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Visual rotation axis and body position relative to the gravitational direction: Effects on circular vection

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Abstract. The visual–vestibular conflict theory asserts that visual–vestibular conflicts reduce vection and that vection strength is reduced with an increasing discrepancy between actual and expected vestibular activity. Most studies support this theory, although researchers have not always accepted them. To ascertain the conditions under which the theory of the visual–vestibular conflict can be applied, we measured circular vection strength accompanied by manipulation of the visual–otolith conflict by setting the axes of visual global motion (pitch, roll, and yaw) as either earth-horizontal or earth-vertical, using three different body positions (supine, left-lateral recumbent, and sitting upright). When the smaller stimulus was used, roll vection strength was greater with the visual–otolith conflict than without it, which contradicts the visual–vestibular conflict theory. We confirmed this result, as observers were able to distinguish circular vection from an illusory body tilt. Moreover, with observers in an upright position, the strength of yaw vection, which does not involve the visual–otolith conflict, increased and was almost equal to that of roll vection, which involves the visual–otolith conflict. This suggests that if the visual stimulus covers the entire visual field, the strength of circular vection around the earth-vertical axis exceeds that around the earth-horizontal axis, which is a finding consistent with the visual–vestibular conflict theory.

Keywords: vection, visual–vestibular conflict, gravitational information, illusory body tilt, body position, self-motion.

1 Introduction

Obtaining information to govern our movement in daily life is important for the actions we perform in dynamic environments. To obtain such information, various types of sensory information are processed and integrated in the brain. Considering the environment, Gibson (1979) has pointed out the importance of visual information, or optic flow, to the process by which we receive information that governs self-motion. In addition, many researchers have reported that our perception of self-motion represents the integration of visual, vestibular, proprioceptive, somatosensory, and other information (Dichgans & Brandt, 1978; Lishman & Lee, 1973; Warren & Wertheim, 1990).

Among various types of sensory information, information from the vestibular and visual systems contributes considerably to the perception of self-motion. Psychophysical studies have revealed that the vestibular system (which is composed of the semicircular canals, which detect the acceleration of self-rotation, and the otolith organs, which detect the linear acceleration of self-motion and gravitational direction) plays a leading role in the perception of self-motion (Benson, Spencer, & Stott, 1986; Greven, Oosterveld, & Rademakers, 1974; Walsh, 1961).

The major role of vision in this perception is also evident. Indeed, self-motion perception induced by visual motion alone is a well-known phenomenon that has been recognized at least since the 19th century (Mach, 1875; Wood, 1895). This phenomenon was named *vection* by Fischer and Kornmüller (1930). Vection can be categorized into two types: (1) linear vection, which consists of linear self-motion perception along one or several of the pitch, yaw, and roll axes, and (2) circular vection, which consists of rotational self-motion perception around one or several of these three axes (Andersen, 1986).

Since vection is induced entirely by visual motion, it necessarily involves a conflict between visual and vestibular information. In linear vection, a conflict between information from the visual system and from the otolith organs arises. In circular vection, two different types of conflict arise, depending upon the visual rotation axis. A conflict between information from the visual system and from the semicircular canals arises for circular vection around both the earth-vertical axis and the earth-horizontal axis. Another conflict between information from the visual system and from the otolith organs arises for circular vection around the earth-horizontal axis. Such conflicts, therefore, are useful for understanding the mechanism of self-motion perception to clarify visual–vestibular interaction using vection. Most studies of vection, however, have focused only on the effects of visual information.

As regards the interaction between the visual and vestibular systems, Zacharias and Young (1981) proposed a model of the *visual–vestibular conflict* to explain the perceptual mechanism of vection. Palmisano, Gillam, and Blackburn (2000) and Palmisano, Burke, and Allison (2003) summarized the effect of the visual–vestibular conflict on circular vection, which was based on the visual–vestibular conflict model, in two concepts: (1) The visual–vestibular conflict (e.g. the absence of expected vestibular activity during the perception of self-motion simulated by visual motion) should always reduce/impair vection. (2) The degree of vection impairment should increase with the discrepancy between the actual and expected vestibular activity.

Most of the literature supports this theory of the perception of vection, as proposed by Zacharias and Young (1981). Howard, Cheung, and Landolt (1987), for example, in their study of visual motion that employed a random dot pattern that covered the inside of a fibreglass sphere with a diameter of 2.74 m, reported that circular vection around the earth-vertical axis was stronger than that around the earth-horizontal axis. They suggested that the absence of expected otolith activity while the visual rotation axis is in the earth-horizontal direction reduces circular vection, in conformance with the visual–vestibular conflict theory. Moreover, they measured the illusory body tilt around the earth-horizontal axis.

The visual–vestibular conflict theory may not always be applicable to the perception involved in circular vection, particularly in the following cases:

1. When the visual stimulus does not completely cover the visual field of the observer.
2. When the degree of the visual–vestibular conflict is not governed by information from the vestibular system, but rather from that of the visual system.

As regards Case 1, much literature that supports the visual–vestibular conflict theory is based upon the use of a visual stimulus that completely covers the visual field of the observer (Brandt, Dichgans, & Büchele, 1974; Howard et al., 1987; Melcher & Henn, 1981; Wong & Frost, 1981; Young, Dichgans, Murphy, & Brandt, 1973; Young, Oman, & Dichgans, 1975). However, Ujike, Yokoi, and Saida (2004) reported that roll vection was the strongest and yaw vection was the weakest among the three types of circular vection (roll, pitch, and yaw) when the visual stimulus (width × height: 82° × 67°) did *not* completely cover the visual field of an observer in an upright position. Their results thus contradict not only those of Howard et al. (1987), but the visual–vestibular conflict theory as well.

As regards Case 2, a number of experiments in the literature that focused on the interaction between visual and vestibular inputs (Melcher & Henn, 1981; Wong & Frost, 1981; Young et al., 1973; Young, Shelhamer, & Modestino, 1986) changed the input of the vestibular information in such a way as to rotate the observer, or put the observer in space in a weightless condition. According to our interpretation, their results indicate that the onset latency of circular vection decreases when the visual–vestibular conflict is reduced. However, Palmisano et al. (2000, 2003) reported that a jittering radial flow stimulus induced vection that commenced earlier and lasted longer than vection produced by a non-jittering radial flow stimulus. This result suggests that the visual–vestibular conflict theory may not be applicable to linear vection when the visual–vestibular conflict is governed by visual information. This suggestion provoked us to speculate that the visual–vestibular conflict theory may not be applicable to circular vection when the visual–vestibular conflict is governed by visual information.

In the present experiments, we sought to ascertain the conditions under which the theory of the visual–vestibular conflict can be applied to the variations in the circular vection strength. To do this, we focused on circular vection, around both the earth-horizontal and earth-vertical directions. The reason for this focus is that the degree of the visual–vestibular conflict is different for these two types of vection. Circular vection around the earth-vertical axis involves a conflict between information from the visual system and from the semicircular canals, while circular vection around the earth-horizontal axis involves a conflict between information from the visual system and from the otolith organs, in addition to the conflict with the semicircular canals. Therefore, we investigated how the strength of circular vection is affected by combinations of conditions involving three different visual global motions (roll, pitch, and yaw) and three different body positions of the observer (supine, left lateral recumbent, and sitting upright), and manipulation of the range of the visual field (180°, 100°, and 70°).

Our aim in Experiment 1 was to investigate how the strength of circular vection is affected by combinations of conditions involving three different visual global motions and three different body positions of the observer, using a visual stimulus whose size was almost the same as that used by Ujike et al. (2004). In Experiment 2, we compared the vection strength and illusory body tilt under the same conditions as in Experiment 1, to confirm that the observers in Experiment 1 could distinguish between the two different types of perception that were occurring concurrently. In Experiment 3, we investigated how the vection strength and illusory body tilt experienced in a sitting upright position are affected by three different sizes of the visual stimulus.

2 Experimental principle

In this study, we investigated how vection strength is reduced by the conflict between visual and vestibular inputs. Two types of conflicts are introduced in circular vection: (1) a conflict between information from the visual system and from the semicircular canals (visual–canal conflict), and (2) a conflict between information from the visual system and from the otolith organs (visual–otolith conflict). The visual–canal conflict arises during circular vection around both the earth-vertical and earth-horizontal axes, whereas the visual–otolith conflict arises during circular vection around the earth-horizontal axis. To examine the effect of the addition of the visual–otolith conflict, we adopted combinations of three different body positions (supine, left lateral recumbent, and sitting upright), and three different types of visual global motions around the pitch, roll, and yaw axes. Each type of global motion produces circular vection around its corresponding axis.

We assume that an addition of the visual–otolith conflict is induced when the visual rotation axis is in the earth-horizontal direction. When the actual motion of the rotation axis is in the earth-vertical direction, the otolith organs are not activated during rotation, since the gravitational direction does not change relative to the body. This is consistent with circular vection around the earth-vertical axis, which also does not activate the otolith organs. However, when the actual motion of the rotation axis is in the earth-horizontal direction, the otolith organs are activated during rotation, since the gravitational direction changes relative to the body. This is inconsistent with circular vection around the earth-horizontal axis, which does not activate the otolith organs. The activation of otolith organs during actual rotation around the earth-horizontal axis was, in fact, indicated in experiments involving the study of a ray (*Raja clavata*) (Lowenstein & Roberts, 1950). Moreover, the simulation model of the relationship between the input of gravity and the otolith organs in man was proposed in a number of studies (e.g. Hudetz, 1973; Twizell, 1980). The visual rotation axis is in the earth-vertical direction under the following combinations of visual global motion and posture: (1) roll motion observed in a supine position, (2) pitch motion observed in a left lateral recumbent position, and (3) yaw motion observed in a sitting upright position.

If the visual–vestibular conflict theory is valid, then in our experiment, the vection around the earth-vertical axis should be stronger than that around the earth-horizontal axis. Considering this idea, we investigated a visual–vestibular interaction as described in the following sections.

3 Experiment 1

To investigate the applicability of the visual–vestibular conflict theory to circular vection, we conducted Experiment 1 under combinations of conditions involving three different types of visual global motions and three different body positions. The visual stimulus size that we used, however, was smaller than that used by Howard et al. (1987).

3.1 Apparatus and methods

3.1.1 Apparatus

We constructed a new apparatus composed of three flat-panel displays (100 cm in height, 120 cm in width), each of which was observed from one of the three different body positions (supine, left lateral

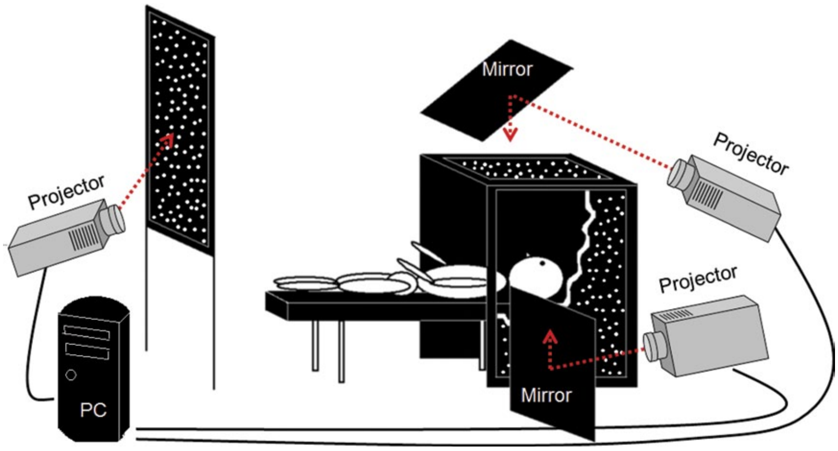

Figure 1. Schematic illustration of the apparatus used in Experiments 1 and 2. Three different LC projectors each back-projected a visual stimulus onto each of three screens; two of the stimuli were projected via mirrors. In the figure, the observer is in a supine position.

recumbent, and sitting upright), as shown in Figure 1. Each of three different LC projectors (Epson EMP-830) back-projected a visual stimulus onto each of the three screens, with two of these stimuli projected via mirrors. When the observer was in a left lateral recumbent or supine position, a screen was installed at the lateral and upper sides of the apparatus, respectively (Figures 2a and b). When the observer was sitting upright, a screen was installed beside the apparatus (Figure 2c). Each of the three different screens was active, depending upon the body posture, and only one screen was used in any condition. A bed (150 cm in length, 70 cm in width, and 55 cm in height) was installed in the apparatus to help the observer maintain the desired position. For the left lateral recumbent and supine positions, the observer lay on the bed, and for the upright sitting position, the observer sat on it.

3.1.2 Stimulus

A visual stimulus that simulated a sphere with a diameter of 120 cm (Figure 3) was rendered in real time as a CG image on a Windows-based PC (Dual Core2, 2.4 GHz) with OpenGL. The frame rate was 60 Hz, and the image size was 1024 × 768 pixels (0.3 mm/pixel), or 93° × 83° from a viewing distance of 57 cm; the vantage point was the centre of perspective projection (Figure 4). The visual context was a random dot pattern consisting of white dots (0.55 cd/m^2) on a black background (0.03 cd/m^2) that was generated on the inner surface of the sphere. The white dots accounted for 33% of the area of the inner surface of the sphere. The visual stimulus simulated rotation of the observer around the pitch, roll, and yaw axes (Figure 3). Both directions of rotation around each of the three axes were used. The rotation velocity was held constant at 60 deg/s.

3.1.3 Procedure

Before the trials were begun, each observer was given time to adapt to the darkness by sitting in a quasi-dark room for 15 min while wearing an eye mask. The observer then viewed the visual stimulus for 140 s, using a bite board to prevent head movement. Each trial began by presenting a stationary

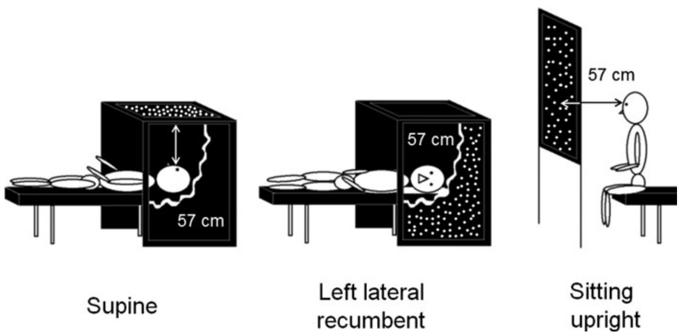

Figure 2. Three different body positions assumed by observers. The observer assumed a different body position for each screen: (a) supine position, (b) left lateral recumbent, and (c) sitting upright.

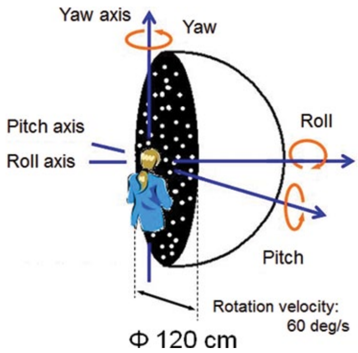

Figure 3. Schematic illustration of the virtual environment. The observer was positioned at the centre of a sphere whose inner surface was textured with a random dot pattern, as shown in Figure 4. Visual stimuli were rotated along three different axes relative to the observer: roll, pitch, and yaw.

image for 10 s, followed by a moving image for 120 s, and then a stationary image again, for 10 s. Two trials were conducted with each of the 18 combinations of two visual rotation directions around three axes—pitch, roll, and yaw—and the three different body positions—supine, left lateral recumbent, and sitting upright. The total number of trials for each observer was 36 and the order of the combinations was counterbalanced across observers and trials.

To measure the vection strength, we adopted two different subjective measurements: continuous measurements during a trial and a simple measurement immediately after a trial. The continuous measurements were adopted based upon a previous study, which reported that observers often experienced intermittent circular vection (Kleinschmidt et al., 2002). During a trial, whenever the observers experienced vection, they continuously indicated the change in vection strength using a subjective response box to evaluate it on a six-point scale. On that scale, "0" represented "no vection was experienced,", and "5" represented "vection so strong that the perceived self-motion could not be differentiated from real physical motion." The observers were able to clearly judge the value of the vection strength without looking at the subjective response box, because a gap, which was tactually perceived, was provided for each value of vection strength on a linear potentiometer. These data were recorded at 60 Hz. After a trial, the observer reported the vection strength over the entire duration of the trial and evaluated that strength on an 11-point scale. Here, "0" represented "no vection was experienced," and "10" represented "vection so strong that the perceived self-motion could not be differentiated from real physical motion."

Upon completion of these tasks, each observer rested for 30 min in the quasi-dark room and then advanced to the next trial. All the observers participated on six different days, with six trials per day.

3.1.4 Observers

Seven adults (one man and six women; 34.9 ± 7.65 years) participated in the study after giving their informed written consent, in accordance with the provisions of the ergonomics experiment policy of

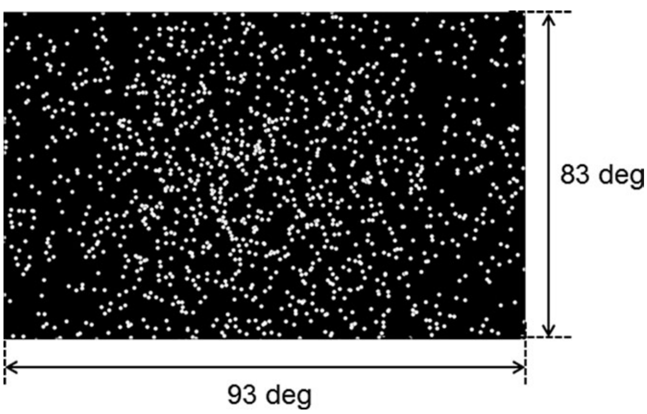

Figure 4. Visual stimulus on each flat-panel display. A random dot pattern was projected onto each of the flat-panel displays.

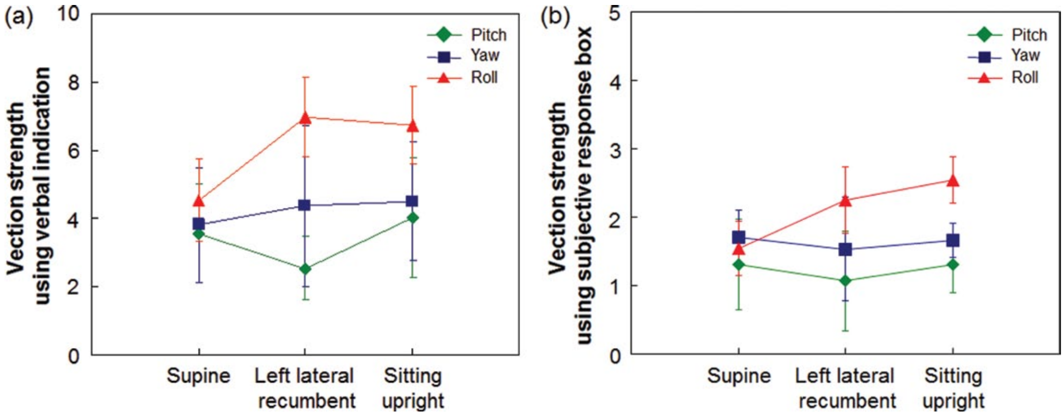

Figure 5. Averaged values of vection strength in Experiment 1 as indicated (a) verbally and (b) with a subjective response box, both as a function of the body position of the observer.

the National Institute of Advanced Industrial Science and Technology (AIST). The observers were free to withdraw at any time during the experiment. The experimental protocol was approved in advance by the Institutional Review Board of AIST. The observers were naïve as to the purpose of the experiment, and had normal or corrected-to-normal visual acuity (based upon testing conducted using the Landolt ring test chart at a distance of 5 m and an optometer). The observers did not have eye disease.

3.1.5 Analysis

We averaged the data of the temporal variation of vection strength, which was continuously measured with a subjective response box during the entire period of visual stimulus motion.

In addition, we evaluated the onset latency of vection (i.e. the time between the onset of optokinetic stimulation and the first subjective report of perceived self-motion) based upon the temporal variation of the vection strength. The statistics shown below are in the form of multiple comparisons, unless otherwise specified.

3.2 Results and discussion

3.2.1 Relationship between vection strength and observation position

The circular vection strength did not show any specific trends in relation to the body position of the observer for any of the three visual rotation axes, when analysed in terms of one-way ANOVA (based on verbal indications: $F(2, 60) = 1.72$, $p = 0.19$; based on the subjective response box: $F(2, 60) = 0.74$, $p = 0.48$) (Figures 5a and b). In the results for the different types of circular vection around the three visual rotation axes, roll vection was significantly stronger than pitch and yaw vection, regardless of the body position, when analysed in terms of the Bonferroni multiple comparison test (based on verbal indications: pitch vs. roll: $t(40) = 5.57$, $p = 1.2 \times 10^{-6}$, yaw vs. roll: $t(40) = 3.36$, $p = 0.0013$; based on the subjective response box: pitch vs. roll: $t(40) = 5.43$, $p = 2.7 \times 10^{-6}$, yaw vs. roll: $t(40) = 2.56$, $p = 0.012$).

3.2.2 Relationship between vection strength and visual–otolith conflict

Our results suggest that the addition of the visual–otolith conflict increases the degree of circular vection (Figures 6a and b). Whether indicated verbally or through the subjective response box, the roll vection strength significantly increased when the visual rotation axis was in the earth-horizontal direction (based on verbal indications: $t(82) = 8.68$, $p = 3.5 \times 10^{-13}$; based on the subjective response box: $t(82) = 10.35$, $p = 1.5 \times 10^{-16}$). Moreover, for measurements based on verbal indications, the pitch vection strength significantly increased when the visual rotation axis was in the earth-horizontal direction ($t(82) = 3.88$, $p = 2.1 \times 10^{-4}$).

For measurements obtained from the subjective response box, the pitch vection strength was not significantly different whether the visual rotation was on the earth-vertical or earth-horizontal axis ($t(82) = 0.98$, $p = 0.32$).

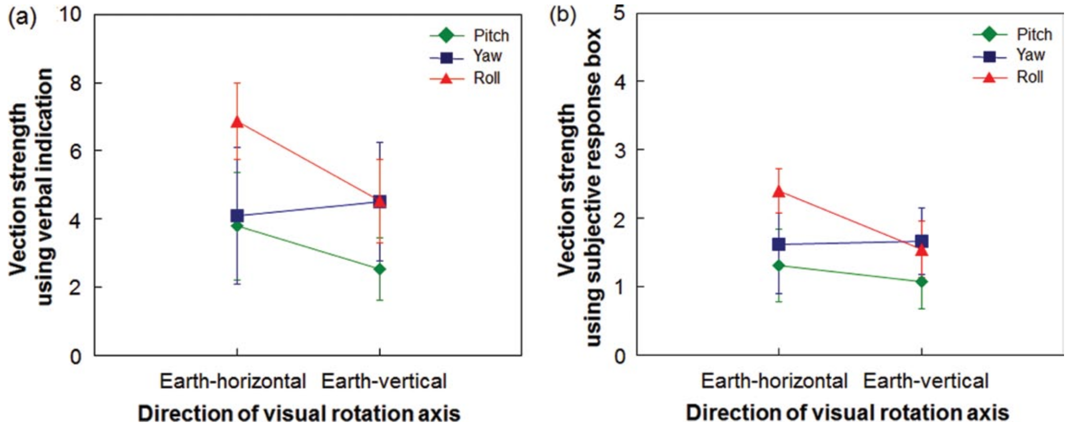

Figure 6. Averaged values of vection strength in Experiment 1 as indicated (a) verbally and (b) with a subjective response box, both as a function of the direction of the visual rotation axis relative to the gravitational direction.

The yaw vection strength was not significantly different whether the visual rotation was on the earth-vertical or earth-horizontal axis (based on verbal indications: $t\,(82) = 0.44$, $p = 0.64$; based on the subjective response box: $t\,(82) = 0.14$, $p = 0.89$).

3.2.3 Onset latency of vection

There were no specific trends in the onset latency of circular vection in relation to the body position of the observer for any of the visual rotation axes (Figure 7a). Moreover, for each of the rotational axes, the averaged value of the onset latency of circular vection was shorter with the addition of the visual–otolith conflict (Figures 7a and b). However, the differences were not significant when analysed in terms of a Student's *t*-test for each type of circular vection (roll: $t\,(82) = 1.19$, $p = 0.22$; pitch: $t\,(82) = 0.33$, $p = 0.73$; yaw: $t\,(82) = 0.52$, $p = 0.58$).

3.2.4 Discussion

The results of the experiment suggest that the addition of the visual–otolith conflict increased the strength of circular vection, a finding that does not conform to the "visual–vestibular conflict" theory proposed by Zacharias and Young (1981). This finding is, however, consistent with Ujike et al. (2004), which was based on experiments in which the visual stimulus did not completely cover the visual field of the observer, as was the case in our Experiment 1.

In that experiment, all the observers perceived circular vection in the direction opposite to that of the visual stimulus motion, as was the case in previously reported research. However, the participants' evaluations of increasing strength of vection around the earth-horizontal axis, especially in the case of roll and pitch vection, may have been distorted by their experience of an illusory body tilt.

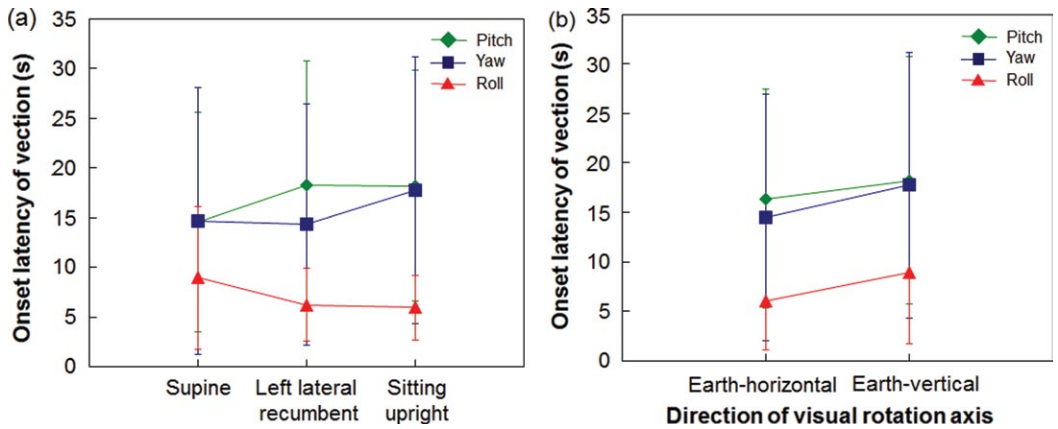

Figure 7. Onset latency of vection, in Experiment 1, as a function of (a) the body position of the observer and (b) the degree of the visual–vestibular conflict.

In the present experiment, we only measured the strength of circular vection and did not measure the illusory body tilt. Therefore, it remains unclear to what degree the observers' responses clearly distinguished the strength of circular vection from the strength of the illusory body tilt. We elucidated this distinction in our next experiment, described below.

4 Experiment 2

In this experiment, observers were asked to intentionally distinguish between vection and the illusory body tilt, using the same apparatus and visual stimulus as used in the previous experiment. They were asked to report upon vection strength, the angle of illusory body tilt, and the degree to which these were convincing.

4.1 Apparatus and methods

4.1.1 Apparatus and stimulus

The experiment was conducted using the same apparatus and stimulus as in Experiment 1.

4.1.2 Procedure

The experiment was conducted using basically the same procedure as used in Experiment 1. One difference, however, is that the time period of the moving image was reduced from 120 to 60 s, because the results of Experiment 1 did not indicate a specific trend for the temporal variation of vection strength. Each participant took part in a trial that consisted of each of the 18 combinations of two visual rotation directions (CW and CCW) around three axes—roll, pitch, and yaw—and three different body positions—supine, left lateral recumbent, and sitting upright. The total number of trials for each observer was 18.

Whenever the observers perceived vection during each trial, they reported its strength using verbal indications and a response box, just as in Experiment 1. In addition, when the visual rotational axis was in the earth-horizontal direction, they reported, after each trial, the extent of the angle to which the body seemed to be tilted or inclined, and also evaluated the degree to which the illusory body tilt was convincing. In the observers' reporting of the angle of the illusory body tilt (up to $\pm 180°$), "0°" represented the original position around the earth-horizontal axis, which was the position when the experimental trial was commenced. In roll motion, "+ value" represented "illusory body tilt is perceived in a CW direction around the roll axis," and "− value" represented "illusory body tilt is perceived in a CCW direction around the roll axis." In pitch motion, "+ value" represented "illusory body tilt is perceived in a forward direction around the pitch axis," and "− value" represented "illusory body tilt is perceived in a backward direction around the pitch axis." In yaw motion, "+ value" represented "illusory body tilt, or a change in position is perceived in a right direction around the yaw axis," and "− value" represented "illusory body tilt, or a change in position is perceived in a left direction around the yaw axis." The degree to which the illusory body tilt was considered convincing was evaluated on an 11-point scale, with "0" representing "no illusory body tilt was experienced," and "10" representing "illusory body tilt so strong that the experienced self-inclination or tilt was indistinguishable from real physical inclination or tilt."

Upon completion of these tasks, each observer rested for 30 min in the quasi-dark room and advanced to the next trial. Each observer participated on two different days, with nine trials per day.

To learn the difference between vection and the illusory body tilt, prior to the main experiment in Experiment 2, all observers participated in a pilot experiment in which roll visual motion was presented in a complete visual field. We chose this motion and visual condition because it enabled all the observers to experience a stable illusory body tilt regardless of the rotational direction (Howard et al., 1987). The result was that they reported that they were able to recognize the two different types of perception, namely vection and illusory body tilt. The pilot experiment was not conducted on the same day as the main experiment.

4.1.3 Observers

Four adults (two men and two women; 42.25 ± 10.53 years) participated in the experiment after giving their informed written consent in accordance with the provisions of the ergonomics experiment policy at AIST, as in Experiment 1. One of the four observers had participated in Experiment 1, and one of the other three observers was one of the authors. Except for the author, the observers were naïve as to the purpose of the experiment, and had normal or corrected-to-normal visual acuity (based on

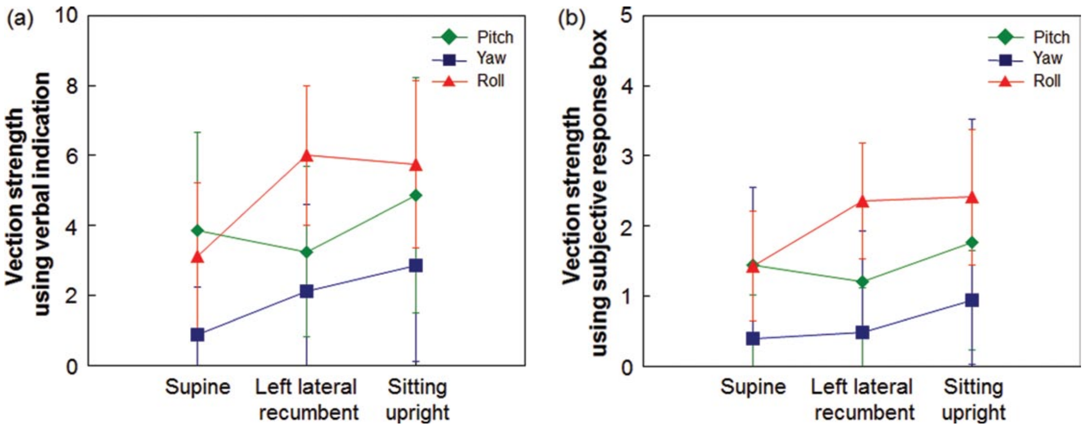

Figure 8. Averaged values of vection strength in Experiment 2, as indicated (a) verbally and (b) with a subjective response box, both as a function of the body position of the observer.

testing conducted using the Landolt ring test chart at a distance of 5 m, and an optometer). The observers did not have eye disease.

4.1.4 Analysis

The method of analysis of vection strength and the onset latency of vection was the same as in Experiment 1. In two different measurements of the illusory body tilt, we averaged the value across observers for each of the conditions in which the illusory body tilt was measured.

4.2 Results and discussion

4.2.1 Vection strength and onset latency of vection

The circular vection strength did not display any specific trends in relation to the body position of the observer for any of the three visual rotation axes, when analysed in terms of one-way ANOVA (based on verbal indications: $F\ (2, 69) = 2.86$, $p = 0.064$; based on the subjective response box: $F\ (2, 69) = 1.85$, $p = 0.16$) (Figures 8a and b).

As with the results of Experiment 1, our results suggest that the addition of the visual–otolith conflict increases the perception of circular vection (Figures 9a and b). Whether indicated verbally or with the subjective response box, the roll vection strength significantly increased under the condition in which the visual rotation axis was in the earth-horizontal direction (based on verbal indications: $t\ (22) = 2.95$, $p = 0.0066$; based on the subjective response box: $t\ (22) = 2.66$, $p = 0.016$) (Figures 9a and b).

However, unlike the results of Experiment 1, the pitch vection strength based on two different subjective measurements, verbal indications, and the subjective response box was not significantly different whether the visual rotation was on the earth-horizontal or the earth-vertical axis (based on verbal indications: $t\ (22) = 0.96$, $p = 0.37$; based on the subjective response box: $t\ (22) = 0.89$, $p = 0.47$).

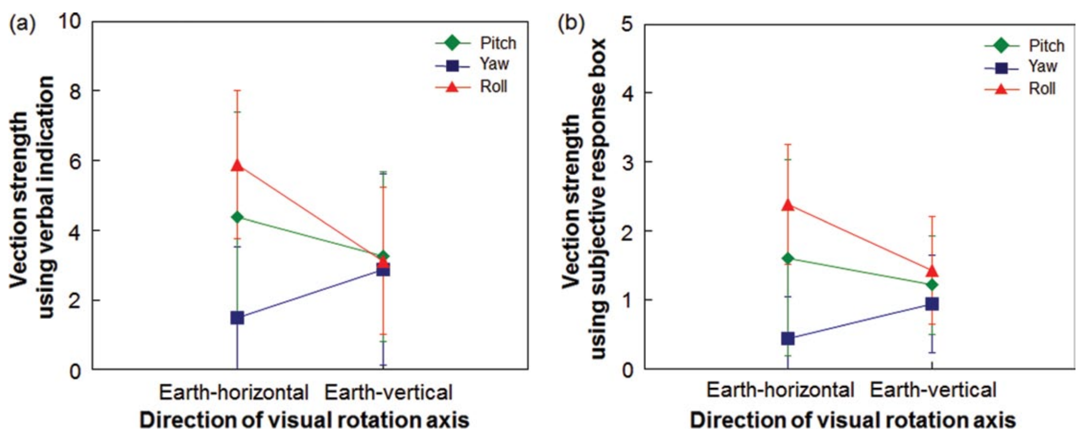

Figure 9. Averaged values of vection strength in Experiment 2 as indicated (a) verbally and (b) with a subjective response box, both as a function of the direction of the visual rotation axis relative to the gravitational direction.

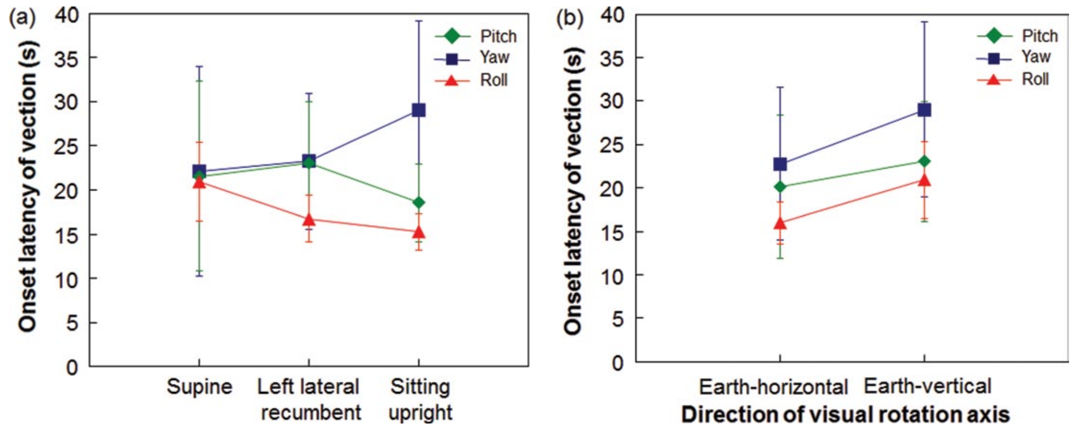

Figure 10. Onset latency of vection, in Experiment 2, as a function of (a) the body position of the observer and (b) the direction of the visual rotation axis relative to the gravitational direction.

Moreover, whether indicated verbally or with the subjective response box, the yaw vection strength was not significantly different whether the visual rotation was on the earth-horizontal or the earth-vertical axis (based on verbal indications: t (22) = 1.35, p = 0.18; based on the subjective response box: t (22) = 1.79, p = 0.085).

There were no specific trends in the onset latency of circular vection in relation to the body position of the observer for any of the visual rotation axes, when analysed in terms of one-way ANOVA (F (2, 55) = 0.09, p = 0.92) (Figure 10a). However, the onset latency of roll vection was shorter when the visual rotation axis was in the earth-horizontal direction (t (22) = 2.85, p = 0.0018) (Figure 10b).

4.2.2 Illusory body tilt

Of the total 48 trials experienced by all participants, the illusory body tilt was perceived in 27 trials (56.3%). The illusory body tilt was induced in the direction opposite to that of the rotation, as was also the case in previous research (Allison, Howard, & Zacher, 1990; Held, Dichgans, & Bauer, 1975; Howard et al., 1987; Young et al., 1975) (Figure 11). The degree to which the illusory body tilt was convincing was always low in each of the conditions in which the illusory body tilt was measured (Figure 12a). Similarly, the angle of the illusory body tilt was also always low in each of the conditions in which the illusory body tilt was measured (Figure 12b).

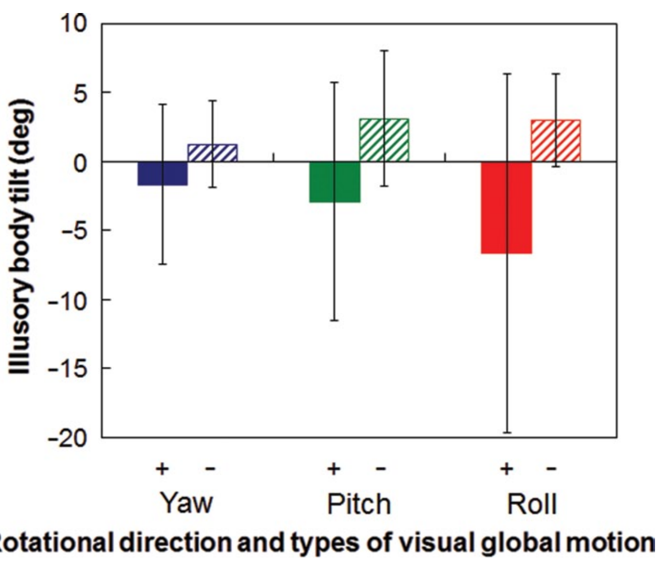

Figure 11. Averaged values of the illusory body tilt angle, in Experiment 2, as a function of the direction and types of visual global motion. All the observers perceived an illusory body tilt in the direction opposite to that of the visual rotational motion.

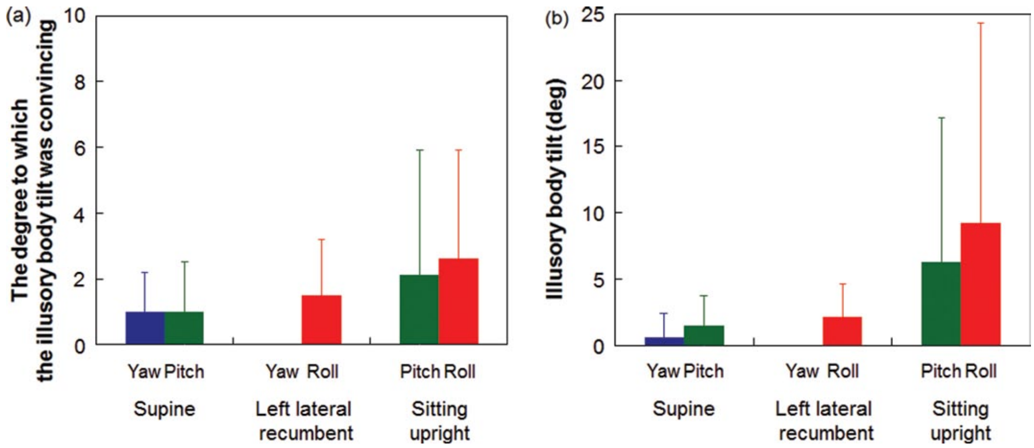

Figure 12. Averaged values in Experiment 2 for (a) the degree to which the illusory body tilt was convincing and (b) the angle of the illusory body tilt, both as a function of the body position of the observer.

The degree to which the angle of the illusory body tilt was perceived and was convincing when the vection strength using verbal indications was more than 5 was significantly higher than when the vection strength using verbal indications was less than 5 (the degree to which the illusory body tilt was convincing: $t\,(70) = 5.10$, $p = 3.1 \times 10^{-6}$; the angle of the illusory body tilt: $t\,(70) = 4.32$, $p = 5.3 \times 10^{-5}$).

4.3 Discussion

The present results suggest that the addition of the visual–otolith conflict increased the strength of circular vection, especially for roll vection. These results therefore confirm the results of Experiment 1. In the present experiment, vection strength was measured as being distinct from the illusory body tilt, because in the pilot experiment, the observers showed their ability to recognize the difference between the two perceptual phenomena of vection and illusory body tilt. As stated above, we confirmed that the vection strength produced under our experimental conditions did not conform to the visual–vestibular conflict theory proposed by Zacharias and Young (1981). The angle of the illusory body tilt and the degree to which it was convincing were weak. In fact, the degree to which the illusory body tilt was convincing was always low, approximately less than 2 on the 11-point scale, in each of the conditions in which the illusory body tilt was measured.

The low values of these results may be due to the following differences in the experimental settings:

1. The size of the visual stimulus was not as large as it was in previous research, in which the stimulus covered the entire visual field.
2. The visual stimulus for circular vection was not a real object, as it was in the previous research.

In Experiment 3, we investigated how the visual–otolith conflict affects circular vection with visual stimuli of various sizes. Moreover, we investigated how the visual stimuli of various sizes affect the illusory body tilt.

5 Experiment 3

We investigated how observers perceive circular vection and the illusory body tilt in response to visual stimuli of various sizes. Specifically, we investigated whether the visual–vestibular conflict theory was applicable to variations of the circular vection strength produced by manipulating the size of the visual field.

5.1 Apparatus and methods

5.1.1 Apparatus

To produce a stimulus with a larger visual field, we used an LC projector (Epson ELP-7700) with a fisheye lens to project a stimulus onto the inside of a hemisphere (with an inner diameter of 150 cm),

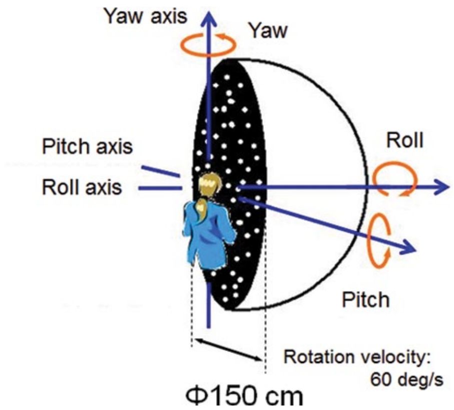

Figure 13. Visual stimulus on the inside of hemisphere display. The random dot pattern that was rotated along three different axes relative to the observer was projected onto the inside of a hemisphere display. In this experiment, the observer was only in an upright sitting position.

as shown in Figure 13. A chair was placed in front of the apparatus to help the observer sit in an upright position. The observer was seated in the chair while viewing the visual stimulus.

5.1.2 Stimulus

A visual stimulus that simulated a sphere with a diameter of 150 cm was rendered in real time as a CG image on a Windows-based PC (Dual Core2, 2.4 GHz) with OpenGL, and projected onto the inside of the hemisphere, as described above. The frame rate was 60 Hz. The visual content was a random dot pattern consisting of white dots (10.5 cd/m^2) on a black background (0.33 cd/m^2), with the white dots accounting for 33% of the area of the inner surface of the sphere. The visual stimulus simulated rotation of the observer around the individual roll, pitch, and yaw axes (Figure 13). The rotation was in either a CW or CCW direction around each of the three axes. The rotation velocity was held constant at 60 deg/s. The visual field of the stimulus was circular, with a diameter that was either 70°, 100°, or 180° from a viewing distance of 50 cm. The area of the 100° visual field corresponded to that of the visual stimulus used in Experiments 1 and 2.

5.1.3 Procedure

The experiment was conducted by basically following the same procedure as used in Experiment 2. Each participant took part in a trial that consisted of each of the 18 combinations of two visual rotation directions (CW and CCW) around three axes—roll, pitch, and yaw—and the three different sizes of visual stimulus—70°, 100°, and 180°. Thus, each observer took part in a total of 18 trials, which were conducted over a period of two days, with nine trials per day.

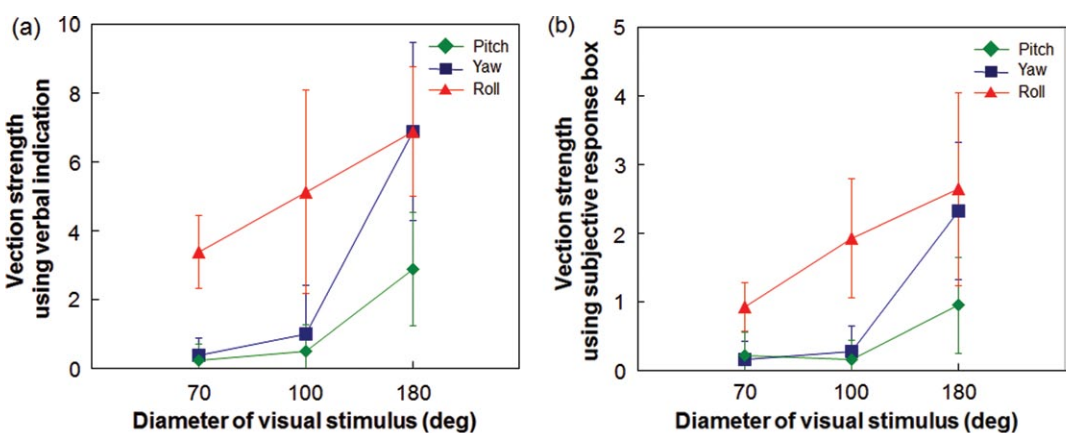

Figure 14. Averaged values in Experiment 3 for vection strength as indicated (a) verbally and (b) with a subjective response box, both as a function of visual stimulus size.

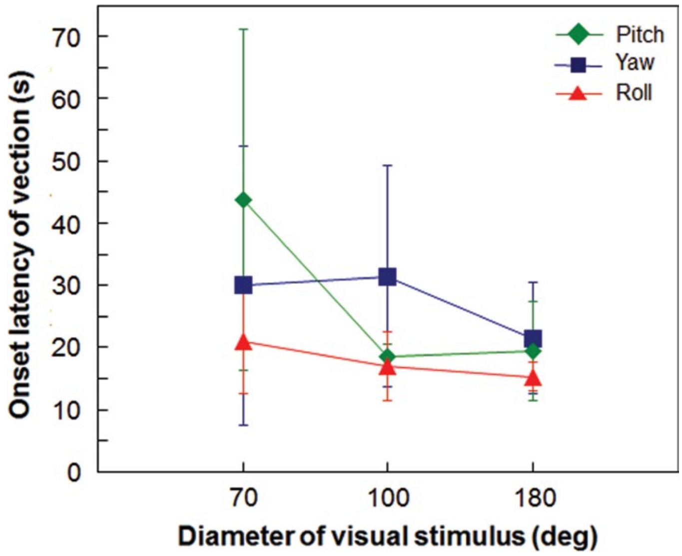

Figure 15. Onset latency of vection, in Experiment 3, as a function of visual stimulus size.

5.1.4 Observers

The observers were the same as in Experiment 2.

5.1.5 Analysis

We analysed the vection strength, the onset latency of vection, the angle of the illusory body tilt, and the degree to which that tilt was convincing, just as in Experiment 2. The method of analysis of the four factors was also the same as in Experiment 2.

5.2 Results and discussion

5.2.1 Relationship between circular vection and stimulus size

Our results suggest that the increment of the visual field of the stimulus increases the strength of circular vection (Figures 14a and b). In fact, the strength of circular vection under the condition of a visual field of 180° was significantly stronger than it was under the other visual field conditions, regardless of the visual global motion, when analysed in terms of the Bonferroni multiple comparison test (70° vs. 180° based on verbal indications: $t\,(46) = 6.28\ p = 6.8 \times 10^{-8}$; 70° vs. 180° based on the subjective response box: $t\,(46) = 5.44\ p = 1.3 \times 10^{-6}$; 100° vs. 180° based on verbal indication: $t\,(46) = 4.05\ p = 1.5 \times 10^{-4}$; 100° vs. 180° based on the subjective response box: $t\,(46) = 3.53\ p = 7.6 \times 10^{-4}$). Moreover, the yaw vection strength significantly increased under the condition of 180°, more than it did under the other conditions of the visual field, becoming almost the same as the roll vection strength (based on verbal indications: $t\,(14) = 0$, $p = 1$; based on the subjective response box: $t\,(14) = 0.49$, $p = 0.56$) (Figures 14a and b). However, there was no significant difference between the strength of the circular vection with a visual field of 70° versus one of 100°, regardless of the visual global motion (based on verbal indications: $t\,(46) = 1.29$, $p = 0.19$; based on the subjective response box: $t\,(46) = 1.53$, $p = 0.12$).

5.2.2 Onset latency of vection

Regardless of the visual global motion, the averaged onset latency of circular vection was the shortest with a visual field of 180° (Figure 15). However, the results were not significant when analysed in terms of one-way ANOVA for each type of circular vection (roll: $F\,(2, 21) = 1.94$, $p = 0.17$; pitch: $F\,(2, 8) = 2.88$, $p = 0.11$; yaw: $F\,(2, 11) = 0.74$, $p = 0.50$).

5.2.3 Illusory body tilt

In roll motion, the increment of the size of the visual stimulus significantly increased both the angle of the illusory body tilt and the degree to which it was convincing (Figures 16a and b). A Bonferroni multiple comparison test showed no significant difference between the angle of the illusory body tilt with a

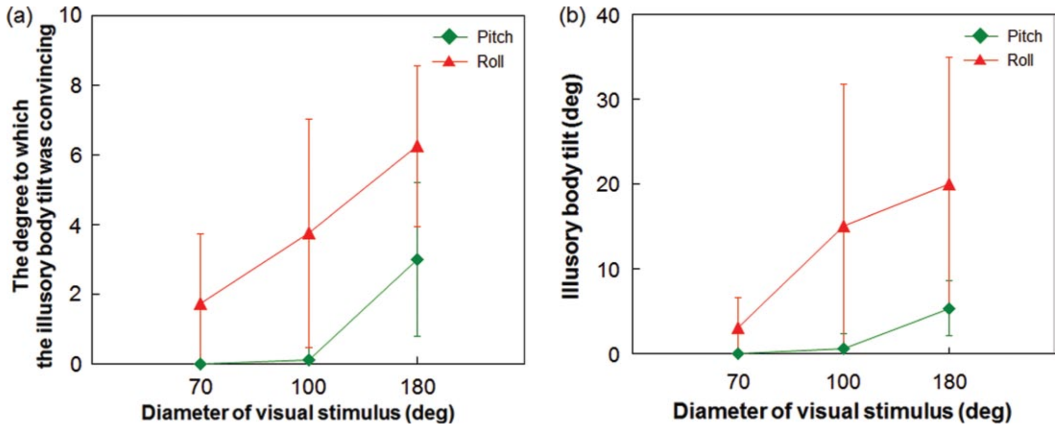

Figure 16. Averaged values in Experiment 3 for (a) the degree to which the illusory body tilt was convincing and (b) the angle of the illusory body tilt, both as a function of the visual stimulus size.

visual stimulus size of 70° versus one of 100° (t (14) = 0.58 p = 0.16), while the angle of the illusory body tilt with a visual stimulus size of 180° was stronger than that with a size of 70° (t (14) = 2.92, p = 9.3×10^{-4}). The variations in the degree to which the illusory body tilt was convincing showed the same tendency as those of the angle of the illusory body tilt, using the Boferroni multiple comparison test (70° vs. 100°: t (14) = 1.65, p = 0.064; 70° vs. 180°: t (14) = 3.91, p = 0.0078).

5.3 Discussion

Our results showed that all the measured parameters—the strength of circular vection, the angle of the illusory body tilt, and the degree to which it was convincing—increased with the size of the visual stimulus. These results are consistent with those of previous research, in light of findings reported for vection strength (Brandt, Dichgans, & Koenig, 1973; Lestienne et al., 1975) and the angle of the illusory body tilt (Allison et al., 1999; Held et al., 1975). The angle of the illusory body tilt and the degree to which it was convincing were not significantly different when the visual stimulus size was 70°. However, the angle of the illusory body tilt and the degree to which it was convincing in roll motion were significantly greater than those in pitch motion when the visual stimulus was 100° or 180°.

Our results suggest that the visual–vestibular conflict theory may be applicable to circular vection when the visual stimulus size is large enough to cover the entire visual field. When the visual stimulus size was 70° or 100°, the strength of the roll vection, which involves the addition of the visual–otolith conflict, was greater than that of the yaw vection. However, with a stimulus of 180°, the strength of the yaw vection was not significantly different from that of the roll vection. In other words, the strength of the yaw vection, which involves a visual–canal conflict, was the same as that of the roll vection, which involves a visual–otolith conflict in addition to the visual–canal conflict. These results suggest that the strength of circular vection around the earth-vertical axis, when the stimulus size is large enough to cover the entire visual field, becomes larger than it is around the earth-horizontal axis. This finding is consistent with Howard et al. (1987), and is thus consistent with the visual–vestibular conflict theory.

The question arises, then, why the stimulus size of 180° was not enough to be consistent with the visual–vestibular conflict theory. The reason for this discrepancy may be the difference in the visual stimulus used as well as its size. The visual stimulus in the present experiment was a projected image, unlike the real object that was used by Howard et al. (1987). Moreover, the visual field size of 180° in the present experiment did not cover the entire visual field, unlike the stimulus used by Howard et al. (1987). Therefore, these conditions related to the stimulus may be a critical factor in the theory of the visual–vestibular conflict.

6 General discussion

The results of our experiments suggest that visual stimulus size is one of the critical factors in the visual–vestibular conflict theory. Experiments 1 and 2, which used a stimulus size of 93° × 83°, showed that the roll vection strength was greater with the addition of the visual–otolith conflict, a finding that opposes the visual–vestibular conflict theory. Experiment 3 with a stimulus size of 180° showed that the yaw vection strength significantly increased and became almost the same as the roll vection strength, which suggests that the vection strength with a larger stimulus size increased with a smaller visual–vestibular conflict. Although the results of Experiment 3 with a stimulus size of 180° do not completely conform to the visual–vestibular conflict theory, the tendency of these results suggests that the stimulus size determines whether or not the theory will be validated.

The pitch and yaw vection strength were not significantly different whether or not there was a visual–otolith conflict. The reason for this may be that the strength of the pitch and yaw vection was not great enough, which may be explained as follows. With roll motion, rotational motion can be perceived regardless of the visual stimulus size. With pitch and yaw motion, however, if we accept Andersen's argument (1986), then the perceived motion may gradually shift from a circular motion around either the interaural or vertical axis to a translational motion along either the vertical or interaural axis, respectively, when the stimulus size becomes smaller. Andersen (1986) indicated that the optical flow is decomposed into two components: a translational component (sometimes referred to as a lamellar or curl-free field) and a rotational component (sometimes referred to as a solenoid or source-free field) by computational approaches. For example, when the visual pitch motion is presented over the entire visual field of the observer, the central visual field mainly includes the translational components of the visual motion and the left and right peripheral visual fields mainly include the rotational components, as shown in Figure 1 in Andersen's (1986) report. Because of the combination of these two components, the observer can recognize that the visual motion indicates pitch motion (circular motion). However, when the visual field is restricted to the central visual field, the observer might recognize that the visual motion indicates vertical motion (linear motion). Moreover, when the peripheral visual field is reduced to some extent when the rotational component remains modest, we would speculate that the recognition of pitch motion becomes ambiguous. In such circumstances, the vection strength may be unstable and may be perceived as being smaller, though we cannot specify the exact size of the visual field that might induce such ambiguous recognition of circular motion.

The illusory body tilt was affected by the increment of the visual stimulus size. In Experiment 2, we did not find a significant difference in the illusory body tilt across experimental conditions, possibly because the angle of the tilt and the degree to which it was convincing were small enough with a small stimulus size. In Experiment 3, however, the angle of the illusory body tilt and the degree to which it was convincing in a roll motion significantly increased with the visual stimulus size, and were significantly different with a stimulus size of 180° from what they were with the other sizes.

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