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Visuospatial orientation: Differential effects of head and body positions

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ABSTRACT

To orientate in space, the brain must integrate sensory information that encodes the position of the body with the visual cues from the surrounding environment. In this process, the extent of reliance on visual information is known as the visual dependence. Here, we asked whether the relative positions of the head and body can modulate such visual dependence (VD). We used the effect of optokinetic stimulation (30°/s) on subjective visual vertical (SVV) to quantify VD as the average optokinetic-induced SVV bias in clockwise and counter-clockwise directions. The VD bias was measured in eight subjects with a head-on-body tilt (HBT) where only the head was tilted on the body, and also with a whole-body tilt (WBT) where the head and body were tilted together. The VD bias with HBT of 20° was in the same direction of the head tilt position (left tilt VD −1.35 ± 0.1.2°; right VD 1.60 ± 0.9°), whereas the VD bias with WBT of 20° was in a direction away from the body tilt position (left tilt VD 2.5 ± 1.1°; right tilt VD −2.1 ± 0.9°). These findings show differential effects of relative head and body positions on visual cue integration, a process which could facilitate optimal interaction with the surrounding environment for spatial orientation.

1. Introduction

Perception of spatial orientation relies on combined processing of allocentric visual information with egocentric sensory inputs that encode the position of the body in space [1–3]. In this process, the extent of reliance on visual inputs or ‘visual dependence’ is vital to maintain a stable spatial orientation, especially in situations where the visuospatial context is in conflict with the sensory inputs that encode the body position in space [4–8]. Experimentally, visual dependence can be measured using the subjective visual vertical (SVV) task in which a visual line is aligned to perceived vertical orientation [4,7–9]. With a background optokinetic stimulation rotating about the visual axis, a bias in SVV response is induced in the same direction of the visual motion along with a sensation of body tilt in the opposite direction. In this scheme, the visual-induced SVV bias can be used to probe modulating effects of body position on visual dependence.

Previous studies have shown that in human observers, visual dependence increases at large body tilt angles where sensory information from the vestibular receptors become less reliable [5,10–13]. Such stronger effect of visual inputs during body tilt can be seen in the presence of either dynamic (e.g. optokinetic stimulation) or static visual stimuli (e.g., panoramic cues) [5,10,13–15]. It is, however, unknown how sensory interactions at various head or body positions may affect visual cue integration for spatial orientation. Psychophysical studies suggest that the brain behaves optimally in this regard by combining each sensory signal in proportion to its reliability [1,3,16,17]. For example, when the head is tilted, the position of the head can be obtained directly from the head sensors (e.g., vestibular inputs), or indirectly from the angle between the head and body through sensory inputs that encode the relative neck and trunk positions (e.g. neck

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Abbreviations: SVV, Subjective Visual Vertical; VD, Visual Dependence; HBT, Head on Body Tilt; WBT, Whole Body Tilt.

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proprioceptors). This overlapping sensory information can be valuable to reduce perceptual uncertainty while encoding the orientation of the body with respect to the visual surroundings. In this study, we asked whether such sensory contributions related to the changes in the head and body positions can modulate the weight of visual inputs for spatial orientation or the visual dependence. To address this question, we probed visual-induced SVV bias at two different states of whole-body tilt and head-on-body tilt positions.

2. Material and methods

This study was approval by the local ethics research committee, and all experiments were performed in accordance with the declaration of Helsinki. Eight healthy volunteers (five females) gave informed consent to participate. The age range was from 21 to 30 y/o (mean 23). All participants were right-handed (self-reported) and reported to be in good health. Exclusion criteria included significant visual impairment (not correctable with glasses), neurological impairment (including history of seizure, stroke, frequent migraines, or vestibular impairment), psychiatric illness, and any current or historical neck pain.

2.1. Experiment setup

Subjects were seated upright in a tilt apparatus in a completely dark room. They were secured into the seat using a safety belt and restrain bars. Cushions were added around the pelvic area and trunk to minimize body motion. The seat was adjusted to ensure that the center of rotation was aligned with the subject's head, which was immobilized using head cushions and a molded bite bar. A computer screen was mounted at 33 cm in front of the subject and the height was adjusted to align the center of the screen with the eye level. To avoid vertical cues, the screen was only visible through a viewing cone that was placed between the screen and the subject. The diameter of the cone at the screen was 24 cm and at the subjects' eyes was 20 cm, subtending a viewing angle of 40°. Subjects performed SVV trials (as described below) first in the upright position and then under two tilt conditions: (i) whole body tilt (WBT) of 20° in the roll plane to the right and left, and (ii) head on body tilt (HBT) of 20° in the roll plane to the right and left (Fig. 1). The order of recording with WBT and HBT was counter-balanced among the subjects. The order of right and left tilts was also counter-balanced among subjects, but a similar order of tilt was used in the WBT and HBT conditions for each subject.

2.2. SVV recording

The visual stimulus consisted of a 6 cm white line on a black background. The line rotated 360° about its midpoint in the central 11° of the visual filed. Outside of this central field, the black background was filled with a set of randomly distributed white dots, each 8 mm (1.5° of visual field) in diameter. Subjects controlled the orientation of the line with a computer mouse and were instructed to align the line to their perceived vertical at each trial using their right hand. Once they clicked on the mouse, their response was recorded and the next trial started. The set up was mounted on the same tilt apparatus in which the subject was seated, and therefore the relative position of the screen did not change when the whole body was tilted. When the head was tilted on the body, the position of the screen was also adjusted so that the fixation dot on the screen remained aligned with the nasion.

SVV recording was done in three sessions: In one session, the dots were stationary (static) and in the other two sessions, they rotated at 30°/s in either clockwise (CW) or counterclockwise (CCW) directions (hence producing an optokinetic effect). In each session, the SVV task consisted of six trials with the line appearing randomly at 20°, 40° or 70° angles to the right and left. The session with stationary dots was always recorded first, but the order of recording between the CW and CCW sessions were counter-balanced among the subjects.

2.3. Data analysis

At each SVV recording session, the SVV was determined as the mean value from the six SVV trials. Visual Dependence (VD) was calculated as the difference between SVV in CW/CCW sessions and the static session: $\mathrm{VD} = [(\mathrm{SVV}_{\mathrm{CW}}\text{-}\mathrm{SVV}_{\mathrm{static}})+(\mathrm{SVV}_{\mathrm{CCW}}\text{-}\mathrm{SVV}_{\mathrm{static}})]/2$ [9,18]. Statistical analyses were done in MATLAB using repeated measures analysis of variance (ANOVA) with the type of tilt (WBT/HBT), direction of visual rotation (CW/CCW), or direction of tilt (left/right) as the independent factors. A p-value<0.05 was considered statistically significant.

3. Results

The SVV results with and without visual rotation for all tilt positions are shown in Fig. 2A. With the head upright, the average SVV values ± standard error of mean (SEM) were −0.61 ± 0.1° for the static background, 5.42 ± 1.5° for the CW visual rotation, and −4.14 ± 0.3° for the CCW visual rotation (positive values indicate CW bias, and negative values CCW bias).

Head on body tilt: The average SVV values with the left HBT were −0.98 ± 0.6° for the static background, 3.85 ± 0.5° for the CW visual rotation, and ± 0.5° for the CCW visual rotation. The average SVV values with the right HBT were −0.62 ± 0.3° for the static background, 10.96 ± 0.6° for the CW visual rotation, and −6.56 ± 0.8° for the CCW visual rotation.

Whole body tilt: The average SVV values with the left WBT were −7.11 ± 0.5° for the static background, 4.48 ± 0.6° for the CW visual rotation, and −11.18 ± 0.6° for the CCW visual rotation. The average SVV values with the right WBT were 1.86 ± 0.2° for the static background, 8.32 ± 1° for the CW visual rotation, and −6.35 ± 1° for the CCW visual rotation.

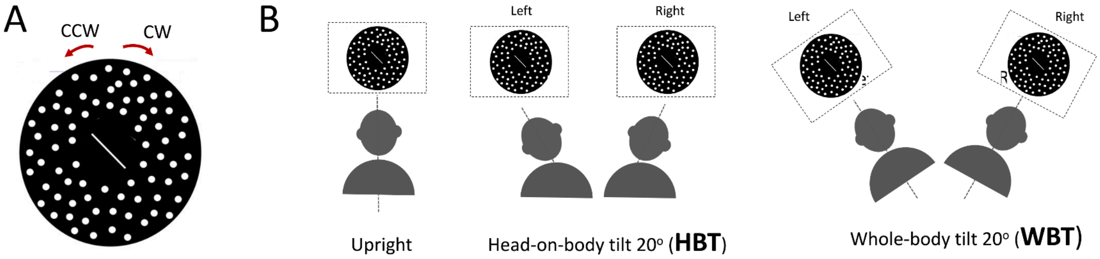

Fig. 1. A: To measure visual dependence, subjective visual vertical (SVV) was measured using a line that had to be set to perceived gravitational vertical with a background that consisted of randomly placed dots. The background was either static or in motion (i.e., roll plane optokinetic stimulation) in clockwise (CW) or counter clockwise (CCW) direction. Visual Dependency was then calculated as the difference between SVV in CW or CCW sessions from the static session. B: The task was performed first in the upright position and then under two tilt conditions: Whole body tilt of 20° (WBT) and head on body tilt (HBT) of 20° to the right and left. The edges of the screen (dotted line) was covered and only the visual stimulus was visible on the screen through a cone.

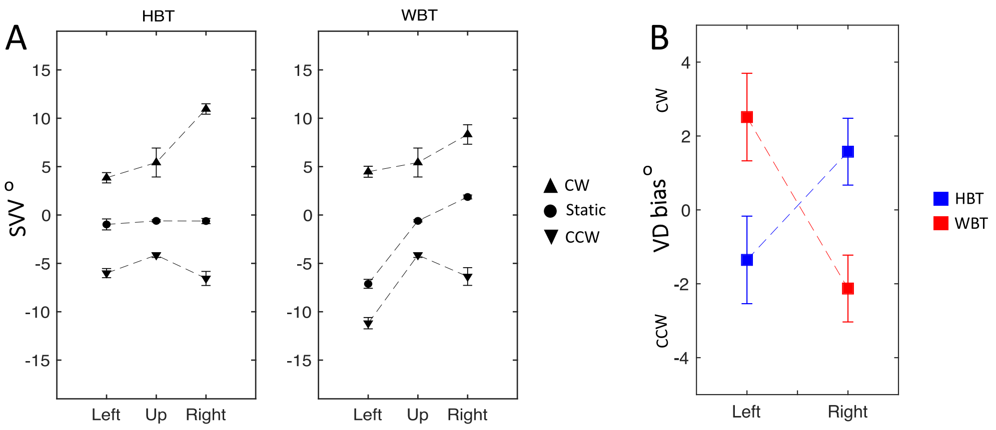

Fig. 2. A: Average SVV without visual rotation (static) and with clockwise (CW) and counter clockwise (CCW) rotations are shown for head-on-body tilt (HBT) and whole-body tilt (WBT). B: Visual Dependence (VD) was calculated as the difference between SVV in CW and CCW sessions from the static session. The tilt-induced bias in VD was calculated as the VD values in each tilt condition from the VD value in the upright position. The VD bias is in the direction of the tilt with HBT, but it is in the opposite direction of the tilt with WBT. The error bars represent SEM.

In both WBT and HBT conditions, a significant main effects of tilt and direction of visual motion were observed (two-way repeated measure ANOVA, HBT tilt $F = 24.3$, $p < 0.001$; HBT visual motion $F = 440.3$, $p < 0.001$; WBT tilt $F = 62.6$, $p < 0.001$; WBT visual motion $F = 257.9$, $p < 0.001$), and there was significant interaction between these two factors (HBT $F = 61.2$, $p < 0.001$; WBT $F = 67.3$, $p < 0.001$).

Tilt-induced bias in visual dependence: To investigate sensory interactions mediating VD, we compared the results between HBT and WBT conditions. The effect of WBT and HBT on VD was accounted for by subtracting the VD values in each tilt condition from the VD value in the upright position (Fig. 2B). The VD was biased in the same direction of the tilt with HBT (left tilt VD −1.35 ± 0.1.2°; right VD 1.60 ± 0.9°), whereas it was biased in the opposite direction of the tilt with WBT (left tilt VD 2.5 ± 1.1°; right tilt VD −2.1 ± 0.9°). A significant interaction between the effects of the tilt direction on VD and tilt type on VD was observed (two-way repeated measure ANOVA, $F = 3.9$, $p = 0.02$).

4. Discussion

In the process of multisensory integration for spatial orientation, the extent of reliance on a sensory signal or its weight is determined by the current state of body position and visual surroundings [1–3,19]. In this study we examined whether changes in the head or body position can modulate the effect of visual inputs on spatial orientation. We used the effect of visual motion on SVV to compare visual dependence with the head tilted on the body and the whole-body tilted en bloc.

Our findings show differential effects of head and body positions on visual dependence, as the visual-induced SVV bias differed depending on whether the head was tilted alone or whether it was tilted along with the trunk (hence no neck flexion). When the head was tilted, there was a visually-induced bias towards the same side of the tilt (e.g., CW with the right tilt; Fig. 2B), but with the whole-body tilt, the visual bias was away from the side of the tilt (e.g., CCW with the right tilt; Fig. 2B). Thus, when the head was tilted on the body, the visual bias was congruent with the direction of the tilt, but it became incongruent with the direction of the tilt when the whole body was tilted. These distinct effects suggest that the spatial weight of visual stimuli is modulated in accordance with the current state of body position. For example, in situations with imposed tilting of the whole body (i.e., falling), the stronger effect of visual motion in the opposite direction of the tilt can help shift spatial attention in the opposite direction to counteract the effect of tilt, whereas when the head is tilted alone, the congruent visually-induced bias can help shift spatial attention in the same direction of the head orientation.

The distinct effects of head and body positions on visuospatial orientation can be mediated by various sensory interactions including (i) head sensors that provide information about the orientation of the head with respect to gravity (e.g., vestibular system), (ii) body sensors that provide an estimate of the orientation of the body in space (e.g., somatic graviceptors), and (iii) neck sensors that provide an estimate of the angle between the head and body positions (e.g., neck proprioceptors) [20,21]. In this context, SVV errors reflect challenges for the brain in maintaining a common reference frame based on sensory information encoding the eye, head and body positions in the absence of visual cues. Commonly, SVV errors are biased toward the direction of the body position at large tilt angles (Known as the A effect), and in the opposite direction of the body position at small tilt angles (known as the E effect) [1–3]. These systematic errors however can be modulated with visual cues, and our results suggest that such modulation would also depend on the head and body positions. Previous studies have shown that when vestibular inputs become less reliable, visual cues have a stronger influence on spatial orientation [10,13,14,22,23]. This effect was present with either a static tilt of the visual background or with optokinetic stimulation. Consistent with our findings, the visually-induced optokinetic bias was in the opposite direction of the whole-body tilt at both small and large tilt angles [10,14,24]. The effect of head-on-body tilt on visual dependence has been also studied [24], however, the differential effects of head versus whole body tilts were not examined previously. In another study, the visually-induced bias was more pronounced in the SVV task than in a task where body tilt position was reported, which is in line with the multisensory aspect of spatial orientation [14]. Changes in the trunk tilt position alone (i.e., without changing head position) could also modulate visual dependence, showing how proprioceptive inputs from the neck or trunk can affect visuospatial orientation [25].

Although the sample size is small in this study, our results suggest non-uniform effects of tilt positions on visual dependence, as the bias induced by CW rotation was larger than the CCW rotation. The larger effect of CW rotation was pronounced during the right head tilt and left whole body tilt (Fig. 2). This asymmetry in visual dependence and its difference between the tilt conditions suggest a lateralized effect from how the interactions of head, neck, and trunk positions can modulate the influence of visual inputs in spatial orientation. Similar lateralized effects have been observed in experiments probing visuo-vestibular interactions [26], and imply a degree of hemispheric dominance for spatial orientation [27]. Here we could not examine this effect as all participants were right handed, and future studies are needed to examine a functional laterality in visual dependence.

In this study we used a roll optokinetic stimulus rotating about the visual axis which can generate a torsional optokinetic nystagmus [28,29]. Whether the torsional nystagmus can affect SVV responses has not been studied directly by measuring eye movements. De Vrijer et al. found a similar optokinetic-induced bias in the SVV task and when the orientation of the body was reported using a visual line, but the bias was not present when the orientation of the body was reported verbally during optokinetic stimulation [14]. These findings suggest that the nystagmus can have a role in producing the visuospatial bias. In our study, although we did not measure eye movements directly, we do not expect a significant difference in the optokinetic nystagmus when the head was in the same orientation, either tilted on the trunk or tilted along with the trunk. Therefore, we postulate that the distinct changes in visual dependence with tilting the head versus the whole body are primarily driven by multimodal sensory interactions.

Strong effect of visual cues has been also shown in other settings such as a visual frame in the SVV task. The frame orientation can bias visual vertical estimate in the same direction, which is known as the rod-and-frame effect [15,22,30,31]. This visual effect also increases with tilting the body, indicating increased reliance on visual cues with reduced reliability of other sensory inputs that encode body position [22,32]. Usually frame tilts close to perceived vertical result in an ‘attractor bias’ towards the frame orientation, whereas a ‘detractor bias’ is seen at larger frame tilts [15,22,33].

In conclusion, here we studied distinct effects of head and body positions on how visual inputs are integrated into spatial orientation. When the head was tilted on the body, the visually-included bias in spatial orientation was in the same direction of the tilt, but when the whole body was tilted, this visually-induced bias was in the opposite direction of the tilt. These findings show how body position can modulate multisensory contributions to spatial orientation, a process that could facilitate optimal interaction with the surrounding environment.

CRediT authorship contribution statement

Patricia Castro Abarca: Methodology, Data curation, Investigation, Formal analysis, Writing – original draft. **Shahvaiz Hussain:** Investigation, Data curation. **Omer G. Mohamed:** Investigation, Data curation. **Diego Kaski:** Writing – review & editing. **Qadeer Arshad:** Conceptualization, Methodology, Validation, Writing – review & editing, Supervision. **Adolfo M. Bronstein:** Conceptualization, Validation, Resources, Writing – review & editing. **Amir Kheradmand:** Conceptualization, Methodology, Data curation, Formal analysis, Validation, Writing – review & editing, Resources, Supervision.

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