Gain of Human Torsional Optokinetic Nystagmus Depends on Horizontal Disparity

Noriaki Washio, Yasuo Suzuki, Masahiro Sawa, and Kenji Ohtsuka

PURPOSE. To investigate the effects of horizontal disparity on torsional optokinetic nystagmus (tOKN) in humans.

METHODS. Ten healthy human subjects were selected for this experiment. Monocular eye movements were recorded three-dimensionally using dual-search coil methods. Torsional OKN was induced by a rotating random-dot pattern (22° in diameter, constant angular velocity: ±54 deg/s) projected on the virtual screen of the optical see-through, head-mounted display (HMD). The optical distance of the HMD’s virtual screen was 2 m. A red LED that could be fixated through the virtual screen of the HMD was located near the center of the rotating random-dot pattern. Horizontal disparity was induced by changing the distance between the fixated target and the subject systematically (1, 1.5, 2, or 3 m; five subjects) or by the prism (+1.5, +0.5, 0, or −0.5 prism-diopter [PD] in each eye; five subjects) in front of the HMD.

RESULTS. The average gain with zero horizontal disparity (0.022 ± 0.008/0.025 ± 0.014, fixated target at 2 m/fixed target with the plain glass) was significantly higher than the gain with crossed disparity (0.017 ± 0.003/0.019 ± 0.008, target at 3 m/with the prism of −0.5 PD) and uncrossed disparity (0.017 ± 0.002, target at 1 m/with the prism of +1.5 PD; one-way ANOVA, P < 0.05).

CONCLUSIONS. The horizontal disparity of optokinetic stimulus affects tOKN. Nonzero horizontal disparity decreases the gain of tOKN. (Invest Ophthal Vis Sci. 2005;46:133–136) DOI: 10.1167/iovs.04-04276

Optokinetic nystagmus (OKN) is an eye movement that stabilizes the retinal image during a movement of the visual field. When the retinal image continuously moves in one direction, the slow phase of OKN in the direction of the retinal image alternates with the fast phase. When the visual field rotates around the line of sight (direction of the gaze), OKN in a torsional direction is induced around the line of sight. OKN consists of the early and later parts, which differ in their dynamics and rotational degrees of freedom. The early and later parts of OKN have been considered to occur via direct and indirect pathways that correspond to the pursuit and the optokinetic systems, respectively. The latter part of OKN has three rotational degrees of freedom and contributes to the visual suppression of the postrotatory nystagmus by decreasing the time constant of slow-phase velocity decay in three dimensions. In contrast, the early part of OKN has only two rotational degrees of freedom and contributes to the visual suppression of the postrotatory nystagmus by decreasing the peak slow-phase velocity in horizontal and vertical directions. Therefore, a visual fixation target suppresses vertical and horizontal OKN completely, but torsional (tOKN) partially.

It has been known that OKN attenuates when convergence is not within the plane of the optokinetic stimulus. When a horizontal binocular disparity is introduced into the vertically moving optokinetic stimulus, the gain of vertical OKN is reduced. The gain of OKN is related to the disparity of optokinetic stimulus; however, it has not yet been clarified whether the horizontal disparity of optokinetic stimulus affects only the gain of tOKN or both (the early and the latter) parts of OKN. To clarify this, we investigated the correlation between the gain of tOKN and horizontal disparity, because tOKN involves only the later part and is not perfectly suppressed by a fixation target.

The gain of tOKN was related to the horizontal disparity of optokinetic stimulus. A part of this work has been presented in a conference report.

METHODS

Subjects and Calibration

Ten healthy subjects (seven men, three women; age range, 20–44 years; mean, 29.8) possessing normal visual acuity (better than 20/20 in each eye, with or without spectacle correction) provided informed consent to participate in the study. All experimental procedures conformed to the tenets of the Declaration of Helsinki for research involving human subjects. None of the subjects had any neurologic disorders on clinical examination. Refractive errors observed in these subjects were myopia or myopia with astigmatism and were not corrected by any devices during experiments. Eye movements were measured three-dimensionally with two orthogonal magnetic fields (side length of cubic field coils was 1 m; EM6, Remel Laboratories, Lenexa, KS), and a double-loop search coil (Skalar Medical BV, Delft, The Netherlands) was worn on the right eye. Four-channel coil signals were filtered (bandwidth for horizontal and vertical eye components was 0–200 Hz, and that for torsional eye components was 0–60 Hz) and digitized at 1000 Hz, written onto the computer hard disk, and processed off-line. The double-loop search coil was calibrated before each experiment by mounting it on a protractor device that could be rotated in horizontal, vertical, and torsional planes (in vitro calibration).

Room lights were turned off, and the calibration and experimental sessions were performed in the dark. Each subject sat upright in a chair with his or her head fixed with a bite bar at the center of the cubic-field coils. The virtual screen size of the optical see-through, head-mounted display (HMD; Glasstron; Sony, Tokyo, Japan) was 52 in. (36.6°) at the optical distance of 2 m. Five targets aligned vertically at intervals of 5° were sequentially presented on the virtual screen for in vivo calibration. After subjects wore the coil, we calculated the orientation of both coil vectors and possible voltage offsets using the four-channel coil signals measured in the in vivo calibration during fixation of the vertically aligned five LEDs. We then carefully checked voltage offsets of the coil signals during each interval between recording sessions and compensated for them if necessary. Calibrated three-dimensional (3D) eye positions were expressed as rotation vectors according to the

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right-hand rule. The direction and the length of the rotation vector represent the axis and the amount of rotation, respectively, from a reference position. Eye position vectors were calculated in coil-frame coordinates in which the torsional axis coincided with the direction of the LED while the subject looked straight ahead. Rotation angles in this study are shown in degrees for clarity. The overall standard deviation of position noise in this study was <0.1° for each component.

**Experimental Protocol**

A round, black pattern (22° in diameter) with randomly spaced white dots generated by custom computer software was projected on the HMD. The random-dot pattern could be rotated about its center at a constant angular velocity, to induce tOKN. The direction of the center of the random-dot pattern coincided with the direction of the target while the subject gazed straight ahead during in vivo calibration.

The horizontal disparity of the torsional optokinetic stimulus was induced by two methods (experiments 1 and 2). A red LED that could be fixated through the virtual screen of the HMD was presented near the center of the rotating random-dot pattern.

In Experiment 1, four different horizontal disparities were induced by changing the distance between the fixation target and the subject (1, 1.5, 2, or 3 m). The size of the LED was not altered, but the brightness was adjusted to maintain a constant target image through the HMD. During the whole session, the visual target was presented near the center of the random-dot pattern, and the subject was asked to fixate on it binocularly. At first, the random-dot pattern was stationary for 30 seconds. Thereafter, it rotated for 30 seconds with a constant angular velocity of 54 deg/s (positive, clockwise rotation) and stopped. After an interval of 10 seconds, the random-dot pattern rerotated for 30 seconds. Thereafter, it rotated for 30 seconds with a constant angular velocity, to induce tOKN. The horizontal disparity of the torsional optokinetic stimulus was induced by two methods (experiments 1 and 2). A red LED that could be fixated through the virtual screen of the HMD was presented near the center of the rotating random-dot pattern.

In Experiment 2, four different horizontal disparities were induced by changing the distance between the fixation target and the subject constant at 2 m. Base-out prisms of 1.5 and 0.5 prism-diopter (PD) and base-in prisms of 0.5 PD were placed in front of the HMD binocularly to induce convergence that corresponded to fixating a target at 1, 1.5, and 3 m in experiment 1. For a convergence corresponding to fixating a target at 2 m, flat glasses having a similar size as the prisms were put in front of the HMD binocularly.

**Data Analysis**

Data were analyzed with custom software used in our previous study. In short, 3D eye position traces were displayed on the computer screen for visual inspection. The onset and the end of the slow phase of tOKN were identified manually, and periods with blinks were discarded. Thereafter, we calculated the average velocity of the slow phase of tOKN [(torsional position at the end of the slow phase – torsional position at the onset of the slow phase)/duration] and the gain to the constant angular velocity of the random-dot pattern. When the slow-phase velocity of tOKN was <1% of the rotational velocity of the random-dot pattern, the data were discarded and not included in our database for further analysis. The average percentages of discarded slow phases were 15.8% ± 10.7% (average ± SD) in experiment 1 and 21.9% ± 18.7% in experiment 2. Because the property of intorsional OKN and extorsional OKN of each subject was not identical, the intorsional slow phase and extorsional slow phase were analyzed separately.

**RESULTS**

**Experiment 1**

Three men and two women participated in the experiment. Figure 1 shows the 3D eye movements during fixation on a target at 2 m (subject YS). Figure 2A shows a typical example of tOKN of a subject during fixation on a target at different distances (same subject as Fig. 1). Faster slow-phase velocity of tOKN was observed during fixation on a target at 2 m with zero horizontal disparity. Table 1 summarizes the mean slow-phase gain of tOKN in five subjects (n = 9). Rhythmical nystagmus with intorsional slow phases was not observed in one subject. Figure 3 shows the grand average and SD of average slow-phase gain of tOKN. The grand average gain (± SD) with zero horizontal disparity (0.023 ± 0.008, fixation target at 2 m) was significantly higher than that with crossed disparity (0.018 ± 0.003, fixation target at 3 m) and that with large uncrossed disparity (0.017 ± 0.002, fixation target at 1 m; one-way ANOVA and multiple comparisons, P < 0.05). The grand aver-
ANOVA and multiple comparisons, with zero disparity was not statistically significant (one way grand average gain with the small uncrossed disparity and that disparity and the zero disparity. The difference between the target at 1.5 m) was between that with the large uncrossed disparity (0.025 ± 0.006, fixation target at 1.5 m) was between that with the large uncrossed disparity and the zero disparity. The difference between the grand average gain with the small uncrossed disparity and that with zero disparity was not statistically significant (one way ANOVA and multiple comparisons, P = 0.38).

**Experiment 2**

Four men and one woman participated in this experiment. Figure 2B shows a typical example of tOKN while the subject fixated on a target through the prism with different prism-diopters (same subject as shown in Fig. 2A). Faster slow-phase velocity of tOKN was observed while fixating on a target through the flat glasses with zero horizontal disparity. Table 2 summarizes the average slow-phase gain of tOKN in five subjects (n = 10), and Figure 3 shows the grand average and SD of average slow-phase gain of tOKN. The grand average gain (± SD) with zero horizontal disparity with binocular flat glasses (0.025 ± 0.013, corresponding to the fixation target at 2 m) was significantly higher than that with crossed disparity with binocular 0.5 PD base-out prisms (0.019 ± 0.008, corresponding to a fixation target at 5 m) and that with uncrossed disparity with binocular 1.5 PD base-in prisms (0.019 ± 0.006, corresponding to a fixation target at 1 m; one way ANOVA and multiple comparisons, P < 0.05). The difference between the grand average gain with zero disparity and that with uncrossed disparity with binocular 0.5 PD base-in prisms (0.02 ± 0.008, corresponding to the fixation target at 1.5 m) was not statistically significant (one-way ANOVA and multiple comparisons, P = 0.08).

**Table 1. Average Slow-Phase Gain of tOKN in Experiment 1**

<table>
<thead>
<tr>
<th>Subject</th>
<th>Direction</th>
<th>1.0 m</th>
<th>1.5 m</th>
<th>2.0 m</th>
<th>3.0 m</th>
</tr>
</thead>
<tbody>
<tr>
<td>YS</td>
<td>Ext.</td>
<td>0.023 (0.010)</td>
<td>0.024 (0.010)</td>
<td>0.037 (0.017)</td>
<td>0.020 (0.008)</td>
</tr>
<tr>
<td></td>
<td>Int.</td>
<td>0.018 (0.007)</td>
<td>0.024 (0.009)</td>
<td>0.024 (0.009)</td>
<td>0.018 (0.008)</td>
</tr>
<tr>
<td>SU</td>
<td>Ext.</td>
<td>0.016 (0.006)</td>
<td>—</td>
<td>0.018 (0.007)</td>
<td>0.017 (0.005)</td>
</tr>
<tr>
<td></td>
<td>Int.</td>
<td>0.017 (0.006)</td>
<td>—</td>
<td>0.034 (0.015)</td>
<td>0.023 (0.008)</td>
</tr>
<tr>
<td>ON</td>
<td>Ext.</td>
<td>0.012 (0.001)</td>
<td>0.015 (0.004)</td>
<td>0.013 (0.002)</td>
<td>0.015 (0.004)</td>
</tr>
<tr>
<td></td>
<td>Int.</td>
<td>0.014 (0.003)</td>
<td>0.018 (0.006)</td>
<td>0.015 (0.004)</td>
<td>0.018 (0.006)</td>
</tr>
<tr>
<td>OK</td>
<td>Ext.</td>
<td>0.015 (0.003)</td>
<td>0.016 (0.005)</td>
<td>0.018 (0.006)</td>
<td>0.016 (0.004)</td>
</tr>
<tr>
<td></td>
<td>Int.</td>
<td>0.017 (0.007)</td>
<td>0.016 (0.004)</td>
<td>0.018 (0.006)</td>
<td>0.015 (0.004)</td>
</tr>
<tr>
<td>MA</td>
<td>Ext.</td>
<td>0.020 (0.007)</td>
<td>0.026 (0.007)</td>
<td>0.030 (0.013)</td>
<td>0.019 (0.009)</td>
</tr>
<tr>
<td></td>
<td>Grand average</td>
<td>0.017 (0.005)</td>
<td>0.020 (0.005)</td>
<td>0.023 (0.009)</td>
<td>0.018 (0.005)</td>
</tr>
</tbody>
</table>

Data are expressed as the mean ± SD in parentheses. n = 9. ext., extortional; int., intortional.

**Discussion**

Horizontal disparity is known to affect OKN6,7; however, the precise manner in which horizontal disparity interacts with the pursuit system (the early part of OKN) and/or the optokinetic system (the later part of OKN) is still uncertain. In this study, we found that the gain of tOKN depends on horizontal disparity and is highest when horizontal disparity is zero (Fig. 3). The gain of tOKN showed high interindividual variability; however, intraindividual variability was low. Because torsional eye movements do not require a shift in the visual axis, the pursuit system does not work in the torsional direction. Therefore, our findings confirmed the effects of horizontal disparity on OKN6,7 and clearly showed that disparity affects not only the pursuit system but also the optokinetic system.

In Experiment 1, the horizontal disparity of the optokinetic stimulus was induced by fixating the target that was not within the plane of the optokinetic stimulus. Although the setup for this experiment was simple, we could not eliminate the effects of accommodation. Therefore, experiment 2 was conducted, in which the horizontal disparity of the optokinetic stimulus was induced by prisms. Under both conditions, the center of the rotating random-dot pattern (torsional optokinetic stimulus) deviated from the visual axis of each eye. The horizontal deviation between the visual axis and the center of the optokinetic stimulus was symmetrical for both eyes and <1° in each eye. Because the gain of tOKN did not change when the fixation target was horizontally shifted from the center of the rotating optokinetic stimulus by 6.5°, the smaller horizontal deviation in these experiments did not affect the gain of tOKN.

Similar results of experiments 1 and 2 suggested that the effects of accommodation on the tOKN were negligible in these experiments. The gain of tOKN with zero horizontal disparity in this study (0.025, 0.025; Tables 1, 2) was smaller than that in our previous study (0.035–0.041).5 The reason for this is partially due to the smaller size of the torsional optokinetic stimulus. The diameter of torsional optokinetic stimulus in our previous study was 52°, whereas that in the current study was 22°. The differences in the optokinetic stimulus setup (rear projection or HMD) are likely to be additional factors. A higher torsional gain of 0.05 was reported with a rotating stimulus of black disks on a white background,11 which was the reverse of our study.

Torsional OKN and optokinetic after nystagmus (OKAN) have been reported by Zupan and Merfeld12 to induce horizontal nystagmus in accordance with gravito-inertial force resolution theory. The duration of each optokinetic stimulation in our study was half that of theirs and we did not observe consistent induction of horizontal nystagmus during torsional optokinetic stimulation.

The effect of viewing distance and accommodation on torsional vestibulo-ocular reflex (VOR) has been studied. The
torsional VOR decreases with viewing distance, but not with accommodation. The gain of tOKN increased from the 1-m to the 2-m viewing distances and decreased from the 2-m to the 3-m viewing distances. The gain of tOKN does not depend on viewing distance; however, it depends on the horizontal disparity. Therefore, we believe that the existence of horizontal disparity decreases the gain of tOKN.

The pursuit system for OKN is found in the cortical and subcortical nervous system of frontal-eyed vertebrates with foveae and stereopsis (e.g., humans, monkeys and cats). The optokinetic system for OKN is found in the subcortical nervous system of the lower lateral-eyed vertebrates without foveae (e.g., rabbits). The main reason for the evolution of the early part of OKN is to enable animals with stereoscopic vision to deal with complex motion signals generated by linear motions of the 3D world. For example, the images of the objects at different distances move at different angular velocities during linear translation along the interocular axis. Cortical neurons with activity responsive to motion and binocular disparity have been found in several areas (e.g., the primary visual cortex and the medial temporal [MT], and medial superior temporal [MST] areas). Howard and Simpson speculated that the cells responding to moving stimuli with zero disparity selectively augment OKN and enable humans to stabilize the images of parts of the scene in the regarded plane while ignoring competing motion signals arising from other distances.

Although much is known about the neurons and projections that concern the early and the later parts of OKN, interaction between them has not yet been reported. The optokinetic system that is evolutionarily old and developed in lower lateral-eyed vertebrates without stereopsis does not require neural activity corresponding to horizontal disparity. Therefore, we speculate that the optokinetic system for the later part of OKN is influenced by the pursuit system in any direction, i.e., three dimensionally. This interaction may prevent the dissociation between the early and the later parts of OKN, especially in horizontal and vertical directions. An anatomic projection from the visual cortical area to the accessory optic system that is involved in the subcortical optokinetic pathway has the possibility of providing this interaction.

References

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**Table 2. Average Slow-Phase Gain of tOKN in Experiment 2**

<table>
<thead>
<tr>
<th>Subject</th>
<th>Direction</th>
<th>3.0 PD</th>
<th>1.0 PD</th>
<th>0.0 PD</th>
<th>−1.0 PD</th>
</tr>
</thead>
<tbody>
<tr>
<td>YS</td>
<td>Ext.</td>
<td>0.031 (0.014)</td>
<td>0.035 (0.013)</td>
<td>0.052 (0.022)</td>
<td>0.037 (0.020)</td>
</tr>
<tr>
<td></td>
<td>Int.</td>
<td>0.028 (0.011)</td>
<td>0.029 (0.012)</td>
<td>0.045 (0.019)</td>
<td>0.025 (0.008)</td>
</tr>
<tr>
<td>SS</td>
<td>Ext.</td>
<td>0.014 (0.004)</td>
<td>0.014 (0.004)</td>
<td>0.016 (0.004)</td>
<td>0.017 (0.004)</td>
</tr>
<tr>
<td></td>
<td>Int.</td>
<td>0.017 (0.006)</td>
<td>0.018 (0.007)</td>
<td>0.026 (0.012)</td>
<td>0.019 (0.007)</td>
</tr>
<tr>
<td>TM</td>
<td>Ext.</td>
<td>0.015 (0.004)</td>
<td>0.017 (0.005)</td>
<td>0.021 (0.008)</td>
<td>0.013 (0.002)</td>
</tr>
<tr>
<td></td>
<td>Int.</td>
<td>0.024 (0.010)</td>
<td>0.032 (0.012)</td>
<td>0.027 (0.010)</td>
<td>0.019 (0.007)</td>
</tr>
<tr>
<td>SY</td>
<td>Ext.</td>
<td>0.015 (0.004)</td>
<td>0.013 (0.003)</td>
<td>0.013 (0.003)</td>
<td>0.012 (0.005)</td>
</tr>
<tr>
<td></td>
<td>Int.</td>
<td>0.014 (0.004)</td>
<td>0.015 (0.004)</td>
<td>0.018 (0.005)</td>
<td>0.015 (0.015)</td>
</tr>
<tr>
<td>KM</td>
<td>Ext.</td>
<td>0.016 (0.005)</td>
<td>0.016 (0.005)</td>
<td>0.014 (0.005)</td>
<td>0.018 (0.007)</td>
</tr>
<tr>
<td></td>
<td>Int.</td>
<td>0.014 (0.004)</td>
<td>0.015 (0.004)</td>
<td>0.015 (0.004)</td>
<td>0.012 (0.001)</td>
</tr>
<tr>
<td>Grand average</td>
<td></td>
<td>0.019 (0.006)</td>
<td>0.020 (0.008)</td>
<td>0.025 (0.013)</td>
<td>0.019 (0.008)</td>
</tr>
</tbody>
</table>

Data and abbreviations are as in Table 1. n = 10. PD, prism diopter.