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ORIGINAL ARTICLE

# Vestibular Perception in Time and Space During Whole-Body Rotation in Humans

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**Abstract**
We investigated the vestibular perception of position, velocity, and time (duration) in humans with rotational stimuli including low velocities and small amplitudes. The participants were categorized into young, middle, and old age groups, and each consisted of 10 subjects. Position perception was assessed after yaw rotations ranged from 30 to 180° in both clockwise and counterclockwise directions. For each position, the rotation was delivered at two or more different velocities ranging from 15 to 120°/s. Position perception tended to underestimate the actual position and was similar during the slow and fast rotations. However, the trends of underestimation disappeared in the old age group. Velocity perception was evaluated by forcing the selection of the faster direction in each pair of rotations toward two positions (30° and 60°) with velocity differences from 0 to 20°/s. Velocity discrimination was similar between the rotation amplitudes or among the age groups. For duration perception, participants chose the rotation of longer duration for three test paradigms with different amplitudes (small vs. large) and durations (short vs. long) of rotation. The accuracy of discriminating duration was similar across the test paradigms or age groups, but the precision was lower in the older group and altered significantly according to the test paradigm. In conclusion, vestibular perception can be assessed using rotations of low velocities and small amplitudes. The perception of position and duration is affected by aging. The precision of duration perception can be influenced by the interactions between the amplitude and duration of motion.

**Keywords** Vestibular perception · Whole-body rotation · Time perception · Spatial navigation

## Introduction

Spatial perception is a high-level brain function essential for daily activities [1]. Accurate spatial perception is ensured by multisensory interactions of visual, vestibular, proprioceptive, and efference copy signals, which occur throughout the brain [2, 3]. Among these cues, the vestibular signals dominate the perception of our body position and velocity in darkness, during visual deprivation, or in the absence of visual landmarks [4]. The vestibular signals originate from the labyrinth [5], are refined in the brainstem and cerebellar circuits [6], and are then relayed to the cortical areas [7]. Diverse cortical regions, especially the parietoinsular cortex, are associated with vestibular motion perception in humans [8, 9]. The temporoparietal cortex comprising the angular and superior temporal gyri has recently been highlighted as the area encoding the position and duration of motion (time) simultaneously or estimating the position by computing the velocity and time information during vestibular-guided navigation [10]. Dysfunction of those brain regions may generate spatial misperception with or without velocity misperception, alternatively called vertigo (false motion sense) or dizziness (spatial disorientation without false motion sense) [11].

From a clinical perspective, evaluating the perception of the body position, the velocity, and duration of motion may be informative in assessing the functional integrity of the higher-level uni-/multi-modal vestibular perceptual pathways [10, 12–14]. In previous studies, the perception of body

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position was evaluated using passive whole-body rotation [10, 14]. The perception of the velocity of motion has also been assessed using the latency of the sensory-perceptual-motor reaction by evaluating the response time when the subjects felt a rotation [10, 12, 13]. Meanwhile, perception of the duration of motion was rated with the discriminative ability using the probability of accurately selecting the longer rotation [10]. These algorithms have been validated through a series of experiments but may require further exploration with different parameters for motion stimuli. Previous studies, however, have adopted rather fast rotation ranging from 80 to 360°/s [10, 14]. Thus, it is required to develop a low-velocity rotation protocol to evaluate vestibular perception in patients with vestibular disorders, especially in those with severe vertigo during rapid motion. For patients with motor dysfunction, the test paradigm for velocity perception needs to be simplified [10, 12, 13]. The perception of the duration of motion seems more complicated. If the temporoparietal cortex perceives body position by simply integrating the velocity over time, precise estimation of the duration as well as velocity is essential for accurate perception of the body position. However, the estimation of duration is known to be altered in experiments using saccadic eye movements or visual stimulation [15, 16]. Thus, the perception of duration may be affected differently when different vestibular stimulus paradigms are adopted. Lastly, the aging effects, if any, should be determined for position, velocity, and duration perception.

This study aimed to determine the applicability of slow rotation for evaluating pure perceptual tasks at the position, velocity, and duration of motion. We also tested the duration perception during diverse vestibular stimuli and tried to probe the way in which the brain codes the duration information associated with vestibular signals. Finally, we investigated the effect of aging on these perceptions.

## Methods

### Subjects

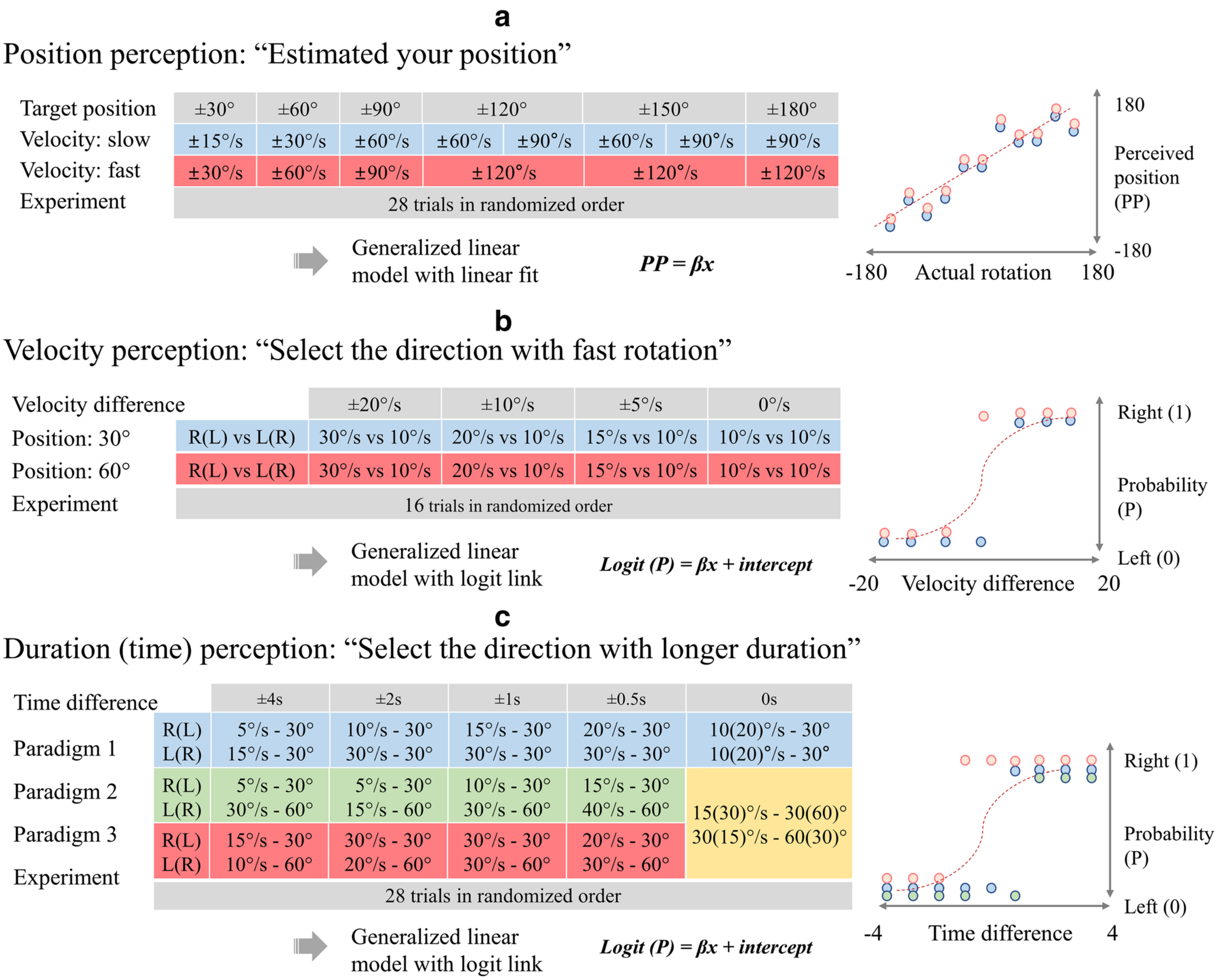
We recruited 30 healthy volunteers (23 women, mean age = 48.5 ± 15.9), 10 for each age group (ages 20–39, 40–59, and 60 or older). The mean age was 29.9 ± 6.1 for the young age group, 49.2 ± 6.3 for the middle age group, and 66.3 ± 2.1 for the old age group. All participants were right handed, and none of them had previous vestibular disorders, hearing loss, or other neurological disorders. The integrity of cognitive function was screened with a mini-mental state examination, and the mean score was 28.5 ± 1.5. The experiments were conducted in accordance with the Declaration of Helsinki. All participants provided written informed consent prior to participation. The experimental protocol and consent form were approved by the Institutional Review Board of Seoul National University Bundang Hospital (B-1801/445-304).

### Experimental Apparatus and Setup

To deliver head-restraint whole-body rotation, we used a rotation chair that was operated with a trapezoid velocity profile, 0.15 s of fixed acceleration and deceleration periods with an intervening period at various constant velocities. The chair acceleration/deceleration applied in the study ranged from 100 to 800°/s$^2$ according to the target velocity. In addition, by changing the velocity and time parameters, we were also able to rotate the chair with various amplitudes. The subjects sat in the chair and fixed their heads and bodies using restraining belts. Goggles with a cover and headphones with white noise were applied to eliminate any visual and auditory cues, as in previous experiments [10, 12, 13]. The experiments consisted of position, velocity, and duration tasks and all participants performed the experiments in the same order (position–velocity–duration).

### Position Task

Vestibular perception of body position was evaluated by rotating the participants rightward or leftward (clockwise or counterclockwise around the yaw axis). The amplitudes of rotation were 30°, 60°, 90°, 120°, 150°, or 180°, and the participants were then instructed to report their positional estimates verbally for the given six positions after each rotation. Because we attempted to determine the applicability of slow velocity rotation, each rotational position was delivered at two or three different velocities ranging from 15 to 120°/s. Specifically, velocities of 15 and 30°/s were used for 30° rotation; 30 and 60°/s for 60° rotation; 60 and 90°/s for 90° rotation; 60, 90, and 120°/s for 120° and 150° rotation; and 90 and 120°/s for 180° rotation. We defined "slow rotation" as 15°/s for 30° rotation; 30°/s for 60°; 60°/s for 90°; 60°/s and 90°/s for 120° and 150°; and 90°/s for 180° rotations. In contrast, "fast rotation" was defined as 30°/s for 30° rotation, 60°/s for 60°, 90°/s for 90°, 120°/s for 120° and 150°, and 120°/s for 180° rotation. In each trial, subjects were rotated back to the starting position after collecting their responses, and a pause of 30 s was given before the next trial to prevent any post-rotational cues that might affect the vestibular perception of position. Before the experiments, the participants had a practice trial for each of the 6 positions (30° to 180°) with auditory feedback for their position estimation. In the experiment, each participant underwent a total of 28 trials without auditory feedback. The order of rotations for different positions and velocities was randomly determined (Fig. 1).



**a**

Position perception: "Estimated your position"

| Target position | ±30° | ±60° | ±90° | ±120° | | ±150° | | ±180° |
|---|---|---|---|---|---|---|---|---|
| Velocity: slow | ±15°/s | ±30°/s | ±60°/s | ±60°/s | ±90°/s | ±60°/s | ±90°/s | ±90°/s |
| Velocity: fast | ±30°/s | ±60°/s | ±90°/s | ±120°/s | | ±120°/s | | ±120°/s |
| Experiment | 28 trials in randomized order | | | | | | | |

Generalized linear model with linear fit

$PP = \beta x$

**b**

Velocity perception: "Select the direction with fast rotation"

| Velocity difference | | ±20°/s | ±10°/s | ±5°/s | 0°/s |
|---|---|---|---|---|---|
| Position: 30° | R(L) vs L(R) | 30°/s vs 10°/s | 20°/s vs 10°/s | 15°/s vs 10°/s | 10°/s vs 10°/s |
| Position: 60° | R(L) vs L(R) | 30°/s vs 10°/s | 20°/s vs 10°/s | 15°/s vs 10°/s | 10°/s vs 10°/s |
| Experiment | 16 trials in randomized order | | | | |

Generalized linear model with logit link

$\mathrm{Logit}\,(P) = \beta x + intercept$

**c**

Duration (time) perception: "Select the direction with longer duration"

| Time difference | | ±4s | ±2s | ±1s | ±0.5s | 0s |
|---|---|---|---|---|---|---|
| Paradigm 1 | R(L)<br>L(R) | 5°/s - 30°<br>15°/s - 30° | 10°/s - 30°<br>30°/s - 30° | 15°/s - 30°<br>30°/s - 30° | 20°/s - 30°<br>30°/s - 30° | 10(20)°/s - 30°<br>10(20)°/s - 30° |
| Paradigm 2 | R(L)<br>L(R) | 5°/s - 30°<br>30°/s - 60° | 5°/s - 30°<br>15°/s - 60° | 10°/s - 30°<br>30°/s - 60° | 15°/s - 30°<br>40°/s - 60° | 15(30)°/s - 30(60)°<br>30(15)°/s - 60(30)° |
| Paradigm 3 | R(L)<br>L(R) | 15°/s - 30°<br>10°/s - 60° | 30°/s - 30°<br>20°/s - 60° | 30°/s - 30°<br>30°/s - 60° | 20°/s - 30°<br>30°/s - 60° | |
| Experiment | 28 trials in randomized order | | | | | |

Generalized linear model with logit link

$\mathrm{Logit}\,(P) = \beta x + intercept$

**Fig. 1** Schematics of experimental design and data analysis for vestibular perception. In the duration (time) perception task, paradigm 1 created a time difference by velocity difference only; paradigm 2 assigned a longer duration of rotation to smaller amplitude; paradigm 3 assigned a longer duration to larger amplitude. $\beta$ = beta coefficient of a generalized linear regression model with a linear fit or logit fit

## Velocity Task

This task assessed the vestibular perception of moving velocity. Unlike previous studies that measured the thresholds for motion perception [10, 12, 13], we adopted a method for evaluating the perception of velocity difference. This was fundamentally identical to the method for assessing duration perception in the previous study [10]. The subjects were rotated either rightward or leftward first, and returned to the original position, and then were rotated in the opposite direction. The rotation velocity was 10°/s, 15°/s, 20°/s, or 30°/s for one direction and 10°/s for the other direction. Thus, the velocity differences between the rotations in either direction were 0°/s, 5°/s, 10°/s, and 20°/s. The velocity task was performed for two different amplitudes of rotation: small (30°) and large (60°). After each rotation, the participants verbally reported the direction of the "faster" rotation. The participants had two practice trials with auditory feedback for their velocity perception and then underwent 16 experimental trials without feedback. The order of rotation within each trial (faster and slower) and for entire test trials was randomly assigned (Fig. 1).

## Duration Task

This task aimed to evaluate the perception of rotation duration. As in the velocity task, the participants were instructed to verbally indicate the direction in which they felt the rotation was "longer." The task comprised a pair of rightward and leftward rotations, and the difference of rotation duration was set to 0, 0.5, 1, 2, and 4 s. In addition, we adopted three different paradigms to evaluate whether duration perception is altered during vestibular-guided navigation. In paradigm 1 (10 trials), we created a difference in the duration of rotation by delivering rotations at different velocities (20 vs. 30°/s) but with a fixed amplitude of 30° in either direction. For the same duration of rotation (duration difference = 0), we tested subjects twice using a 30° rotation at 10°/s and 20°/s in either direction. In paradigm 2 (8 trials), we adopted different velocities and amplitudes to assign longer durations for smaller amplitudes (i.e., 0.5 s longer for the rightward rotation by applying 30° rightward rotation at a velocity of 15°/s and 60° leftward rotation at a velocity of 40°/s). In paradigm 3 (8 trials), different velocities and amplitudes were used to assign a longer duration for rotation of larger amplitude (i.e., 0.5 s longer for rightward rotation of 60° at a velocity of 30°/s and leftward rotation of 30° at a velocity of 20°/s). During the second and third paradigms, the same duration of rotation (duration difference = 0) could not be adopted. Thus, we provided a pairwise rotation consisting of 60° rightward at 30°/s and 30° leftward at 15°/s, or vice versa (2 trials).

We hypothesized that the responses do not differ among the paradigms if a common, centralized, and dedicated timing mechanism operates for vestibular perception. All participants underwent 6 practice trials with auditory feedback for the duration perception. After then, a total of 28 experimental trials were randomly conducted without feedback (Fig. 1).

### Statistical Analyses

We calculated the mean and standard deviation of the participants' responses for each amplitude of rotation in the position task, and those of the probability choosing "rightward rotation was faster or longer" for the velocity and duration tasks. We, then, compared the perception of position, velocity, and duration with the ideal values using a single-tailed paired *t* test. The ideal values for the position task corresponded to the rotational amplitude. The ideal value for the velocity and duration tasks was 0.5 when the velocity or duration of rotation was equal in both directions. In contrast, the ideal value was 1 (when the rightward rotation was faster or longer) or 0 (when the leftward rotation was faster or longer) when the velocity or duration of rotation differed between the directions. These analyses were performed for the data of entire subjects and each subgroup.

The relationship between vestibular perception and actual stimuli during the position, velocity, and duration tasks was explored using a generalized linear model (Fig. 1). For the position task, we used a linear fit without an intercept term. The regression slope, $\beta$, represents the amount of change in the perceived position corresponding to the amount of change for the actual stimuli (delivered position). Thus, a $\beta$ value of 1 indicates an ideal positional perception. In contrast, perceptual underestimation or overestimation is indicated when $\beta$ is less than or larger than 1. For the velocity and duration tasks, we adopted a logit fit. The intercept value of the regression equation could determine the probability to select "rightward rotation was faster or longer" in the rotation without a velocity or duration difference between the rightward or leftward rotation. $\beta$ is the amount of change in the logarithm of the odds, log ($p/[1 - p]$), in response to the amount of change in the velocity or duration difference. With a higher $\beta$ value, the discrimination in velocity or duration occurs within a narrow range. Therefore, the accuracy and precision of discriminative ability increase with an ideal intercept value and higher $\beta$ value.

The univariate model was adopted to estimate the regression value for the whole group and each subgroup. The multivariate model with an interaction term, which is one of the ways of testing the homogeneity of the regression slope, was adopted to evaluate any difference among the subgroups in the vestibular perception of position, velocity, and duration. For this, the covariates (i.e., the rotational velocity (slow vs. fast) for the position task, the rotational amplitude (small vs. large) for the velocity task, the paradigms (1, 2, and 3) of rotation for the duration task, and the age groups (young, middle, old) for all tested tasks) and their interactions with the actual stimuli were included in each model. A *p* value of less than 0.05 was defined as the level of statistical significance. All statistical analyses were performed using the MATLAB statistical toolbox (Matlab R2018a, The MathWorks, Inc., USA).

### Data Availability Statement

Anonymized data will be shared by request from any qualified investigator.

## Results

### Position Task

The descriptive results of vestibular perception of position for the whole group and subgroups are presented in Table 1. In the whole group, the participants underestimated the rotated position for the rightward rotation of 60° and 120–180° and for the leftward rotation of 90–180° (single-tailed paired *t* test). This perceptual underestimation for each position was similarly observed during both slow and fast rotations in the young and middle-aged groups but not in the old age group.

The generalized linear model with a linear fit showed that, for the whole data set, the perceived position was clearly correlated, even though underestimated, with the actual rotational position ($\beta = 0.850$ (95% CI = 0.832–0.867), $p < 0.001$). In the subgroup analyses, the estimated $\beta$ was similar between slow and fast rotation ($\beta = 0.850$ vs. 0.851, $p > 0.05$). The old age group ($\beta = 0.921$) had a larger regression value than the young ($\beta = 0.824$, $p < 0.001$) and middle ($\beta = 0.806$, $p < 0.001$) age groups (Fig. 2).

**Table 1** Dataset for experiments

Position task

| Stimulation (°) | − 180 | − 150 | − 120 | − 90 | − 60 | − 30 | 30 | 60 | 90 | 120 | 150 | 180 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Ideal perception (°) | − 180 | − 150 | − 120 | − 90 | − 60 | − 30 | 30 | 60 | 90 | 120 | 150 | 180 |
| Whole group | − 151 | − 128 | − 101 | − 77 | − 56 | − 33 | 33 | 49 | 82 | 101 | 128 | 151 |
| Slow rotation | − 153 | − 125 | − 105 | − 79 | − 57 | − 33 | 32 | 49 | 79 | 101 | 128 | 147 |
| Fast rotation | − 149 | − 130 | − 97 | − 75 | − 54 | − 32 | 33 | 48 | 85 | 101 | 127 | 154 |
| Young age group | − 149 | − 129 | − 102 | − 75 | − 59 | − 30 | 32 | 48 | 77 | 87 | 127 | 141 |
| Middle age group | − 149 | − 119 | − 94 | − 71 | − 48 | − 30 | 32 | 48 | 75 | 98 | 118 | 146 |
| Old age group | − 156 | − 137 | − 107 | − 86 | − 60 | − 38 | 35 | 50 | 95 | 118 | 138 | 165 |

Velocity task

| Stimulation | − 20 | − 10 | − 5 | 0 | 5 | 10 | 20 |
|---|---|---|---|---|---|---|---|
| Ideal probability† | 0 | 0 | 0 | 0.5 | 1 | 1 | 1 |
| Whole group | 0.00 | 0.03 | 0.08 | 0.46 | 0.92 | 0.97 | 0.98 |
| Short rotation | 0.00 | 0.07 | 0.10 | 0.47 | 0.93 | 0.97 | 1.00 |
| Long rotation | 0.00 | 0.00 | 0.07 | 0.45 | 0.90 | 0.97 | 0.97 |
| Young age group | 0.00 | 0.00 | 0.05 | 0.55 | 0.90 | 0.95 | 1.00 |
| Middle age group | 0.00 | 0.05 | 0.10 | 0.38 | 0.95 | 0.95 | 1.00 |
| Old age group | 0.00 | 0.05 | 0.10 | 0.45 | 0.90 | 1.00 | 0.95 |

Time task

| Stimulation | − 4 | − 2 | − 1 | − 0.5 | 0 | 0.5 | 1 | 2 | 4 |
|---|---|---|---|---|---|---|---|---|---|
| Ideal probability† | 0 | 0 | 0 | 0 | 0.5 | 1 | 1 | 1 | 1 |
| Whole group | 0.07 | 0.18 | 0.19 | 0.19 | 0.43 | 0.80 | 0.88 | 0.87 | 0.89 |
| Paradigm 1‡ | 0.00 | 0.10 | 0.10 | 0.10 | 0.38 | 0.90 | 0.93 | 1.00 | 0.97 |
| Paradigm 2‡ | 0.20 | 0.40 | 0.43 | 0.33 | $R = 0.60$* | 0.63 | 0.70 | 0.60 | 0.70 |
| Paradigm 3‡ | 0.00 | 0.03 | 0.03 | 0.13 | $L = 0.33$* | 0.87 | 1.00 | 1.00 | 1.00 |
| Young age group | 0.03 | 0.17 | 0.20 | 0.13 | 0.48 | 0.90 | 0.90 | 0.97 | 0.97 |
| Middle age group | 0.03 | 0.13 | 0.17 | 0.27 | 0.35 | 0.77 | 0.97 | 0.80 | 0.90 |
| Old age group | 0.13 | 0.23 | 0.20 | 0.17 | 0.45 | 0.73 | 0.77 | 0.83 | 0.80 |

The value in the light-gray cell is statistically different from the ideal value (single-tailed *t* test, $p < 0.05$)

† The probability of choosing the right is denoted by 1 while that of selecting the left is denoted by 0

‡ In paradigm 1, duration difference was created by only velocity difference. In paradigms 2 and 3, a longer duration of rotation assigned to smaller and larger amplitude of rotation, respectively

*In paradigms 2 and 3, the same duration of rotation was impossible to set. For those paradigms, a pairwise rotation consisting of 60° rightward at 30°/s and 30° leftward at 15°/s, or vice versa were applied. The probability was 0.33 when the leftward rotation ($L = 0.33$) was larger and 0.60 when the rightward rotation was larger ($R = 0.60$)

## Velocity Task

The descriptive results of the probabilities of correctly choosing the direction with a faster rotation at each velocity difference are presented in Table 1. For the whole data set, the probabilities were near ideal except for a velocity difference of 5°/s (single-tailed paired *t* test). In the subgroup analyses for each age and position group, the probabilities were also ideal across the entire range of velocity differences tested.

The generalized linear model with a logit fit showed that, for the entire data set, the intercept and $\beta$ values were − 0.129 (− 0.425–0.168) and 0.374 (0.295–0.453). Thus, the probability of selecting "rightward rotation was faster" was 0.47 (0.38–0.56) when equal velocity was applied in both directions. None of the subgroups showed an intercept significantly apart from 0 (ideal value). The probability of selecting "rightward rotation was faster" at zero velocity difference, therefore, was not significantly different from the ideal probability (0.5) in all subgroups. Likewise, the estimated $\beta$ was also similar between short and long rotation ($\beta = 0.373$ vs. 0.377, $p > 0.05$) and among the young (0.439), middle-aged (0.385), and old-aged (0.323) groups ($p > 0.05$) (Fig. 3).

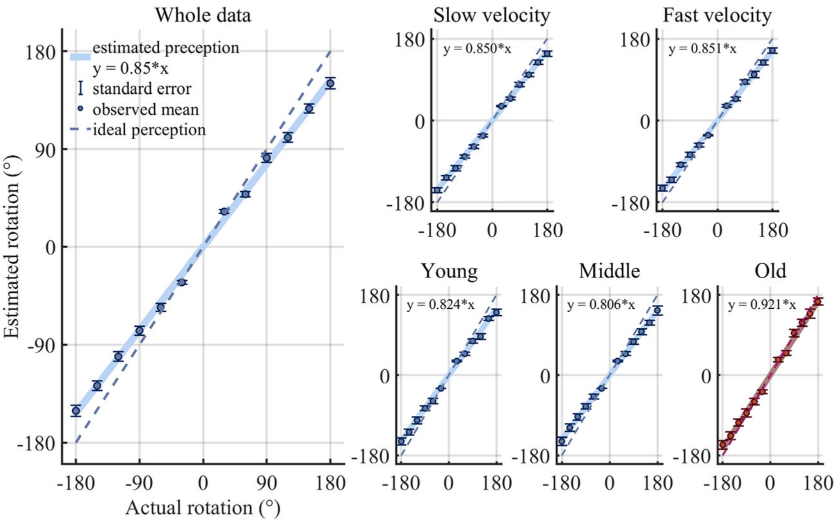


**Fig. 2** The result of position task. The generalized linear regression model with a linear fit shows a perceptual underestimation on position. The regression slopes are similar in slow and fast rotations. In contrast, the old age group (red regression line) showed a significantly higher regression slope than the middle and young age group (blue regression lines)

## Duration Task

The descriptive results of the probabilities of correctly deciding the direction of rotation with a longer duration are presented in Table 1. For the whole data set, the probabilities were generally close to but significantly different from the ideal values across all the differences tested except when the difference in the rotation duration was 0 (single-tailed paired *t* test). In the subgroup analyses, however, the results were dissimilar among the three paradigms tested. When the difference was created by the velocity difference alone, the probabilities were ideal for each duration difference. When a longer duration was applied to smaller amplitudes of rotation, the probabilities significantly deviated from the ideal values for all differences tested. In contrast, when a longer duration was applied to larger amplitudes of rotations, the probabilities were ideal, except when the difference of duration was 0.5 s. In a pairwise rotation consisting of 60° rightward at 30°/s and 30° leftward at 15°/s or vice versa (the duration was equal, but the rotational velocity was different), the probability was 0.6 when the rightward rotation had a larger amplitude (60°). In the reverse situation, the probability was 0.33. In both cases, the values were not different from the ideal value (0.5) but were significantly different from each other ($p$ = 0.039, paired *t* test). With aging, the probabilities were more likely to deviate from the ideal values.

The generalized linear model with a logit fit showed that, for the entire data set, the intercept and β values were − 0.016 (− 0.195–0.163) and 0.862 (0.730–0.995). The probability of responding that the "rightward rotation was longer" was 0.50 (0.45–0.54) after the rotations with equal duration. None of the subgroups had an intercept value significantly different from 0 (ideal value), which indicates that the probability of selecting "rightward rotation was longer" after the rotations with the same duration were not different from the ideal value (0.5). In other words, duration

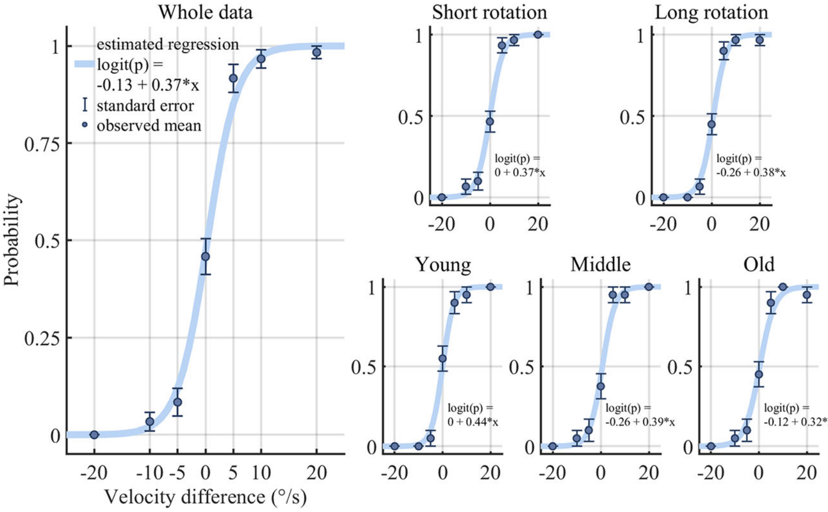


**Fig. 3** The result of the velocity task. The generalized linear regression model with a logit fit shows the relationship between the estimated probability and actual velocity difference. The regression slope is similar regardless of the subgroup by rotation amplitude or age

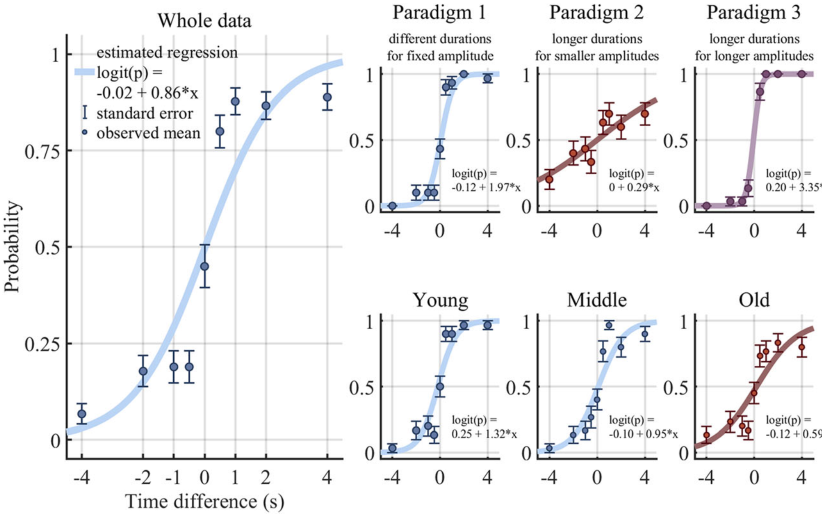


**Fig. 4** The result of duration task. The generalized linear regression with a logit fit shows the relationship between the estimated probability and actual time difference. Compared to paradigm 1 (the difference in rotation duration was created by the velocity difference only), the regression slope decreases in paradigm 2 (a longer duration of rotation was assigned to small amplitude, red regression line) and increases in the reverse paradigm (paradigm 3, purple regression line). In the old age group (red regression line), the regression slope significantly decreases compared to young and middle age groups

discrimination was accurate. In contrast, the estimated $\beta$, the indicator for precision, was significantly different across the test paradigms and age groups. Compared with $\beta$ in paradigm 1 (1.966), in which the difference in rotation duration was created by the velocity difference only, the $\beta$ value decreased significantly in paradigm 2 (0.288, $p < 0.001$), in which a longer duration was applied to a smaller amplitude of rotation, and increased significantly in paradigm 3 (3.352, $p = 0.013$), in which a longer duration was applied to the larger amplitude of rotation. In the analyses by age subgroups, the $\beta$ value was significantly decreased in the old (0.589) compared with the young (1.332, $p < 0.001$) and middle (0.946, $p = 0.021$) age groups (Fig. 4).

## Discussion

This study evaluated the perception of position, velocity, and duration upon vestibular stimulation in healthy subjects. Position perception tended to underestimate the rotational position, which was apparent for the larger amplitude of rotation. The position perception did not differ between slow and fast rotations. Velocity and duration perception could be successfully evaluated using the discrimination task. Velocity perception did not differ by the amplitude (small vs. large) of rotation, while duration perception depended on the interactions between the amplitude (smaller vs. larger) and duration (short vs. long) of rotation. Lastly, in the old age group, the trend of underestimation of positional perception was absent and the precision of discriminative ability for motion duration was reduced while accuracy remained intact.

In the position task, the vestibular perception was significantly lower than the actual rotational position. Previous studies have shown that the accuracy of position perception may differ according to the study paradigm. In a study that adopted four rotational positions at 90, 180, 270, and 360° in each direction [14], position perception was near perfect. However, the protocol with a wide position interval and a small number of choices may not be enough to evaluate spatial perception precisely. In contrast, a study that adopted 12 positions with a 30° interval in each direction demonstrated perceptual underestimation for the rotational position [10]. Furthermore, a simplified protocol having adopted six positions with a 30° interval in each direction also showed a trend of perceptual underestimation for the position, which was identical to that of the previous study [10]. In detail, the regression slope between the perceived and actual positions in healthy participants was approximately 0.87 in the previous study [10] and 0.85 in our study. The reason for underestimation may be the decay of velocity information in the peripheral vestibular nerve or central velocity storage networks that are engaged in both self-motion perception and reflexive eye movements [17]. During constant velocity rotation, the velocity information to move the eyes is rapidly reduced, with a time constant of 4 to 5 s in the peripheral nerve [18], while it reduced three times more slowly in the central vestibular system [6, 19]. However, given that all the rotations were delivered for less than 2 s, the loss of velocity information in the peripheral nerve or central velocity storage could not account for the perceptual underestimation of position. Instead, we propose two explanations. First, if there is a neural integrator in the temporoparietal cortex that computes position from the velocity and time signals, the underestimation may be attributed to the physiologic leak (preventing the bias accumulation from biological noises) of the neural integrator likewise in the velocity and position neural integrator located in the brainstem and cerebellum [6, 19–21]. Second, in normal conditions, the cortical regions coding the velocity information may be tuned to use velocity information from both vestibular and visual systems. Thus, vestibular information alone may be insufficient to estimate the velocity perfectly, which in turn leads to positional underestimation. In this regard, the effect of aging on the relationship between the perception and actual position also has a twofold hypothetical explanation. With aging, the physiological leak of the neural integrator may decrease or the cortical area for velocity coding may bias toward the vestibular system than the visual system, resulting in paradoxical near-perfect positional estimation in the old age group.

Lastly, one of the objectives of this study was to test whether the relatively low-velocity rotation is also useful in evaluating vestibular position perception. No significant difference was found in the relationship between the perceptual and actual positions according to the velocity applied, indicating that slow rotation can also reliably evaluate the vestibular perception of position.

In the velocity task, the healthy participants accurately and precisely discriminated the velocity regardless of the rotation amplitude in all age groups. Previous studies evaluated motion perception in comparison with the vestibulo-ocular reflex (VOR) using an acceleration ($°/s^2$) threshold [10, 12, 13]. The VOR thresholds were lower than the perceptual thresholds in both young and older subjects. The VOR was generated more sensitively for the young than for the old, but the threshold for motion perception was similar between young and old subjects [12]. Therefore, the similar accuracy for determining the velocity difference across age groups in our study was similar to previous results. When evaluating motion perception, determining the velocity difference may be less straightforward than the methods adopted in previous studies [10, 12, 13]. However, compared with previous studies that required the integrity of perceptual-motor reaction, the method adopted in this study may be useful for patients with motor dysfunction. The feasibility should be further evaluated in patients with vestibular symptoms from various causes.

Lastly, we evaluated the ability to determine the rotation duration. A previous study showed that healthy subjects can accurately discriminate differences in rotation duration with a velocity from 60 to 90°/s and rotation amplitude from 0 to 180° [10]. In this study, the discriminative ability was accurate (determined by the intercept value of the generalized linear model with a logit fit) regardless of the test paradigm or age group. However, the precision (evaluated by the $\beta$ values of the generalized linear model) differed significantly across the test paradigms or age groups. The precision was strongly dependent on the interactions between the amplitude (smaller vs. larger) and duration (short vs. long) of rotation. Compared to paradigm 1 in which the time difference was created only by the velocity difference with fixed rotational amplitude, the precision increased when the direction of the longer duration of rotation was the same as that of the larger amplitude of rotation. In the reverse paradigm, the precision decreased significantly. It is still uncertain whether our brain has a centralized dedicated or distributed intrinsic timing mechanism [15]. The former encodes the duration in an absolute manner, while the latter does so in a relative manner [15]. Therefore, the alteration of precision in discriminating the duration would favor the distributed and intrinsic timing mechanism in the vestibular system. Another finding was that aging significantly modulated the relationship between perceived and actual duration differences. Time information encoded by either the central or distributed timing mechanism requires further processing that compares the encoded time to the reference memory to decide the duration [15]. The prior memory that it takes more time to travel longer distances may affect duration perception. Hence, older adults may depend more on the prior memory for the decision of duration than the younger subjects. Alternatively, the timing mechanism may actually decrease with aging. This postulation may be in line with the increase in the prevalence of dizziness (spatial disorientation without a sense of false motion) in aged people [22]. In addition, patients with vestibular disorders should be evaluated further regarding their patterns of duration perception using different methods applied in this study. However, the question remains as to whether the temporoparietal region has a common neural substrate perceiving both position and duration during vestibular-guided navigation or, alternatively, whether it is a computing hub for the perception of position ($p = \int v\, dt$) [10]. Although our results do not strongly favor one possibility over the other, the dependency of duration perception on the interactions between the amplitude and duration of rotation would favor the former, or at least suggests the presence of another neural substrate encoding the duration for position perception, and the idea of a distributed timing mechanism.

In conclusion, vestibular perception can be assessed using pure perceptual tasks, even using rotations of slow velocities and short amplitudes. Position and duration perception are affected by aging during vestibular navigation. The precision of duration perception can be influenced even in healthy subjects by the interactions between amplitude and duration of motion.

**Authors' Contributions** Dr. E Kwon analyzed and interpreted the data and wrote the manuscript. Dr. J.Y. Lee, J.M. Song, and H.J. Kim analyzed and interpreted the data and revised the manuscript. Drs. J.Y. Choi and J.S. Kim designed and conceptualized the study, interpreted the data, and revised the manuscript.

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## Compliance with Ethical Standards

**Conflict of Interest** Drs. E Kwon, J.Y. Lee, H.J. Kim, J.M. Song, and J.Y. Choi report no disclosures. Dr. J.S. Kim serves as an associate editor of Frontiers in Neuro-otology and on the editorial boards of the Journal of Clinical Neurology, Frontiers in Neuro-ophthalmology, Journal of Neuro-ophthalmology, Journal of Vestibular Research, Journal of Neurology, and Medicine.

**Ethical Standard** This study followed the tenets of the Declaration of Helsinki and was performed according to the guidelines of the Institutional Review Board of the Seoul National University Bundang Hospital (B-1801/445-304).

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