

The effect of supine body position on human heading perception

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The use of virtual environments in functional imaging experiments is a promising method to investigate and understand the neural basis of human navigation and self-motion perception. However, the supine position in the fMRI scanner is unnatural for everyday motion. In particular, the head-horizontal self-motion plane is parallel rather than perpendicular to gravity. Earlier studies have shown that perception of heading from visual self-motion stimuli, such as optic flow, can be modified due to visuo-vestibular interactions. With this study, we aimed to identify the effects of the supine body position on visual heading estimation, which is a basic component of human navigation. Visual and vestibular heading judgments were measured separately in 11 healthy subjects in upright and supine body positions. We measured two planes of self-motion, the transverse and the coronal plane, and found that, although vestibular heading perception was strongly

modified in a supine position, visual performance, in particular for the preferred head-horizontal (i.e., transverse) plane, did not change. This provides behavioral evidence in humans that direction estimation from self-motion consistent optic flow is not modified by supine body orientation, demonstrating that visual heading estimation is one component of human navigation that is not influenced by the supine body position required for functional brain imaging experiments.

Introduction

The use of virtual environments in combination with functional brain imaging provides an important meth-

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odological tool for understanding human spatial navigation and self-motion perception. Because fMRI does not allow for actual physical movement, these studies rely on visual stimulation to simulate self-motion (e.g., Cardin & Smith, 2010; Kovacs, Raabe, & Greenlee, 2008; Wall & Smith, 2008). The visual input is usually provided in the form of a self-motion consistent optic flow stimulus, from which the direction, speed, and duration of self-motion can be successfully estimated (Bremmer & Lappe, 1999; Gibson, 1950; Warren & Hannon, 1988).

One assumption inherent to performing these tasks during fMRI is that perceptual performance is comparable between upright and supine body positions. However, the differing vestibular and proprioceptive signals between upright and supine body positions may modify heading perception. We are not accustomed to move in a supine body position, and this prior experience could lead to differential performance between upright and supine postures. Such differential performance may generalize for heading perception across both visual and vestibular modalities. Alternatively, effects of body orientation on heading perception may depend on modality. For the vestibular system, a change in body orientation amounts to changing the direction of the static gravitational stimulus, which could directly impact low-level processing of dynamic vestibular heading stimuli. In contrast, low-level visual processing will be unaffected by the direction of the static gravitational vestibular stimulus. To determine whether effects of body orientation on heading perception are modality-specific, it is necessary to measure and compare heading perception across modalities.

In an upright body position, humans show systematic biases when estimating heading directions from optic flow (Crane, 2012; Cuturi & MacNeilage, 2013). These biases have been ascribed to a neuronal preference for lateral motion. When the same visual stimuli are rendered to subjects in a supine body position, multisensory interactions may prompt the interpretation of movement in the earth vertical plane because nonvisual sensory signals indicate that subjects are lying on their back. Could this affect the appearance of the visual heading biases?

On a neuronal level, visual and vestibular signals are combined relatively early in sensory processing pathways (Dichgans, Diener, & Brandt, 1974; Gu, DeAngelis, & Angelaki, 2007), suggesting a close interdependence between visual and vestibular processing. Body tilts away from upright lead to decreased reliability of vestibular sensory estimates (Graybiel & Patterson, 1955; Quix, 1925), causing a reweighting of other sensory inputs, including vision (Dichgans et al., 1974; Fetsch, Turner, DeAngelis, & Angelaki, 2009). This can lead to modifications in visual perception, for

example, in the perception of the orientation of lines or objects (Aubert, 1861; Mikellidou, Cicchini, Thompson, & Burr, 2015). The perception of the own body and its orientation relative to extrapersonal space is created by a combination of vision, body position, and gravity (Dyde, Jenkin, Jenkin, Zacher, & Harris, 2009; Harris, Herpers, Hofhammer, & Jenkin, 2014). In a supine body position, the direction of gravity in relation to the body changes, causing a shift in the perceptual upright that could also affect visual motion perception. Varying the body position can lead to systematic biases in estimating the direction of forward movements relative to the horizon from optic flow (Bourrelly, Vercher, & Bringoux, 2010) and increase the threshold of vestibular as well as visual heading direction discrimination close to straight ahead (MacNeilage, Banks, DeAngelis, & Angelaki, 2010). Similarly, effects of body orientation have been found for distance estimation (Harris & Mander, 2014) and the sensation ofvection (i.e., the illusory perception of self-motion that develops during prolonged viewing of optic flow) (Kano, 1991; Thilo, Guerraz, Bronstein, & Gresty, 2002).

The aim of this study was to investigate the influence of the supine body position on visual heading estimation performance in humans. For comparison purposes, we also acquired supine and upright vestibular heading performance as a behavioral measure for the effect of a supine body position on vestibular perception. Biases and variability in heading estimation were compared between upright and supine body positions as a measure of performance and uncertainty. Because heading perception depends strongly on the stimulus type (Fetsch et al., 2009), motion plane (Crane, 2014a; MacNeilage et al., 2010), and heading angle (Crane, 2012; Cuturi & MacNeilage, 2013), we chose a paradigm that covered different factor combinations of visual and vestibular stimulation, transverse and coronal stimulus planes, and 24 heading angles within each plane. We expected stronger biases and larger errors in both visual and vestibular heading estimation in the supine position than in the upright position because human self-motion systems are most specialized for processing heading with upright posture.

Methods

Subjects

Eleven subjects (five females), mean age 27.55, range 24–32 years, participated in the study. They had normal or corrected-to-normal vision and no history of neurological disorders. All subjects gave written informed consent to participate in the study, which was

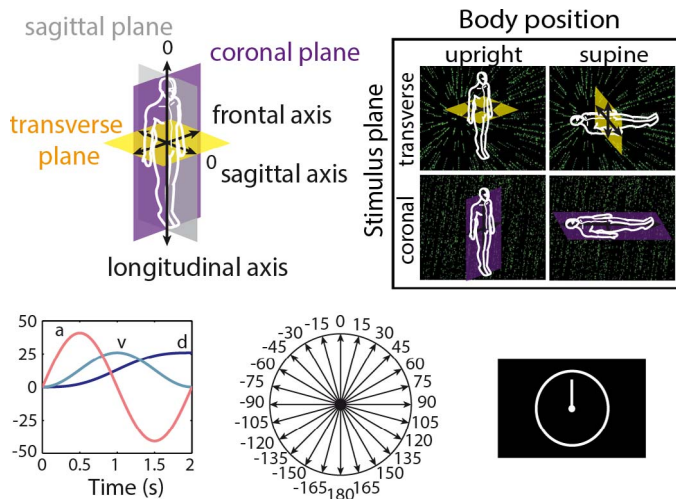


Figure 1. Experimental procedure, conditions, and nomenclature. During the experiment, all combinations of the three factors, body position (supine/upright), stimulus type (visual/vestibular), and stimulus plane (transverse/coronal), were tested. The stimulus profile (lower left corner) shows acceleration in cm/s^2 (a), velocity in cm/s (v), and displacement in cm (d) during the 2-s stimuli for both optic flow and platform motion. Twenty-four heading directions (lower row, center) were presented in the coronal and the transverse plane, respectively (six repetitions). Zero degrees corresponded to a movement straight forward or upward. Negative heading directions refer to leftward self-motion, positive heading directions to rightward self-motion. After each stimulus, the response screen (lower right corner) was shown. Subjects estimated their perceived heading direction by moving the arrow around the dial via button press.

approved by the ethics committee of the medical faculty of the Ludwig Maximilians University and performed in accordance with the Declaration of Helsinki.

Stimuli

Stimuli were either visual (optic flow) or vestibular (passive acceleration/deceleration) with identical stimulus profiles for both types of stimulation. One stimulus profile lasted 2 s and represented a linear translation in one of 24 directions. All translations had a sinusoidal acceleration profile with a total displacement of 26 cm, a peak velocity of 26 cm/s , and a peak acceleration/deceleration of 41 cm/s^2 (Figure 1). Translational motion can be described in world-centered, i.e., earth-horizontal or earth-vertical, or body-centered coordinates, i.e., sagittal, coronal, and transverse. However, previous research has shown that heading discrimination is influenced by changes in the stimulus plane in body-centered and not world-centered coordinates (MacNeilage et al., 2010). Therefore, we refer to the two stimulus planes in the present study with respect to

body coordinates as transverse and coronal translations (Figure 1). Body-centered optic flow stimulus planes also correspond to the same physical stimulus projected onto the head mounted display (HMD), see Visual stimuli; therefore, we define stimulus planes in body-centered coordinates in this study. Both visual and vestibular heading estimation were tested in each stimulus plane in both an upright and a supine body position.

For each plane, we tested 24 heading directions covering the whole plane in 15° steps, i.e., 0° , 15° , 30° , 45° , etc. All directions are labeled in relation to 0° or straight ahead/upward such that left (counterclockwise) heading directions are negative (-15° to -165°) and right (clockwise) directions are positive (15° to 165° , Figure 1). All trials took place in a darkened room, and in the vestibular condition, subjects were additionally instructed to close their eyes during stimulus presentation. Acoustic white noise was played over headphones during stimulus presentation to eliminate auditory self-motion cues. In the upright position, the subject sat in a racing chair; his or her head was positioned against a form-fitting vacuum headrest, and a headband fixated the forehead to the chair. In the supine position, the subject was placed on a form-fitting vacuum mattress, and forehead, body, and legs were fixated with mattress belts.

Visual stimuli

Three-dimensional optic flow stimuli were created in Matlab (The Mathworks Inc., Version R2009b) using the OpenGL library and Psychtoolbox-3 (Brainard, 1997). Stimuli were rendered on a head-mounted stereo display (HMZ-T2, Sony Corporation) with a binocular horizontal field of view of 45° , a display resolution of $1,280 \times 720$ pixels and a refresh rate of 60 Hz. Stimuli simulated linear transitions through a cloud of randomly placed triangles. For stimulus creation, 13,366 green, two-dimensional, frontoparallel triangles (base and height 0.5 cm) were placed at a density of 0.04 triangles/ cm^3 in a black rectangular room with a three-dimensional volume of $122.30 \times 170.76 \times 210 \text{ cm}^3$ (height, width, depth). The near and far clipping planes were at 50 cm and 400 cm, respectively.

Vestibular stimuli

Vestibular stimuli were delivered by a six-degree-of-freedom motion platform (Moog© 6DOF2000E). Subjects were placed, either seated (upright position) or lying (supine) on the platform. The subject was then moved passively in one of the directions described above following the motion profile described above. After response collection, the platform moved to the origin that was required for the next trial.

Experimental procedure

The procedure was identical in all trials: After an acoustic signal, subjects started the trial via button press. The heading stimulus was presented, and afterward, subjects indicated the perceived heading direction by adjusting the orientation of an arrow on the screen via button press. The arrow was presented within a white circle on a black background (Figure 1). Four buttons allowed for rough adjustments of 2° and fine adjustments of 0.2° per registered key press. Subjects confirmed their estimate by pressing a different button. Haptic cues on the buttons allowed subjects to distinguish all five buttons without visual feedback, and subjects quickly learned the positions of the buttons without seeing them.

The experiment was performed over 4 days, and stimuli were presented block-wise with four blocks per day. Each block consisted of 74 trials. Within one block, only one stimulus type (visual or vestibular), one body orientation (upright or supine), and one stimulus plane (coronal or transverse) was presented. This means, three (of, in total, six) repetitions of the 24 heading directions of one specific condition were presented in random order. Within the same day, stimulus type and body orientation never changed, but two blocks of each stimulus plane were acquired. The order of presentation of stimulus type, body orientation, and stimulus plane was counterbalanced across subjects. Before a new condition began, subjects received 10 training trials that accustomed them to the new condition.

Feedback as to subject's performance was only given during the 10 training trials. This was done primarily to ensure that subjects were not judging object motion in the visual heading conditions, which would lead to errors of $\sim 180^\circ$ (see also Crane, 2012; Cuturi & MacNeilage, 2013). Despite training, subjects occasionally judged object motion instead of self-motion, leading to large errors that are unrelated to the perceptual biases under investigation. Therefore, a deviation of more than 90° from the target angle was considered an erroneous estimate of subjective heading (see also Crane, 2012; Cuturi & MacNeilage, 2013). This was the case in 54 out of 6,336 visual trials (0.85%). These trials were identified immediately, recollected at a later time within the same block, and excluded from further analysis.

Control condition for response bias

Response collection methods may lead to systematic differences between the intended and indicated heading direction. As our response dial was slightly different than what has been used in the past (Cuturi & MacNeilage, 2013), we performed two additional

blocks in which we measured heading estimation for “written” directions, similar to the spoken condition in Crane's (2012) study. Instead of presenting a motion stimulus, the actual direction was presented as a written number on the screen, e.g., “ -45° .” Using this measure helped us to identify to what extent responses given by subjects were biased by their interpretation of the angles on the response device. For example, subjects may not be able to set the line accurately to 45° although, if asked what visual or vestibular heading angle they received, they would respond “ 45° .” For this control experiment, six repetitions of each direction were acquired, again with 15° spacing, once in a supine and once in an upright body orientation. To ensure that the additional knowledge of stimulus magnitude did not affect heading estimation, the control experiment was always performed after the main experiment. Subjects were informed about the relationship between each written value and its relative location within the circle prior to performing the task.

Analysis

The error between the response direction and the actual heading direction was extracted from each trial by subtracting the final position of the arrow within the dial in each trial from the presented heading direction, resulting in the heading bias (Crane, 2012; Cuturi & MacNeilage, 2013). Additionally, we calculated absolute bias to obtain a measure of the magnitude of the heading bias, independent of its direction. This is convenient, for example, for comparing accuracy of heading perception across body orientations. In addition, variability was calculated as the standard deviation of the bias across the six repetitions.

We performed a 2×24 repeated-measures (rm-)ANOVA with factors body orientation (upright/supine) and heading direction (24 directions per plane) for each of the three measures in each stimulus plane for visual stimuli as well as for vestibular stimuli and for the written control condition. If significant interactions between body orientation and heading direction were found (i.e., $p < 0.05$), we evaluated the differences by calculating paired t tests for each heading direction.

Results

In this study, we compared visual heading estimation for upright and supine body positions to test whether the change in vestibular sensory information (i.e., the direction of gravity in head coordinates) influences optic flow-based heading perception. We also tested

	Visual						Vestibular						Written							
	BP		HD		BP-HD		BP		HD		BP-HD		BP		HD		BP-HD			
	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p		
Bias																				
Transverse	0.37	0.55	89.76	<0.0001	1.44	0.093	5.52	0.041	2.85	<0.0001	7.19	<0.0001	0.61	0.45	3.37	<0.0001	0.77	0.77	0.77	0.77
Coronal	5.50	0.041	10.23	<0.0001	1.21	0.24	25.29	0.00051	3.30	<0.0001	4.59	<0.0001	7.01	0.024	4.04	<0.0001	1.50	0.072	1.50	0.072
Variability																				
Transverse	0.27	0.61	11.08	<0.0001	1.58	0.049	6.78	0.026	4.59	<0.0001	1.62	0.041								
Coronal	0.018	0.90	7.60	<0.0001	1.65	0.034	11.65	0.0066	5.66	<0.0001	2.58	0.00019								
Absolute bias																				
Transverse	1.05	0.33	32.54	<0.0001	1.31	0.16	0.018	0.90	3.42	<0.0001	1.00	0.47	4.23	0.067	3.39	<0.0001	0.86	0.65	0.86	0.65
Coronal	0.050	0.83	5.78	<0.0001	0.98	0.49	25.68	0.00049	4.68	<0.0001	1.77	0.019								

Table 1. F values and p values for the repeated-measures ANOVAs performed. Notes: BP = main effect of body position, df: 1,10; HD = main effect of heading direction, df: 23, 230; BP-HD = interaction between the body position and heading direction, df: 23, 230.

vestibular heading estimation performance in both body positions to estimate the change in vestibular heading perception induced by a change in body orientation.

The rm-ANOVAs revealed a main effect of heading direction for all conditions, consistent with what has been shown previously in an upright position (Crane, 2012, 2014a; Cuturi & MacNeilage, 2013). However, because we were interested in the effects of body orientation, we have focused the results on the main effect of body orientation and the interactions with heading direction. The results of the rm-ANOVAs are summarized in Table 1.

Visual heading perception

Similar heading biases were found between upright (Figure 2A, green) and supine (Figure 2A, blue) body positions using optic flow. This was true in both the transverse and coronal stimulus planes although heading bias showed a very different pattern between stimulus planes. For transverse stimuli, no main effect of body position or interaction between body position and heading direction was found. For stimuli in the coronal plane, a weak main effect of body position existed, $F(23, 230) = 5.50, p = 0.041$, but no interaction, $F(23, 230) = 1.21, p = 0.24$. Inspection revealed that this effect is due to a small offset between supine and upright heading estimates. Biases were in general more positive (i.e., clockwise) when subjects were sitting than when they were lying on their back.

This offset was not correlated to the effects of body position we measured for vestibular heading perception in the same stimulus plane ($r = -0.019, p = 0.76$). It could also not be explained by differences in the absolute bias or variability. Both of these variables showed no main effect of body position (Figure 2B, C), suggesting that the bias offset is neither caused by a change in the subjects' uncertainty about heading direction nor by generally greater or smaller errors. Bias variability showed a significant interaction between body position and heading direction for both stimulus planes. The interaction was due to a difference in bias variability between upright and supine body position for individual heading directions (Figure 2C), but no consistent pattern of significance across similar heading directions was found that could explain the general offset in heading bias.

Vestibular heading perception

The lack of effect of body position on visual heading estimation could result from little or no effect of body position on heading judgments in general. However,

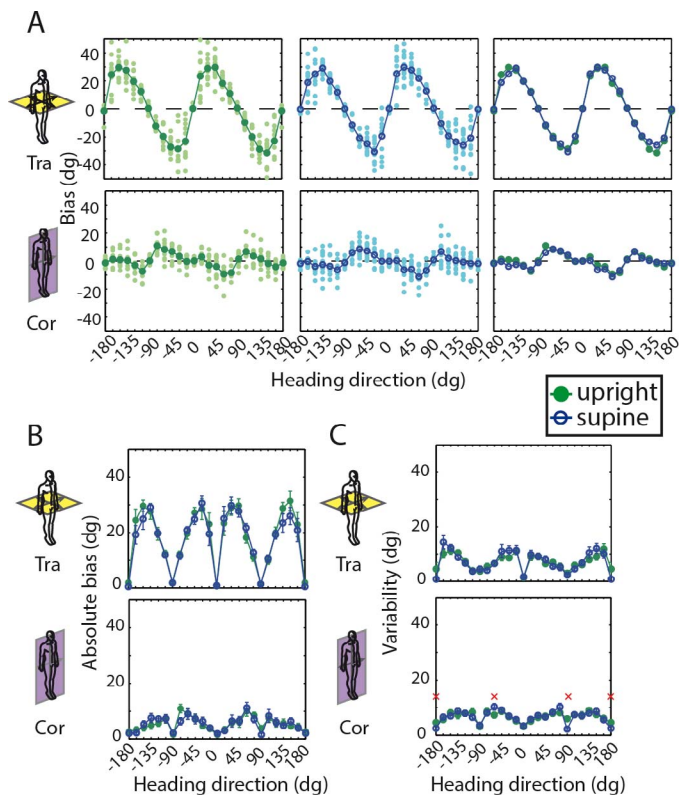


Figure 2. Visual heading perception. Top rows always show results in the transverse stimulus plane and bottom rows the coronal stimulus plane. Green: upright body orientation, blue: supine body orientation. (A) Biases in heading direction estimation. Left: mean bias across subjects ($n = 11$, green) and mean bias for each individual ($n = 6$, bright green) for the upright body orientation. Center: mean bias across subjects ($n = 11$, blue) and mean bias for each individual ($n = 6$, cyan) for the supine body orientation. Right: Mean bias across subjects plotted for both upright versus supine body orientations. (B) Mean absolute bias \pm SE across subjects. (C) Mean variability (standard deviation of the biases) \pm SE across subjects. Red ticks delineate significant differences between upright and supine as calculated by t tests ($p < 0.05$).

consistent with previous research, vestibular heading biases were strongly affected by body position (Figure 3). These effects varied depending on the stimulus plane.

In the transverse stimulus plane, oblique direction biases went in approximately opposite directions for upright (Figure 3A, top row, green) versus supine (Figure 3A, top row, blue) body position, corresponding to a weak main effect of body position and a significant interaction (Table 1). Significant differences between supine and upright biases were seen in almost all oblique heading directions (-165° , -150° , -135° , -60° , -45° , -30° , -15° , 45° , 120° , 135° , 150° , and 165° , $p < 0.05$). In the coronal stimulus plane, a strong main effect of body position and significant interaction was found (Table 1). The upright (Figure 3A, bottom row,

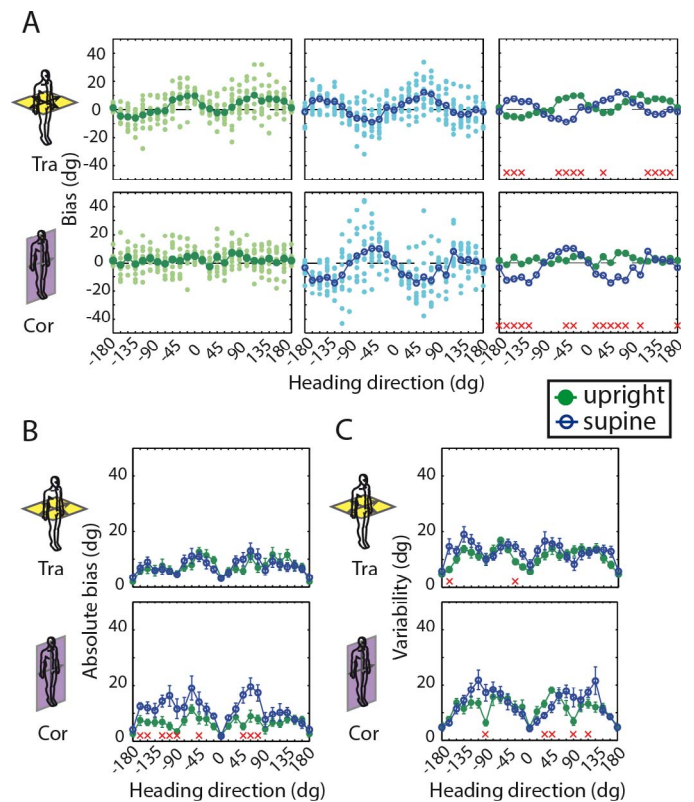


Figure 3. Vestibular heading perception. Color coding for body orientation and location for stimulus plane are the same as in Figure 2. (A) Left: mean bias across subjects ($n = 11$, green) and mean bias for each individual ($n = 6$, bright green) for the upright body orientation. Center: mean bias across subjects ($n = 11$, blue) and mean bias for each individual ($n = 6$, cyan) for the supine body orientation. Right: Mean bias across subjects plotted for both upright versus supine body orientations. (B) Mean absolute bias \pm SE across subjects. (C) Mean variability (standard deviation of the biases) \pm SE across subjects. Red ticks delineate significant differences between upright and supine as calculated by t tests ($p < 0.05$).

green) body position showed no obvious directionality in heading bias. However, distinct heading biases were seen in the supine (Figure 3A, bottom row, blue) body position. Oblique forward heading directions were underestimated and oblique backward heading directions, in particular movements to the left, were overestimated. In other words, subjects showed a bias toward the longitudinal body axis for supine heading estimates, which they did not show in an upright position.

Absolute bias and variability (Figure 3B, C) were further analyzed to determine the effects of body position on vestibular heading accuracy and precision. For transverse movements, absolute biases did not show significant effects of body position, but variability increased significantly in a supine body position (Table 1). For coronal stimuli, both absolute bias and

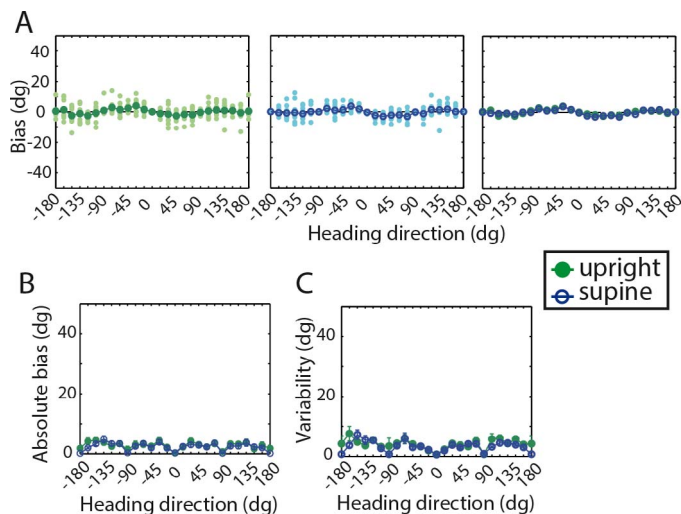


Figure 4. Written heading estimation. Color coding for body orientation is the same as in Figure 2 and 3. (A) Left: mean bias across subjects ($n = 11$, green) and mean bias for each individual ($n = 6$, bright green) for the upright body orientation. Center: mean bias across subjects ($n = 11$, blue) and mean bias for each individual ($n = 6$, cyan) for the supine body orientation. Right: Mean bias across subjects plotted for both upright versus supine body orientations. (B) Mean absolute bias \pm SE across subjects. (C) Mean variability (standard deviation of the biases) \pm SE across subjects.

variability showed a significant main effect of body position (greater values in supine position) and an interaction between heading direction and body position. In general, the effects of body position were stronger for the coronal stimulus plane than for the transverse plane.

Written heading estimation

To explore possible effects of response modality on heading errors, subjects were also asked to move the arrow to angles that were written out numerically on the screen. Subjects tended to underestimate forward/upward and to overestimate backward/downward directions. The magnitude of the biases measured was much smaller than those seen for visual and vestibular heading estimation (Figure 4), suggesting that response bias cannot explain the heading biases. Statistics on heading biases corrected for response bias (i.e., after subtraction of the response bias from the heading bias), showed very similar results as on the original heading biases. However, the weak main effects we found for body position for visual stimuli in the coronal plane, before correction: $F(1, 10) = 5.50$; $p = 0.041$; after correction: $F(1, 10) = 2.78$; $p = 0.13$, and vestibular stimuli in the transverse plane, before correction: $F(1, 10) = 5.52$; $p = 0.041$; after correction: $F(1, 10) = 2.52$; $p =$

0.14 , lost significance when accounting for the response bias. Body position had a significant main effect on variability and, by trend, also on the absolute response bias but in the opposite direction than the expected one. Greater errors and higher variability were seen for the upright rather than the supine condition. This may be attributable to the fact that the HMD was more comfortable and more stable in a supine position. However, the main effect was opposite from the effects we found for visual and vestibular heading biases. Thus, the results of the written experiment do not explain the overall effects of body position on heading biases.

Discussion

In this study, we compared visual and vestibular heading biases between upright and supine body positions. We found that visual heading perception is basically unaffected by the change in body position. Vestibular heading biases, on the other hand, were strongly modified. The effect of a supine body position extended to the direction, size, and variability of the vestibular heading biases and depended on the heading angle and the stimulus plane.

Visual heading perception

Humans can estimate their heading direction based solely on optic flow stimuli (Warren & Hannon, 1988). However, heading estimates can be strongly modified by other sensory inputs, such as vestibular, proprioceptive, and somatosensory cues (DeAngelis & Angelaki, 2012). The supine body position that is required during functional imaging scanning is very uncommon when we move in everyday life; during supine orientation, gravity acts along the sagittal rather than the longitudinal axis of the head and body. Is visual heading performance, when measured in a supine body position, comparable to upright performance? We found that visual heading estimates are very similar between upright and supine body positions. In particular for the transverse plane, the most common plane of movement, we do not find significant differences in performance. This suggests that visual heading performance is not affected by a supine position and that the estimates are based exclusively on the visual stimuli, which are identical between body positions. A change in body position appears to affect vestibular heading perception as supported by the results of our vestibular heading experiment. However, the vestibular and proprioceptive sensory signals that differ between upright and supine body positions seem not to interfere

with our visual perception. This is consistent with the theories of optimal Bayesian cue integration in heading perception (Knill & Pouget, 2004; Saunders, 2014). When only visual stimuli are provided for heading perception, input from nonvisual sensory systems may be considered inaccurate or unreliable. This results in a predominant weighting of the more reliable, visual input (Fetsch et al., 2009). It has further been suggested that if a sensory system is considered inaccurate or unreliable, it can be eliminated from the weighting process (Brandt et al., 2002). If a purely visual heading stimulus is shown, vestibular brain regions are even deactivated (and vice versa) (Brandt, Bartenstein, Janek, & Dieterich, 1998; Brandt et al., 2002; Wenzel et al., 1996). Thus, although noisy or conflicting information may exist between visual and nonvisual systems due to the supine body position, this suppression could explain why our visual estimates are unaffected.

For visual stimuli in the coronal body plane, the differences we find between upright and supine body positions are very small. There is weak evidence that subjects perceived the presented heading direction more counterclockwise in the supine position compared to when they were upright. Because biases may exist in both body positions, we cannot say whether the estimates improve or deteriorate in a supine position. Such an offset may be a true property of perceptual processing or an artifact of the experimental manipulation. Correcting the heading biases for errors induced by the response device removes the reported main effect, favoring the latter explanation.

Taken together, we found no evidence that visual heading estimation performance is impaired by a supine body position. Although this first appears in conflict with previous work (Bourrelly et al., 2010; MacNeilage et al., 2010), we believe that the effects are a result of the different experiments performed. MacNeilage et al. (2010) examined heading discrimination for roll-, not pitch-tilts, of the body. The task in Bourrelly et al. (2010) was to judge heading elevation in the sagittal plane, and they did not examine supine body orientation. In addition, subjects were instructed to judge heading in world rather than body coordinates. Visual motion perception may still depend on the task and the complexity of the visual stimulus. Studies on navigation, for instance, usually use complex structured environments (Doeller, Barry, & Burgess, 2010; Spiers & Maguire, 2006) that might be less compatible with the supine body position. The relative weighting of earth- to body-related reference frames will likely play a stronger role in these more complex structured environments (Bourrelly et al., 2010).

Although heading biases have not been investigated previously for a supine body position, heading accuracy and precision based on optic flow stimuli have been extensively studied for an upright body position (see

Lappe, Bremmer, & van den Berg, 1999, for review). The systematic heading biases we observe for upright individuals estimating heading directions from coronal and transverse optic flow are consistent with previous studies using similar heading range, optic flow type, and stimulus characteristics (Crane, 2012, 2014a; Cuturi & MacNeilage, 2013; however, see de Winkel, Katliar, & Bulthoff, 2015). In the transverse plane, biases are systematically oriented toward lateral directions (Crane, 2012; Cuturi & MacNeilage, 2013). These biases have been explained using population vector decoding models based on the distribution of directionally selective neurons in the dorsal medial superior temporal areas (MSTd) of primates (Gu, Fetsch, Adeyemo, DeAngelis, & Angelaki, 2010). MSTd is known to integrate visual and vestibular stimuli, and a larger number of left/right-sensitive neurons have been found compared to fore/aft-sensitive neurons, which may lead to the lateral bias. For coronal optic flow, we find biases similar to those described by Crane (2014a). He also reports weak visual biases with a high precision compared to vestibular estimates and a tendency to overestimate the vertical component of the heading directions. Our error sizes are considerably larger (around twice as large) than those found in Crane's (2014a) study, and our subject's variabilities are considerably smaller, which may be due to the higher number of repetitions in our study.

Vestibular heading perception

We also measured the effect of a supine body position on vestibular heading perception. The vestibular system is directly affected by the change in body position because the otoliths transduce the combination of gravity and linear acceleration stimuli. We hypothesized that a supine body orientation would have a significant effect on vestibular heading perception, and this hypothesis was confirmed. The effect extended to the direction, magnitude, and variability of the vestibular heading biases. We assume that this is caused by the change in the position of the otoliths relative to gravity (i.e., a pure effect of body orientation regardless of movement direction). Alternatively, it could be due to a change in the orientation of the stimulus plane relative to gravity (i.e., an effect of movement direction in world coordinates). Our experimental design does not allow us to tease apart these two possibilities. However, heading discrimination has been shown to depend on body orientation relative to gravity and not on movement direction in world coordinates (MacNeilage et al., 2010). We therefore favor the same explanation for the current effects. In MacNeilage et al. (2010), the best performance (i.e., the smallest thresholds) on the heading discrimination task was observed in an upright position with a horizontal (transverse) accelera-

tion, and the worst performance was observed in a side-down body position together with a vertical (sagittal) stimulus plane. Here, we found that the effect of the supine body position on absolute bias and variability was larger in the coronal plane than in the transverse plane in support of previous results. Because we most often move in the horizontal (transverse) plane, it is conceivable that we are better able to compensate for the effects of a supine position on vestibular sensitivity when moving in the transverse plane than for vertical planes of movement, such as the coronal plane.

Analogous to visual heading biases, previous studies have most frequently investigated upright vestibular heading biases in horizontal and vertical stimulus planes (Crane, 2012; Cuturi & MacNeilage, 2013; Telford & Howard, 1996). In the present study, upright, transverse, vestibular heading estimates were systematically biased toward straight ahead, similar to the findings of Telford and Howard (1996), who measured visual and nonvisual heading biases for a limited range of heading directions. However, our results are contrary to the biases shown in Crane (2012) and Cuturi and MacNeilage (2013), who reported the biases to be systematically biased toward lateral directions. For visual biases, the absolute bias was much larger than the variability (i.e., constant error was large relative to variable error; Figure 2B, C) whereas approximately equal values of absolute bias and variability were found for vestibular heading perception (Figure 3B, C). This suggests that the subjects were relatively uncertain when giving their estimates (i.e., variable error was large relative to constant error). As a consequence, small variations in the experimental design might affect the biases measured. Our study used a HMD for presenting the response dial. This adds inertia to the head that must be stabilized by neck muscle commands, which have been recently shown to impact perception of linear translation (Crane, 2014b). This stabilization behavior could lead to a reversal in the direction of the observed biases relative to prior research. Additionally, the amount of stabilization will obviously differ between upright and supine positions, contributing to differences in the observed biases depending on body orientation. Indeed, the pattern of biases observed in the supine orientation, in which HMD inertia would play less of a role, are more similar to biases reported previously for the transverse plane in upright subjects (i.e., overestimation of oblique heading angles). Our response dial did not include tick marks for various angles as in Cuturi and MacNeilage (2013), and the written heading estimates show slight biases toward straight ahead (Figure 4A). Control data (not shown) suggest that the absence of tick marks may have also contributed slightly to observing biases toward rather than away from straight ahead in the upright, transverse condition.

Only one previous study has looked at vestibular heading biases in the coronal plane (Crane, 2014a) and

only with subjects upright. This study described stronger vestibular biases than visual biases and in the opposite direction. Vestibular biases were consistent with overestimation of the horizontal component of the heading stimulus. The vestibular biases we observed for the coronal plane were smaller and showed no systematic pattern. This difference could again be due to the HMD adding inertia to the head, leading to increased estimates of the vertical motion component. Biases observed while supine were in the direction opposite to those reported by Crane (2014a), inconsistent with explanations based on a generalized underestimation of head-vertical relative to head-horizontal motion components. Within-subject variability was considerably lower in our study compared with Crane's (2014a). In general, we suggest that due to the high degree of variability in vestibular heading estimation, a high number of repetitions per heading direction should be acquired.

Conclusions

In this study, we explored the effects of a supine body position on visual heading perception in order to understand the behavioral consequences of the position imposed by functional imaging data acquisition. We found that vestibular heading perception is strongly modified by a change in position; however, our perception of heading direction from 3-D optic flow is not affected. Visual motion direction identification is comparable for supine and upright body orientation.

Keywords: spatial orientation, egomotion, passive motion, supine, body tilt, optic flow, vestibular, visuo-vestibular, heading, fMRI, gravity, navigation, cue integration

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