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The saccule and gravity

Hiroaki Ichijo and Hisako Ichijo

Ichijo Ear, Nose and Throat Clinic, Hirosaki, Japan

Abstract

Background. The important role of the saccule is the sensing of gravity. In other words, gravity always stimulates the macula of the saccule.

Objectives. The aim of this study was to clarify whether nystagmus and dizziness occur by intentional changes upon stimulation to the saccules.

Methods. The subjects were eight healthy humans. Experiment 1: Subjects were asked to maintain a supine position to check for nystagmus and dizziness. Experiment 2: Subjects were asked to tilt their heads 45° to the left in the supine position to check for nystagmus and dizziness. Experiment 3: Subjects were asked to maintain a left-ear-down 90° position to check for nystagmus and dizziness.

Results. In all the experiments, no one revealed nystagmus and no one complained of dizziness.

Conclusion. Neither nystagmus nor dizziness occurs by intentional changes in the stimulation to the saccules.

Main Article

Hiroaki Ichijo takes responsibility for the integrity of the content of the paper

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Corresponding author: Hiroaki Ichijo; Email: hiro3387@mvj.biglobe.ne.jp

Introduction

Otolithic organs are the utricle and saccule, the important role of which is the sensing of gravity. The earth's gravity has been constant for billions of years, and all forms of life experience it. Plants sense gravity leading to their stems growing towards the sky and roots towards the earth. Animals maintain their posture by sensing gravity using their otolithic organs. Otolithic organs are phylogenetically the oldest sensory organs, and are even present in primitive organisms such as jellyfish.[1] Animals have evolved to move faster and may also sense acceleration.

The human saccule is an ellipsoidal organ located at the level of stapes (Figure 1), close to the bottom of the internal auditory meatus, and the macula is attached to the bone wall. The length of its major axis is almost the same as the base of the stapes, and it is about 3000 μm.

The microstructure of the saccule is known (Figure 2). The jelly-like otolithic membrane is attached to the side of the hair cells with a group of otoconia.[2] The thickness of the group of otoconia is about 40 μm. Gravity is sensed by the weight applied to the otoconia, which are heavier than endolymph.

Since the direction of gravity acting on the otoconium is always towards the centre of the earth, a head tilt is sensed by how much the angle differs from this direction. This is caused by the flexion of the cilia of hair cells.

Figure 2 shows the state of the saccule in the supine position. If the mass of the group of otoconia is m, a force, mg, is generated in the direction to the earth (g is gravitational acceleration). This force leads to mild bending of the cilia. In other words, even if a man is stationary, action potentials are emitted from the saccule. When the head is tilted in a plane parallel to the XY plane, the direction of gravity exerted on the otoconia changes, and the angle of flexion of the cilia also changes. When nodding in a plane parallel to the YZ plane, the angle of flexion of the cilia changes. However, tilting in a plane parallel to the XZ plane does not change the bending of cilia.

To calculate the mass of the otoconia in the human saccule, Igarashi *et al.*[3] reported that the area of the saccular macula is about 2.2×10^6 μm^2. Although few studies have measured the thickness of the group of otoconia, we have estimated it from some tissue samples to be about 40 μm.[4–6] Therefore, the volume of the otoconia group is $2.2\times10^6\times40 = 8.8\times10^7$ μm^3. The mass of water of the same volume is 8.8×10^{-2} mg. Since the specific gravity of otoconia is 2.7, its mass is $2.7\times8.8\times10^{-2} = 23.8\times10^{-2}$ mg.

Endolymph is a liquid next to the otoconia that produces water pressure that pushes or pulls the saccular macula during head position changes.

To calculate the mass of the endolymph in the saccule. Igarashi *et al.*[3] reported that the volume of the saccule is about 2×10^9 μm^3. The mass of water in the same volume is 2 mg. Since the specific gravity of the endolymph is almost 1, its mass is 2 mg. Since $2/(23.8\times10^{-2})$ is approximately 8.4, the mass of endolymph in saccule is 8.4 times greater than the mass of the otoconia group.

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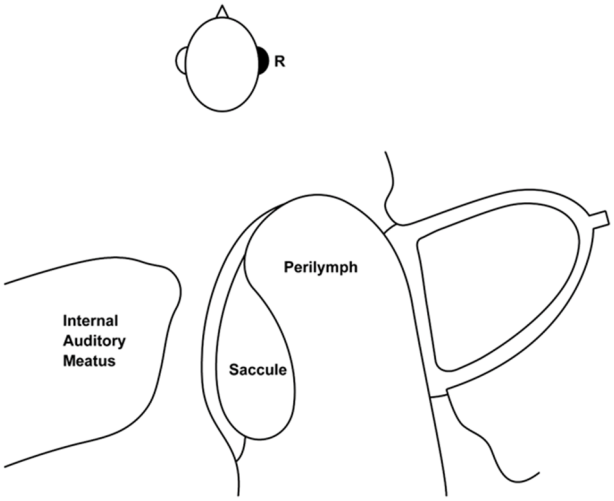


Figure 1. The position of the right saccule. The saccule is filled with endolymph, and perilymph is present around it. R = right.

Naturally, gravity also acts on the endolymph and affects the macula as water pressure. Outside the endolymph, perilymph is present. It also produces water pressure on the macula. This fact has been overlooked until now.

Since the discovery of ocular counter-roll, it has been thought that the otolithic organs are involved in eye movements. In animal experiments, there have been some studies that eye movements were caused by nerve stimulation,[7–9] and Sadeghpour *et al.*[10] reported that the otolithic organ function can be evaluated by measuring eye movements due to head tilt. However, this theory has been questioned because nystagmus does not occur in the sitting position immediately after the canalith repositioning procedure in patients with benign paroxysmal positional vertigo.[11]

Morphologically, otolithic organs and semicircular canals are completely different. The arrangement of hair cells in the utricle is not linear but a loose C-shape and is arranged like the seats of a coliseum, and in the saccule, the arrangement is U-shaped. On the other hand, the cells of the semicircular canal crista are arranged in an orderly manner, and their direction selectivity 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 the difference of function. The curvilinear cell arrangement of the saccule may be advantageous for sensing forces (gravity and inertial force) in all directions. Since force is a vector, it has direction and magnitude. There are thousands of hair cells to sense both direction and magnitude. Sensing gravity is important to maintain posture even when in a stationary position. In other words, even if a human is stationary, cilia are bent. Twenty-four hours a day, the otolithic organs are constantly sending action potentials to the vestibular nucleus. If nystagmus is caused by cilia flexion, then all animals should constantly produce nystagmus. However, this is not the case, which raises questions about the very existence of the otolith–ocular reflex.

Murofushi *et al.*[12] proposed a concept of idiopathic otolithic vertigo with endolymphatic hydrops in the otolithic organs. However, Ichijo[13] reported that no patient with benign paroxysmal positional vertigo complained of dizziness just after the Epley maneuver, despite direct stimulation to the utricle by pathological

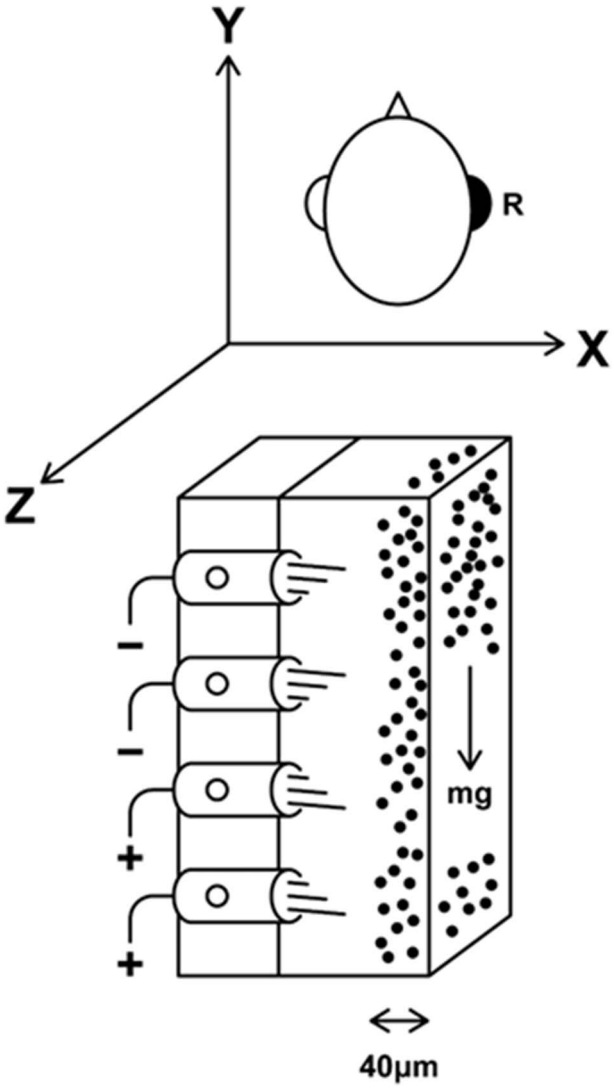


Figure 2. Microstructure of the right saccule. The macula is vertical in the supine position. The weight of the otoconia group causes a small ciliary bend. m = mass of otoconia group. g = gravitational acceleration; R = right.

debris. Therefore, it is controversial whether the left–right difference of the otolithic organs causes dizziness. As mentioned above, there is no consensus on the function of the otolithic organs.

To investigate the function of the saccule, we conducted three experiments on human beings. The aim of this study was to clarify whether nystagmus and dizziness occur by intentional changes upon stimulation to the saccules.

Methods

The subjects were eight healthy individuals.

Experiment 1

Subjects were asked to maintain a supine position for 30 seconds to check for nystagmus and dizziness.

Experiment 2

Subjects were asked to tilt their heads 45° to the left for 30 seconds in the supine position to check for nystagmus and dizziness.

Experiment 3

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Table 1. Results

	y		Experiment 1		Experiment 2		Experiment 3	
Subject	Age (years)	Sex	Nystagmus	Dizziness	Nystagmus	Dizziness	Nystagmus	Dizziness
1	42	Female	–	–	–	–	–	–
2	54	Female	–	–	–	–	–	–
3	58	Male	–	–	–	–	–	–
4	59	Female	–	–	–	–	–	–
5	60	Female	–	–	–	–	–	–
6	62	Female	–	–	–	–	–	–
7	66	Male	–	–	–	–	–	–
8	72	Female	–	–	–	–	–	–

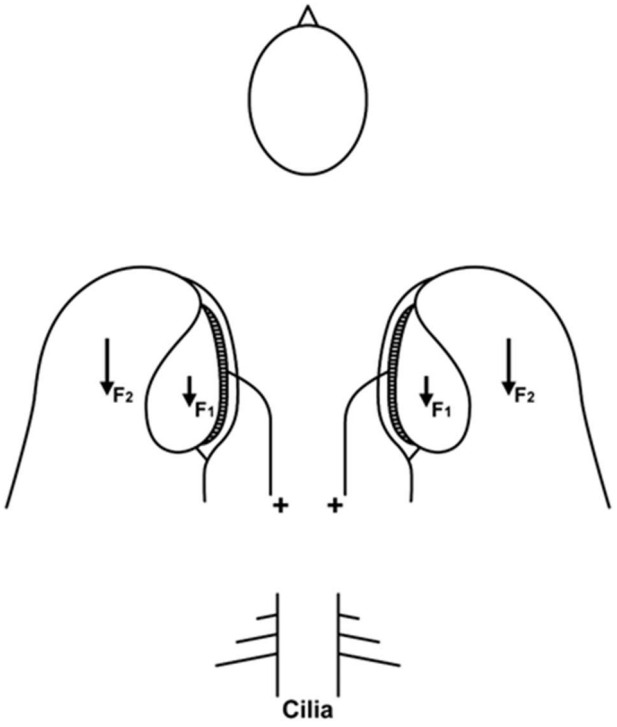


Figure 3. In the supine position, only the weight of the otoconia group is applied to the cilia, and the stimulation of the macula is weak. F_1 = weight of endolymph; F_2 = weight of perilymph.

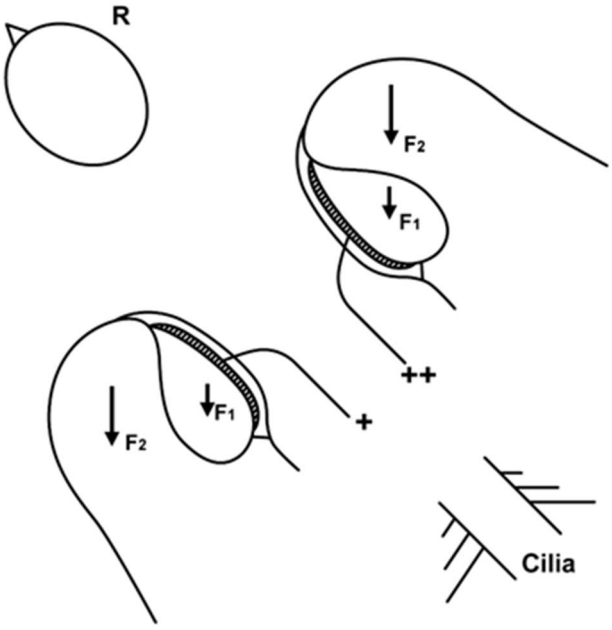


Figure 4. In the left-ear-down 45º position, the right macula perceives positive water pressure, and the left macula perceives negative water pressure. The state of stimulation on the left and right is completely different. F_1 = weight of endolymph; F_2 = weight of perilymph; R = Right.

Subjects were asked to maintain a left-ear-down 90º position for 30 seconds to check for nystagmus and dizziness.

Eye movements in the dark were observed and recorded using an infrared camera.

Results

In all the experiments, no one revealed nystagmus and no one complained of dizziness (Table 1).

Discussion

We found that nystagmus and dizziness do not occur upon changing the stimulation of the saccules (ciliary flexion). Hair cells emit action potentials by ciliary flexion. For example, in the semicircular canal, the greater the flexion of the cupula, the greater the flexion of the cilia, and the stronger the nystagmus. Even in the cochlea, the louder the sound transmitted to the perilymph, the greater the flexion of the cilia. Similarly for otolithic organs, the greater the flexion of the cilia, the greater the excitation of the cells.

In Experiment 1 (Figure 3), the position of the saccular macula is almost vertical in the supine position. Thus, the cilia are almost horizontal. In this state, the water pressure of the endolymph (F_1) and perilymph (F_2) on the macula is weak, only the weight of the otoconia group is applied to the cilia, and the stimulation of the macula is weak. There is no nystagmus and dizziness due to no difference between the left and right.

Therefore, we intentionally made a left–right difference. In Experiment 2, the right macula is subjected to endolymphatic water pressure and perilymphatic water pressure (Figure 4). The weight of the otoconia is also applied to the macula, but it is overwhelmingly small compared to the water pressure of the

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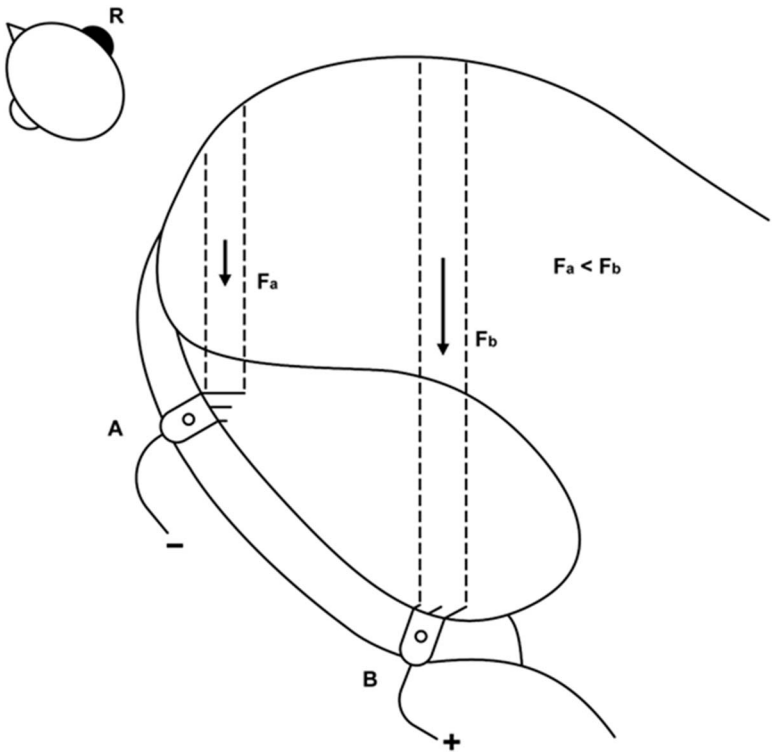


Figure 5. The state of the right macula in the left-ear-down 45° position. The water pressure exerted on cell A is less than that exerted on cell B. Therefore, the excitability of the two is different. Fa = water pressure on the cell A; Fb = water pressure on the cell B; R = Right.

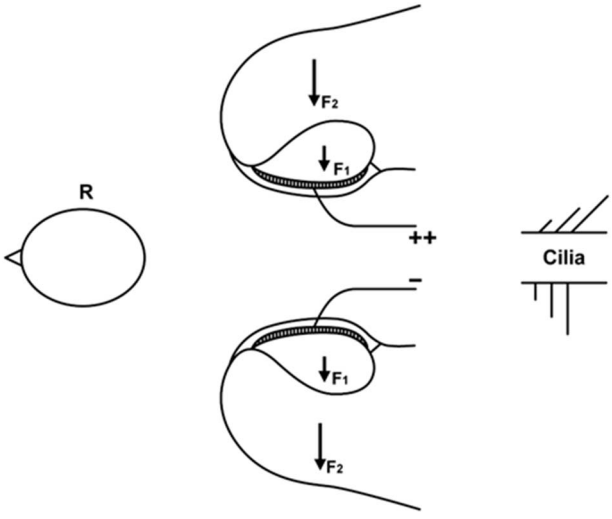


Figure 6. In the left-ear-down 90° position, the left-right difference of stimulation is maximized. F_1 = weight of endolymph; F_2 = weight of perilymph; R = right.

endolymph, so it is omitted for convenience. Negative pressure is applied to the left macula in the same direction, and the excitability of the cells decreases, resulting in a significant left–right difference. However, neither nystagmus nor dizziness occurred.

Focusing on two hair cells, A and B, equidistant from the centre of the right macula (Figure 5). The water pressure on cell A is *Fa*, and that on cell B is *Fb*. Since the magnitude of the water pressure is proportional to the mass of water above the cell, *Fa* is completely smaller than *Fb*. Moreover, ciliary polarization is different above and below the striola. In cell A, an inhibitory stimulus occurs, while in cell B, an excitatory stimulus occurs. Therefore, the excitability of the two is different. This illustrates an important fact. The change of the head position causes an uneven degree of excitation of the macula. We speculate that this unevenness is an important factor for sensing head tilt.

Excitation can be uneven. Strictly speaking, the flexion angle of cilia of each cell is not the same, because the macula is slightly curved rather than planar.[2] Furthermore, since the arrangement of cilia is not linear and the polarity of each cell is not in the same direction, there will be a difference in ciliary flexion. This phenomenon is concerned about the recovery of balance system. For example, a patient who has undergone labyrinthectomy with unilateral acoustic neuroma will have no balance problem after a while. It is thought that the ability to sense the tilt of the head even with one-sided inner ear is due to this ability to sense uneven excitation.

Next, in Experiment 3, the left-ear-down 90° position, the right macula is perpendicularly subjected to endolymphatic pressure (F_1) and perilymphatic pressure (F_2), and the ciliary flexion is maximized (Figure 6). On the other hand, in the left macula, negative endolymphatic pressure and negative perilymphatic pressure are applied in the same direction, and ciliary flexion is minimized. In other words, the left–right difference in input in the vestibular nucleus is maximized. However, no nystagmus occurred and no one complained of dizziness.

As described above, even if the left–right difference was intentionally created in the maculae, dizziness and nystagmus did not occur. Therefore, nystagmus does not emanate from the saccule. For example, as in the caloric test, if there is a left–right difference in the stimulation of the lateral semicircular canals, nystagmus and dizziness occur. The fact that nystagmus does not occur even if there is a difference between the left and right saccules means

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that the function of the saccule completely differs from that of the semicircular canal.

Rather, we considered that the important role of the saccules is to create a left–right difference in excitability, and the central nervous system can sense head tilt by this difference.

Since our results indicate that eye movements analysis cannot evaluate the function of the saccule, VEMP (vestibular-evoked myogenic potentials) testing is needed to test it. By combining VEMP and head position changes,[14] it may be possible to examine abnormalities in the saccule. We expect further research.

- Gravity always stimulates the macula of the saccule
- Endolymph is a liquid that pushes or pulls the saccular macula during head position changes
- The function of the saccule completely differs from that of the semicircular canal
- Neither nystagmus nor dizziness occurs by intentional changes in the stimulation to the saccules

Conclusions

Neither nystagmus nor dizziness occurs by intentional changes in the stimulation to the saccules. When the head is tilted, the excited state of hair cells becomes uneven. We speculate that this unevenness and the left–right difference in input to the vestibular nucleus may contribute to perceive head tilt.

Disclosures. All authors of this manuscript have read and agreed to its content and are accountable for all aspects of the accuracy and integrity of the manuscript. This article is original work that is not being considered or reviewed by any other publication and has not been published elsewhere in the same or a similar form.

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Competing interests. We declare that we have no conflicts of interest.

Ethical approval. All procedures performed in this study were in accordance with the ethical board of the Hirosaki Medical Association (certificate number is 2024-118).

Informed consent. Informed consent was obtained from all individual participants included in this study.

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