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Four Kinds of Forces Exerted on the Utricle

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Abstract

Objective:

The utricle is commonly understood to detect gravity and horizontal linear acceleration. We hypothesized that it may also respond to vertical linear acceleration, horizontal angular acceleration, and centrifugal force.

Methods:

We performed six physical analogy experiments using deformable media, spring-mounted masses, and human squatting tasks (five healthy humans). Observations included deformation patterns and eye movement recordings.

Results:

(1) Submerged lead deformed the pudding, modeling gravitational deformation. (2–3) Spring-mounted masses deflected opposite to the direction of acceleration. (4) Human vertical motion did not elicit nystagmus. (5) Sudden rotation caused tangential deflection. (6) Constant-speed circular motion led to outward (centrifugal) deflection.

Conclusion:

The utricle can detect four distinct forces—gravity, horizontal and vertical linear acceleration, tangential angular acceleration, and centrifugal force—which suggests broader roles in postural control. Although utricular hair cells are continuously stimulated by Earth's gravity, no nystagmus is observed under static conditions. Thus, static utricular activation alone does not elicit nystagmus. However, further studies are needed to quantify these effects and determine their physiological significance.

Keywords: otolithic organ, gravity, linear acceleration, angular acceleration, centrifugal force

1. Introduction

The otolithic organs, the utricle and saccule, are thought to be involved in sensing gravity and linear acceleration. By design, the utricle's horizontal macula primarily detects head tilt and acceleration in the horizontal plane. However, given the utricle's mass (otoconia) and gelatinous coupling [1], it is plausible that other inertial forces (e.g. angular or centrifugal) might also deform the macula. No definitive study has clarified which forces truly stimulate the utricle. We therefore hypothesized that, in addition to gravity and horizontal acceleration, the utricle may respond to vertical linear acceleration, tangential (horizontal) angular acceleration, and centrifugal force.

Notably, the head's center of rotation lies near the second cervical vertebra (C2), not at the inner ear. This eccentric rotation means that during head turns the labyrinth experiences off-center motion, potentially exposing the utricle to tangential inertial forces.

Some studies indicate that utricular stimulation can drive eye movements [2]. Animal studies have shown that direct utricular nerve stimulation can evoke eye movements [3,4]. Off-vertical axis rotation in humans also elicits nystagmus [5], reflecting both semicircular canal and otolith inputs. However, the origin of this nystagmus is debated.

In benign paroxysmal positional vertigo, canalith repositioning [6] moves debris into the utricle, yet patients often have little or no nystagmus in the sitting position post-treatment [7,8]. This suggests that pure utricular stimulation may not induce nystagmus. Such observations have led to debate over an "otolith-ocular reflex".

Herein, we present a series of physical and human experiments designed to clarify which inertial forces act upon the utricle. Our goal was to determine the type and direction of forces that could deflect the utricular otolithic membrane and hair cells.

2. Materials and Methods

Experiment 1

We used a 4cm layer of gelatin dessert (agar pudding) submerged in water to simulate the utricular macula. A 7g lead weight (specific gravity, 11.4) was gently placed on top of the gelatin. We repeated the same experiment twice. The condition of the pudding was observed.

Experiment 2

A plastic ball (2.5g) was connected to the top of a spring which was then moved laterally. Estimated linear acceleration was 0.92m/s^2. Spring constant (k) of the spring was 0.63N/m. We repeated the same experiment twice. Spring constant (k) was calculated based on the Hooke's law. It states that the force is proportional to the extension.

Experiment 3

A plastic ball (2.5g) was connected to the top of a spring which was then sharply moved vertically (upward). Estimated linear acceleration was 0.82m/s^2. Spring constant (k) of the spring was 0.63N/m. We repeated the same experiment twice.

Experiment 4

After confirming the vestibulo-ocular reflex in darkness (horizontal, vertical, and torsional) of five healthy subjects, we asked them to perform squat three times with their necks fixed and observed eye movements. The frequency was approximately 0.33Hz and the amplitude was approximately 0.3m. 0.33 Hz has no special meaning; it is a frequency that can be repeated comfortably, at 20 times per minute. Estimated peak head acceleration was 0.53m/s^2.

Experiment 5

A plastic ball (2.5g) connected to the top of a spring was placed on a swivel chair which was then rotated suddenly. Estimated angular acceleration was 284°/s^2. Spring constant (k) of the spring was 0.63N/m. We repeated the same experiment twice.

Experiment 6

A T-shaped wooden stick was placed in the center of a rotating disk, and a plastic ball (1g) was hung on one arm of the wooden stick at a distance of 20cm from the center of rotation. The disk was rotated in a circular motion with a constant velocity (angular velocity, 200°/s). We repeated the same experiment twice.

All experiments were recorded. An infrared charge-coupled device camera was used to observe eye movements in healthy human subjects.

3. Results

All results are shown in the movie [9].

Experiment 1

The submerged lead caused a visible depression (1cm) in the pudding. The pudding deformed under the weight of the lead, analogous to how gravity deforms the utricular otolithic membrane.

Experiment 2

Immediately after applying force to induce motion, the spring bent, and the plastic ball moved away opposite to the direction of acceleration. Maximum displacement of the plastic ball was 29°.

Experiment 3

Immediately after applying force to induce motion, the spring bent, and the plastic ball moved away opposite to the direction of acceleration. Maximum displacement of the plastic ball was 32°.

Experiment 4

None of the five subjects exhibited any nystagmus during the squat movements (Table 1).

Experiment 5

Immediately after applying force to induce motion, the spring bent, and the plastic ball moved away opposite to the direction of rotation. Its direction was tangential. Maximum displacement of the plastic ball was 39°.

Experiment 6

After several rotations, the plastic ball moved outward and stabilized. Displacement of the plastic ball was 18°.

Table 1. Results of Experiment 4

			Experiment 4
Subject	Age (years)	Sex	Nystagmus
1	33	Female	—
2	43	Female	—
3	53	Female	—
4	64	Male	—
5	65	Male	—

4. Discussion

Our experiments support the idea that the utricle can be stimulated by four types of forces: (1) gravity, (2) horizontal and vertical linear acceleration, (3) angular acceleration, and (4) centrifugal force.

Experiment 1

Although simple, this experiment illustrates a fundamental principle. A dense otoconium (specific gravity, 2.7) lies on a gelatinous membrane; under Earth's gravity, the membrane will deform downward, continuously bending the hair cell cilia. In vivo, even when the head is upright and stationary, the utricular nerve remains tonically active due to this gravitational load. Thus, standing subjects maintain posture via constant utricular input

Assuming that there is one otoconium placed on the top of one hair cell. If the mass of otoconium is m_1, then a force F_1 (=m_1g) is experienced by the otolithic membrane, where *'g'* is the gravitational acceleration (9.8m/s^2). F_1 is a vector, the direction of which is the center of the Earth. Since the otolithic membrane is gelatinous, it is easily deformed. Furthermore, if the mass of the endolymph present on the otoconium is m_2, a force F_2 (=m_2g) directed toward the center of the Earth is experienced by the otolithic membrane. Similarly, perilymph is also present above the utricle, and if the mass of perilymph is m_3, a force F_3 (=m_3g) is experienced by the otolithic membrane. F_3 is also a vector whose direction is toward the center of the Earth. Thus, the net force experienced by the otolithic membrane is $F_1 + F_2 + F_3$. This force bends the cilia of the hair cell (Figure 1). This shows that while standing upright, the gravity of the Earth stimulates the utricle naturally. Since humans do not show nystagmus while stationary, we have doubts on the authenticity of "otolith-ocular reflex".

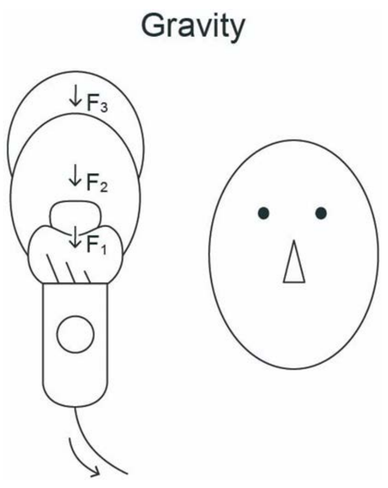

Figure 1.

Within the utricle, the otolithic membrane is always deformed and the hair cell is always stimulated due to gravity. Although action potentials are always induced, no one shows nystagmus.

F_1 = Weight of otoconium, F_2 = Weight of endolymph, F_3 = Weight of perilymph.

Experiment 2

Immediately after inducing motion, the plastic ball moved relatively. According to Newton's first law, an object at rest tends to stay at rest. The force was experienced by the ball in a direction opposite to that of acceleration. This force is called inertial force, and its magnitude is the product of mass and acceleration. When horizontal linear acceleration is applied to the human head, the otoconia of the utricle move relatively due to inertial force and sense linear acceleration. This is the conventional theory (Figure 2A).

Experiment 3

It was observed that the plastic ball showed relative motion due to the vertical inertial force, and its direction was opposite to that of acceleration. Thus, vertical linear acceleration should also activate the utricle. This extends the conventional view (which usually considers only horizontal acceleration) to include vertical motion. Our result suggests that the utricle can respond to vertical acceleration, a factor often overlooked. In practical terms, a sudden upward jerk of the head creates a downward inertial force on otoconium (Figure 2B), further deflecting the otolithic membrane and increasing cilia bending.

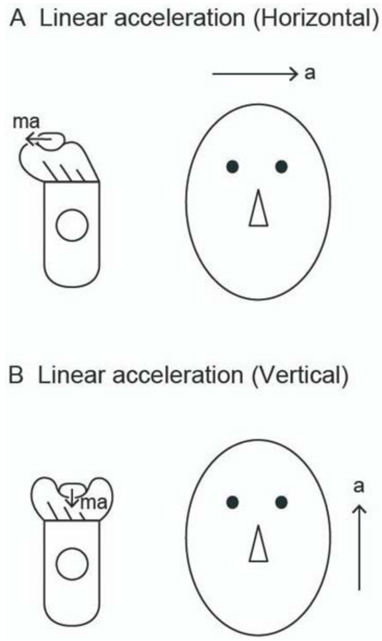

Figure 2.

A: When horizontal linear acceleration is applied to the human head, the otoconium moves relatively due to the inertial force and sense linear acceleration.

B: When acceleration is applied to the human head in the upward direction, an inertial force is generated in the downward direction, hence the pressure on the otolithic membrane and the bending of cilia increase.

m = Mass of otoconium, a = Acceleration.

Experiment 4

Despite the above, our human test (squatting) produced no observable nystagmus in any subject. This aligns with our spring model (Experiment 3) in that the utricle was indeed mechanically stimulated by vertical motion, but it did not trigger ocular reflexes. Consistent with Ichijo & Ichijo [10], who found no nystagmus from vertical head translations, this suggests that the classical “otolith-ocular reflex” may not produce overt eye movements under these conditions. In other words, utricular deflection from vertical acceleration does not by itself induce nystagmus. We note that our squat frequency (0.33Hz) and amplitude were physiologically relevant (normal gait perturbations), so if a robust otolith-driven nystagmus existed it should have appeared. Because it did not, we question the link between pure otolith stimulus and nystagmus generation.

Experiment 5

When the chair was rotated quickly, the spring-ball apparatus deflected tangentially (perpendicular to the radius of rotation) opposite to the direction of motion (Figure 3). This indicates that the utricle should likewise experience a tangential inertial force during head rotation. In fact, because the head rotates around C2 (axis), the otoconia in the utricle will lag in a tangential direction. Thus, the utricle is likely sensitive to horizontal angular acceleration (tangential inertial force) as well as linear. This phenomenon has not been widely emphasized in the literature.

If ocular counter-roll originates from the utricle, the nystagmus induced by horizontal rotation should contain a torsional component. However, a three-dimensional analysis of this nystagmus showed that it is purely horizontal [11]. This is also evidence that nystagmus does not originate from the utricle.

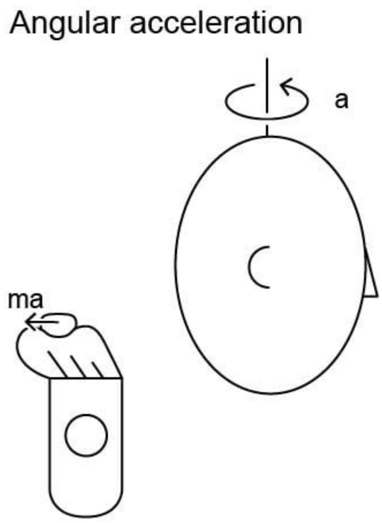

Figure 3.

Since the center of rotation of the head is the second cervical vertebra (eccentric rotation), when a person looks back, the otoconium of the utricle experiences an inertial force in the tangential direction.

m = Mass of otoconium, a = Acceleration.

Experiment 6

During the constant circular motion, the plastic ball was displaced outward. This is due to the centrifugal force, a kind of inertial force whose direction is opposite to that of acceleration (Figure 4). In the case of constant velocity circular motion, since acceleration occurs in the direction of the center of rotation, the centrifugal force is directed outward from the axis of rotation, and its magnitude is $mr\omega^2$ (*m* = Mass of plastic ball, *r* = Radius of rotation, ω = Angular velocity of rotation). If the head moves in a constant circular motion, the otoconium of the utricle experiences a centrifugal force. This fact has been overlooked in the past.

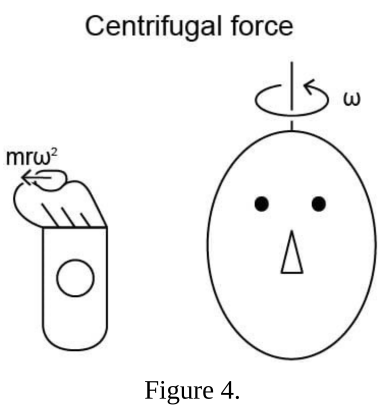

Figure 4.

If the head moves in a constant circular motion, the otoconium of the utricle experiences a centrifugal force. The direction of this force is outward and the magnitude is $mr\omega^2$.

m = Mass of otoconium, r = Radius of rotation, ω = Angular velocity of rotation.

5. Conclusion

Our results indicate that the utricle is mechanically responsive to four distinct forces: gravity, horizontal and vertical linear acceleration, tangential angular acceleration, and centrifugal force (its direction is outward). Even at rest, Earth's gravity induces a sustained utricular input (via cilia deflection). However, this static input does not produce nystagmus, suggesting that utricular stimulation alone may not drive ocular reflexes in a straightforward way. Collectively, these findings imply that the utricle's functional role in balance is broader than traditionally thought, potentially contributing to postural control via multiple inertial cues.

Acknowledgments

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