Effects of Earth-Fixed vs Head-Fixed Targets on Static Ocular Counterroll

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Objective: To investigate whether static ocular counterroll (OCR) gain is reduced during viewing of an earth-fixed vs a head-fixed target.

Methods: Twelve healthy individuals were recruited. The target consisted of a red fixation cross against a grid pattern at a viewing distance of 33 cm. The target was mounted on a wall (earth fixed) or was coupled to the head (head fixed). Changes in mean torsional eye position were plotted as a function of head position steps (0°±25° in 5° steps), and sigmoidal fits were performed. Mean static OCR gain was calculated by taking the derivative of the fitted functions.

Results: Mean static OCR gain was 40% lower with a head-fixed target (−0.084) than with an earth-fixed target (−0.141) ($P < .001$).

Conclusion: The reduction in static OCR gain during viewing of a head-fixed target indicates that static OCR is partially negated when a target moves with the head.

Arch Ophthalmol. 2010;128(4):413-417

Ocular counterroll (OCR) generates torsional eye movements during static head tilt, although this compensatory response is only partial.[1-11] Static OCR is important from a clinical standpoint because this otolith-driven reflex forms the basis of the Bielschowsky head-tilt test, and it explains the abnormal compensatory head tilt in patients with trochlear nerve palsy. In healthy individuals, for example, during right head tilt, static OCR activates the right superior oblique and superior rectus muscles, causing the right eye to incyclotort and elevate slightly.[12] Simultaneously, static OCR activates the left inferior oblique and inferior rectus muscles, causing the left eye to excyclotort and depress slightly.[12] In a patient with right trochlear nerve palsy, however, during right head tilt, the elevating action of the superior rectus muscle is unopposed by the palsied superior oblique muscle in the right eye; thus, right hypertropia increases during right head tilt, constituting a positive Bielschowsky head-tilt test result. Similarly, static OCR also explains why many patients with right trochlear nerve palsy adopt a compensatory left head tilt; in this position, vertical strabismus and diplopia are minimized.

The existence of static OCR was challenged by some studies.[13,14] Using a head-fixed target, these studies[13,14] concluded that static OCR does not exist and that the static OCR reported previously resulted from an artifact called "false torsion" (ie, geometrically derived apparent torsion associated with eye rotation around an oblique axis). However, some investigators[3,15] have carefully controlled for false torsion yet still found a significant compensatory static OCR response.

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One possible explanation for the failure of the previous studies[13,14] to detect static OCR may be related to their use of a head-fixed target. When the target moves with the head, the vestibuloocular reflex (VOR) must be nulled to stabilize the target image on the fovea during dynamic head movements.[16-21] Likewise, during sustained lateral head tilt, static OCR might also be suppressed during viewing of a head-fixed target. However, evidence of static OCR negation has been sparse, and the results are contradictory. Reports of gains in static OCR elicited by head-fixed targets are generally lower[7,11] than those evoked by earth-fixed targets[1,2,5,8-10]; however, direct comparison cannot be made because testing conditions that are known to affect static OCR gains (eg, testing distance, vergence angle, and degree of head

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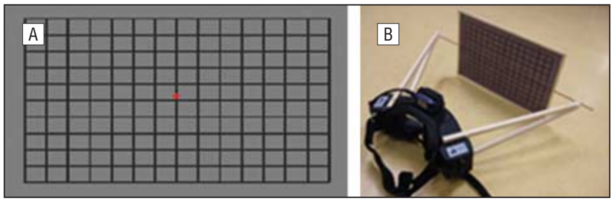

Figure 1. The wall-mounted (earth-fixed) (A) and goggle-mounted (head-fixed) (B) targets used in this study. The stimuli (red) were scaled so that they subtended the same visual angle in the earth-fixed and head-fixed conditions.

tilt) varied widely across studies. A previous study[4] compared static OCR gains in an earth-fixed vs a head-fixed target under the same testing conditions but found no difference in gains between the 2 targets. This may have resulted from their use of a transient stimulus that was inadequate to evoke static OCR negation. In the present study, we used a constant visual stimulus with strong spatial orientation cues to test the hypothesis that static OCR gains are decreased during viewing of a head-fixed target compared with an earth-fixed target in healthy individuals.

METHODS

PARTICIPANTS

Twelve healthy individuals (mean age, 31.8 years; median age, 31.5 years; age range, 17-51 years; 5 females) with normal vision without any vestibular, neurologic, or eye diseases participated in this study. The research protocol was approved by the research ethics board of The Hospital for Sick Children and adhered to the tenets of the Declaration of Helsinki. All of the participants gave informed consent. Participants wore corrective contact lenses during the experiments if needed.

VISUAL STIMULI

While wearing a pair of eye-tracking goggles (see the "3-Dimensional Video-Based Eye Tracking" subsection), participants underwent testing in 2 target conditions—earth fixed and head fixed—to evaluate the effects of visual stimuli on static OCR. In the earth-fixed condition, participants viewed a small (1.1°) red cross target in the center of a grid pattern back-projected onto a stationary screen (**Figure 1**A). The head-fixed condition had the identical grid pattern and red cross target but the stimulus was affixed to the goggles such that it tilted with the individual's head (Figure 1B). The viewing distance was 33 cm in both conditions. The stimuli in each condition were scaled so that they subtended the same visual angle (wide field, 42° vertically and 28° horizontally). The head-fixed apparatus attached to the goggles was lightweight (30 g) yet rigidly constructed of balsa wood so that participants could move their head freely with the stimulus tightly coupled to it. All of the experiments were performed during binocular viewing.

3-DIMENSIONAL VIDEO-BASED EYE TRACKING

A commercially available infrared video-based system was used (3D VOG; SensoMotoric Instruments GmbH, Teltow, Germany) to measure 3-dimensional eye movements (horizontal, vertical, and torsional). Eye positions were acquired in both eyes simultaneously using 2 miniature charge-coupled device infrared-illuminated video cameras mounted on a pair of goggles. Three infrared LEDs at a wavelength of 920 nm and an intensity of less than 1 mW/cm^2 illuminated each eye. The sampling frequency was 60 Hz for all 3 dimensions. For image processing, the monochrome image was digitized with 256 gray levels (8-bit accuracy). The spatial resolution of the system for ocular torsion was approximately 0.1°. Maximum deviation of torsion linearity was ±1.4% at a range of ±20°.[9] Trials in which horizontal or vertical eye movements exceeded ±20° and portions of trial records containing blinks were excluded from further analysis.

Goggle slippage was prevented by coupling the goggles firmly to the person's head by fitting an elastic strap tightly around the back of the head and by using a bite bar made of disposable balsa wood attached to the nasal bridge of the goggles. Care was taken to adjust the height of the testing chair relative to the target for each participant to avoid significant head pitch and to ensure that gaze was in the straight-ahead direction.

HEAD-ROLL TILT PARADIGMS

Before each experiment, monocular horizontal and vertical calibration was performed using a red fixation cross (visual angle, 1.1°) at 9 locations: 0° and ±10° and ±15° torsionally, horizontally and vertically. At the beginning of the experiment, the participant was instructed to maintain fixation on the target while keeping the head in the upright position. This allowed us to obtain reference images of the iris of each eye to compare with images taken subsequently at different head-tilt positions for the computation of torsion. After the reference images were obtained, the participant's head was tilted in the roll plane in 5° steps over a range of 25° toward either the right (clockwise, ie, positive) or left (counterclockwise, ie, negative) shoulder 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 (earth fixed vs head fixed). At each head-tilt position, the head was held steady for at least 15 to 20 seconds to allow the canal-mediated dynamic torsional response (time constant of approximately 6 seconds[3,22]) to subside. Head movements were controlled by placement of the experimenter's hands on each parietal area of the person's skull. Static pitch and roll angles were calculated using ratios of the gravity vector from the 3-axis signals of a linear accelerometer mounted on top of the goggles. These angles were displayed onscreen so that the experimenter could view the amplitude of the tilt angles in real time and make adjustments accordingly. The participant was instructed to maintain fixation on the target throughout the experiment. The total duration of 1 tilt series in both directions (clockwise and counterclockwise) was approximately 5 minutes.

DATA ANALYSIS

Horizontal, vertical, and torsional eye positions for each eye were recorded in pixels; were converted from pixels to degrees of eye rotation; and were exported in ASCII format. Positive directions were defined as right for horizontal, up for vertical, and clockwise for torsional angles, all from the participant's viewpoint. Horizontal and vertical eye positions were computed using the black pupil technique by calculating the center of the lowest infrared reflection (ie, the center of the pupil) geometrically. Ocular torsion was computed by calculating the angular displacement of a user-defined iris segment selected after acquisition of the reference image. This was achieved by measuring luminance levels of the user-defined iris segment, which was then cross-correlated with that of the same iris segment in each consecutive video frame (every 16.67 millisec-

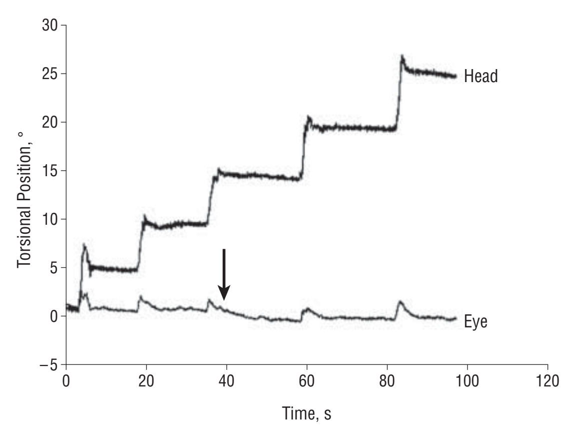

Figure 2. Representative tracings of clockwise head tilt (ie, head roll toward the right shoulder) from 0° to 25° and the corresponding partially compensatory torsional eye movements in a representative participant. Positive values indicate clockwise; negative values, counterclockwise; and arrow, nystagmus beats that superimposed on the torsional peak, with slow phases in the opposite direction of the head tilt.

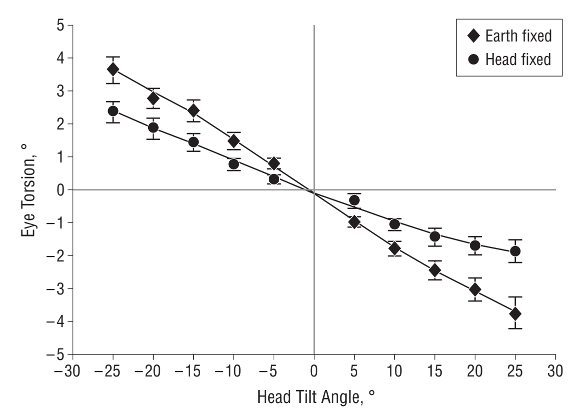

Figure 3. The relationship between mean torsional eye movement and head-tilt angle during viewing of earth-fixed vs head-fixed targets. Each data point represents the group mean torsional response for all 12 participants for a given head-tilt angle. Error bars represent SEM.

onds) throughout the recording. The concordance between the user-defined iris segment and that of the same iris segment in each consecutive frame was computed and was called *torsion quality*, which could range from 0.0 (no concordance) to 1.0 (maximum concordance). Although data with a torsion quality of 0.3 or greater are considered reliable by the manufacturer of the system, we included only frames with torsion quality of 0.6 or greater in this analysis to ensure that we obtained the most robust torsional data. All eye movements were recorded using Fick coordinates, and false torsion associated with Fick geometry was eliminated from the torsional data using a rotation vector algorithm in the 3D VOG system software.

For each participant, 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 to 20 seconds. While eye movements were recorded continuously throughout the experiment, we analyzed a 1-second epoch (constituting 60 samples at a sampling frequency of 60 Hz) of this continuous record at the end of each 15- to 20-second tilt period. This was to ensure that the dynamic VOR canal signal had decayed and that the static torsional eye responses had stabilized. These values were then averaged across participants to acquire a group mean response. To compare group static OCR responses between conditions, changes in mean torsional eye position were plotted as a function of head position steps (0° ± 25° in 5° steps), and 5-parameter sigmoidal fits were performed. The sigmoidal fits were excellent, with r^2 values consistently greater than 0.99. Mean static OCR gain was calculated by taking the derivative of the fitted functions for each participant for each condition.

Analysis of variance was performed to assess the effects of earth-fixed vs head-fixed targets on static OCR gains. Static OCR responses did not differ between right and left eyes; accordingly, we combined the data from both eyes for all subsequent analyses.

RESULTS

A representative tracing of the torsional eye position during stepwise clockwise head tilts is shown in **Figure 2**. Consistent with previous studies,[22,23] after initiation of a head tilt, a rapid torsional eye movement (ie, torsional peak[22]) occurred in the direction of the head movement. This was followed by a nystagmus beat that was superimposed on this torsional peak, with compensatory slow phase in the opposite direction of 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 to 20 seconds.[23,24]

For earth-fixed and head-fixed targets, all of the participants exhibited partially compensatory torsional eye movements that increased with increasing head-tilt angle. The relationship between head-tilt angle and torsional eye position across all of the individuals during viewing of earth-fixed and head-fixed targets is shown in **Figure 3**. In the head-tilt range of 0° to approximately ±10°, torsional eye position varied approximately linearly with head-tilt angles; however, as head-tilt angles increased, torsional eye response per degree of head tilt (ie, gain) started to decrease, which could be explained by saturation of OCR, as has been previously observed.[2-4,7,9,11] This attenuation of OCR gain with increasing head tilt was well captured by 5-parameter sigmoidal fits, with $r^2 = 0.998$ for earth-fixed targets and $r^2 = 0.996$ for head-fixed targets.

The mean (SEM) static OCR gain for earth-fixed targets (−0.141 [0.018]) was consistently higher than that for head-fixed targets (−0.084 [0.014]) ($P < .001$) across all head-tilt angles. This represents a 40% reduction in static OCR gain. No statistically significant interactions between head-tilt angle and target condition were found. The earth-fixed target elicited small disconjugate vertical eye movements that seemed to be larger than those for the head-fixed target; however, the difference was not statistically significant ($P = .88$).

COMMENT

Static OCR is a well-documented physiologic phenomenon that is often used clinically to diagnose abnormal functioning of cyclovertical muscles. Some study researchers,[13,14] however, have asserted that static OCR does not exist and have argued that the static OCR demonstrated in previous studies[1-11] was an artifact arising from false torsion, a geometric consequence that occurs when the angles of a curved surface (eg, a globe) are projected onto a flat surface during eye rotation around an oblique axis. To address this issue, Hamasaki et al[3] developed a novel method to measure static OCR that removed false torsion and demonstrated irrefutably the presence of partially compensatory static OCR. In this study, we eliminated false torsion and found a mean static OCR gain of 14% for an earth-fixed target, which decreased to 8% for a head-fixed target. Potential limitations of this study include the effects of proprioceptive cues from the neck or trunk and the effects of differential pressure cues exerted by the goggles on the head, which may affect OCR gains. However, because we used identical head-tilt protocols to compare the difference in OCR gains between earth-fixed and head-fixed conditions, these effects were minimized. These results are in good agreement with previously reported values[1-11] and support the existence of static OCR.

So, why did these studies[13,14] fail to detect static OCR? Three factors may contribute.[3,25,26] First, the use of a fixation target at a very short distance (32 cm) may be a factor. Static OCR responses are reduced when viewing a near target. Ooi et al[7] reported that decreasing the viewing distance from 130 to 30 cm reduced mean static OCR gain by 35%. Similarly, decreasing the viewing distance from 150 to 10 cm reduced static OCR gain by 70% in nonhuman primates.[27] It is suggested that the lower OCR gains elicited by near targets may reflect a mechanism to minimize the vertical disparity induced by torsion during convergence, thereby optimizing stereopsis.[27]

A second contributing factor may be related to the use of a fixation target that moved with the head. The function of the VOR is to stabilize a target image on the fovea during head rotation. Dynamic VOR is mediated by the semicircular canals and otolith organs during horizontal, vertical, and torsional head rotations. Static OCR, in contrast, is primarily driven by the otolith organs during sustained head tilt in response to a change in direction of gravitational acceleration.[22,28,29] In this light, the VOR is driven by visual and vestibular inputs. When a target moves with the head, the VOR must be negated to stabilize the target image. Negation of VOR has been demonstrated in animals[30] and humans[21,31] when a visual display moves with the head; however, unlike its horizontal and vertical counterparts, the gain reduction for dynamic torsional VOR is only partial (approximately 36%).[21,30,31] We postulated that VOR negation could also be elicited by a head-fixed target during sustained and static head tilt. To our knowledge, only 1 previous study[4] has compared static OCR gains directly between an earth-fixed and a head-fixed target, but they reported no difference in gains. This might be related to their[4] choice of visual stimulus, which consisted of a horizontal grating that oscillated sinusoidally in a frontal plane at 0 to 0.6 Hz with amplitude that varied from 6° to 33°. The transient nature of this stimulus may not be strong enough to evoke VOR negation. In the present study, we used a constant visual stimulus with strong spatial orientation cues to elicit VOR negation. As predicted, we found a reduction in static OCR gain (40%) when participants viewed a head-fixed target compared with an earth-fixed target.

A third contributing factor was related to measurement methods. In previous studies,[13,14] a heavy apparatus (700 g) was used that was attached to the head with a headband only, with no additional control for camera movements relative to the eye. The apparatus was also long, which, combined with its significant mass, created a moment arm for gravity to act on. Variation of the camera position during head roll may have reduced their measurement precision. In the present study, we minimized the weight of the apparatus (30 g) by using balsa wood, and we prevented goggle and camera slippage by using the combination of an elastic strap and a bite bar attached to the goggle. Together, the low static OCR gain elicited by a head-fixed target at a short viewing distance may have been too small to be detected reliably with the apparatus and analytical tools used in these studies[13,14] and may explain their failure to detect a systematic compensatory OCR response.

What mechanism negates the VOR when a person fixates a target that moves with the head? There are 2 main theories to explain VOR negation. One theory suggests that VOR is canceled by a smooth pursuit signal when a target moves with the head. It proposes that the moving target elicits smooth pursuit eye movements that add to and effectively cancel the VOR.[16,18,19,32-34] This is further supported by the finding that in patients with vestibular dysfunction, a pursuit signal is absent during combined eye-head movements because there is no VOR to cancel.[33,35] A second theory suggests that a central process attenuates the VOR gain.[17,20,21,36-38] This is supported by the finding that during dynamic head roll using a head-fixed target, the torsional VOR gain was reduced despite the absence of torsional smooth pursuit,[21] suggesting that a mechanism other than smooth pursuit must be responsible for the VOR negation. Because there is no torsional smooth pursuit during static lateral head tilt, the present findings provide further support to the second theory. Further studies are needed to elucidate whether a central process attenuates the VOR gain or other mechanisms are responsible for the reduction in static OCR responses we observed.

The magnitude of the static OCR response, which is believed to be the basis of the Bielschowsky head-tilt test, depends on stimulus features, including the viewing distance and whether the stimulus moves with the head or remains stationary. Clinically, when testing a patient with suspected trochlear nerve palsy, to elicit a strong OCR response such that the increase in hypertropia on ipsilateral head tilt is maximal (ie, to increase the sensitivity of the Bielschowsky head-tilt test), one should use a distant stationary target (eg, a Snellen or Early Treatment Diabetic Retinopathy Study chart mounted on a wall) rather than a near target (eg, a near visual acuity card held by a patient, which may also move as the patient's head is tilted). This observation is in agreement with a previous study[39] that showed that the vertical deviation in trochlear nerve palsy increases with distant fixation and provides evidence that the same otolithic mechanism (static OCR) is operative in generating vertical and torsional eye movements during the Bielschowsky head-tilt test.

Submitted for Publication: December 5, 2008; final revision received April 16, 2009; accepted May 12, 2009.
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Financial Disclosure: None reported.
Funding/Support: This study was supported by New Investigator Award MSH 55058 and grant MOP 57853 from the Canadian Institutes of Health Research, by the University Health Network Ophthalmology Practice Plan, and by the Department of Ophthalmology and Vision Sciences at The Hospital for Sick Children (all support to Dr Wong).

REFERENCES

1. Averbuch-Heller L, Rottach KG, Zivotofsky AZ, et al. Torsional eye movements in patients with skew deviation and spasmodic torticollis: responses to static and dynamic head roll. *Neurology*. 1997;48(2):506-514.
2. Bockisch CJ, Haslwanter T. Three-dimensional eye position during static roll and pitch in humans. *Vision Res*. 2001;41(16):2127-2137.
3. Hamasaki I, Hasebe S, Ohtsuki H. Static ocular counterroll: video-based analysis after minimizing the false-torsion factors. *Jpn J Ophthalmol*. 2005;49(6):497-504.
4. Kingma H, Stegeman P, Vogels R. Ocular torsion induced by static and dynamic visual stimulation and static whole body roll. *Eur Arch Otorhinolaryngol*. 1997;254(suppl 1):S61-S63.
5. Klier EM, Crawford JD. Human oculomotor system accounts for 3-D eye orientation in the visual-motor transformation for saccades. *J Neurophysiol*. 1998;80(5):2274-2294.
6. Markham CH, Diamond SG. Ocular counterrolling differs in dynamic and static stimulation. *Acta Otolaryngol Suppl*. 2001;545:97-100.
7. Ooi D, Cornell ED, Curthoys IS, Burgess AM, MacDougall HG. Convergence reduces ocular counterroll (OCR) during static roll-tilt. *Vision Res*. 2004;44(24):2825-2833.
8. Schmid-Priscoveanu A, Straumann D, Böhmer A, Obzina H. Vestibulo-ocular responses during static head roll and three-dimensional head impulses after vestibular neuritis. *Acta Otolaryngol*. 1999;119(7):750-757.
9. Schworm HD, Ygge J, Pansell T, Lennerstrand G. Assessment of ocular counterroll during head tilt using binocular video oculography. *Invest Ophthalmol Vis Sci*. 2002;43(3):662-667.
10. Wong AM, Sharpe JA. Cerebellar skew deviation and the torsional vestibuloocular reflex. *Neurology*. 2005;65(3):412-419.
11. Zingler VC, Kryvoshey D, Schneider E, Glasauer S, Brandt T, Strupp M. A clinical test of otolith function: static ocular counterroll with passive head tilt. *Neuroreport*. 2006;17(6):611-615.
12. Harris L, Beykirch K, Fetter M. The visual consequences of deviations in the orientation of the axis of rotation of the human vestibulo-ocular reflex. *Vision Res*. 2001;41(25-26):3271-3281.
13. Jampel RS. The myth of static ocular counter-rolling: the response of the eyes to head tilt. *Ann N Y Acad Sci*. 2002;956:568-571.
14. Jampel RS, Shi DX. The absence of so-called compensatory ocular countertorsion: the response of the eyes to head tilt. *Arch Ophthalmol*. 2002;120(10):1331-1340.
15. Kushner BJ, Kraft S. Ocular torsional movements in normal humans. *Am J Ophthalmol*. 1983;95(6):752-762.
16. Barnes GR, Benson AJ, Prior AR. Visual-vestibular interaction in the control of eye movement. *Aviat Space Environ Med*. 1978;49(4):557-564.
17. Cullen KE, Belton T, McCrea RA. A non-visual mechanism for voluntary cancellation of the vestibulo-ocular reflex. *Exp Brain Res*. 1991;83(2):237-252.
18. Gauthier GM, Vercher JL. Visual vestibular interaction: vestibulo-ocular reflex suppression with head-fixed target fixation. *Exp Brain Res*. 1990;81(1):150-160.
19. Huebner WP, Leigh RJ, Seidman SH, et al. Experimental tests of a superposition hypothesis to explain the relationship between the vestibuloocular reflex and smooth pursuit during horizontal combined eye-head tracking in humans. *J Neurophysiol*. 1992;68(5):1775-1792.
20. Koenig E, Dichgans J, Dengler W. Fixation suppression of the vestibulo-ocular reflex (VOR) during sinusoidal stimulation in humans as related to the performance of the pursuit system. *Acta Otolaryngol*. 1986;102(5-6):423-431.
21. Leigh RJ, Maas EF, Grossman GE, Robinson DA. Visual cancellation of the torsional vestibulo-ocular reflex in humans. *Exp Brain Res*. 1989;75(2):221-226.
22. Morrow MJ, Sharpe JA. The effects of head and trunk position on torsional vestibular and optokinetic eye movements in humans. *Exp Brain Res*. 1993;95(1):144-150.
23. Collewijn H, Van der Steen J, Ferman L, Jansen TC. Human ocular counterroll: assessment of static and dynamic properties from electromagnetic scleral coil recordings. *Exp Brain Res*. 1985;59(1):185-196.
24. Pansell T, Schworm HD, Ygge J. Torsional and vertical eye movements during head tilt dynamic characteristics. *Invest Ophthalmol Vis Sci*. 2003;44(7):2986-2990.
25. Hasebe S, Hamasaki I, Ohtsuki H. Random measurement error in assessing compensatory ocular countertorsion. *Arch Ophthalmol*. 2003;121(12):1805-1807.
26. Kushner BJ. Compensatory ocular torsion. *Arch Ophthalmol*. 2003;121(12):1806-1807.
27. Misslisch H, Tweed D, Hess BJ. Stereopsis outweighs gravity in the control of the eyes. *J Neurosci*. 2001;21(3):RC126.
28. Groen E, Bos JE, de Graaf B. Contribution of the otoliths to the human torsional vestibulo-ocular reflex. *J Vestib Res*. 1999;9(1):27-36.
29. Schmid-Priscoveanu A, Straumann D, Kori AA. Torsional vestibulo-ocular reflex during whole-body oscillation in the upright and the supine position, I: responses in healthy human subjects. *Exp Brain Res*. 2000;134(2):212-219.
30. Straumann D, Suzuki M, Henn V, Hess BJ, Haslwanter T. Visual suppression of torsional vestibular nystagmus in rhesus monkeys. *Vision Res*. 1992;32(6):1067-1074.
31. Barr CC, Schultheis LW, Robinson DA. Voluntary, non-visual control of the human vestibulo-ocular reflex. *Acta Otolaryngol*. 1976;81(5-6):365-375.
32. Lanman J, Bizzi E, Allum J. The coordination of eye and head movement during smooth pursuit. *Brain Res*. 1978;153(1):39-53.
33. Leigh RJ, Sharpe JA, Ranalli PJ, Thurston SE, Hamid MA. Comparison of smooth pursuit and combined eye-head tracking in human subjects with deficient labyrinthine function. *Exp Brain Res*. 1987;66(3):458-464.
34. Misslisch H, Tweed D, Fetter M, Dichgans J, Vilis T. Interaction of smooth pursuit and the vestibuloocular reflex in three dimensions. *J Neurophysiol*. 1996;75(6):2520-2532.
35. Leigh RJ, Zee DS. *The Neurology of Eye Movements*. 4th ed. Oxford, England: Oxford University Press; 2006.
36. Lisberger SG. Visual tracking in monkeys: evidence for short-latency suppression of the vestibuloocular reflex. *J Neurophysiol*. 1990;63(4):676-688.
37. McKinley PA, Peterson BW. Voluntary modulation of the vestibuloocular reflex in humans and its relation to smooth pursuit. *Exp Brain Res*. 1985;60(3):454-464.
38. Robinson DA. *Functional Basis of Ocular Motility Disorders*. Oxford, England: Pergamon Press; 1982.
39. Ohtsuki H, Hasebe S, Furuse T, Nonaka F, Nakatsuka C, Shiraga F. Contribution of vergence adaptation to difference in vertical deviation between distance and near viewing in patients with superior oblique palsy. *Am J Ophthalmol*. 2002;134(2):252-260.