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Visual perception of upright: Head tilt, visual errors and viewing eye

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Abstract

BACKGROUND—Perception of upright is often assessed by aligning a luminous line to the subjective visual vertical (SVV).

OBJECTIVE—Here we investigated the effects of visual line rotation and viewing eye on SVV responses and whether there was any change with head tilt.

METHODS—SVV was measured using a forced-choice paradigm and by combining the following conditions in 22 healthy subjects: head position (20° left tilt, upright and 20° right tilt), viewing eye (left eye, both eyes and right eye) and direction of visual line rotation (clockwise [CW] and counter clockwise [CCW]).

RESULTS—The accuracy and precision of SVV responses were not different between the viewing eye conditions in all head positions ($P > 0.05$, Kruskal-Wallis test). The accuracy of SVV responses was different between the CW and CCW line rotations ($p \approx 0.0001$; Kruskal-Wallis test) and SVV was tilted in the same direction as the line rotation. This effect of line rotation was however not consistent across head tilts and was only present in the upright and right tilt head positions. The accuracy of SVV responses showed a higher variability among subjects in the left head tilt position with no significant difference between the CW and CCW line rotations ($P > 0.05$; post-hoc Dunn's test).

CONCLUSIONS—In spite of the challenges to the estimate of upright with head tilt, normal subjects did remarkably well irrespective of the viewing eye. The physiological significance of the asymmetry in the effect of line rotation between the head tilt positions is unclear but it suggests a lateralizing effect of head tilt on the visual perception of upright.

Keywords

Subjective visual vertical; head tilt; line rotation; monocular; binocular

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1. Introduction

As an individual interacts with the surrounding environment the projection of the scene onto the retina changes due to movement of the eyes and change in the head and body position. Despite all these movements the visual world continues to appear stable along the earth-vertical axis (up and down). One way to examine this internal reference to gravity is by aligning an illuminated line with the perceived pull of gravity, referred to as the 'subjective visual vertical' (SVV). Normally, in the upright position, one can adjust the visual line into vertical orientation with an error of about 2 degrees in an otherwise completely dark room [8,18].

The visual perception of upright is based on the integration of visual information with other sensory modalities including those from the vestibular and somatosensory systems, as well as the ocular inputs that encode orientation of the globe within the orbit. In the upright position, sensory inputs that encode head and body positions are naturally aligned with the gravity axis. With a head tilt, however, images would also be tilted on the retina unless there is a perfect compensatory (counter-roll) response of the globe to keep the retina oriented along the pull of gravity. In fact, this compensatory response is far less than the amount of head tilt (usually in the range of 5–25%) and images do become tilted on the retina [2]. Thus, tilting the head can pose a challenge to integration of visual and vestibular information into a coherent perception of upright. This is reflected in the systematic errors of SVV when the head is tilted away from upright. The true vertical orientation is underestimated at the tilt angles greater than 70° with responses biased toward the side of the head tilt (known as the A-effect) [10,18,19]. At smaller tilt angles less than 60°, SVV responses might be overestimated toward the opposite side of the head tilt (known as the E-effect) [8,18,22]. Generally, the E-effect is less consistent and presents less often compared to the A-effect [3,16]. Bayesian analysis suggests that the systematic errors of SVV represent a precision-accuracy trade off in the visual perception of upright, aiming at a high precision (i.e., how consistent are the responses from trial to trial) with the cost of reducing accuracy (i.e., how close the overall estimate is to true vertical) [3]. The errors of upright perception are reduced by using haptic adjustments in which there is no perceptual error associated with the ocular counter-roll [14,22]. This error reduction correlated with the amount of ocular counter-roll in the haptic horizontal adjustments, whereas in the haptic vertical adjustments the error reduction was larger than it could be entirely explained by the absence of perceptual errors related to the ocular counter-roll [14,22].

The visual exposure in SVV paradigm is limited to a line stimulus without providing other orientation cues. The line stimulus, however, may itself alter SVV responses [11,17]. For example, the initial orientation of the line can bias how subjects adjust the line into vertical orientation [11]. Previous studies found no difference in SVV responses between monocular and binocular measurements in the absence of torsional misalignment of the eyes [6,13]. The effects of the visual line and viewing eye on SVV responses both have been studied in the upright position, and neither has been investigated with the head tilted where maintaining a coherent estimate of upright is more challenging for the brain. Here we addressed these effects by examining the accuracy and precision of SVV responses in the upright and roll-tilted head positions. Overall, in spite of the challenges to the estimate of upright with the

head tilted, normal subjects did remarkably well in this task, whether viewing with one or both eyes and with or without using an optical correction.

2. Materials and methods

2.1. Experimental conditions

Twenty two healthy volunteers (age 21–52, 8 females) participated in the study and all underwent refraction measurement and visual acuity examination (Supplementary Table). Twenty were right-handed and two were left-handed by self report. The experiments were done late in the morning or early afternoon. Three conditions were assessed: Viewing eye (right eye [OD], binocular [OU] and left eye [OS]), head position (20° right tilt, upright and 20° left tilt), and direction of the visual line rotation (clockwise [CW] and counterclockwise [CCW]). There were total of 18 recording sessions for each subject (Fig. 1). We used a small head tilt angle of 20° to minimize the variability related to the effect of head tilt and allow for better evaluation of the effects of viewing eye and line rotation on SVV responses. The order of recordings between the eye viewing conditions and head positions were randomized in each subject.

2.2. SVV paradigm

Subjects sat upright in a chair with their head immobilized by a molded bite bar. A red laser line (length: 34.5 cm, width: 2 mm), covering 15° of the binocular visual field, was back-projected on a semitransparent screen 135 cm away in front of the subject. The center of rotation was at the bottom of the laser line, which was marked by a red dot positioned at the subject's eye level (diameter: 3 mm). A black patch was applied to cover one eye for monocular viewing. The SVV paradigm consisted of two blocks that were displayed five minutes apart (Fig. 1). In each block the laser line rotated only in CW and CCW direction. The order of recordings between the CW and CCW blocks was randomized among subjects, but it was fixed for each subject in order to control for a possible visual tilt effect from consecutive runs of CW and CCW line rotations. There was a total of 8 runs per block. In each run the line started from either 16° to the left (CW block) or 16° to the right (CCW block) of the earth vertical and rotated in steps of 2° in between trials to reach 16° on the opposite side (negative values for the left angles and positive values for the right angles). Therefore, there were 136 trials in each block from 17 projected angles in a run (between $\pm 16^\circ$) and a total of 8 runs. At each trial, subjects rotated a potentiometer to three different positions to indicate their perception of line orientation as either tilted to the left, upright, or tilted to the right and then pressed a button to accept the response and move to the next trial (i.e., a forced-choice paradigm). In each run, the SVV was measured as the angles with upright response or alternatively, in case of no upright response, an average of two angles at which responses switched from either left to right tilt (CW block) or right to left tilt (CCW block).

2.3. Data acquisition and analysis

The data collected from CW and CCW blocks were processed offline using Matlab™. The SVV responses from each block were used to obtain *accuracy*, i.e. the degree of veracity as reflected by the *median* of SVV responses from 8 runs in each block, and *precision*, i.e. the

degree of reproducibility as reflected by *interquartile range* of SVV responses from 8 runs in each block. The accuracy and precision of SVV responses were then compared between the viewing eye conditions, directions of line rotation and head positions using nonparametric statistical analysis. We used Kruskal-wallis test which does not assume normal distribution of the data and is the non-parametric equivalent of one-way analysis of variance (ANOVA). Dunn's multiple comparison was used for post-hoc analysis and comparing specific pairs of data from different conditions.

3. Results

3.1. Effect of head tilt position on SVV accuracy and precision

The accuracy and precision values are provided in Fig. 2 and Table 1 for head position, viewing eye and direction of line rotation. There was no significant difference in the accuracy of SVV responses between the head positions with comparisons only in the CW or CCW direction (CW $p = 0.97$ and CCW $p = 0.43$; *Kruskal-Wallis test*) (Fig. 2A). For this comparison, in each subject we first averaged the accuracy of SVV responses from three viewing eye conditions for each head position. The average values from all subjects were not normally distributed and we used *Kruskal-Wallis test* to compare between the three head positions. The comparison was done separately for each direction of line rotation (CW and CCW).

Unlike the results for accuracy of SVV responses, there was a significant difference in the precision of SVV responses between the head positions in each direction of line rotation (CW, $p = 0.038$ and CCW, $p = 0.01$; *Kruskal-Wallis test*). Similar to the comparison for accuracy of SVV responses, here we used the average precision values between three viewing eye conditions for each head position. The average values from all subjects (not normally distributed) were then compared between three head positions. The comparison was done separately for each direction of line rotation (CW and CCW). The post hoc analysis showed a significant difference between the right and left tilt positions in both CW and CCW directions ($P < 0.05$; *post-hoc Dunn's test*). In the CCW direction, there was also a significant difference between the upright and right tilt positions ($P < 0.05$; *post-hoc Dunn's test*) (Fig. 2B).

3.2. Effect of direction of line rotation on SVV accuracy and precision

There was a significant difference between the accuracy of SVV responses in the CW and CCW directions ($p \approx 0.0001$; *Kruskal-Wallis test*) (Fig. 2A). For this comparison we also used the average accuracy of SVV responses between three viewing eye conditions for each head position. The average values from all subjects (not normally distributed) were then compared between the three head positions. Both directions of line rotation (CW and CCW) were included in this comparison. The post hoc analysis showed a significant difference between the CW and CCW directions in the right head tilt and upright positions ($p < 0.05$; *post-hoc Dunn's test*) whereas in the left head tilt position there was no significant difference between the CW and CCW directions ($p > 0.05$; *post-hoc Dunn's test*) (Fig. 2A; gray box). The distributions for the accuracy of SVV responses are shown in Fig. 3 with

wider distributions in the left head tilt position ($p = 0.01$; Bartlett's test). This finding is consistent with a higher variability across subjects in the left head tilt position.

There was no significant difference between the precision of SVV responses in the CW and CCW directions ($p > 0.05$ *Kruskal-Wallis with post-hoc Dunn's test*). Here we also used the average precision value between the three viewing eye conditions for each head position. The average values from all subjects (not normally distributed) were then compared between the three head positions. Both directions of line rotation (CW and CCW) were included in this comparison.

3.3. Effect of viewing eye on SVV accuracy and precision

The accuracy of SVV responses was not significantly different between the viewing eye conditions for all head positions (right tilt $p = 0.92$, upright $p = 0.9$, left tilt $p = 0.91$; *Kruskal-Wallis test*). In this comparison, we first averaged the accuracy of SVV responses between the CW and CCW directions for each viewing eye condition. The average values from all subjects (not normally distributed) were then compared between the three viewing eye conditions. This was done separately for each head position. Nine subjects did not wear their habitual corrections for the experiment, five subjects wore contact lenses, and eight subjects were emmetropic (Supplementary Table). Similar analysis in each of these subgroups showed no significant difference in the accuracy of SVV responses between the viewing eye conditions for all head positions (no-refractive correction subgroup: right tilt $p = 0.84$, upright $p = 0.37$, left tilt $p = 0.66$; refractive correction subgroup: right tilt $p = 0.9$, upright $p = 0.79$, left tilt $p = 0.76$; emmetropic subgroup: right tilt $p = 0.3$, upright $p = 0.99$, left tilt $p = 0.83$, *Kruskal-Wallis test*).

There was also no significant difference in the precision of SVV responses between the viewing eye conditions in each head position (right tilt $p = 0.67$, upright $p = 0.62$, left tilt $p = 0.68$; *Kruskal-Wallis test*). Similar to the accuracy of SVV response, here we used the average precision of SVV responses between the CW and CCW directions for each viewing eye condition. The average values from all subjects (not normally distributed) were then compared between the three viewing eye conditions. This was done separately for each head position.

4. Discussion

Here we investigated the effects of visual line rotation and viewing eye on SVV responses and whether there was any change with head tilt. Overall, there was no significant difference in the accuracy of SVV responses irrespective of the viewing eye (monocular or binocular) or using optical correction among subjects. These findings suggest that, in the absence of ocular misalignment or large refractive differences, visual disparities between both eyes do not significantly affect SVV irrespective of head position. In our SVV paradigm the perception of line orientation was not affected by stereopsis as the line stimulus was projected on a flat screen in front of the subjects and there was no difference in the SVV responses between monocular and binocular viewings.

The accuracy of SVV responses was not different between head positions when compared only within one direction of line rotation (CW or CCW). This can be related to the small angle of head tilt in our study (20°) resulting in the SVV errors not significantly different from upright. There was however a significant difference in the accuracy of SVV responses between the CW and CCW line rotations. The SVV was tilted in the same direction as the line rotation, resulting in a rightward SVV tilt with the line movement in the CW direction and a leftward SVV tilt with the line movement in the CCW direction. Therefore, upright responses appeared biased by previous line orientations within the same block (i.e., a hysteresis effect). This effect, however, was not apparent in the left head tilt position, in which there was a higher intersubject variability in the accuracy of SVV responses (Figs 2A and 3). The precision of SVV responses was not different between CW and CCW line rotations in all head positions. Therefore, a variability in the precision of SVV responses among subjects may not account for the difference in accuracy of SVV responses from the line rotation. The effect of visual line stimulus has been previously described and should be considered when designing paradigms to measure SVV [11,17]. Tarnutzer et al. found a drift of SVV adjustments over time, suggesting that the upright estimate was not stable due to a trial-to-trial dependency of perceived visual line orientation. Pagrakar et al. observed a significant difference in the SVV responses between CW and CCW adjustments. In both of these studies SVV was measured with the head only in upright position. Other studies have shown that SVV responses can be affected by relative orientation of the visual line stimulus to the head position [7,12]. For example, if the starting position of the line was in the opposite direction of the head tilt, the SVV was shifted toward the starting position of the line.

SVV is a multisensory process using information from various sensory modalities including vision, head orientation and ocular position. In this context, retinal information is highly accurate in detecting orientation of a visual stimulus [20]. On the other hand sensory inputs that encode head or eye position are inherently more variable [15]. It has been shown that at larger head tilt angles, where head orientation inputs become more inaccurate, visual cues (e.g., a static tilt of the visual background) have stronger influence on SVV responses [21]. Therefore, it is possible that at small head tilt angles such as the one in this study, SVV responses are less affected by the visual line rotation than the variability in inputs encoding head position or torsional position of the eyes among subjects. A similar pattern has been described with a background motion, showing larger visually-induced SVV tilts by increasing the head tilt angle [4,23]. For example, exposure to an optokinetic stimulus induced larger shifts of SVV if the head was tilted in the opposite direction of the optokinetic flow. Here a similar effect from the visual line rotation could be seen in the precision of SVV responses, which showed a significant difference between the right and left head tilts in each direction of the line rotation.

The torsional position of the eyes may also change in response to and in the direction of a visual line rotation, described as 'torsional entrainment' [9]. Here we did not measure ocular torsion and could not examine the variability in the torsional eye position among subjects or the effect of torsional entrainment on SVV responses. Regardless of these potential effects, the accuracy of SVV responses was more variable among subjects only in the left head tilt position. This finding suggests an asymmetric effect of head tilt on SVV errors which,

despite a small number of subjects in this study, was consistently present across all viewing eye conditions (see Figs 2A and 3; left head tilt). Since the majority of participants were right-handed and SVV was more variable in the left head tilt position, this finding may suggest a link between handedness and asymmetric effect of head tilt on SVV errors. Such a handedness-related modulation has been demonstrated in cortical vestibular function with dominant involvement of the right hemisphere in right handers and the left hemisphere in left handers [1,5]. Future experiments will have to examine whether this lateralization extends to the effect of head tilt on SVV errors.

In conclusion, our results show that in spite of the challenges to the estimate of upright with head tilt normal subjects did remarkably well in the SVV task irrespective of the viewing eye (monocular or binocular). The accuracy of upright responses was altered by the direction of visual line rotation in the SVV paradigm. This effect was not similar across head tilts and there was a higher variability among subjects in the left head tilt position. The physiological significance of this asymmetry is unclear but it may suggest a lateralizing effect of head tilt on the visual perception of upright.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Fig. 1.

SVV was recorded by combining the following conditions in each subject: Three head tilt positions, three viewing eye conditions and two directions of visual line rotation (18 sessions per subject). The SVV paradigm consisted of two blocks, one in CW and one in CCW direction that were displayed five minutes apart. In each block the laser line was projected in 8 runs. In each run, the line started from either 16° to the left (CW block) or 16° to the right (CCW block) of earth vertical and rotated in steps of 2° between trials to reach 16° on the opposite side (total of 136 trials as a result of 17 angles presented in 8 runs). At each trial,

the task was to report the perceived orientation of the line by setting a potentiometer to one of three different positions: left tilt, upright, or right tilt. OD: right viewing eye, OS: left viewing eye, OU: binocular viewing, CW: clockwise, CCW: counterclockwise.

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Fig. 2.

The group data are shown in Tukey plots for *accuracy* (A) and *precision* of SVV responses (B). The actual median values are provided in Table 1. The data for each direction of line rotation is presented separately (CW in white and CCW in gray). The accuracy from all three viewing eye conditions was significantly different between the CW and CCW blocks in the upright and right head tilt positions but not in the left head tilt position (gray box). The precision from all three viewing eye was different between the right and left head tilt positions in both CW and CCW blocks and also between the upright and right head tilt positions in the CCW blocks ($p < 0.05$). IQR: Interquartile range, OD: right viewing eye, OS: left viewing eye, OU: binocular viewing, CW: clockwise, CCW: counterclockwise.

Fig. 3.

The group distributions for SVV medians (*accuracy*) are shown with respect to the head tilt, viewing eye and visual line conditions. The dashed lines at zero indicate earth vertical and there is a rightward shift with respect to the dashed line in the CW distributions and a leftward shift in the CCW distributions. In the left head tilt position the distributions are wider with less number of subjects in each bin. OD: right viewing eye, OS: left viewing eye, OU: binocular viewing, CW: clockwise, CCW: counterclockwise.

Table 1

The accuracy and precision of SVV responses for all conditions including head position, viewing eye and direction of line rotation

Head position	Right tilt				Upright				Left tilt			
	OD	OU	OS	OS	OD	OU	OS	OS	OD	OU	OS	OS
Viewing eye	OD	OU	OS	OS	OD	OU	OS	OS	OD	OU	OS	OS
Line rotation	CW	CCW	CW	CCW	CW	CCW	CW	CCW	CW	CCW	CW	CCW
SVV accuracy (group median)	1°	-2°	0°	-2°	0°	-2°	0°	-2°	0°	-1.2°	0°	-2°
SVV precision (group median)	2°	2.2°	2°	2.4°	1.7°	1.9°	2°	2°	2.2°	2.1°	2.5°	2.4°

OD: right viewing eye, OS: left viewing eye, OU: binocular viewing, CW: clockwise, CCW: counterclockwise.