Research Article

Human Visual and Vestibular Heading Perception in the Vertical Planes

BENJAMIN T. CRANE^{1,2,3}

¹*Department of Otolaryngology, University of Rochester, 601 Elmwood Avenue, Box 629, Rochester, NY 14642, USA*

²*Department of Neurobiology and Anatomy, University of Rochester, Rochester, NY, USA*

³*Department of Bioengineering, University of Rochester, Rochester, NY, USA*

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ABSTRACT

Heading estimation has not previously been reported in the vertical planes. This is a potentially interesting issue because although distribution of neuronal direction sensitivities is near uniform for vertical headings, there is an overrepresentation of otolith organs sensitive to motion in the horizontal relative to the vertical plane. Furthermore, thresholds of horizontal motion perception are considerably lower than those of vertical motion which has the potential to bias heading perception. The current data from 14 human subjects (age 19 to 67) measured heading estimation in response to vestibular motion of 14 cm (28 cm/s) over a 360° of headings at 5° intervals. An analogous visual motion was tested in separate trials. In this study, earth and head vertical/horizontal were always aligned. Results demonstrated that the horizontal component of heading was overestimated relative to the vertical component for vestibular heading stimuli in the coronal (skew) and sagittal (elevation) planes. For visual headings, the bias was much smaller and in the opposite direction such that the vertical component of heading was overestimated. Subjects older than 50 had significantly worse precision and larger biases relative to that of younger subjects for the vestibular conditions, although visual heading estimates were similar. A vector addition model was fit to the data which explains the observed heading biases by the known distribution of otolith organs in humans. The greatly decreased precision with age is explained by the model with decreases in end

organ numbers, and relatively greater loss of otoliths that are sensitive to vertical motion.

Keywords: otolith, optic flow, MSTd, vision

INTRODUCTION

Recent data has demonstrated that humans overestimate azimuth relative to straight ahead in a similar way for both visual and vestibular stimuli (Crane 2012; Cuturi and Macneilage 2013), a trend which was also reported by some earlier studies that looked at visual headings (Warren 1976; Telford and Howard 1996). This type of direction-dependent perceptual bias was predicted by a population vector decoder (PVD) model which was developed based on the known distributions of neuronal sensitivities in medial superior temporal area (MSTd) of primates (Gu et al. 2010). According to the PVD model, the overestimation occurs because there are more neurons with preferred left/right sensitivities relative to other directions. In addition to predicting a direction specific bias, the PVD model also predicts that discrimination of two headings will be best near straight ahead, which has been established for visual (Crowell and Banks 1996) and vestibular (Gu et al. 2010; MacNeilage et al. 2010; Crane 2012) heading. Such PVD models have previously been proposed in motor systems (Georgopoulos et al. 1986) including in the MSTd (Page and Duffy 2003), so it is a biologically plausible explanation.

There is evidence that lateral direction specificity exists not only in MSTd, but also at the level of the

Correspondence to: Benjamin T. Crane · Department of Otolaryngology · University of Rochester · 601 Elmwood Avenue, Box 629, Rochester, NY 14642, USA. Telephone: +1-585-7585700; fax: (585) 271-8552; e-mail: craneb@gmail.com

otolith organs. In the monkey, $\frac{3}{4}$ of otolith afferents respond to ipsilateral tilt (Fernandez and Goldberg 1976), the human utricle orientation also suggests better sensitivity to lateral motion (Rosenhall 1972; Rosenhall and Engstrom 1974), and the otoconia sensitive to lateral motion outnumber those sensitive to vertical motion (Igarashi et al. 1993). Although the PVD model tells us that differences in directional specificity can predict directional biases, the model does not necessarily tell us if it is the otoliths or central units in MSTd that cause these biases, or if the same units are causing the biases in both the visual and vestibular sensory modalities (Crane 2012; Cuturi and Macneilage 2013). The current paper aims to address this issue by studying heading perception in the coronal (skew) and sagittal (elevation) planes which include a horizontal and vertical component. Preferred directions in MSTd neurons are more evenly distributed in elevation (Gu et al. 2006), which suggests bias in heading perception would not be introduced in MSTd and may be more likely to reflect peripheral distributions. For vertical headings, there is a much larger difference in otolith/saccular representation with humans having a much lower threshold for motion in the horizontal plane in comparison with motion in the vertical plane (Benson et al. 1986; MacNeilage et al. 2010; Roditi and Crane 2012). Thus otolith sensitivity is much more direction specific in the horizontal versus vertical plane than MSTd. Performing heading estimation in the vertical plane has the power to investigate the possibility that visual and vestibular biases occur via a common mechanism in MSTd and determine if these biases can originate with the peripheral sensory organs.

The current paper reports the results of visual and vestibular heading estimation in the coronal and sagittal planes, and demonstrates that the observed biases in vestibular headings may be explained by the distribution of the otoliths in the saccule and utricle.

MATERIALS AND METHODS

Equipment

Motion stimuli were delivered using a six-degree-of-freedom motion platform (Moog, East Aurora, NY, model 6DOF2000E) similar to that used in other laboratories for human motion perception studies (Grabherr et al. 2008; Fetsch et al. 2009; MacNeilage et al. 2010; Cuturi and Macneilage 2013) and previously described in the current laboratory (Roditi and Crane 2012), including for heading perception experiments in the horizontal plane (Crane 2012). Subjects were seated in a padded racing seat (Corbeau, Sandy UT, model FX-1) mounted on the platform. A four-point racing style harness held the body in place. The

head was held in place using an American football helmet (Riddell, Eyría, OH) with the facemask removed to improve visibility. The helmet had an inflatable liner to insure a snug fit as previously described (Crane 2012).

During both visual and vestibular stimuli, an audible white noise was reproduced as previously described (Roditi and Crane 2012). Although no masking noise was needed for the visual condition, it was still used for consistency.

Responses were collected using a control box with a dial in the middle that could be freely rotated about the axis perpendicular to the plane being tested without any discontinuity points (Crane 2012). The dial itself was a plastic triangle 1.5 cm high, 6 cm long, and 1 cm wide at the back. The orientation was determined by feel. The box with the dial was mounted 20 cm anterior to the subject just above waist level below the viewing screen. It was oriented in the vertical plane so that it was facing towards the subject (for coronal plane headings) or facing towards the right (for sagittal plane headings). The dial was connected to a 14 bit rotary encoder (Contelec, model VertX1332, Biel Switzerland) which was calibrated to a $<0.1^\circ$ angular resolution.

The two buttons on either side of the dial had a similar function. After an audible tone indicated that the next stimulus was ready, a button could be pressed to deliver the stimulus. After the heading was selected, one of the buttons was pressed again so the subject could signal that they had finished their selection. The dial was only moved by the subject and remained in the position it was left for the next stimulus presentation. Although the heading direction and residual position from the previous trial may have influenced the response to the subsequent trial, any effect likely evened out in the aggregate data as the stimuli were given in a random order which was different for each block of trials. There were no explicit orientation markers on the dial (such as a divot at the zero position).

Stimulus

The visual and vestibular stimuli consisted of a 2 s (0.5 Hz) sine wave in acceleration. This motion profile was chosen because it contains no discontinuities in acceleration, velocity, or position, and they have previously been used for threshold determination (Benson et al. 1989; Grabherr et al. 2008; Roditi and Crane 2012) as well as for heading determination in the horizontal plane (Crane 2012).

Visual stimuli were presented on a color LCD screen measuring 115.6 by 64.8 cm with a resolution of $1,920 \times 1,080$ pixels (Samsung model LN52B75OU1FXZA). The subject was seated 50 cm

from the screen that filled a 98° horizontal field of view. A fixation point for the visual stimulus consisted of a 2×2 cm midline cross at eye level; the vestibular experiments were done in darkness. The visual stimulus consisted of a star field which simulated movement of the observer through a random-dot cloud similar to that used previously for horizontal plane headings (Crane 2012). Disparity was provided using red-green anaglyph glasses made with Kodak (Rochester, NY) Wratten filters #29 (dark red) and #61 (deep green). The colors were adjusted such that the intensities of the two were similar when viewed through the respective filters and rejection ratio was better than tenfold.

For both stimuli, the displacement was 14 cm with a peak velocity of 14 cm/s, and a peak acceleration of 22 cm/s/s.

Each block consisted of 72 stimulus presentations. The stimuli were headings at 5° increments such that all 360° was equally represented. The headings were delivered in random order throughout the trial block with each heading delivered once. Each block was delivered twice, usually on separate days. Thus for each subject and condition, there were 144 stimulus presentations. Each testing session included motion in only the sagittal or coronal planes.

Experimental procedure

Subjects were instructed that each stimulus would move or simulate motion along a vector in either the coronal or sagittal plane. Prior to testing, subjects were shown how to orient the dial. Occasionally, subjects were seen to make systematic errors early in a session such as identifying the direction the star field was moving rather than their direction through the star field in the visual system. These types of errors were rare and identified in the first few trials. Other than correcting these systematic errors, no feedback was given. When this occurred, the subject was given further instruction and the trial block was restarted. An audible cue marked the end of the stimulus alerting the subject to orient a dial towards the perceived direction. Subjects were encouraged to guess if uncertain. The experiment was practiced a few times in the light to ensure comprehension of the task prior to data collection in darkness.

Prior to stimulus delivery, the subject heard a 500 Hz, 0.125 s single tone to signal that the next stimulus was ready and the start button could be pressed. The stimulus was delivered immediately after the subject pressed the start button. After the stimulus was delivered, two 0.125 s tones were played in rapid succession to indicate that the stimulus had been delivered and the perceived direction could be entered. If no response was entered, a “time out

sound” was played (a low frequency buzz). The time out occurred at 3 s. Subjects were not told they had a time limit to enter responses and time outs were rare (on average 1 in 432 stimulus presentations, or 1 in 6 blocks of trials). Only 4 of the 14 subjects experienced any time outs. Although the time to respond was not recorded, it was generally much shorter than the time limit (~ 1 s). The time out was so intended to allow no response to be entered if subjects were not paying attention to the stimulus, to discourage cognitive strategies which may be more time consuming, and to make this study as similar as possible to the prior study on horizontal plane headings (Crane 2012). After either a response or time out, the platform returned to the center starting position using a motion profile similar to the stimulus but taking 2.5 s.

Subjects

The research was conducted according to the principles expressed in the Declaration of Helsinki. Written informed consent was obtained from all participants. The protocol and written consent form were approved by the University of Rochester Research Science Review Board.

A total of 14 subjects (5 female) participated in the study, all of which completed the entire protocol. The range of ages was 19 to 67 with a mean and standard deviation (SD) of 41 ± 18 . There were 5 subjects over the age of 50. Two subjects (#3 and #9) were familiar with the design of the experiment; the other subjects had participated in previous experiments in the lab using the motion platform but were otherwise naive to the design and purpose of the experiment. Subjects were screened prior to participation for normal peripheral vestibular function and hearing as previously described (Roditi and Crane 2011).

Analysis

The dial setting was compared with the actual heading for each trial to calculate an error. The coordinate system used is shown in Figure 1. This direct method allowed the error to be calculated across subjects. Due to the large number of headings (72) and the limited number of repetitions of each heading, simply taking the average at each heading was susceptible to noise when applied to the data of an individual subject. The averaging method also does not provide a reliable measure of precision (reproducibility) of responses since there were small numbers of trials at each heading. These issues were addressed using a psychometric technique that was previously applied to headings in the horizontal plane (Crane 2012). Each of the 72 possible stimulus headings was used as a reference heading. The

FIG. 1. Coordinate system used for heading determination in the vertical plane. For both planes of motion to 0°, headings were defined as up and ±180° as down. For headings in the coronal plane, 90° defined as right. For sagittal headings, 90° was defined as forward. Each of the 72 headings that was tested in each condition is shown with a line.

responses to all the headings within ±90° of this heading were examined to determine if the response heading were right or left of the reference heading. When plotted this way, the headings appeared to follow a cumulative distribution function. A cumulative distribution function could then be fit to these responses using a standard psychometric function fitting technique (Wichmann and Hill 2001). Each fit was reiterated 100 times using resampled responses to permit determination of confidence intervals (Wichmann and Hill 2001). A lapse rate of 0 to 0.05 was fit to the responses. Using this method, for each reference heading, the mean of the psychometric function or point of subjective equality (PSE) represented the heading at which subjects were equally likely to perceive a heading left or right of the reference heading. The PSE was never assumed to be negligible. The width of the psychometric function (sigma) represented a measure of the precision or reproducibility of the responses.

Statistical significance was determined using ANOVA in Prism (GraphPad, La Jolla, CA) with the threshold for significance set at $p < 0.01$. Correlations between continuous variables were analyzed using Pearson's correlation coefficient.

The results modeled using a version of a population vector decoder model (Georgopoulos et al. 1986; Seung and Sompolinsky 1993; Gu et al. 2010). Population vector decoder models can be generally described using the equation as follows:

$$\vec{P} = \sum_{i=1}^n w_i \vec{C}_i \quad (1)$$

Where P is the population vector, w is the weight of each unit, and C is the individual unit vector. The distributions of the directional sensitivities of the utricle and saccule are not well known in humans but for the purpose of analysis will be estimated as a

population which includes two vectors: a utricle vector which is sensitive only to motion in the horizontal plane and a saccule vector which is sensitive only to motion in the vertical plane. Although the actual utricle and saccule are sensitive to motion in a number of directions and the direction of greatest sensitivity may be offset from these directions, this assumption is used for simplicity because the direction of greatest sensitivity is not known in humans, and because it makes it easy to compare to prior that have measured sensitivity in the horizontal and vertical directions. Thus for this situation, the population vector model can be simplified and the accuracy can be described such that for any heading angle (θ) the perceived angle (θ_p) is given as follows:

$$\theta_p = \tan^{-1} \left(\frac{w_u \sin(\theta)}{w_s \cos(\theta)} \right) = \tan^{-1}(r \tan(\theta)) \quad (2)$$

Where w_u is the weight of the utricle vector (horizontal component), w_s is the weight of the saccule (vertical component), and r is proportional to the ratio between the two. The dependence of error on population size (N) has previously been established as $1/\sqrt{N}$ (Paradiso 1988; Snippe and Koenderink 1992; Seung and Sompolinsky 1993). The precision of the estimate (σ) at any heading is given as follows:

$$\sigma = \sqrt{(w_u \cos \theta)^2 + (w_s \sin \theta)^2} = \frac{K}{\sqrt{N}} \sqrt{\frac{(\cos \theta)^2}{r^2} + (\sin \theta)^2} \quad (3)$$

Where K is a constant which was arbitrarily chosen as 1,000 so that N values remain above unity. Using these two equations, the unknown parameters r and N were determined by fitting this model to the data using the `fminbnd` function in Matlab (Mathworks, Natick, Massachusetts). First, the ratio w_u/w_s or r was determined by fitting the observed biases using Eq. (2). Afterwards, using this fixed ratio, the number of units was estimated using the observed precision (3), only $N > 0$ were allowed. This order was used for fitting the data because the bias was not sensitive to N and fitting both sigma and bias simultaneously using the combined error would not be appropriate because the sigma values were much larger than the bias for several of the conditions.

RESULTS

Early in the analysis, it was noticed that age was strongly correlated with subject performance with older subjects having significantly greater errors in determining the motion direction with the vestibular

stimulus in both planes and with the visual stimulus in the sagittal plane (Fig. 2). For both the vestibular conditions, the correlation between age and mean error were highly significant ($p < 0.001$ for both). Although for visual stimuli in the sagittal plane there was a strong correlation between age and larger errors ($p < 0.001$), this correlation with visual stimuli was not significant in the coronal plane ($p = 0.19$). Although there was no clear cutoff point, there was a clear effect

FIG. 2. Mean heading error by subject's age. The mean heading error was calculated from the absolute value of each error so that there were no negative values. **Panel A:** In the coronal plane there was a significant correlation between age and mean error for vestibular headings ($p < 0.001$) but not for visual headings ($p = 0.19$). **Panel B:** In the sagittal plane, there was a significant correlation between age and the mean error for both vestibular and visual stimuli ($p < 0.001$ for both).

of age. The data was analyzed in two age groups: under 50 and over 50. These groups were chosen based on examining the data in Figure 2, and is a cutoff point previously used in studies of vestibular perception (Roditi and Crane 2012). The age difference was not likely due to differences in the time required to orient the dial. Timeouts occurred after 0.09 % of stimulus presentations in older subjects and were limited to a single subject. In younger subjects, time outs occurred in 0.29 % of stimulus presentations and these were limited to three subjects. These fractions were not significantly different (Fischer's exact test, $p > 0.1$). No time outs occurred in ten of the subjects. When time outs occurred, it was thought to be due to lapses of attention and not due to the subject not having enough time to complete the task.

A psychometric technique was applied to determine the precision of the subjects' responses. This technique was used instead of simply averaging the responses for each heading because it decreased the noise by allowing a 180 ° range of headings to be used to determine the bias for each heading direction. This technique can be applied to individual subjects (Fig. 3) as well as data combined across subjects (Fig. 4). When this technique is applied across the range of angles tested, the direction specific bias (error) and thresholds can be determined. This is shown for a typical individual subject (Fig. 5). In this subject, there was a tendency to overestimate the horizontal aspect of vestibular headings in the coronal plane with the best accuracy near straight ahead and straight down. Biases for visual headings were smaller and thresholds more uniform.

When the data was combined across subjects, biases were similar to those in individual subjects. When determining heading in the coronal plane (Fig. 6), subjects tended to overestimate the horizontal component of the heading when the stimulus was purely vestibular (Fig. 6A, B). Thus, for headings up to 90 °, bias (error) was positive, and for headings between 90 and 180 °, the bias was negative. Similarly for headings to the subject's left, the lateral component of the heading was overestimated. Although the trend in biases was true for both age groups, the bias was about three times larger for subjects over the age of 50 (Fig. 6E). The precision (Sigma) of the heading estimates were best (lowest) for movements close to straight up (0 °) or down (180 °) in both age groups (Fig. 6B, F), even though the sigma was much higher in the over 50 age group (Fig. 6F). For each condition when the bias and threshold were compared between the over and under 50 age groups, there was a highly significant difference ($p < 0.005$ for each, paired t test). The ratio of sigma to PSE was > 2 in all conditions for the younger subjects and > 1.75 for all conditions in the older subjects.

FIG. 3. Sample data from an individual subject (a 47-year-old female) for vestibular heading estimation in the coronal plane. *Upper panel:* The actual error for each stimulus presentation. Ideal performance would be represented by a horizontal line at zero. The mean of the two responses for each heading is shown as a gray line. *Lower panel:* The psychometric method of determining perceived heading corresponding to a stimulus at 45° (up and to the right). Each data point represents two stimulus presentations. The ordinate represents the fraction of responses clockwise relative to the reference heading. With ideal performance, all the headings to the left of the reference heading would be 0 and all the headings to the right would be 1. The solid line represents the cumulative distribution function which best approximates the data.

For visual heading determination in the coronal plane, the biases were smaller when compared with the vestibular condition (Fig. 6C, G) and the precision was also better (Fig. 6D, H) with less variation across the range of stimuli. For the subjects under age 50, there was a slight trend in the biases in the opposite direction seen with the vestibular heading such that the vertical component of the heading tended to be slightly overestimated.

When vestibular headings were estimated in the sagittal plane, there was a trend towards overestimation of the horizontal (in this case surge or fore-aft) component of motion relative to the heave (up-down) component (Fig. 7A, E). Similarly, the precision was the worse for forward (90°) and backward

FIG. 4. Sample data, from subjects under age 50 during the sagittal heading estimation using a visual stimulus. *Panel A:* Heading error across the range of stimuli. Ideal performance would be represented by a horizontal line at zero. Individual responses are shown as gray circles. The median of individual responses is shown as a dark, solid line. Thin lines represent the 25th and 75th percentiles. The angle 0 represents straight up, 90° is right, -90° is left and ±180° is down. *Panel B:* The psychometric method of determining perceived heading for a sample stimulus of 45° (up and forward). The plot contains data from all subjects each of whom completed two blocks of trials with the visual stimulus. Thus each data point represents 20 stimulus presentations. The ordinate represents the fraction of responses which were clockwise to the reference heading as viewed from the subject's right. With ideal performance, all the headings to the left of the reference heading would be 0 and all the headings to the right would be 1. The solid line represents the cumulative distribution function which best approximated the data.

(-90°) relative to headings with a larger vertical component (Fig. 7B, F). For the visual headings in the sagittal plane, there was a trend towards overestimation of the vertical component of headings, thus it was opposite that seen for vestibular stimuli in this plane (Fig. 7C, G). The precision also got worse as headings

FIG. 5. Visual and vestibular heading error (bias) and sigma (precision) for a typical individual subject. The subject was a 52-year-old male. Coronal plane headings are shown in the right column and sagittal plane headings are shown on the left. The thick line represents the PSE relative to the reference heading on error plots (panels A, C, E,

and G) and the sigma of the best fit to the psychometric function for the sigma plots (panels B, D, F, and H). Thin lines represent the 95 % CI based on multiple resampling and refitting the data. On error plots, a gray dashed line at zero represents ideal performance.

moved away from straight ahead, although this trend was largest for the subjects older than 50 (Fig. 7H).

There was a poor ($R=0.61$ and 0.69) but significant ($p<0.001$ for both age groups) correlation between vestibular and visual heading biases in the coronal plane (Fig. 8A). There was no significant correlation ($p>0.1$) between visual and vestibular biases in either the sagittal plane (Fig. 8B).

A model with two free parameters was proposed to explain the direction specific biases (accuracy) and sigma (precision) for vestibular heading estimation in the vertical planes as described in Methods. The basis of the model is the utricle and saccule having different relative weights described in methods and shown graphically in Figure 9. The two free parameters are the ratio of the utricle to saccule (r) and the

FIG. 6. Coronal plane direction specific bias (error) and precision (sigma) for data combined across subjects under age 50 (*left side, A–D*) and over 50 (*right side, E–H*). The *thick line* represents the mean value and the two thin lines represent the 95 % CI based on multiple fits resampling data in each iteration. The *dashed gray line* represents the ideal performance and is shown only in plots of bias.

number of units (N) which are calculated based on the thresholds being proportional to $1/\sqrt{N}$. Although visual headings are obviously not determined using the utricle and saccule, the same model could be applied to the visual system to predict the relative numbers of units focused on horizontal and vertical

heading. This model provided a good approximation of individual data (Fig. 10). Fitting the model to individual data demonstrated individual variation with a tendency for r to be higher and N to be lower in vestibular heading conditions relative to visual conditions (Fig. 11). There was a significant difference in r

FIG. 7. Sagittal plane direction specific bias and precision (sigma) for subjects under age 50 (left side, A–D) and over 50 (right side, E–H). The thick line represents the mean value and the two thin lines represent the 95 % CI based on 100 fits with resampled data in each iteration.

based on test condition (one-way ANOVA, $F=4.66$, $p=0.03$). The mean r for visual conditions was 1.1 ± 0.4 (mean $\pm$ SD) and for vestibular conditions it was 2.0 ± 1.5 . There was also a significant difference in N based between these conditions (ANOVA, $F=6.76$, $p=0.003$). The mean N was higher for visual headings at $15,660 \pm$

$13,773$ versus $3,697 \pm 8,547$ for vestibular headings, indicating greater uncertainty in vestibular headings which may be explained by a lower number of units. With the individually determined parameters fits, there was a poor correlation between age and r for each condition ($p > 0.1$). With both the visual and

FIG. 8. Correlation between visual and vestibular biases for coronal and sagittal heading estimation. *Solid symbols* represent subjects under 50 and *open symbols* represent subjects over 50. The best fit linear regression is represented by a *solid* (under 50) or *dashed* (over 50) line. The correlation was significant only in the coronal plane.

vestibular conditions, there was a tendency for N to decrease with age but the trend was not significant ($p > 0.1$). The model was also fit to the combined data (Fig. 12) with r for the vestibular condition found to be slightly lower than the fits to the individual data and N significantly lower due to the decreased noise when combining multiple datasets. Although the fits to the visual combined data are not plotted in every case, N was higher than for the vestibular conditions (mean 4,171, range 1,991–8,408), and r was 0.98 and 1.16 for the coronal and sagittal conditions in young

FIG. 9. Model to explain the relative contributions of the utricle and saccule on vertical heading perception. A sample heading of 45° is shown (*gray arrow*) in which the utricle and saccule would experience equal translation. However, if we assume that the utricles outnumber of saccule 2:1 then the relative representation of the movement will be as shown on the right side. In this case, instead of 45° being perceived, the angle would be less at 26.7°, such that the bias or error would be 18.3°. This magnitude of error would be typical for a 45° stimulus. The precision or sigma would be a function of the ability to discriminate small changes in heading and thus the fraction of the response perpendicular to the heading.

subjects and 1.47 and 1.76 for the corresponding conditions in subjects over 50.

DISCUSSION

It has been previously demonstrated that humans overestimate both visual and vestibular headings in the horizontal plane relative to the fore-aft axis when a full range of headings is considered (Crane 2012; Cuturi and Macneilage 2013). These biases in visual and vestibular headings in the horizontal were predicted by a population vector decoder (PVD) model (Gu et al. 2010) based on the known distributions of neuronal sensitivities in the medial superior temporal area (MSTd) of monkeys. These model predictions are predicated on the fact that neurons with preferred sensitivities which differentiate left versus right outnumber those sensitive to fore-aft directions. The model then makes two related predictions which are both supported by data as follows: First, that the precision of heading estimates will be best for headings near straight ahead, a prediction now well established for both visual and vestibular headings (Crowell and Banks 1996; Gu et al. 2007; Gu et al. 2010; MacNeilage et al. 2010). Second, that the lateral component of heading is overestimated (Crane 2012; Cuturi and Macneilage 2013). Although the previously described PVD model was based on neuronal sensitivities in MSTd (Gu et al. 2010), there is also the potential for these asymmetries to exist at the level of the peripheral vestibular end organs (Rosenhall 1972; Rosenhall and Engstrom 1974; Fernandez and Goldberg 1976).

Since both visual and vestibular signals are available in MSTd (Duffy 1998; Gu et al. 2007; Chowdhury et al. 2009), it is biologically plausible that sensitivities in MSTd

addition model. The ratio of the utricle/sacculle weights is shown (r) as well as the relative number of otoliths (N) which best fit the observations. The quality of each fit was estimated using a correlation coefficient (R).

could be responsible for the similar biases in visual and vestibular headings in the horizontal plane. The current

data sought to further test this hypothesis by examining visual and vestibular heading estimation in vertical

FIG. 11. Results of model fit to individual subject data. *Solid symbols* represent vestibular headings with *open symbols* represent visual headings. Coronal headings are represented by *circles* and sagittal headings by *squares*. In *panels A, B*, the mean value is shown by a *solid vertical line*. In *panels C, D* plot, the model fit parameters against age.

planes. These conditions are potentially useful for addressing this issue because human thresholds for heave (up–down) translation are 2–3-fold higher than thresholds of translation in the horizontal plane (Benson et al. 1986; Roditi and Crane 2012; Valko et al. 2012). These sensitivity differences likely originate in the periphery where higher gains have been found for otolith afferents preferring horizontal motion relative to those preferring vertical motion (Fernandez et al. 1972; Fernandez and Goldberg 1976), although a central origin cannot be ruled out. Heading discrimination is also more sensitive in the horizontal plane than in the vertical plane (MacNeilage et al. 2010), although heading estimation had not previously been examined. Furthermore, the number of otoconia in the human utricle is significantly more than in the saccule (Igarashi et al. 1993). Thus, differences in vestibular end-organ sensitivity are more likely to bias heading perception in the vertical plans than in the horizontal plane where thresholds of lateral and fore–aft translation have previously been reported to be similar (Benson et al. 1986; Roditi and Crane 2012). Furthermore, in MSTd, the distribution of neuronal direction sensitivities to headings in vertical directions are more uniform (Gu et al. 2010) so any direction-specific biases introduced in MSTd would likely be less.

Thus if peripheral vestibular sensitivity is driving the direction specific bias, heading estimation in the vertical planes may cause a pattern of biases that are different in the visual and vestibular tasks. In the current study as well as previous studies of heading estimation (Crane 2012; Cuturi and Macneilage 2013), there was no effort to differentiate head-horizontal/vertical from earth-horizontal/vertical as the head was always upright. Although it is believed the differences described are related to the direction of movement relative to the head, as previous studies have shown that thresholds do not change based on the direction of movement relative to gravity (MacNeilage et al. 2010).

Unlike estimation of headings in the horizontal planes, the current data demonstrated different trends in direction specific biases between visual and vestibular headings. The biases for both visual and vestibular headings were large when compared with the noise (Sigma) indicating they are likely true perceptual biases rather than just error-related noise. The direction-specific biases in visual headings were less than those for the vestibular headings. For vestibular conditions, the horizontal heading component was always overestimated relative to the vertical component, where this was not always true for vision.

FIG. 12. Experimental observations and model predictions for the vector addition model of vestibular heading perception. The *gray lines* represent the observed data and are the same as those reported in Figures 4 and 5. The *solid black line* in each figure represents the predictions of the vector addition model. The ratio of the utricle/

sacculi weights is shown (r) for each age group and condition as well as the relative number of otoliths (N) which best fit the observations. The correlation coefficient (R) represents the correlation between the model predictions and the observations.

Furthermore, there were large differences in performance based on age in both vestibular heading tasks, while for the visual task, it was only significant in the sagittal plane. These differences further suggest that sensory organ sensitivity may lead to different biases in perceived visual and vestibular headings.

The possibility that these heading biases might be explained by haptic influences was considered. This consideration was also relevant to the prior paper on heading estimation in the horizontal plane where an overestimation of the lateral aspect of headings was observed for both visual and vestibular headings (Crane 2012). In the prior paper, attempts were made to control this by giving spoken headings, which greatly decreased this bias, although this task was more difficult and generally took subjects longer to complete. Additionally, in that previous study, sub threshold vestibular headings were delivered to see if subjects tended to be more likely to orient the dial in certain positions which also did not occur. Neither these control experiment were repeated in the current series. A subsequent paper which examined heading estimation in the horizontal plane independently found similar results with a different haptic task—orienting a point on a screen rather than a physical pointer (Cuturi and Macneilage 2013). Thus, even with a separate task, the biases were similar suggesting they were unlikely to be haptic in origin. The current results make haptic effects even less likely because the direction of the biases in the visual and vestibular conditions was different and the correlation between visual and vestibular heading estimates were poor (Fig. 8), despite a common haptic task.

Although, it is believed that the vestibular heading estimates were primarily determined from motion sensed in the inner ear and proprioceptive component cannot be completely ruled out. Previously when examining vertical translation thresholds in humans without vestibular function, it was found that the thresholds were much higher than the 14 cm/s stimulus used here at a similar frequency (Valko et al. 2012). Thus, the vertical component of translation was almost certainly vestibular in origin. However, the translation component of the heading used here was above threshold for most of the stimuli tested in subjects with bilateral vestibular loss (Valko et al. 2012), suggesting a possible proprioceptive component of translation perception.

An unexpected finding of this paper is that heading estimation was strongly dependent on the subject's age for both the visual and vestibular conditions, the sagittal plane, and for the vestibular condition in the coronal plane (Fig. 2). Although this was a significant effect on heading error, the effect on best fit parameters to the model was more subtle (Fig. 11C, D). A previous study that included a similar age range did not find any significant effect of age in for heading estimation in the

horizontal plane even though efforts were made to look for potential age effects (Crane 2012). Most previous studies of vestibular heading discrimination have not been designed to consider age effects as all the subjects were under age 35 (MacNeilage et al. 2010; Cuturi and Macneilage 2013). However, thresholds of translation perception significant increase after age 50 (Roditi and Crane 2012), so it is not surprising that heading estimation also deteriorates in this age group. The number of otoconia decreases with age in humans (Igarashi et al. 1993), and this decrease is greater for otoconia in the saccule which has implications for biasing heading estimation.

A model was fit to the data which explains the observed heading biases and precisions as a result of two vectors: horizontal (utricle) and vertical (saccule). Although the utricle/saccule distinction is made for the vestibular system, the model could also be applied to visual headings. Given that sensitivity horizontal motion is better, this model predicts the best heading estimation for headings near vertical. This is because precise estimation of headings near vertical depends largely on the horizontal component of motion which will have the greatest change in activity for small changes in the angle relative to vertical. This model provided a good approximation of the observed heading biases or accuracy and heading precision or sigma both for individuals (Figs. 10, 11) and for data combined across subjects (Fig. 12). Although the weights of the utricle and saccule used in the model are probably not directly proportional to the number of otoconia because the gain of the system is likely adjusted. However, the ratio (r) of utricle to saccule weights may be explained by the ratio of end organs. In humans, this ratio of otoconia has been found to be 1.4 in the utricle for every 1 in the saccule in infants (Igarashi et al. 1993). In the current dataset, the model predicts only a very similar ratio at 1.56 (coronal) and 1.34 (sagittal) for adult subjects under age 50 in the combined data. When the model fits to individual subjects were examined (Fig. 11), the median ratios were similar at 1.84 (coronal) and 1.21 (sagittal). In their elder population, who had a mean age of 65, this ratio increased to 2.9 (Igarashi et al. 1993). The model of the current data also predicts a similar change in the ratio of utricle to saccule representation at 2.33 (coronal) and 1.45 (sagittal) in the subjects >50 when the model was fit to the combined data. When the median ratios of the individual fits of those >50 were considered, it was 2.47 (coronal) and 2.52 (sagittal). The magnitude of the ratio change with age with this model was similar to that seen in the Igarashi et al. histological study; however, there was a lot of interindividual variation in both the current data and the previous histology. Furthermore, there may be mechanisms of compensation at other

levels in the system which would prevent the model predictions from exactly matching the histology.

The model was also able to predict the relative numbers of peripheral otoliths. Which for the older group were only 24 % of that seen in the young population for the sagittal analysis and 5 % of that seen in the young population for the coronal analysis for the fits to the combined data. When the median values of N for the individual fits were considered, the number of peripheral otoliths in the older population was 18 % for coronal and 15 % for sagittal headings. In the histological analysis, the decrease in otolith volume was such that the elderly population had only 33 % of the volume seen in their young population (Igarashi et al. 1993). Thus, the model predicts a greater decrease than the histological study. This greater decrease may be because the histology only examined loss of volume and did not consider functional decline. The thresholds of translation perception were previously described to be about twofold higher in those over 50 relative to the under 50 population (Roditi and Crane 2012). If the thresholds are proportion to $1/\sqrt{N}$ as previously suggested (Paradiso 1988; Snippe and Koenderink 1992; Seung and Sompolinsky 1993), this finding also suggests that otolith function in the older population is about 25 % that of the younger population.

The current data suggest that directional differences in vestibular end organ sensitivity cause biases in vertical heading perception. It is perhaps not surprising that more resources are dedicated to determining lateral and fore-aft translation because this is the plane in which most human navigator occurs. A consequence of this is that the vertical component of heading is underestimated and this directional bias increases with age due to the relatively greater loss of otolith function in the saccule. This may have implications for the increase for fall risk which is much higher in the elderly population (Kelsey et al. 2012).

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