

Reevaluating the Role of Otolith Organs in Nystagmus Generation: An Experimental Approach

Hiroaki Ichijo¹ & Hisako Ichijo¹

¹ Ichijo Ear, Nose and Throat Clinic, 3-2-1, Ekimae, Hirosaki, Japan

Correspondence: Hiroaki Ichijo, MD, PhD, Ichijo Ear, Nose and Throat Clinic, 3-2-1, Ekimae, Hirosaki, Japan 036-8002. Tel: 081-172-39-6222. Fax: 081-172-39-6222. E-mail: hiro3387@mvj.biglobe.ne.jp

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Abstract

This study investigates whether the otolith organs—the utricle and saccule—are involved in generating nystagmus. Using both human subject experiments (sway and squat tests) and inertial physical models, we demonstrate that linear accelerations do not produce nystagmus, challenging the prevailing view of an otolith-ocular reflex. Our results suggest that nystagmus is primarily mediated by the semicircular canals, while the otolith organs remain essential for body balance and gravity sensing. These findings prompt a reevaluation of vestibular reflex pathways and highlight the need for further investigation into vestibular physiology.

Keywords: utricle, saccule, linear acceleration, video-oculography, inertial force

1. Introduction

The otolith organs, comprising the utricle and saccule, contain tiny calcium carbonate crystals (otoconia) embedded in a gelatinous matrix (otolithic membrane) that bends hair cell cilia in response to gravity and linear acceleration. Hair cells in the otolith organs are always transmitting crucial information regarding head position to the vestibular nucleus. Therefore, in patients with unilateral vestibular neuritis, strong spontaneous nystagmus and severe disequilibrium occur.

The mechanism of sensation is the bending of the cilia. Have you ever wondered why we do not see continuous eye movements even though our otolith organs are constantly active? This puzzling observation inspired our study.

Once the ocular counter-roll was discovered, it was assumed that the otolith organs are involved in eye movements. Curthoys [1] reported that upward eye movements were evoked by stimulation to the unilateral macula of the utricle, while Goto et al. [2] showed that horizontal eye movements were evoked by the selective stimulation of the utricular nerve in cats. Additionally, Furman et al. [3] reported that off-vertical axis rotation has the potential of becoming a useful method for clinical assessing both the otolith-ocular reflex and semicircular canal otolith interaction.

However, these findings should be treated with caution because of the Epley maneuver [4]. Pathophysiology of benign paroxysmal positional vertigo is pathological debris in the semicircular canal. The principle of the Epley maneuver is moving debris from a long arm to the utricle. We have noticed that no one showed nystagmus in the sitting position after the treatment. Just after the Epley maneuver, pathological debris stimulates the macula of the utricle. Nevertheless, no patient complained of vertigo and no patient revealed nystagmus.

Morphologically, otolith organs and semicircular canals are completely different. The arrangement of hair cells in the utricle is not linear. It is loose C-shaped and is arranged like the seats of a coliseum. This tendency is strong in the saccule, where the arrangement of cells is U-shaped. On the other hand, the cells of the semicircular canal crista are arranged in an orderly manner and the direction selectivity of them is strong. For example, if only the lateral semicircular canal is stimulated by the caloric test, horizontal nystagmus occurs.

The difference in cell arrangement means that they are also functionally different. The curvilinear cell arrangement of otolith organs may be advantageous for sensing forces in all directions of 360 deg. The forces here are gravity and inertial forces. Since force is a vector, it has direction and magnitude.

It is necessary to sense gravity for maintenance of posture even in a stationary state. That is to say, even if a human is stationary, the otolith organs cilia are bent. Twenty-four hours a day, the otolith organs are constantly sending action potentials to the vestibular nucleus. If nystagmus is caused by the cilia flexion, then all animals should be constantly producing nystagmus. However, this is not the case, which raises questions concerning the very existence of the otolith-ocular reflex.

Murofushi et al. [5] proposed a concept of idiopathic otolithic vertigo with endolymphatic hydrops in the otolith organ. However, Ichijo [6] reported that no patient with benign paroxysmal positional vertigo complained of dizziness just after the canalith repositioning procedure, despite of direct stimulation to the utricle by the pathological debris. So, it is controversial whether the left-right difference of otolith organs causes dizziness.

We hypothesize that the otolith organs do not produce nystagmus and that the vestibulo-ocular reflex is exclusively mediated by the semicircular canals. To test this, we conducted controlled experiments that produce the forces acting on the otolith organs and observed the resultant eye movements.

In this study, we first test whether lateral head translations (sway) and vertical squats stimulate the utricle and saccule, respectively, leading to nystagmus. Then, using controlled physical experiments with inertial objects, we further validate our hypothesis.

2. Materials and Methods

Subjects of Experiments 1 and 2 were five healthy humans with no ear pathologies.

Experiment 1 (sway)

This experiment was designed to examine whether lateral acceleration (sway) triggers the expected inertial forces on the utricle that, according to some theories, would lead to nystagmus. First, it was confirmed that yaw, pitch, and roll rotations of the head can develop good horizontal, vertical, and torsional nystagmus. Second, each subject stood with their feet shoulder-width apart while keeping their neck in a fixed position. They were instructed to perform a controlled sway by alternately lifting their left and right heels, resulting in a lateral head translation. Each subject completed three full cycles at an average frequency of 0.33 Hz, covering a distance of approximately 0.3 m per cycle. This setup was designed to selectively stimulate the utricle by generating lateral inertial forces. Eye movements were recorded and converted to digital data.

Experiment 2 (squat)

This experiment was designed to examine whether vertical acceleration (squat) triggers the expected inertial forces on the saccule that, according to some theories, would lead to nystagmus. Subjects performed three vertical squats while maintaining a consistent shoulder-width stance. The movement was executed at a controlled frequency of 0.33 Hz, with an approximate vertical displacement of 0.3 m. This procedure was intended to activate the saccule through vertical inertial forces. Eye movements were recorded and converted to digital data.

In Experiments 3 and 4, we modeled inertial forces using a simple physical system. An orange plastic cap was attached to the tip of a spring to simulate an otoconium's behavior. In Experiment 3, the assembly was jerked sideways to observe the inertial response, while in Experiment 4, it was jerked downward. The movement of the cap was recorded and analyzed to determine the direction of the inertial force, which we expected to be opposite to the direction of acceleration.

Eye Movements Analysis (Figure 1)

Experiments 1 and 2 were performed in the dark with the subjects' eyes open using an infrared charge-coupled device camera. Eye movements were recorded and converted to digital data. Three-dimensional video-oculography was performed using ImageJ version 1.36 software (a public domain, Java-based image-processing program developed at the National Institutes of Health). For analysis of the horizontal and vertical components, the XY center of the pupil was calculated. For analysis of the torsional component, the whole iris pattern, which was rotated in steps of 0.1° , was overlaid with the same area of the next iris pattern, and the angle at which both iris patterns showed the greatest match was calculated [7].

3. Results

Table 1 shows the results of Experiments 1 and 2. Movies show the results of all experiments [8].

Experiment 1

None of the subjects exhibited nystagmus. Although jerky nystagmus did not occur, slight drift of eye balls arose. The average of maximum deviation of the horizontal component from the baseline was 3.9 deg. Figure 2 shows the video-oculography of Subject 5.

Experiment 2

None of the subjects exhibited nystagmus. Although jerky nystagmus did not occur, slight drift of eye balls arose. The average of maximum deviation of the vertical component from the baseline was 4.8 deg. Figure 3 shows the video-oculography of Subject 5.

Experiment 3

At the beginning of the movement, the orange cap moved to the left, in the opposite direction to the acceleration.

Experiment 4

At the beginning of the movement, the orange cap moved upward, in the opposite direction to the acceleration.

Table 1. Results of Experiments 1 and 2

Subject	Age (years)	Sex	Experiment 1	Experiment 1	Experiment 2	Experiment 2
			Nystagmus	Maximum deviation of horizontal component (deg)	Nystagmus	Maximum deviation of vertical component (deg)
1	33	Female	—	5.7	—	4.3
2	43	Female	—	4.3	—	5.7
3	53	Female	—	4.3	—	10
4	64	Male	—	4.0	—	1.4
5	65	Male	—	1.4	—	2.8
Mean	51.6			3.9		4.8

4. Discussion

Our experiments demonstrate that neither lateral translations (sway) nor vertical movements (squat) induce nystagmus, even though the otolith organs are undoubtedly stimulated by these movements. If the otolith organs were responsible for initiating nystagmus, then the constant gravitational stimulation should result in continuous nystagmus. However, since no nystagmus is observed under static conditions, this supports the alternative hypothesis that nystagmus arises only from semicircular canal stimulation.

The results of Experiment 3 show that an object receives an inertial force in the opposite direction to the acceleration. This is Newton's first law, which states that anything at rest has the tendency to stay at rest. The resulting inertial force is the product of mass and acceleration.

In Experiment 1 (sway), lateral linear acceleration should have induced inertial forces on the otoconia, stimulating the utricle. The results showed that no nystagmus occurred, confirming that nystagmus does not arise from the utricle.

For convenience, we assumed that one otoconium sits on the top of one hair cell in the utricle (Figure 4). Where the mass of an otoconium is m , the weight of the otoconium is mg . Because the otoconium is present in the endolymph, a buoyancy is generated with a magnitude of ρVg (Archimedes' principle). Therefore, the force $F1$ that the otoconium presses against the otolithic membrane is $mg - \rho Vg$. If an acceleration (magnitude of it is a) is applied to the left, the resulting inertial force $F2$ is the apparent mass $(m - \rho V)$ multiplied by a . This force deforms the otolithic membrane and causes the bending of cilia toward the right. However, no nystagmus was observed, confirming that the utricle does not cause nystagmus.

The results of Experiment 4 show that an inertial force also occurs in the vertical direction, in the opposite direction to the acceleration. In Experiment 2 (squat), the saccule should be stimulated by the inertial force generated by the vertical linear acceleration. However, the fact that nystagmus does not occur is evidence that nystagmus does not arise from the saccule.

Again, for convenience, we assumed that one otoconium sits on the top of one hair cell (Figure 5). If the mass of the otoconium in the saccule is m , the weight of the otoconium is mg . Because the otoconium is present in the endolymph, a buoyancy is generated, with a magnitude of ρVg . Therefore, the force $F3$ exerted on the otoconium is $mg - \rho Vg$. When a downward acceleration (magnitude of it is a) is applied by squatting, the resulting inertial force $F4$ is the apparent mass $(m - \rho V)$ multiplied by a . This force deforms the otolithic membrane of the saccule, bending the hair cell cilia upward. However, no nystagmus was produced, confirming that the saccule does not cause nystagmus.

Theoretical physics can explain why nystagmus does not originate from the otolith organs. All animals, including humans, sense gravity through their otolith organs. Specifically, both saccule and utricle are constantly stimulated by gravity. Even in an upright position, action potential occurs in a hair cell, because the weight of otoconia pushes the cilia. Even if the head is stationary, a hair cell is transmitting crucial information regarding head position to the vestibular nucleus. Namely, vestibular nerves are continuously stimulated throughout the lifetime of every animal on Earth. If nystagmus were to be generated by the action potential of hair cells, all animals should be constantly producing nystagmus. However, this is not the case. Therefore, we can conclude that nystagmus is not caused by the otolith organs.

Maximising the angle of flexion of the cilia of the utricle can be easily achieved by lying in a lateral position. In the right lower lateral position, gravity pushes the cilia to the right (Figure 6). If the ocular counter-roll was the utricle ocular reflex, leftward torsional nystagmus should continue with this head position. However, nothing happens, which proves that nystagmus does not originate from the utricle.

The vestibulo-ocular reflex is a kind of spinal reflex, with gaze maintained by involuntary compensatory eye movements in the opposite direction to head rotation. Usually, the receptor for a spinal reflex is one organ, such as the cochlea for the stapedial reflex, and the retina for the pupillary light reflex. In the vestibulo-ocular reflex, if the receptors are two organs, the semicircular canals and the otolith organs, there will be two input systems, which will confuse the central nervous system. Semicircular canals are the only receptors for the vestibulo-ocular reflex, and the otolith organs are thought to be primarily involved in body balance.

Phylogenetically, otolith organs predate semicircular canals. For example, jellyfishes do not have semicircular canals, but they do have otolith organs [9]. Since primitive animals moved slowly, the otolith organs that sense gravity were probably sufficient. Later on, as vision evolved and the eyeballs began to move, semicircular canals became necessary to maintain vision, which is when the three semicircular canals were thought to have developed in order to control eye movements. The role of the otolith organs is to sense gravity, and it is thought that this has not changed since the time of lower animals because the basic structure of the otolith organ is the same in all animals.

Several researchers have attempted to evaluate the otolith organs' function using eye movements. Darlot et al. [10] reported that horizontal nystagmus was induced by off-vertical axis rotation and speculated that it originates from the otolith organs. Sadeghpour et al. [11] determined that the function of otolith organs can be measured by ocular counter-roll (torsional eye movements). It is unlikely that two types of nystagmus can be caused by one organ since the mechanism of stimulus perception is a simple movement, namely the flexion of cilia. Horizontal nystagmus and torsional nystagmus occurring at different times is highly improbable.

The absence of nystagmus following otolithic stimulation suggests that clinical tests relying solely on nystagmus may not accurately assess otolith function. This could lead to a revision of diagnostic protocols for vestibular disorders.

Ocular counter-roll caused by roll rotation can be explained if it originates in the semicircular canals rather than the utricles. There are three semicircular canals on each side, positioned so that they can sense angular acceleration in all directions. It is reasonable, therefore, to assume that the bilateral posterior and anterior semicircular canals are stimulated simultaneously during roll rotation, resulting in torsional nystagmus.

Although semicircular canals sense angular acceleration, our experiments showed that they do not respond to linear acceleration. Ichijo [12] speculated that the cupula receives inertial forces induced by linear acceleration. However, our results showed that this is incorrect and that the cupula responds to only angular acceleration.

This study has a limitation. Five subjects were selected as a pilot study to provide preliminary insights into the otolith-ocular relationship. Future studies with larger cohorts will be necessary to generalize these findings.

5. Conclusions

Our study not only challenges the long-held belief that the otolith organs generate nystagmus but also paves the way for improved diagnostic strategies in vestibular disorders. Our results support the hypothesis that the ocular counter-roll is a semicircular canal ocular reflex.

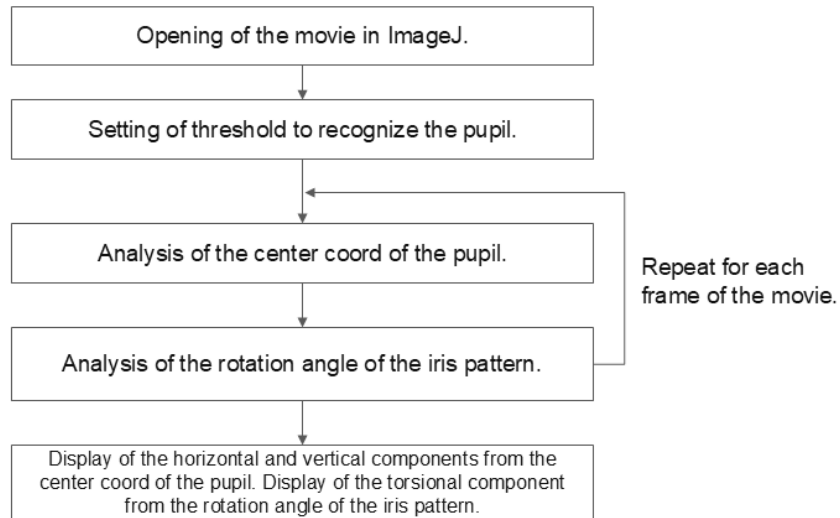


Figure 1. Flowchart of eye movements analysis.

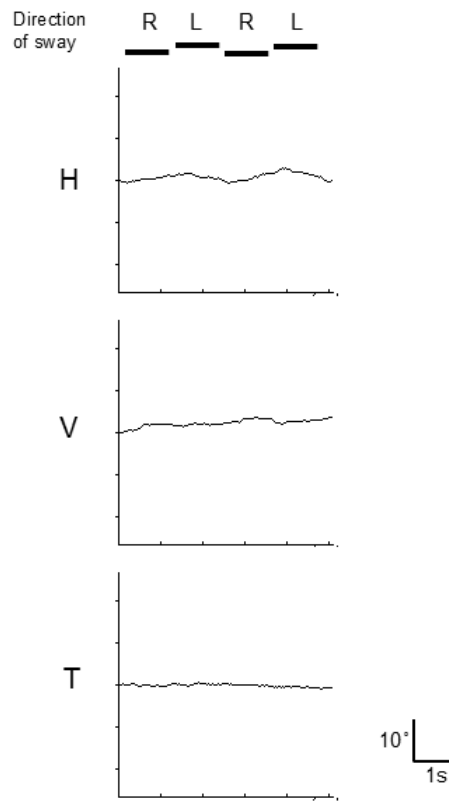


Figure 2.

Video-oculography (position trace) of Subject 5. Sway did not produce nystagmus. The upward deflections in horizontal (H), vertical (V), and torsional (T) eye movements are indicated as being toward the right, upward, and right, respectively. R = Right, L = Left.

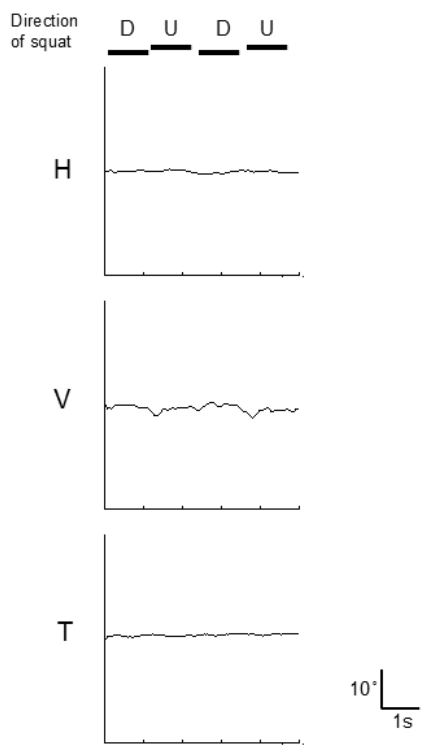


Figure 3.

Video-oculography (position trace) of Subject 5. Squat did not produce nystagmus. The upward deflections in horizontal (H), vertical (V), and torsional (T) eye movements are indicated as being toward the right, upward, and right, respectively. D = Downward, U = Upward.

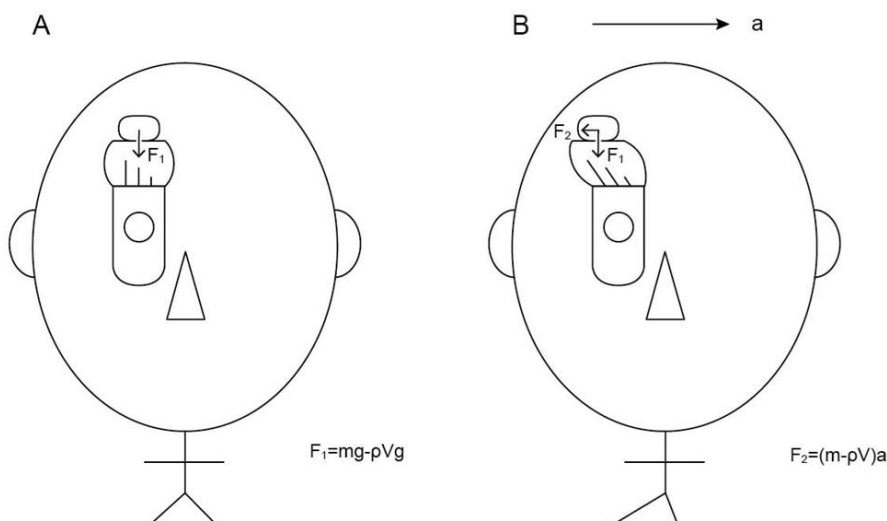


Figure 4.

A: Rest.

B: Sway to the left. Inertial force deforms the otolithic membrane and causes the cilia to bend to the right. However, the eyeballs did not move, confirming that the utricle does not produce nystagmus. a = Acceleration of the head. m = Mass of the otoconium. g = Gravitational acceleration. ρ = Density of endolymph. V = Volume of the otoconium.

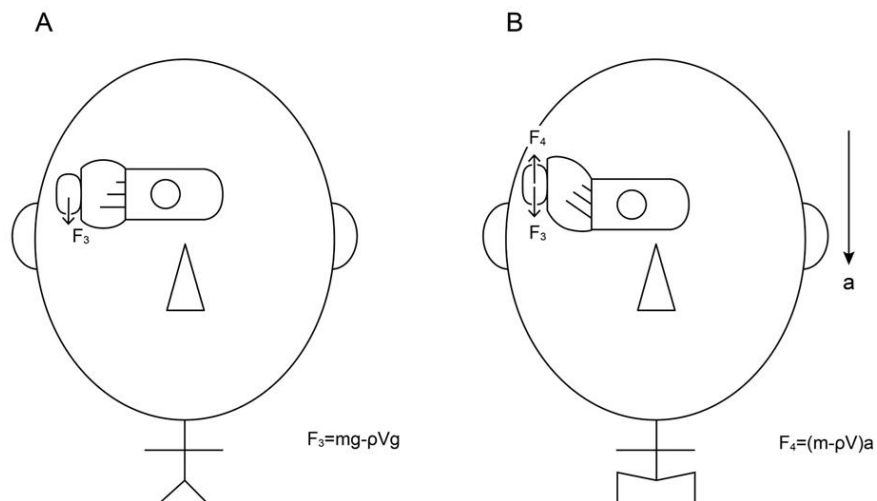


Figure 5.

A: Rest.

B: Squat down. Inertial force deforms the otolithic membrane of the saccule, bending the cilia of the hair cell upward. However, the eyeballs did not move, meaning that the saccule does not produce nystagmus. a = Acceleration of the head. m = Mass of the otoconium. g = Gravitational acceleration. ρ = Density of endolymph. V = Volume of the otoconium.

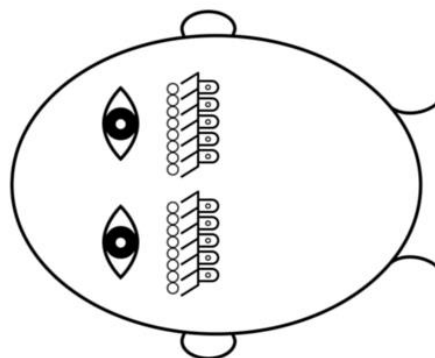


Figure 6.

Maximizing the angle of flexion of the cilia of the utricle can be easily achieved by lying in a lateral position. In the right lower lateral position, gravity pushes the cilia to the right. If the ocular counter-roll was the utricle ocular reflex, leftward torsional nystagmus should continue with this head position. However, nothing happens, which proves that nystagmus does not originate from the utricle.

Conflict of Interest

We declare that we have no conflict of interest.

Acknowledgments

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