The effects of dynamic arm movements during prolonged whole-body tilt on the perception of gravitational direction

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ABSTRACT

Do body movements contribute to the perception of the gravitational space? To answer this question, we investigated the influence of arm movements against gravity on the estimation of the gravitational direction or body tilt orientation. In Experiment 1, we asked the participants to perform static or dynamic arm movements during prolonged whole-body tilt and evaluated their effect on subjective visual vertical (SVV) at the tilt position (during-tilt session) and after tilting back to upright position (post-tilt session). In Experiment 2, we assessed how these arm movements at the tilt position affected subjective postural vertical (SPV). We observed that shifts of SVV induced by prolonged tilt were suppressed only by dynamic arm movements. On the other hand, SPV also shifted after prolonged tilt but was not influenced by either static or dynamic arm movements. The present results suggest that the central nervous system (CNS) utilises not only vestibular or static body somatosensory signals, but also additional cues generated by dynamic body movements for the perception of the gravitational direction.

Keywords

Spatial orientation; Gravitational direction; Arm movement; Subjective visual vertical (SVV); Subjective postural vertical (SPV); Prolonged whole-body tilt

INTRODUCTION

To appropriately achieve aimed actions in the gravitational field, the central nervous system (CNS) plans and executes movements based on spatial information, such as gravitational direction and body tilt orientation. Therefore, accurately perceiving one's directions is an important factor determining the quality of motor performance. Previous studies support this assumption by demonstrating that stroke patients, having impaired perception of their directions, experience difficulty in postural control of sitting and standing [1-5].

The CNS builds the internal representation of the gravitational direction and body tilt orientation by integrating multisensory inputs from vision, somatosensory, and vestibular organs with a weighting based on reliability [6-9]. One common method to evaluate the perception of the gravitational direction is the subjective visual vertical (SVV) task, where participants are asked to adjust a visual line to the perceived vertical [10]. Although SVV closely coincides with the actual gravitational direction in the upright position, the estimation error in other positions depends on the body tilt angle. For example, SVV shifts towards the opposite direction of body tilt for a relatively small tilt angle (< 60°, E-effect), but shifts towards the direction of body tilt for a large tilt angle (> 60°, A-effect) [11-14].

When we maintain a tilted body posture for a certain time, referred to as prolonged tilt, SVV gradually shifts towards the side of body tilt regardless of the angle and direction of body tilt [15-20], and SVV remains deviated towards the previous tilted side even after a return to the upright position [15,19,20]. In addition, previous studies have demonstrated that prolonged tilt influences the perception of body tilt orientation [21-24]. This time-dependent change in the perception of the gravitational direction and body tilt orientation seems to be mainly attributed to sensory adaptation. For instance, Fernandez and Goldberg (1976) showed that the otolith afferent firing rate in primates gradually decreased in the roll head-tilt position [25]. Other studies suggest the possibility that somatosensory adaptation derived from trunk receptors may also contribute to SVV shift during prolonged tilt [11,16]. Taken together, head and body angle relative to gravity would be sensed to be smaller due to vestibular and somatosensory adaptation, leading to the shifts of the perceived direction of gravity towards the tilt side [26].

The purpose of this study was to investigate how arm movements during prolonged tilt influence the perception of the gravitational direction and body tilt orientation. Performing arm movements against gravity generates additional information, such as proprioceptive feedback from muscle spindles, skin and joint receptors, and the Golgi tendon organ, and efferent copy [27], which would provide cues about gravitational force on the arm. Moreover, the gravitational torque the shoulder of an extended arm during arm lifting depends on the arm position relative to gravity [28,29]. Given these facts, we expected that the gravitational cues generated by arm movements would improve accuracy in estimating the gravitational direction and body tilt orientation. If the CNS utilises the additional cues

to internally estimate the gravitational space, the decrease of sensed head/body tilt angle due to sensory adaptation would be compensated by the execution of arm movements during prolonged tilt, resulting in the suppression of the alteration of the perceived direction of gravity or body tilt orientation. Contrary to this hypothesis, previous studies have shown that the perception of body tilt orientation or earth-horizontal direction is not improved by the execution of arm movements [29-31]. In these studies, however, the participants were asked to perform the estimation task immediately after the body was tilted or while the body was being tilted. Thus, sensory adaptation would not have occurred in these studies, which might make it difficult to observe the effects of arm movements on the perception of the gravitational space. To address this possibility, the present study evaluated whether or how static or dynamic arm movements during prolonged tilt influenced the perception of visual vertical (Experiment 1) and body tilt orientation (Experiment 2).

METHODS

Experiment 1

Participants

Fifteen healthy volunteers (13 males and 2 females, aged 19–33 years) participated in this experiment after giving written informed consent. All of them had normal vision and no neurological, muscular, or cognitive disorders. This study was approved by the Ethics Committee of the Graduate School of Human and Environmental Studies, Kyoto University, and was conducted in accordance with the Declaration of Helsinki (2013).

Apparatus

The participants sat on a seat (RSR-7 KK100, RECARO Japan, Japan) mounted on a tilt-table in a completely dark room. The head, trunk, and legs were firmly secured to the seat with Velcro bands and a four-point safety belt in a natural position (Fig. 1). An axis under the tilt-table was expanded or contracted via a servo motor, enabling the tilt table to be tilted in the roll plane around a rotation centre located 18 cm underneath the bottom of the seat. The tilting velocity and initial acceleration were respectively 0.44°/s and 0.09°/s^2, which is below the rotational acceleration threshold [32]. Therefore, in the present study, the contribution of the semi-circular canal to the estimation of visual vertical was negligible.

A display (LTN097QL01, SAMSUNG, Korea; 19.6 cm × 14.7 cm) was placed 35 cm in front of the participant's face. To prevent any spatial cues such as the edge of the display, a black-coloured cylinder (26 cm diameter) one end of which was covered by a black board with a hole (10 cm diameter) in the centre, was fixed between the face and the display. During the SVV task, a white line (length, 4 cm; width, 0.1 cm) which could be rotated via a digital controller (BSGP1204, iBUFFALO, Japan) was presented in the centre of the display. An anti-aliasing mode was applied for the projection to avoid any orientational cues derived from the pixel alignment. The display was mounted on the tilt table via metal frames (Green Frame, SUS, Japan), maintaining the display position identical relative to the participants regardless of body tilt angle. At the centre of a vertical frame positioned on the left side of the tilt table was the hinge structure, enabling it to rotate the display portion in the horizontal plane independently from the tilting chair. During the action task, an experimenter rotated the display portion to the left side of the participants, preventing them from hitting their arm against the display or frames. An electric magnet was set between the display portion and the horizontal frame positioned at the right side of the tilt table. The display portion and frame were firmly fixed via the electrification of the electric magnet, enabling it to be set in front of the face.

To temporarily restrict vision, the participants wore a mechanical shutter goggle controlled via

microcomputer (Arduino UNO, Arduino SRL, United States) during the experiment. They also wore earphones via which white noise was provided to avoid auditory cues from the environment.

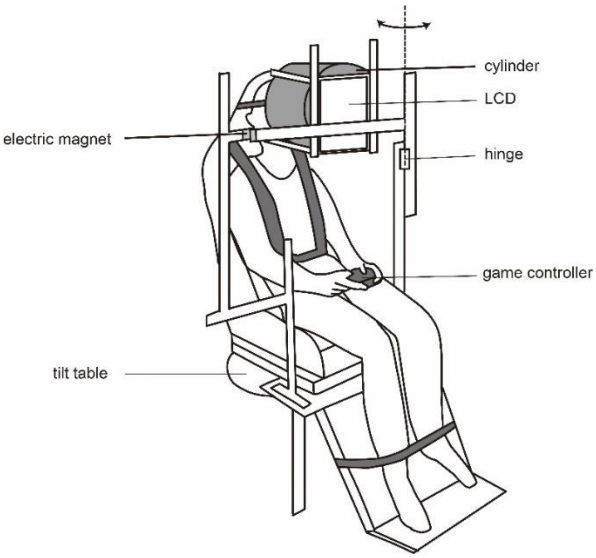

Figure 1

Schema of the experimental setup.

Procedure

This experiment consisted of two sessions, during-tilt and post-tilt sessions. In the former, we evaluated how SVV was influenced by an action task at the tilt position. In the latter, we confirmed whether the effects of an action task performed during prolonged body tilt influenced SVV after returning to the around upright position. Each session was conducted in a randomised order for each participant.

During-tilt session

Figure 2A shows the experimental procedure in the during-tilt session. After the experimenter announced the start of the trial, the shutter closed and the tilt table was tilted leftward. One second later, after the tilt table came to the left-side-down (LSD) 16° position, the shutter opened again, and a white line was presented on the display. The participants were asked to adjust the line to the gravitational vertical via the controller (SVV task). The initial angle of the line was set at ±45°, ±60°, or 90° relative to the body longitudinal axis in a randomised order. The participants repeated 5 trials within 40 seconds. Then the shutter closed and the display portion was moved leftward by the experimenter. The participants were asked to execute one of three action tasks (see the *Action*

Condition section). After the display portion was returned to the initial position (i.e. in front of the participant's face), the shutter opened and the participants were asked to perform the SVV task again for five trials. After the SVV task, they were tilted back to upright. Approximately two minutes of rest was given between trials. Prior to the beginning of this experiment, the participants practiced the SVV task a few times to be able to accomplish five SVV trials within 40s.

Each participant performed the SVV task for 30 trials in total [3 action conditions × 2 phase (before and after action task) × 5 trials]. The order of action conditions was randomised for each participant.

Post-tilt session

Figure 2B shows the experimental procedure in the post-tilt session. After the participants were tilted to LSD 16° position, the display portion was moved leftward by the experimenter and the participants were asked to perform an action task. The display portion was then moved back to the original position and the tilt table was tilted to one of the following positions: upright, right-side-down (RSD) 4°, or LSD 4° position. The shutter opened and the participants were asked to repeat the SVV task for five trials. After the SVV task, the tilt table was tilted back to upright via RSD 16° to avoid providing feedback about body angle to the participants. To prevent the participants from performing the SVV task based on prior knowledge about the experimental protocol, they were not informed about their final tilt position.

Each participant performed the SVV task for 45 trials [3 action task conditions × 3 final tilted angles × 5 trials] in total. The order of presentation of the action task was randomised for each participant. After all trials were accomplished, the participants performed the SVV task for 5 trials at each final tilt position (0° and ±4°) immediately after being tilted from upright without prolonged tilt, referred to as Control condition (Fig. 2C). Therefore, SVV angle in the Control condition does not reflect the effects of prolonged tilt.

Action task

The participants performed one of three action tasks during prolonged tilt as follows: No-movement, Static, or Dynamic tasks. In the No-movement task, both preparation and action sounds were not presented, and the participants were asked to just maintain the tilt posture. In the Static task, a preparation sound was first presented via the earphones, prompting the participants to switch the controller to their left hand and to point to the front of the face using their right index finger with the right arm extended. The participants were instructed to maintain this posture until another preparation sound was presented. In the Dynamic task, a preparation sound was first presented and participants were asked to set the pointing posture as with the Static condition. Three seconds after the preparation sound, an action sound was presented every 3 seconds for a total of 10 times. The participants were asked to move their arm upward and then down parallel to their body's longitudinal axis once per one

action sound with their arm extended. The length of arm movement was set from the height of the eye to the navel. Then another preparation sound was presented, prompting them to hold the controller again.

Prior to the beginning of the experiments, participants sufficiently practiced each action task. The duration time of each action condition (i.e. duration of prolonged tilt) was identical across all conditions (34 seconds). The order of the action tasks was randomised across participants.

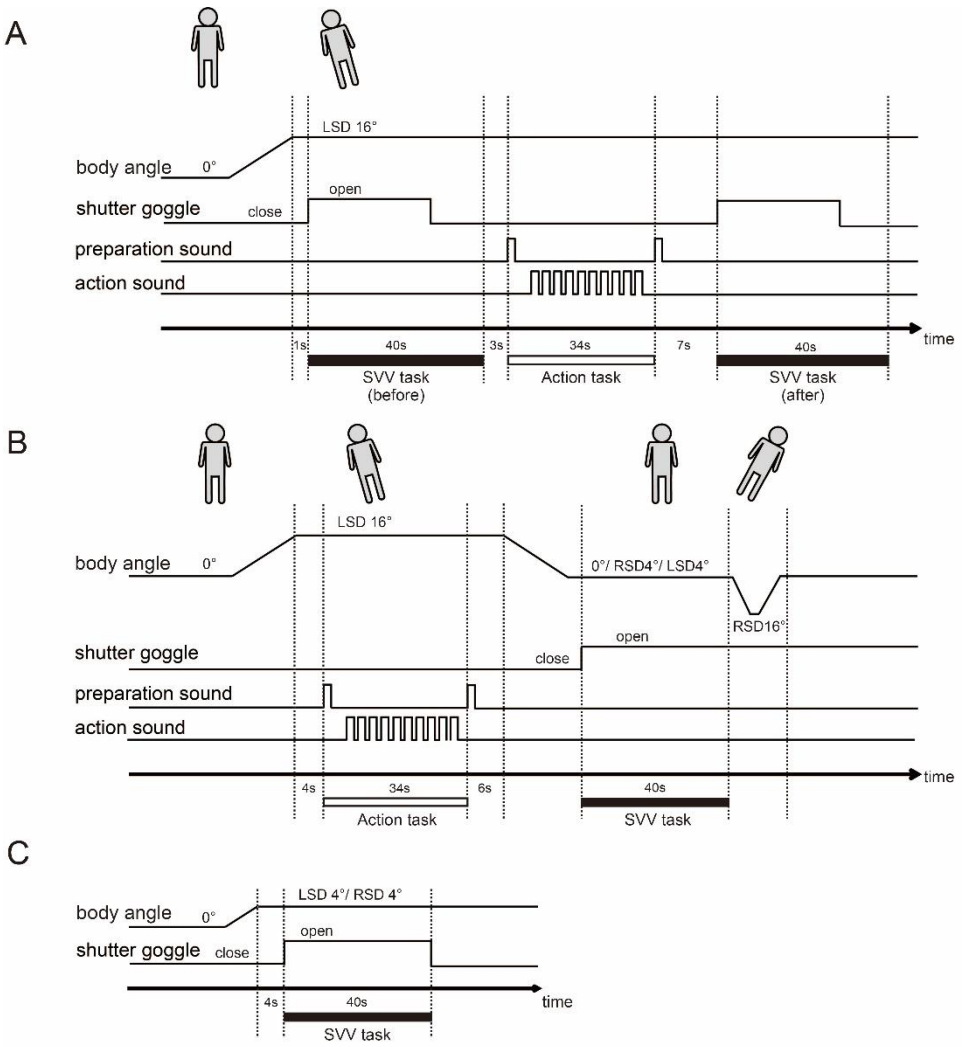

Figure 2

Schema of the experimental procedure in the during-tilt (**A**) and the post-tilt sessions (**B** for the No-movement, Static, and Dynamic conditions; **C** for the Control condition). These figures represent the Dynamic condition.

Data Analysis

We calculated SVV angle as a deviation between the subjective vertical and the actual gravitational vertical for each trial. Since the trial number of SVV tasks (5 trials) was small, the median was applied as the representative value in each action condition for each participant. Kolmogorov-Smirnov tests showed that SVV angles were normally distributed across participants in all conditions for both sessions (all at $p > 0.05$). Therefore, to compare SVV angles between each action condition, we conducted 2-way analyses of variance (ANOVA) with repeated measures [2 phases (before, after) × 3 action conditions (No-movement, Static, Dynamic) for the during-tilt session; 4 conditions (Control, No-movement, Static, Dynamic) × 3 final tilt positions (0°, ±4°) for the post-tilt session].

In addition, we calculated the effect of each action task on SVV angles (SVV_{effect}) by subtracting the SVV angle before the action task from the SVV angle after it for the during-tilt session, or by subtracting the SVV angle in the Control condition from the SVV angle in each action condition (No-movement, Static, Dynamic) for the post-tilt session. Finally, we compared the SVV_{effect} of each action task with one-way [3 action conditions (No-movement, Static, Dynamic)] and two-way [3 conditions (No-movement, Static, Dynamic) × 3 final tilt positions (0°, ±4°)] ANOVAs with repeated measures for the during-tilt and the post-tilt session, respectively.

If sphericity was found to be violated by Mauchly's sphericity test, the degree of freedom was corrected using Greenhouse-Geisser correction coefficient epsilon, and the *p*-value was recalculated. For post-hoc comparisons, Bonferroni's tests were applied. The significance level for all comparisons was set to 0.05. All statistical analyses were conducted using JPSP software version 0.11.1 (Amsterdam, the Netherlands).

Experiment 2

Participants

Twelve healthy volunteers (8 males and 4 females, aged 22–26 years) participated in this experiment after giving written informed consents.

Apparatus

As in Experiment 1, the participants sat on the tilting chair, and the head, trunk, and legs were firmly fastened to the seat. In this experiment, the velocities of the tilt table were different from in Experiment 1. The velocity of the tilt-chair during the subjective postural vertical (SPV) task (see *Procedure* paragraph) was set at 1.0°/s (initial acceleration: 0.52°/s^2) to avoid the stimulation of semi-circular canals [32]. The velocity of the chair from upright to LSD 16° (before SPV task) and from RSD 16° to upright (after SPV task) was relatively fast (8.0°/s), but this would not affect the results for SPV angles because sustained nystagmus was not observed in the preliminary experiment of our previous study [33].

The participants held a custom-made controller with a press-button to indicate the position of the perceived body vertical. The roll-tilt angle of the chair was monitored via an accelerometer module (KXM52-1050, Kionix, U.S.A.) mounted under the centre of the tilt table. The signals from the accelerometer and from the controller were recorded via a data acquisition system (Power Lab 16sp, AD Instruments, Australia). The sampling frequency was set at 100Hz.

During the experiment, the participants wore an eye-mask and were provided white noise via earphones so as not to provide visual or auditory cues from the environment. To prevent the participants from being fatigued, a rest for about ten minutes was inserted per ten SPV trials.

Procedure

The blindfolded participants were first tilted to LSD 16°. In this position, they were presented with one of four action task conditions (No-movement, Static, Dynamic, Control). Under the former three conditions, as with Experiment 2, they were asked to perform each action task based on the preparation and action sounds (see *Action task* paragraph), and then they were tilted to RSD 16°. While tilted from LSD 16° to RSD16°, they were asked to press the bottom of the controller at the point when the body was upright (SPV task). In the Control condition, they were tilted to RSD 16° immediately after arriving at LSD 16° (i.e. without prolonged tilt) and performed the SPV task. After each SPV task, they were tilted back toward upright. As with Experiment 1, the duration time of each action condition was 34 seconds.

Each participant performed the SPV task in 7 trials in each action condition, i.e. 28 trials in total. The order of presentation of the action task conditions was randomised for each participant.

Data Analysis

We calculated SPV angle as the deviation between the subjective vertical and actual gravitational vertical for each trial. The median was used as the representative value of SPV angles in each action condition for each participant. Since Kolmogorov-Smirnov tests revealed a normal distribution of SPV angles across participants in all conditions (all $p > 0.05$), we conducted one-way ANOVA with repeated measures [4 action conditions (Control, No-movement, Static, Dynamic)] to compare SPV angles between action conditions.

RESULTS

Experiment 1

We first checked whether prolonged tilt induced the shifts of SVV in the present experimental set-up. Figure 3 shows the angular changes of SVV in the No-movement condition in each session. Positive and negative values of SVV correspond to rightward and leftward deviation, respectively. Mean SVV across participants tended to shift towards the side of prolonged tilt.

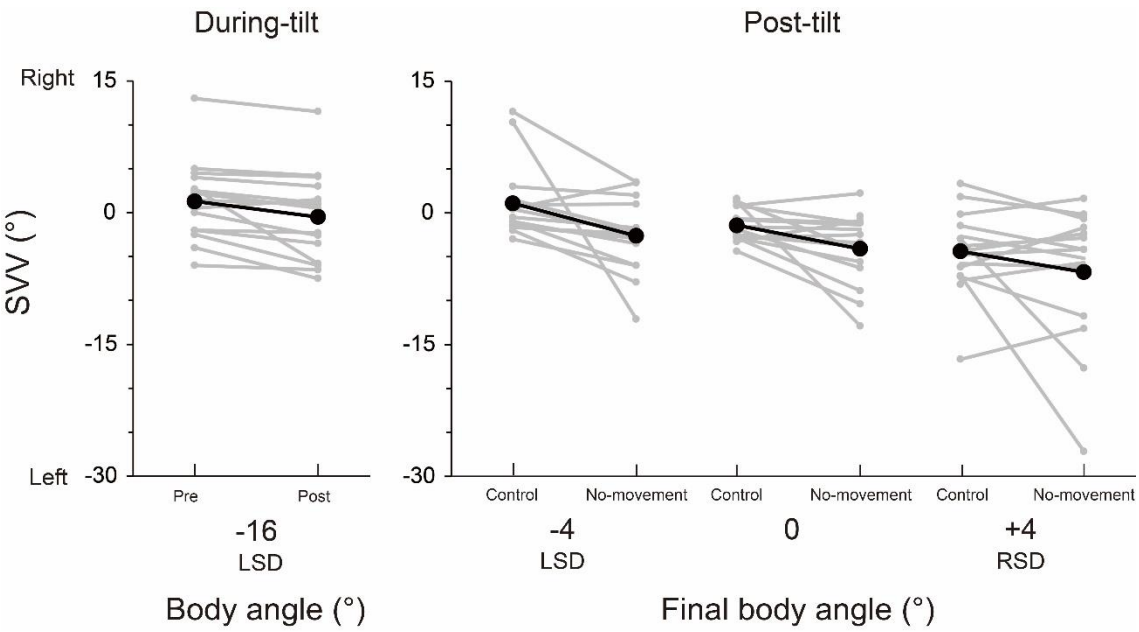

Figure 3

The alteration of SVV angles in the No-movement condition. Grey bars denote the data of each participant and black bars denote the mean data across all participants.

During-tilt session

Figure 4A shows mean SVV angles before and after each action task. ANOVA revealed a significant main effect of phase [$F(1, 14) = 5.21$, $p < 0.05$], but the main effect of action condition was not significant [$F(2, 28) = 1.51$, $p = 0.24$]. There was a significant interaction between phase and action condition [$F(2, 28) = 6.60$, $p < 0.01$]. Post-hoc tests revealed that SVV angle after action task was significantly smaller than that before action task in the No-movement (before, 1.3 ± 1.2°; after, −0.5 ± 1.3°) ($p < 0.05$) and the Static conditions (before, 1.9 ± 1.6°; after, 0.9 ± 1.4°) ($p < 0.05$). In contrast,

in the Dynamic condition, SVV angles before and after the action tasks were not significantly different (before, 1.0 ± 1.1°; after, 1.3 ± 1.0°; $p = 0.55$).

Subsequently, we compared the effect of each action task on SVV (SVV_{effect}). One-way ANOVA revealed a significant main effect of action task condition [$F(2, 28) = 6.60$, $p < 0.01$]. Post-hoc tests showed that SVV_{effect} in the Dynamic condition (0.3 ± 1.6°) was significantly larger than in the Control condition (−1.8 ± 2.2°, $p < 0.01$) (Fig. 2B). On the other hand, there were no significant differences between the Static (−1.0 ± 1.8°, $p < 0.01$) and Control conditions ($p = 0.66$), or between the Static and Dynamic conditions ($p = 0.11$). These results indicate that the shifts of SVV during prolonged tilt were suppressed only by dynamic arm movements.

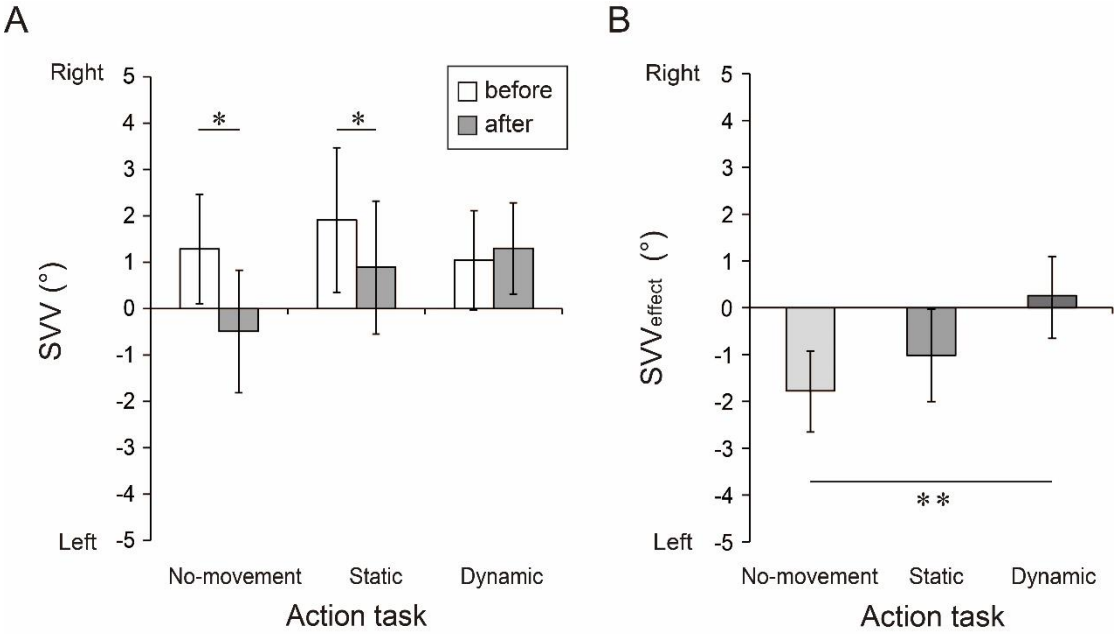

Figure 4

The mean SVV angles before and after action task **(A)** and the SVV_{effect} **(B)** in each action condition in the during-tilt session. Error bars represent standard errors. *: $p < 0.05$, **: $p < 0.01$

Post-tilt session

Figure 5A shows mean SVV angle at each final tilt position in each action condition. ANOVA revealed significant main effects of action condition [$F(3, 42) = 4.90$, $p < 0.01$] and final tilt position [$F(2, 28) = 5.25$, $p < 0.05$], but no significant interaction between them [$F(6, 84) = 0.56$, $p = 0.59$]. Post-hoc tests for action condition revealed that SVV angles in the No-movement (−4.3 ± 0.9°) and in the Static conditions (−4.4 ± 0.9°) were significantly smaller than in the Control condition (−1.4 ± 0.6°) (both at

$p < 0.05$), while there was no significant difference between the Control and Dynamic conditions ($p = 0.27$).

Figure 5B shows the results for SVV_{effect} in each action condition. ANOVA revealed that SVV_{effect} in the Dynamic condition (−1.1 ± 5.0°) tended to be larger than in the other conditions (Static, −3.0 ± 6.6°; No-movement, −2.9 ± 5.5°), but a main effect of action task condition was not statistically significant [$F(2, 28) = 2.32$, $p = 0.12$]. In addition, a main effect of final tilted position [$F(2, 28) = 0.91$, $p = 0.10$] and the interaction effect [$F(4, 56) = 0.86$, $p = 0.41$] were not significant.

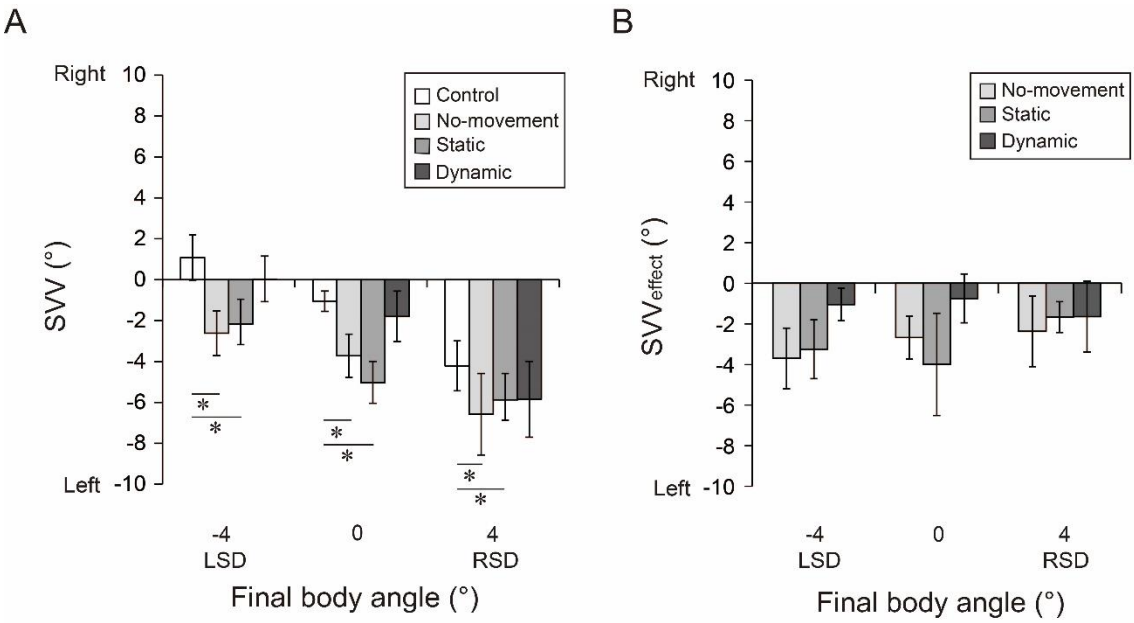

Figure 5

The mean SVV angles (A) and the SVVeffect (B) in each action condition in the post-tilt session. Error bars represent standard errors. *: p < 0.05

The absence of significant differences in SVV angles between the Control and Dynamic conditions regardless of final tilt positions (Fig. 3A) implies that dynamic arm movements could suppress the shifts of SVV after prolonged tilt. However, since conventional statistical testing (i.e. frequentist analysis) cannot allow us to accept the null hypothesis even though the null hypothesis is not rejected due to a non-small p-value, we still did not obtain evidence regarding the absence of a difference in SVV angles between these conditions. Therefore, we carried out a Bayesian analysis using JSPS, and computed Bayesian factors (BF_{01}) as an indication of which of the null (H_0, absence of the difference) or the alternative hypotheses (H_1, presence of the difference) the observed data preferentially explains. We conducted a Bayesian two-way repeated-measures (4 action task conditions × 3 final tilt positions)

ANOVA followed by post-hoc tests. In these analyses, we applied a Cauchy prior distribution with σ = 0, $r = 0.707$ (default of JSPS). As a result, this analysis revealed that the two-main-effect model was most supported ($BF_M = 10.63$) of the models. A post-hoc test for the comparison between the Control and Dynamic conditions showed that the data were twice as likely under the null hypothesis as the alternative hypothesis ($BF_{01} = 2.06$), which supports the result of the frequentist analysis, although the evidence level was weak [34].

Experiment 2

Figure 6 shows mean SPV angle in each action condition. ANOVA revealed a significant main effect of action tasks [$F(3, 33) = 20.75$, $p < 0.001$]. Post-hoc tests showed that SPV angle in the Control condition (−0.8 ± 1.2°) was significantly smaller than in other conditions (No-movement, −5.0 ± 0.9°, $p < 0.001$; Static, −4.2 ± 0.9°, $p < 0.01$; Dynamic, −4.6 ± 0.9°, $p < 0.01$). SPV angle in the No-movement condition was not significantly different from in the Static ($p = 0.32$) or the Dynamic conditions ($p = 1.00$). These results indicate that prolonged tilt induced shifts of SPV toward the side of body tilt, but the shifts were not suppressed by either static or dynamic arm movements.

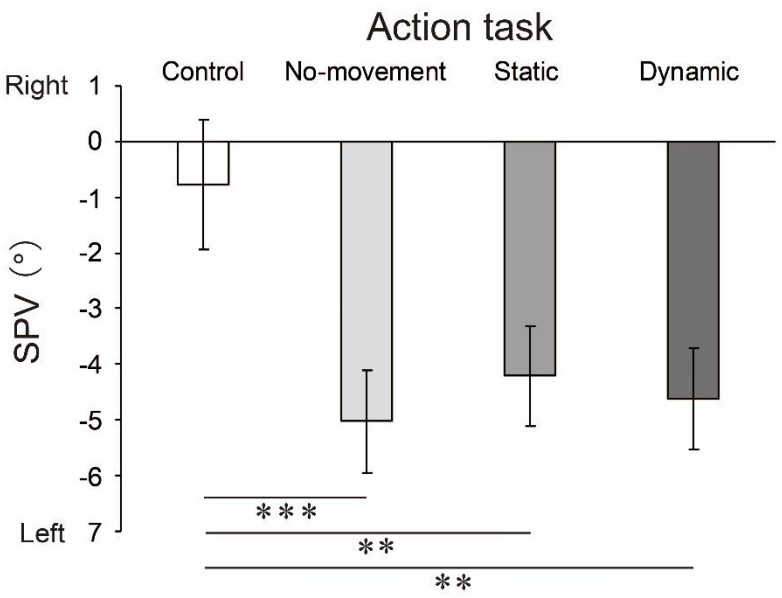

Figure 6

The mean SPV angles in each action condition. Error bars represent standard errors. **: $p < 0.01$, ***: $p < 0.001$

DISCUSSION

In the present study, we evaluated how static or dynamic arm movements during prolonged tilt influenced the estimation of the gravitational direction (SVV) and body tilt orientation (SPV). We found that the shifts of SVV towards the tilted side induced by prolonged tilt were suppressed only by dynamic arm movements. On the other hand, SPV angles were not clearly influenced by either static or dynamic arm movements. Based on these results, we discuss the relationship between the action and the perception of the gravitational space in the following paragraphs.

Consistently with previous studies [15-20], the shifts of SVV towards the side of prolonged tilt (i.e. leftward) were observed, but these shifts were effectively suppressed at the tilt position (*during-tilt* session, Fig. 4) and after returning upright (*post-tilt* session, Fig. 5) when the participants performed dynamic arm movements during prolonged tilt. As mentioned above, the SVV shifts during prolonged tilt are mainly due to sensory adaptation in the vestibular and body somatosensory systems [11,26]. The present results support our hypothesis that the CNS would utilize not only vestibular or static body somatosensory signals, but also the additional cues generated by dynamic body movements to internally represent the gravitational direction.

On the other hand, we found no clear effects of static arm movements on SVV even though the gravitational force on the arm dependent on body tilt angle are generated by both static and dynamic arm movements. The lack of an effect of static arm movements implies that the dynamic property of arm movements plays an important role in the estimation of the gravitational direction. The gravitational force on the arm during arm movements can be perceived as a sense of heaviness based on the afferent information about muscle tension from the Golgi tendon organ (GTO) located at the muscle-tendon junction [35,36]. Psychophysical studies have shown that estimation of the heaviness of an object with concurrent dynamic movements, such as lifting or wielding, is more accurate than estimation with static holding [37,38]. In addition, a physiological study has demonstrated that when constant tension is persistently applied to a muscle, the firing rate and the sensitivity of the GTO to the force gradually deteriorate [39]. These findings suggest that the information about the gravitational force on the arm would be more accurately conveyed to the CNS when performing dynamic arm movements than static arm movements, which would lead to the effective suppression of SVV shifts.

Although dynamic arm movements suppressed the shifts of SVV in both the during-tilt and the post-tilt sessions, the magnitude of the effect differed between them. Specifically, SVV_{effect} was significantly larger in the Dynamic condition than the No-movement condition in the during-tilt session, while no significant difference was observed between them in the post-tilt session. These results allow us to consider that the effect of dynamic arm movements would be relatively small in the post-tilt session compared with in the during-tilt session. This could be related to the time from the arm movements. In the during-tilt session, the participants performed SVV tasks immediately after arm movement task.

On the other hand, in the post-tilt session, they performed SVV tasks after slowly tilting back to upright, and thus the duration between dynamic arm movements and SVV tasks was relatively long (about 20s). It is likely that the contribution of the additional cues derived from arm movements to the estimation of the visual vertical would diminish with the passage of the time after the action task, resulting in a small influence of dynamic arm movements on SVV.

Similar to SVV, SPV also shifted towards the side of prolonged tilt. However, SPV was not clearly influenced by dynamic arm movements. This result was in line with the result of a previous study demonstrating that self-tilt perception was not influenced by vertical arm movements while the body was being tilted [29]. A possible reason for the difference in the effect of dynamic arm movement between SVV and SPV could be related to the different process for the perception of the gravitational direction and body tilt orientation. Indeed, previous studies have demonstrated that the errors in the estimation task of visual vertical and body tilt angle show different patterns during whole-body tilt [9,13,40,41]. For the estimation of visual vertical, the CNS would primarily rely on head-in-space information from the otolith organ [7,9,22]. In addition, body-in-space information from trunk receptors [42,43] and information about the head orientation relative to the trunk originating from neck proprioceptors [44,45] also contribute to the estimation of visual vertical. On the other hand, body tilt orientation in space is estimated based on body-in-space information [7,41], while other information such as vestibular or neck proprioceptive signals would hardly be involved in the perception of body tilt orientation [7,46]. These facts suggest that additional cues derived from arm movements would be incorporated into the estimation process of gravitational direction but not into the estimation of body tilt orientation. Consequently, no clear effects of dynamic arm movements would be observed on SPV.

In conclusion, the present study demonstrated that dynamic arm movements could suppress the shifts of SVV induced by prolonged tilt, suggesting that the supplementary information generated by dynamic body movements would contribute to the perception of the earth-gravitational direction. To better understand the relationship between the effects of action on the perception of the gravitational space, we need to further examine how performance in the estimation of the gravitational direction and body tilt orientation would be influenced by the manipulation of temporal (e.g. movement velocity and acceleration) and spatial properties (e.g. movement direction) of arm movements.

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