($p < 0.001$; Fig. 3). Peak OCR gains occurred by the smallest head-tilt angle tested for both far and near targets. For far targets, mean group OCR gain was -0.280 at 5° head tilt, which decreased linearly as the head-tilt angle increased and was reduced to -0.170 at 40° head tilt. Similar patterns were also observed for near targets; where the mean group OCR gain peaked by 5° of head tilt with a gain of -0.218 , which then decreased linearly to -0.141 at 40° head tilt (Fig. 3).

Subjects were divided into two groups by a median split based on age (i.e., 30 years old) to assess the effects of aging on OCR. The main effect of age on OCR gain was not significant ($p = 0.086$). There was, however, a significant interaction between age and viewing distance, with subjects 31 years and older exhibiting low-

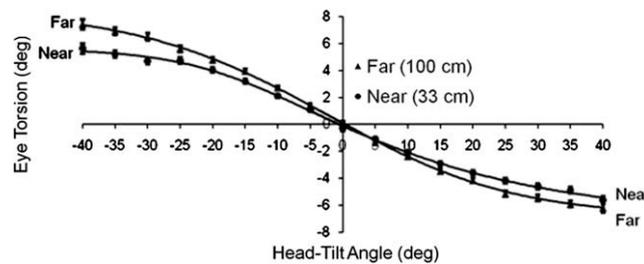


Fig. 2. Sigmoidal relationship between mean torsional eye movement and head-tilt angle during far vs. near viewing. Each data point represents the group mean torsional response for all 47 subjects for a given head-tilt angle. Error bars represent the standard error of the mean.

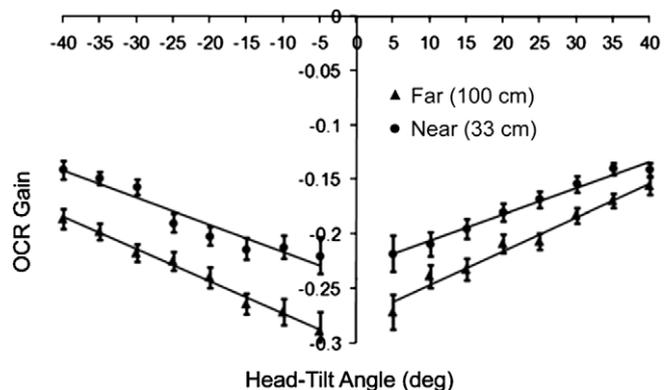


Fig. 3. Linear relationship between mean OCR gain and head-tilt angles for both far and near targets across all 47 subjects. Error bars represent the standard error of the mean.

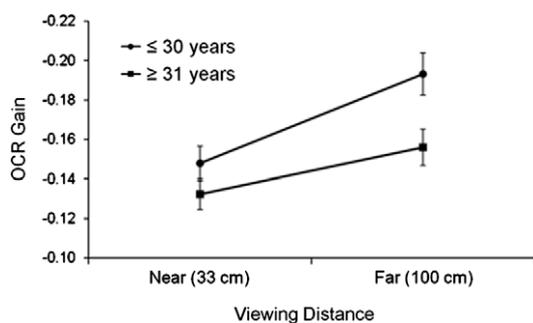


Fig. 4. Interaction of age and viewing distance on OCR gain. During viewing of a far target, older subjects (≥ 31 years) exhibited significantly lower OCR gain than younger subjects (≤ 30 years). This difference, however, was not significant during viewing of a near target. Error bars represent standard error of the mean.

er OCR gains (-0.156 ± 0.010) than those aged 30 and under (-0.193 ± 0.012 ; $p < 0.024$) during far viewing (Fig. 4).

OCR responses were symmetrical during CW and CCW head tilt (i.e., $\leq 1^\circ$ difference in ocular torsion) in 79% of subjects. Seventeen percent of subjects had greater responses during CW head tilt, while 6% had greater responses during CCW head tilt. The mean gain difference (i.e., CW minus CCW head-tilt gain) across all 47 subjects was -0.030 ± 0.007 . There was no significant difference in OCR gains between viewing of a simple (-0.180 ± 0.008) vs. complex target (-0.193 ± 0.007 ; $p = 0.061$).

4. Discussion

Vestibular function is known to be influenced by age, with lower rotational VOR gain and increased phase lead in the elderly (Baloh et al., 1993, 2001; Paige, 1992; Peterka et al., 1990a, 1990b), especially during stimulation at low frequencies and high rotation speeds. Older subjects also have more difficulty visually suppressing the modulation component during off-vertical axis rotation (Furman & Redfern, 2001a, 2001b), as well as prolonged latency and reduced sensitivity during linear VOR (Tian et al., 2002), indicating that aging also affects the otolith-ocular reflex. Only one previous study (Furman & Schor, 2003) has examined the effects of senescence on OCR; however, they reported no difference in OCR gain between young (< 30 years; $n = 8$) and elderly (> 65 years; $n = 10$) subjects, when complex targets were presented at 44 cm. In this study, we investigated the OCR in 47 subjects across the age span (19–63 years), and found that although the main effect of age was not significant, there was a significant interaction between age and viewing distance, with subjects 31 years and older exhibiting lower OCR gains ($\sim 19\%$ less than subjects aged 30 years and under) during far viewing at 1 m (but not at 33 cm). Taken together, our findings and that of others (Furman & Schor, 2003) suggest that the effects of aging on OCR responses are most prominent when viewing a far target (at 1 m). It is noteworthy, and perhaps a little surprising, that this OCR gain reduction becomes manifest at a relatively young age (31 years and over); but this could be explained by the progressive loss of primary and secondary vestibular neurons that starts at about age 40 years (Engstrom et al., 1974; Lopez et al., 1997).

Our study revealed that compensatory ocular torsion is dependent strongly on the amount of head tilt. The maximum OCR gain we observed was $\sim 28\%$ at 5° head tilt. As the head-tilt angle increased, OCR gains decreased progressively such that at 40° head tilt, gain was only 17% (for far targets). Saturation of static OCR as head-tilt angle increases has been suggested by previous studies (Bockisch & Haslwanter, 2001; Hamasaki et al., 2005; Kingma et al., 1997; Ooi et al., 2004; Schworm et al., 2002). Our study extends previous findings by showing that a robust sigmoidal relationship

exists between compensatory ocular torsion and head-tilt angle within the tested range of head roll tilt during passive head-on-body tilt. Whether this saturation of OCR response is due to the limited torsional range inherent in the ocular motor system, or whether it simply reflects the vestigial nature of the OCR reflex in frontal-eyed animals, remains to be elucidated.

We found that while converging on the near targets (33 cm), subjects displayed a significant reduction in OCR ($\sim 17\%$ compared to far targets at 1 m). This gain reduction is consistent with that reported by others (Ooi et al., 2004), who used a head-fixed target during en-bloc tilting of the head and body. By comparing the OCR gains during symmetric and asymmetric vergence, they demonstrated that this OCR reduction is mediated by convergence command, rather than horizontal eye position (Ooi et al., 2004). It has been proposed that lower OCR gains elicited by near targets may reflect a mechanism to minimize the vertical disparity associated with torsion during convergence, thus optimizing stereopsis (Misslisch, Tweed, & Hess, 2001). In this study, we used a different target and tilt protocol than Ooi et al. (2004), and confirmed that OCR gain reduction could also be observed with an earth-fixed target during passive head-on-body tilt.

Another interesting result we found in the present study is that about 20% of subjects exhibited gain asymmetry when they tilted their heads CW vs. CCW. Although most previous studies (Averbuch-Heller et al., 1997; Bockisch & Haslwanter, 2001; Collewijn et al., 1985; Klier & Crawford, 1998; Kori et al., 2001; Ooi et al., 2004; Schmid-Priscoveanu et al., 1999; Wong & Sharpe, 2005; Zingler et al., 2006) using small sample sizes did not report any asymmetry, asymmetry between tilt directions, as well as ocular torsional disconjugacy have been reported during static OCR (Markham & Diamond, 2001) and during parabolic flight when gravitational force changed (Markham, Diamond, & Stoller, 2000). Some investigators have attributed the asymmetry to hysteresis, both for static (Schworm et al., 2002) and dynamic (Palla, Bockisch, Bergamin, & Straumann, 2006) OCR. Interaural linear VOR, another otolith-mediated reflex, has also been shown to be asymmetric in 50% of subjects tested ($n = 6$) (Ramat & Zee, 2003). It is plausible that this asymmetry/disconjugacy may arise from intrinsic asymmetry in the otolith receptors (e.g., otoconia mass) on each side of the head. Because a small tilt asymmetry exists in 20% of the normal population, this asymmetry should be taken into consideration when using OCR as a clinical laboratory tool to evaluate patients with peripheral or central vestibular disorders.

Our study confirmed the findings from previous studies (Collewijn et al., 1985; Krejcová et al., 1971; Markham & Diamond, 2001; Schworm et al., 2002) that target complexity plays little role in OCR gains. Collewijn and coworkers (1985) showed minimal change in OCR gains between viewing a simple fixation spot and a wide-field checkerboard in two subjects. Schworm and co-workers (2002) also evaluated the effects of target complexity. Although their stimulus was only described qualitatively (a photograph of a Swedish historical castle) and the sample size was small ($n = 5$), they also concluded that visual stimulation contributes little to the OCR. In this study, we used a well-defined visual stimulus with strong vertical and horizontal spatial cues in a large number of subjects, and found that target complexity did not exert significant influence on OCR gains. Taken together, it is reasonable to conclude that the OCR response is primarily driven by the otoliths, and that the role of vision in the OCR is primarily to maintain vergence.

In summary, the present study demonstrated that OCR responses begin to decrease after 30 years of age, and this decrease is dependent upon the viewing distance. On the basis of this finding, we would predict a larger reduction in OCR gains in the elderly. Further studies on elderly subjects (≥ 65 years) using a far target (at 1 m) would further clarify the effects of senescence on the OCR.

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References

- Averbuch-Heller, L., Rottach, K. G., Zivotofsky, A. Z., Suarez, J. I., Pettee, A. D., Remler, B. F., et al. (1997). Torsional eye movements in patients with skew deviation and spasmodic torticollis: Responses to static and dynamic head roll. *Neurology*, *48*, 506–514.
- Baloh, R. W., Enrietto, J., Jacobson, K. M., & Lin, A. (2001). Age-related changes in torsional vestibular function: A longitudinal study. *Annals of the New York Academy of Sciences*, *942*, 210–219.
- Baloh, R. W., Jacobson, K. M., & Socotch, T. M. (1993). The effect of aging on visual-vestibuloocular responses. *Experimental Brain Research*, *95*(3), 509–516.
- Bergamin, O., & Straumann, D. (2001). Three-dimensional binocular kinematics of torsional vestibular nystagmus during convergence on head-fixed targets in humans. *Journal of Neurophysiology*, *86*(1), 113–122.
- Bergstrom, B. (1973). Morphology of the vestibular nerve. II. The number of myelinated vestibular nerve fibers in man at various ages. *Acta Oto-Laryngologica*, *76*(2), 173–179.
- Bockisch, C. J., & Haslwanter, T. (2001). Three-dimensional eye position during static roll and pitch in humans. *Vision Research*, *41*(16), 2127–2137.
- Brody, H. (1976). An examination of cerebral cortex and brainstem aging. In R. D. Terry (Ed.), *Neurology of aging* (pp. 177–181). New York: Raven.
- Brzezny, R., Glasauer, S., Bayer, O., Siebold, C., & Buttner, U. (2003). Head impulses in three orthogonal planes of space: Influence of age. *Annals of the New York Academy of Sciences*, *1004*, 473–477.
- Collewijn, H., Van der Steen, J., Ferman, L., & Jansen, T. C. (1985). Human ocular counterroll: Assessment of static and dynamic properties from electromagnetic scleral coil recordings. *Experimental Brain Research*, *59*, 185–196.
- De Graaf, B., Bos, J. E., & Groen, E. (1996). Saccular impact on ocular torsion. *Brain Research Bulletin*, *40*(5–6), 321–326.
- Demer, J. L. (1994). Effect of aging on vertical visual tracking and visual-vestibular interaction. *Journal of Vestibular Research*, *4*(5), 355–370.
- Engstrom, H., Bergstrom, B., & Rosenhall, U. (1974). Vestibular sensory epithelia. *Arch Otolaryngol*, *100*(6), 411–418.
- Furman, J. M., & Redfern, M. S. (2001a). Effect of aging on the otolith-ocular reflex. *Journal of Vestibular Research*, *11*(2), 91–103.
- Furman, J. M., & Redfern, M. S. (2001b). Visual-vestibular interaction during OVAR in the elderly. *Journal of Vestibular Research*, *11*(6), 365–370.
- Furman, J. M., & Schor, R. H. (2003). Orientation of Listing's plane during static tilt in young and older human subjects. *Vision Research*, *43*(1), 67–76.
- Groen, E., Bos, J. E., & de Graaf, B. (1999). Contribution of the otoliths to the human torsional vestibulo-ocular reflex. *Journal of Vestibular Research*, *9*(1), 27–36.
- Hamasaki, I., Hasebe, S., & Ohtsuki, H. (2005). Static ocular counterroll: Video-based analysis after minimizing the false-torsion factors. *Japanese Journal of Ophthalmology*, *49*(6), 497–504.
- Jampel, R. S. (2002). The myth of static ocular counter-rolling: The response of the eyes to head tilt. *Annals of the New York Academy of Sciences*, *956*, 568–571.
- Jampel, R. S., & Shi, D. X. (2002). The absence of so-called compensatory ocular counter-torsion: The response of the eyes to head tilt. *Archives of Ophthalmology*, *120*(10), 1331–1340.
- Johnsson, L. G. (1971). Degenerative changes and anomalies of the vestibular system in man. *Laryngoscope*, *81*(10), 1682–1694.
- Kingma, H., Stegeman, P., & Vogels, R. (1997). Ocular torsion induced by static and dynamic visual stimulation and static whole body roll. *European Archives of Oto-Rhino-Laryngology*, *254*(Suppl. 1), S61–63.
- Klier, E. M., & Crawford, J. D. (1998). Human oculomotor system accounts for 3-D eye orientation in the visual-motor transformation for saccades. *Journal of Neurophysiology*, *80*(5), 2274–2294.
- Kori, A. A., Schmid-Priscoveanu, A., & Straumann, D. (2001). Vertical divergence and counterroll eye movements evoked by whole-body position steps about the roll axis of the head in humans. *Journal of Neurophysiology*, *85*(2), 671–678.
- Krejcová, H., Highstein, S., & Cohen, B. (1971). Labyrinthine and extra-labyrinthine effects on ocular counter-rolling. *Acta Oto-Laryngologica*, *72*(3), 165–171.
- Lichtenberg, B. K., Young, L. R., & Arrott, A. P. (1982). Human ocular counterrolling induced by varying linear accelerations. *Experimental Brain Research*, *48*(1), 127–136.
- Lopez, I., Honrubia, V., & Baloh, R. W. (1997). Aging and the human vestibular nucleus. *Journal of Vestibular Research*, *7*(1), 77–85.
- Markham, C. H., & Diamond, S. G. (2001). Ocular counterrolling differs in dynamic and static stimulation. *Acta Oto-Laryngologica*, *545*(Suppl.), 97–100.
- Markham, C. H., Diamond, S. G., & Stoller, D. F. (2000). Parabolic flight reveals independent binocular control of otolith-induced eye torsion. *Archives Italiennes de Biologie*, *138*(1), 73–86.
- Misslisch, H., Tweed, D., & Hess, B. J. M. (2001). Stereopsis outweighs gravity in the control of the eyes. *Journal of Neuroscience*, *21*, RC126.
- Moore, S. T., Clement, G., Raphan, T., & Cohen, B. (2001). Ocular counterrolling induced by centrifugation during orbital space flight. *Experimental Brain Research*, *137*(3–4), 323–335.
- Morrow, M. J., & Sharpe, J. A. (1993). The effects of head and trunk position on torsional vestibular and optokinetic eye movements in humans. *Experimental Brain Research*, *95*, 144–150.
- Ooi, D., Cornell, E. D., Curthoys, I. S., Burgess, A. M., & MacDougall, H. G. (2004). Convergence reduces ocular counterroll (OCR) during static roll-tilt. *Vision Research*, *44*, 2825–2833.
- Paige, G. D. (1992). Senescence of human visual-vestibular interactions. 1. Vestibulo-ocular reflex and adaptive plasticity with aging. *Journal of Vestibular Research*, *2*(2), 133–151.
- Palla, A., Bockisch, C. J., Bergamin, O., & Straumann, D. (2006). Dissociated hysteresis of static ocular counterroll in humans. *Journal of Neurophysiology*, *95*(4), 2222–2232.
- Pansell, T., Schworm, H. D., & Ygge, J. (2003). Torsional and vertical eye movements during head tilt dynamic characteristics. *Investigative Ophthalmology and Visual Science*, *44*, 2986–2990.
- Peterka, R. J., Black, F. O., & Schoenhoff, M. B. (1990a). Age-related changes in human vestibulo-ocular and optokinetic reflexes: Pseudorandom rotation tests. *Journal of Vestibular Research*, *1*(1), 61–71.
- Peterka, R. J., Black, F. O., & Schoenhoff, M. B. (1990b). Age-related changes in human vestibulo-ocular reflexes: Sinusoidal rotation and caloric tests. *Journal of Vestibular Research*, *1*(1), 49–59.
- Ramat, S., & Zee, D. S. (2003). Ocular motor responses to abrupt interaural head translation in normal humans. *Journal of Neurophysiology*, *90*, 887–902.
- Richter, E. (1980). Quantitative study of human Scarpa's ganglion and vestibular sensory epithelia. *Acta Oto-Laryngologica*, *90*(3–4), 199–208.
- Rosenhall, U. (1973). Degenerative patterns in the aging human vestibular neuro-epithelia. *Acta Oto-Laryngologica*, *76*(2), 208–220.
- Schmid-Priscoveanu, A., Straumann, D., Bohmer, A., & Obzina, H. (1999). Vestibulo-ocular responses during static head roll and three-dimensional head impulses after vestibular neuritis. *Acta Oto-Laryngologica*, *119*(7), 750–757.
- Schmid-Priscoveanu, A., Straumann, D., & Kori, A. A. (2000). Torsional vestibulo-ocular reflex during whole-body oscillation in the upright and the supine position. I. Responses in healthy human subjects. *Experimental Brain Research*, *134*(2), 212–219.
- Schworm, H. D., Ygge, J., Pansell, T., & Lennerstrand, G. (2002). Assessment of ocular counterroll during head tilt using binocular video oculography. *Investigative Ophthalmology and Visual Science*, *43*(3), 662–667.
- Sloane, P. D., Baloh, R. W., & Honrubia, V. (1989). The vestibular system in the elderly: Clinical implications. *American Journal of Otolaryngology*, *10*(6), 422–429.
- Tian, J. R., Crane, B. T., Wiest, G., & Demer, J. L. (2002). Effect of aging on the human initial interaural linear vestibulo-ocular reflex. *Experimental Brain Research*, *145*(2), 142–149.
- Torvik, A., Torp, S., & Lindboe, C. F. (1986). Atrophy of the cerebellar vermis in ageing. A morphometric and histologic study. *Journal of the Neurological Sciences*, *76*(2–3), 283–294.
- Wall, C., 3rd., Black, F. O., & Hunt, A. E. (1984). Effects of age, sex and stimulus parameters upon vestibulo-ocular responses to sinusoidal rotation. *Acta Oto-Laryngologica*, *98*(3–4), 270–278.
- Wong, A. M., & Sharpe, J. A. (2005). Cerebellar skew deviation and the torsional vestibulo-ocular reflex. *Neurology*, *65*, 412–419.
- Zingler, V. C., Kryvoshey, D., Schneider, E., Glasauer, S., Brandt, T., & Strupp, M. (2006). A clinical test of otolith function: Static ocular counterroll with passive head tilt. *NeuroReport*, *17*(6), 611–615.