

The effect of head roll on perceived auditory zenith

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Abstract We studied the influence of static head roll on the perceived auditory zenith in head-centred and world-centred coordinates. Subjects sat either upright, or with their head left/right rolled sideways by about 35° relative to gravity, whilst judging whether a broadband sound was heard left or right from the head-centred or world-centred zenith. When upright, these reference frames coincide. Results show that subjects judged the zenith accurately within different planes, although response variability increased for the midsagittal plane. With the head rolled, head-centred auditory zenith shifted by the same amount and was located as accurately as for upright, indicating unaltered localisation cues by head-on-body roll. Interestingly, when judging world-centred zenith subjects made large systematic errors (10–15°) in the direction of head roll, and response variability increased, which resembles the visual Aubert effect. These results demonstrate a significant influence of the vestibular-collic system on auditory spatial awareness, which sheds new light on the mechanisms underlying multisensory integration and spatial updating in sound localisation behaviour.

Keywords Spatial updating · Audio-vestibular integration · Aubert effect · Sound localisation · Vestibular-collic reflex · Reference frames

Introduction

Spatial awareness relies on the integration of multisensory inputs, but as accuracy and variability of signals may differ and change under varying conditions, an interesting question is how different sources are integrated to construct a unified percept.

Spatial perception has been studied extensively with visual stimuli (Aubert 1861; Mittelstaedt 1983; Van Beuzekom et al. 2001; Kaptein and Van Gisbergen 2004, 2005; De Vrijer et al. 2008). In visual-vestibular experiments, subjects set the orientation of a luminous line, either parallel to their own body axis, or to the perceived earth-vertical (i.e. gravity). Subjects accurately estimate their body orientation, even in the absence of visual cues (e.g. Mittelstaedt 1983; Mast and Jarchow 1996; Van Beuzekom et al. 2001). However, when subjects have to set the luminous line earth-vertical, responses depend on body roll (Mittelstaedt 1983; Kaptein and Van Gisbergen 2004; Fig. 1) or on head-on-neck orientation (Van Beuzekom et al. 2001). For near-upright orientations, errors are typically negligible, but at intermediate tilt angles (around 30°), data may show a small overcompensation (E-effect; Müller 1916). At larger rolls (>60°), however, the luminous line setting is tilted in the direction of head roll (Aubert (A)-effect; Aubert 1861), and response variability increases with roll angle.

Mittelstaedt (1983) explained the A-effect as a compromise between an imperfect gravicentric signal from the otoliths and a head-centred internal bias, called the

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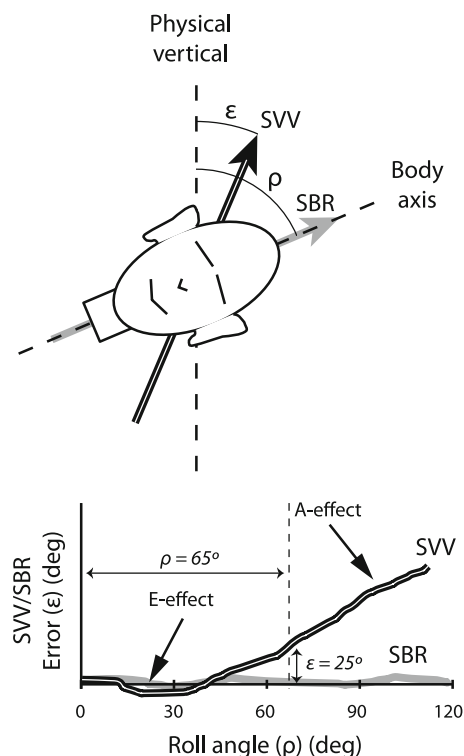


Fig. 1 Visual-vestibular integration. Subject sets a luminous line either parallel to the perceived earth-vertical (*black-white arrow*), or estimate body orientation in space (*grey arrow*). With the body rolled over a large angle (ρ), the subjective visual vertical (SVV) deviates from physical vertical (error ϵ ; A-effect). For small roll angles, subjects may slightly overcompensate roll (E-effect). The error varies systematically with roll angle (*black-white line, bottom, schematic data*). The subjective body roll (SBR) aligns well with the actual body orientation for all roll angles (*grey, schematic data*)

idiotropic vector. According to this hypothesis, the otolith estimate is not aligned with gravity because of an imperfect fusion of utricle and saccule information. The head-roll estimate will then be biased towards the head axis after adding the imperfect otolith signal with the idiotropic vector. This computation minimises the E-effect but enhances the A-effect.

An alternative theory proposes a Bayesian principle (De Vrijer et al. 2008). This model is based on the summation of precise and accurate retinal information of the luminous line with a biased, but statistically optimal, estimate of head orientation in space. In contrast to Mittelstaedt's proposal, the otoliths are assumed accurate, but contaminated with noise, which increases with roll angle. To cope with this neural variability, the Bayesian hypothesis assumes that in the visual task, the brain uses prior assumptions about head orientations, e.g., upright is more likely than rolled. A Bayesian estimate (Dayan and Abbott 2001) of head orientation is then biased towards the prior distribution (which explains the A-effect) but is less variable than the otoliths.

This study focuses on the integration of head posture and acoustic spatial information. We wondered whether the auditory system is subjected to an A-effect when estimating a spatial auditory percept.

Sound localisation

In contrast to the luminous line, the spatial representation of sound is far from perfect (Wightman and Kistler 1989; Middlebrooks 1992; Hofman and Van Opstal 1998). Sound localisation relies on implicit acoustic cues that are processed by independent neural pathways. Interaural time (ITD) and level (ILD) differences define locations in the horizontal plane (azimuth; Blauert 1997); spectral-shape cues from the pinna encode vertical locations (elevation). Psychophysical experiments indicate that human sound localisation is accurate, but less precise when compared to visual localisation (Frens and Van Opstal 1995). Response variability is typically larger in elevation than in azimuth (Perrott and Saberi 1990; Hofman and Van Opstal 1998; Grantham et al. 2003) and varies with target eccentricity (Middlebrooks and Green 1991; Frens and Van Opstal 1995). Spatial resolution for azimuth decreases for far-lateral locations, and for elevation near the zenith (Hofman and Van Opstal 1998).

Audio-vestibular integration

As there is no obvious equivalent of a vertical luminous line at straight ahead for audition, we presented auditory stimuli around the zenith, which for an upright head is straight above. We measured how subjects estimated the auditory zenith either straight above their head, or relative to the earth (i.e. opposite to gravity). In case of an auditory A-effect, one expects the world-centred zenith to shift in the direction of head roll.

To our knowledge, the only study on this topic is by Lechner-Steinleitner et al. (1981), who investigated how localisation of a pure tone moving towards the zenith is influenced by head orientation. Their data did not show an auditory A-effect.

By letting subjects actively roll their head either left-ear down, or right-ear down, we investigated the influence of head posture on perceived head-centred and earth-centred auditory zenith. We also determined the resolution of the auditory system around the zenith for sounds within different planes. We presented well-localisable broadband sounds at pseudo-random locations around the zenith, to prevent a potential effect of attention or prediction. Subjects indicated whether they perceived sounds left or right from the head- or world-centred zenith. In this way, listeners never indicated the zenith directly. Instead, we estimated perceived zenith (and its precision) by fitting

psychometric curves through the responses for the different head-roll and plane conditions.

Our results show that subjects indicated the correct head-centred zenith regardless head roll for all stimulus conditions, but that the resolution for midsagittal plane locations is much worse than for other planes. Moreover, we found a strong effect of head roll on the world-centred subjective auditory zenith, which provides the first evidence for an auditory A-effect.

Methods

Listeners

Four male subjects (age-range, 20–22) participated in the experiments on a voluntary basis, including author BA. Subjects were free from vestibular or other neurological disorders and had no hearing deficit.

Experimental setup

The listener sat in a completely dark, sound-attenuated room, in which black sound-absorbing foam effectively reduced echoes down to 500 Hz. A circular hoop with 58 speakers could rotate around the subject about a vertical axis with an angular resolution below 1° . Speakers were mounted with 5° spacing in elevation, but the 29 speakers on the frontal versus back halves of the hoop were offset by 2.5° . Three orthogonal magnetic fields were generated by three pairs of squared coils along the edges of the room, which induced alternating voltages in a dual-search coil mounted on the subject's head to record 3-D head orientation (Robinson 1963). The coil signals verified whether the subject's head remained stable throughout the experiment. Apart from the coil signals, we recorded button presses on a button box. All signals were digitised at 1,017.25 Hz/channel on Tucker Davis Technologies equipment (System 3).

Stimuli

Sounds were 150 ms of Gaussian White Noise (cut-off frequencies: 200 Hz HP and 20 kHz LP; e.g., Hofman and Van Opstal 1998) with an intensity of 60 dB(A) (measured at the subject's head with a Brüel and Kjaer microphone B&K 3134, and measuring amplifier B&K 2610). In contrast to tones, these noise bursts provided optimal localisation cues to the auditory system. By varying the relative intensities of two nearby speakers on the hoop, we implemented a spatial resolution down to 1.25° (Bremen et al. 2010).

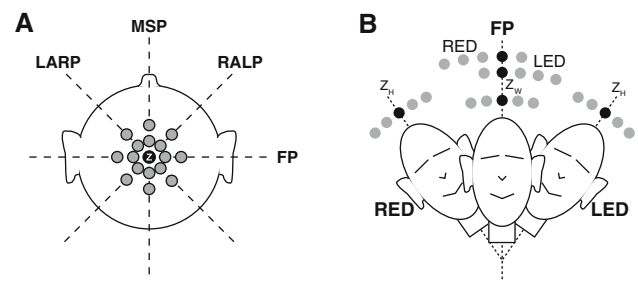


Fig. 2 **a** With the head upright, sounds were presented in different planes around the auditory zenith (Z ; top-view head). *FP* frontal plane, *MSP* midsagittal plane, *LARP* left-anterior/right-posterior plane, *RALP* right-anterior/left-posterior plane. **b** Stimulus presentation in the FP with the head upright, or during a static active head roll of 35° *RED*, or *LED*. Subjects responded whether the sound (grey dots) was presented left or right from either the head-centred zenith (Z_H), or left or right from the world-centred zenith (Z_W). Note asymmetrical stimulus arrays around Z_W for the *RED/LED* conditions

Experimental paradigms

Listeners were positioned with their head in the centre of the hoop. They responded in a two-alternative forced choice (2AFC) approach, by pressing either one of two buttons on the button box. When upright, the listener responded to stimuli within four different stimulus planes presented in different blocks: frontal plane (FP), midsagittal plane (MSP), left-anterior/right-posterior plane (LARP) and right-anterior/left-posterior (RALP) plane (Fig. 2a). The subject had to indicate whether the sound was perceived to the left versus right of the zenith in the FP, LARP and RALP planes or at front versus back in the MSP plane.

In a subsequent experimental session with the head in a static rolled position (either left-ear down or right-ear down by about 35°), stimuli were presented in the FP, and listeners indicated whether the sound was heard left versus right of the head-centred (Z_H), or world-centred (Z_W) zenith (Fig. 2b). Subjects responded open loop, as they never received any feedback about performance. That way we avoided potential effects of perceptual learning. If perceptual learning would have occurred in this fixed-order block design, response precision should improve over trials/blocks, which was not the case: MSP precision was always much worse than FP precision (see “Results”).

The subjects' answers were converted into psychometric curves (see “Data analysis”). For a reliable fit, data should symmetrically cover the full perceptual range that includes the threshold (50% correct) and the upper (100% correct) and lower ends (0% correct). Therefore, to prevent over-sampling (leading to unnecessarily long experiments), or measuring irrelevant regions of the psychometric curve, we used different physical speaker locations, resolutions and

ranges for the different conditions, which were determined by pilot experiments.

In the FP, sounds were at $[0 \pm 1.25 \pm 2.5 \pm 5 \pm 7.5]^\circ$ (right positive) with respect to head-centred zenith. Because pilot experiments indicated a much poorer auditory spatial resolution in elevation around zenith, sounds were presented over a broader range in the MSP: $[0 \pm 5 \pm 10 \pm 15 \pm 20 \pm 30 \pm 40]^\circ$ (front positive). In the LARP/RALP planes, we presented sounds at $[0 \pm 2.5 \pm 5 \pm 7.5 \pm 12.5]^\circ$ (anterior positive).

In static roll experiments, the subject actively rolled the head by 35° (right-ear down, RED), or -35° (left-ear down, LED; Fig. 2b), which was about the maximal roll subjects could comfortably maintain. In the head-centred zenith task, sounds were presented between $[-7.5, +7.5]^\circ$ around the head-centred zenith (resolution as in upright FP). In the world-centred zenith task, sounds were presented at $[-40, -35, -30, -20, -15, -10, -5, +5, +10]^\circ$ around the gravity zenith for LED, and at $[-10, -5, +5, +10, +15, +20, +30, +35, +40]^\circ$ re. zenith for RED. These physically asymmetrical target sequences were chosen, as pilot experiments indicated that *perceptually* these target ranges were heard approximately symmetrical around the perceived world-centred zenith. In this way, the listeners' responses covered the entire perceptual range in an unbiased way, which was required for a reliable psychometric measurement. For all conditions, each sound location was presented 20 times, resulting in experimental blocks of about 8 min. The experiments with static head roll were divided in two blocks of 10 repetitions per sound location, to prevent discomfort for the listener.

Although the number of physical stimulus locations differed slightly for the different stimulus planes (13 for MSP vs. 9 for FP), we think it is unlikely that response accuracy and precision were influenced by these differences, as all stimuli (20 repetitions each) were always presented in pseudorandom order, and subjects responded open loop, never receiving any feedback about performance.

Data analysis

Off-line data analysis used custom-made routines in Matlab (Matlab 7.6, The Mathworks). Psychometric data were analysed by calculating the proportion of 'right' (or 'front') responses for each stimulus location and fitting a cumulative normalised Gaussian through the data by using the method of maximum likelihood (Wichmann and Hill 2001). The psychometric curve, $\psi(x)$ (x is stimulus location), is thus given by:

$$\psi(x) = \lambda + (1 - 2\lambda) \cdot \text{erf}(x; \mu, \sigma) \quad (1)$$

in which $\text{erf}(x; \mu, \sigma)$ is the error function (mean μ , standard deviation σ). The mean (threshold) represents the location of the subjective auditory zenith, which serves as a measure of accuracy. The standard deviation, which reflects the slope around threshold, measures response precision. The lapse parameter, λ , represents stimulus-independent errors that may be due to mistakes, a bias, or random guessing. It was constrained to maximally 10%.

Results

The auditory zenith in upright listening

Fig. 3 shows results for the four stimulus planes of listener KA sitting upright (Fig. 2a). The thresholds of the psychometric curves indicate an accurate percept of the auditory zenith in all four planes (mean close to zero: $0.08 \pm 0.33^\circ$), but response precision was direction dependent. As standard deviations (precision) for the RALP/LARP and FP planes were highly similar (mean \pm SD: $3.7 \pm 1.3^\circ$), for the MSP it was clearly higher (11°).

Figure 4 presents accuracy and precision results of all listeners when estimating the head-centred auditory zenith for the different stimulus planes. All thresholds were within 5° ($0.65 \pm 0.57^\circ$; Fig. 4a) of the physical head/gravity zenith. The only exception concerned listener BA, whose responses to MSP stimuli were virtually random, leading to

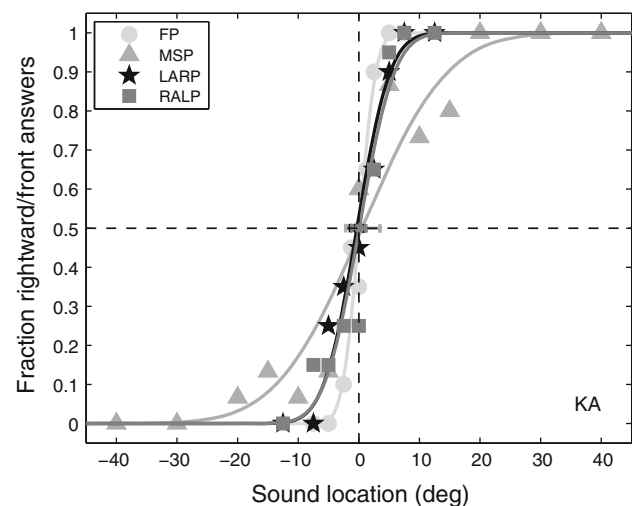


Fig. 3 Responses to stimuli in the four planes with the head upright (subject KA): Psychometric curves for frontal plane (dots), midsagittal plane (triangles) and the LARP (stars) and RALP (squares) planes. Thresholds are determined by 50% rightward responses (horizontal/vertical dashed line), and measures response accuracy; the slope at threshold measures response precision (variance). In all four cases, accuracy is high, as thresholds are close to 0° . MSP precision, however, is worse than for the other three planes

an unreliable psychometric fit. Excluding this one condition, the main trend is that upright listeners were quite accurate in defining the true auditory zenith (two-sided t test between true and estimated zenith: $P > 0.25$ for all conditions).

Figure 4b shows a clear effect of stimulation plane on response precision (ANOVA with stimulation plane as factor: $F(3,11) = 14$, $P = 0.0004$; excluding BA_{MSP}). The precision measures for the FP, RALP and LARP planes were very similar, but the standard deviations for MSP stimuli were much higher (Bonferroni-corrected t tests: $P < 0.005$).

Compensation for head roll

Figure 5 compares the results of listener BA for the craniocentric zenith task for FP stimuli when sitting upright (black triangles), with the head rolls of 35° RED (grey stars) and LED (grey squares). Note that the thresholds (small squares) in all three curves were close to the actual head axis (vertical dashed lines), indicating good accuracy for the three head postures. The figure also shows the

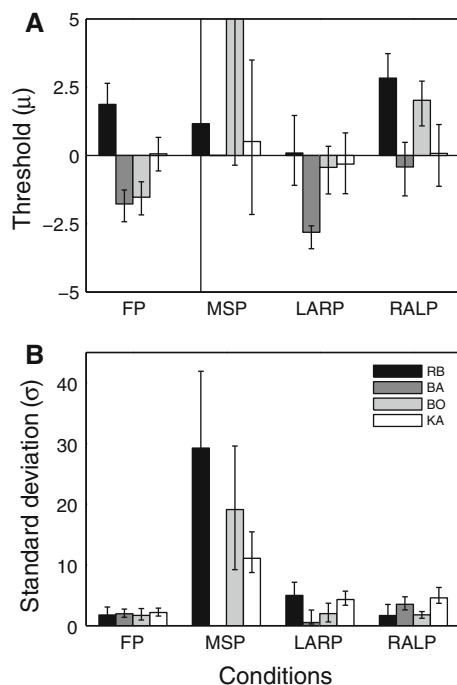


Fig. 4 **a** Accuracy of the psychometric curves for all four subjects and stimulus planes with the head upright. All thresholds are within a few deg (mean \pm SD: $0.62 \pm 0.57^\circ$) of the true auditory zenith, except for the MSP data of subject BA. All four subjects are quite accurate in determining craniocentric auditory zenith. Error bars denote 95% confidence intervals of fit. **b** Precision data. For all subjects, precision was high in FP and in the RALP/LARP planes, but much worse for MSP stimuli. Error bars denote 95% confidence intervals of fit

results of the world-centred zenith task for the head-roll conditions (LED: light-grey triangles, RED: light-grey dots). For an accurate world-zenith estimate, the curves should coincide with the central (FP) response curve around 0° . This is clearly not the case, as the two curves shifted in the direction of head roll (LED: -17° , RED: 12°). Note that also their standard deviations (LED: 10° , RED: 6.0° , FP: 1.9°) differ from the upright condition, indicating increased response variability.

Figure 6 presents the results for all subjects. The left-hand column shows thresholds (A) and standard deviations (B) of the psychometric curves for the head-centred zenith task under LED and RED conditions. The dashed lines correspond to the true head zenith. All subjects accurately estimated the craniocentric auditory zenith (two-sided t test between true and estimated zenith: $P > 0.12$ for all conditions). The right-hand side shows the results of the world-centred task, with the upright FP data for comparison. The data indicate a substantial and consistent shift of the perceived auditory earth-vertical into the direction of head roll by about 10 – 15° (ANOVA with head roll as factor: $F(2,9) = 56$, $P \ll 0.0001$).

The precision data of the head-centred (Fig. 6b, left) and world-centred (right) settings for the different head postures show an effect of head roll on response variability when compared to the upright FP estimates (ANOVA with head roll as factor: head-centred: $F(2,9) = 6.4$, $P = 0.019$; world-centred: $F(2,9) = 65$, $P \ll 0.0001$). Specifically, precision decreased for all listeners and for both tasks when

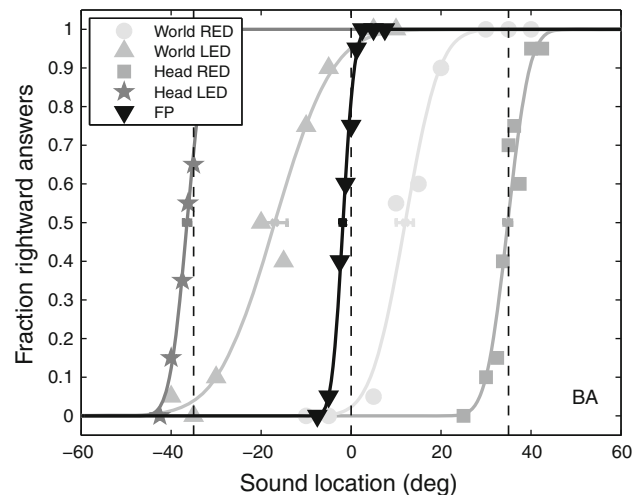


Fig. 5 Psychometric curves during head roll of $\pm 35^\circ$ (subject BA). Stars and squares show the curves for the head-centred task. Vertical dashed lines: true head-centred zenith. Subject is accurate in localising the head-centred zenith, as thresholds are close to the true locations (vertical dashed lines). Circles and grey triangles: world-centred zenith task for head rolls of $\pm 35^\circ$. Thresholds shifted into the direction of head roll, and response variability increased when compared with head-upright data for FP stimuli (black triangles)

they rolled their head (two-sided t tests on precision differences between FP and head tilt: $P < 0.05$ for all conditions).

Discussion

Effect of auditory cues

We tested accuracy and precision in determining the auditory zenith, either straight above the head, or along the direction of gravity. With the head upright, we found (1) accurate localisation of the zenith for all stimulus planes but (2) lower precision for sounds within the MSP, than for the other three planes (Fig. 4). Differences in accuracy and precision for FP versus LARP/RALP were minor. These results therefore suggest that binaural difference cues dominated around head-centred auditory zenith, and only for the MSP configuration subjects exclusively relied on poorly defined spectral-shape cues.

Auditory Aubert effect

Accuracy of the craniocentric auditory zenith under the two head-roll orientations was similar as for head upright (Figs. 5, 6a, left). However, precision of the head-centred estimates in roll was worse than for FP upright (Fig. 6b, left), which suggests an influence of head orientation on the precision of processing binaural difference cues.

When estimating the world-centred auditory zenith, however, subjects were inaccurate, with 10–15° errors in the direction of head roll (Fig. 6a, right). This finding resembles the visual Aubert effect (see “Introduction”), and may therefore be termed Auditory Aubert (AA)-effect. Compared to the visual A-effect, which starts for roll angles beyond about 60°, the AA-effect kicks in at a much smaller roll angle. The precise behaviour of the effect will have to be assessed in future experiments; for this report, we only determined the effect for a particular roll angle.

In addition, the variability of the world-centred responses was higher when compared to head-centred roll and head-upright data in the FP (Fig. 6b). It is not immediately obvious whether this increased variability is due to a (slight) deterioration of the binaural difference cues at more lateral azimuth angles, to an influence of head roll, or to both. Spatial resolution of the auditory system is about 1° around zero azimuth and declines with azimuth angle (Grantham et al. 2003; Perrott and Saberi 1990; Hofman and Van Opstal 1998), with poorest performance near the interaural axis. Under roll conditions, stimuli were presented (in head-centred coordinates) around $[\alpha, \varepsilon] = [0, 90]^\circ$ (head-centred task) and $[\alpha, \varepsilon] = [\pm 20, 70]^\circ$ (world-centred task). Therefore, an effect of cue resolution on response variability may have played only a minor role.

Other studies

Few studies investigated the influence of changes in head orientation on sound localisation. Goossens and Van Opstal (1999) studied eye movements to pure tones with the head pitched and found that responses were directed towards a location between a head-centred and world-centred reference frame, depending on tone frequency. Since eye movements towards broadband noise stimuli were accurate, the authors suggested that a static head-orientation signal interacts within the tonotopically organised auditory system. Although the interaction might be due to a gravitational signal from the otoliths, Kopinska and Harris (2003) found that pointing errors towards dichotic auditory stimuli were mostly attributed to (yaw-induced) head-on-neck signals. In a visual remembered-saccade task, Klier et al. (2005) showed that both efference copies of head movement (yaw rotation only) and gravitational signals (pitch and roll head orientations) contribute to spatial

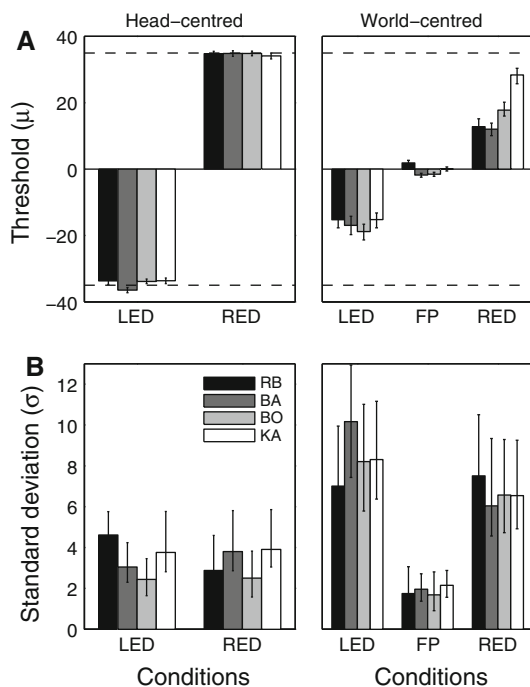


Fig. 6 **a** Response accuracy for all subjects during head roll for head-centred (left) and world-centred (right) zenith localisation. Dashed lines: actual craniocentric zenith locations. All subjects were accurate in the head-centred task, whereas they made large systematic errors in the direction of head roll for the world-centred task (auditory A-effect). Error bars denote 95% confidence intervals of fit. **b** During head roll, response precision was lower than for the upright orientation (FP) for either task. Error bars denote 95% confidence intervals of fit

updating of saccades, and it is conceivable that this holds true for audition as well. Indeed, Goossens and Van Opstal (1999) and Vliegen et al. (2004) showed that intervening movements of the head in rapid eye-head gaze shifts are fully incorporated in sound localisation responses to broadband noises, suggesting the accurate on-line use of efferent feedback signals. This high accuracy contrasts with the errors observed in perceptual tasks employed in (off-line) lateralisation experiments, or pointing tasks.

Others have also assessed the effect of changes in head orientation on sound lateralisation. For example, passive whole-body rotational vestibular stimulation around the earth-vertical axis affects sound lateralisation (audiogyral illusion), in which the auditory median plane (where ITDs and ILDs are perceived as zero) shifts in the direction of rotation (Clark and Graybiel 1949; Lewald and Karnath 2001). Recently, Van Barneveld and Van Opstal (2010) argued that this effect is due to changes in mean eye position, caused by quick phases of vestibular nystagmus.

Stimulation of the otoliths by linear acceleration in a centrifuge (Graybiel and Niven 1951; Dizio et al. 2001) or by passive whole-body roll (Lewald and Karnath 2002) also affects sound lateralisation: sounds at straight ahead shift a small amount towards the (perceived) upper ear

(audiogyral illusion). In the head-centred zenith task, we did not observe this effect (Fig. 6a, left). Possibly, the illusion disappears around the zenith, where the spectral cues are less reliable.

To our knowledge, the only study on the influence of static head roll on perceived world-centred auditory zenith was by Lechner-Steinleitner et al. (1981), who found no net effect of LED head roll after averaging their data from leftward to rightward sound presentations. However, they reported hysteresis; when sounds approached from the right, the perceived zenith shifted rightward, whereas a leftward shift was found for sounds on the left side. The origin of the hysteresis is not clear, but perhaps the repeated presentation of sounds on the same side may have drawn attention, or expectation, of sound locations towards that side. In the presence of such a biased nonlinearity, averaging data does not seem appropriate. A second difference with our study is the use of a low-frequency tone (323 Hz), instead of a well-localisable broadband noise burst. Such a tone only contains ITD information, as ILDs and spectral pinna cues are negligible. As a result, the ill-defined sound elevation could have caused the actual spatial percept of stimuli to move along a frontal straight-ahead path in azimuth. In any case, it seems unlikely that

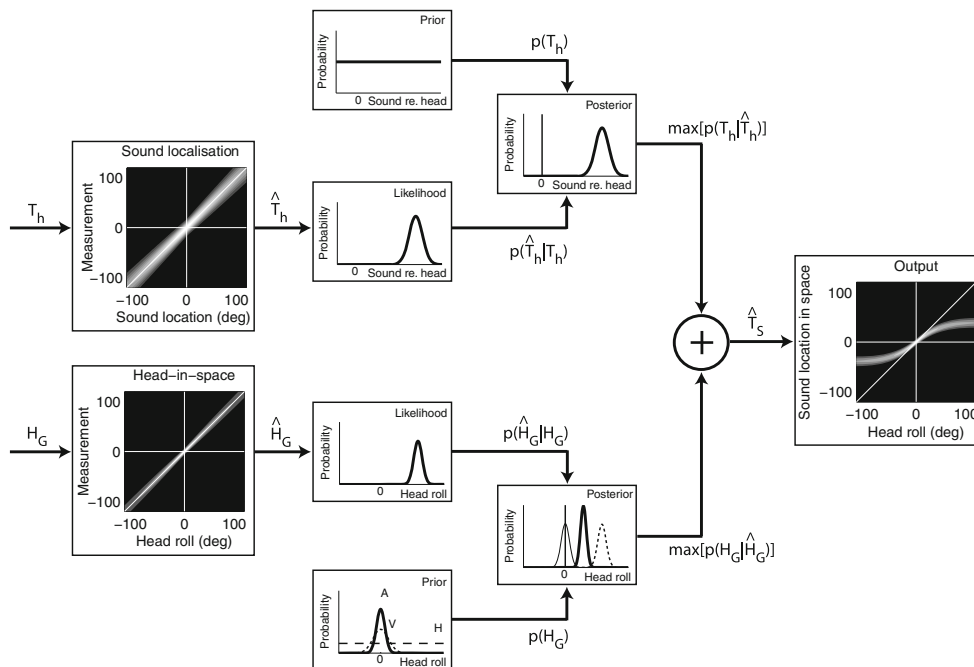


Fig. 7 Model that explains the auditory A-effect. The head-re-gravity estimation is based on the same Bayesian mechanism as discussed in De Vrijer et al. (2008); the actual head orientation re-gravity (H_G) induces an ambiguous otolith signal (\hat{H}_G) (the same neural signal corresponds to many potential head orientations). This is represented by the likelihood function that is weighted against the prior expectation of possible head orientations, which peaks around upright (0°). The prior in the auditory task (A) is narrower than for

visual stimuli (V), or for head-estimation (H, flat). The posterior distribution has smaller variance than the prior (thin black line) and likelihood (dashed line) but is biased towards the prior (Eq. 2). The auditory cues are noisy too, but the prior expectation of sounds is assumed uniform. As a result, the posterior estimate equals the likelihood. At the output, the sound location in space (\hat{T}_S) estimate is biased towards the head-centred zenith

subjects perceived such stimuli around the world-centred zenith. We have attempted to use an unbiased approach: subjects were tested open loop and never directly indicated the perceived zenith. They responded to broadband, well-localisable stimuli that were symmetrically arranged around the perceived task-related zenith. In addition, sounds were drawn at random, so that the likelihood of left versus right was the same. Under these conditions, we obtained a clear AA-effect on the percept of a world-centred auditory zenith.

Implications for models

The Bayesian model of De Vrijer et al. (2008) cannot readily explain our results. First, head-on-body roll in our experiments was only 35°, whilst the (visual) Aubert effect starts beyond 50–60°. Second, in the Bayesian model, the retinal representation of the luminous line is close to perfect with little variability, so that the likelihood for visual stimuli resembles a delta peak at the actual retinal location. For audition, however, this is not the case: sound localisation relies on the integration of different acoustic cues, each with varying reliabilities. It may be assumed that the acoustic likelihood function peaks around the true head-centred location, as sound localisation is accurate, but with considerable direction-dependent variability. In a Bayesian model, this would invoke a prior about craniocentric sound locations to get optimal estimates with smaller variance. For example, the auditory system could assume that sounds typically originate from straight ahead. The Bayesian estimate for a sound at the left would then shift towards the centre. Hence, in LED roll, a stimulus at the world-centred zenith (i.e. rightward with respect to the head) would be perceived left from the zenith. However, our results indicate an opposite effect (Fig. 5)!

The Bayesian model could account for our data under the assumption that the estimate of head orientation is biased, like in De Vrijer et al. (2008), in combination with an accurate representation of the sound's location (Fig. 7). Thus, sound locations have a uniform prior; they can originate anywhere with equal probability. To explain the earlier onset of the AA-effect, the prior for head orientation should have a narrower peak around upright for auditory than for visual stimuli, as the Bayesian posterior for head orientation is determined by:

$$\hat{H}_{\text{post}} = \frac{\sigma_{\text{prior}}^2}{\sigma_{\text{prior}}^2 + \sigma_{\text{otolith}}^2} \cdot \hat{H}_{\text{otolith}} + \frac{\sigma_{\text{otolith}}^2}{\sigma_{\text{prior}}^2 + \sigma_{\text{otolith}}^2} \cdot \hat{H}_{\text{prior}} \quad (2)$$

with σ_X the standard deviation of signal X, and \hat{H}_X its mean. In case $\sigma_{\text{prior}} \ll \sigma_{\text{otolith}}$, Eq. 2 is dominated by the prior, resulting in a strong A-effect. In the head-centred

task, the head prior is supposed to be uniform, yielding an accurate estimate of head orientation. In other words, the influence of the prior would be task and modality dependent. The modality dependence underlies differences for auditory, visual, vestibular, and tactile stimuli and could be determined by the reliability of the respective sensory inputs.

The results of response variability (Fig. 6b) may be qualitatively understood from the model too. The final stage adds two independent stochastic signals ($\hat{T}_G = \hat{T}_H + \hat{H}_G$), and therefore the response variability increases as $\sigma_{H+A} = \sqrt{\sigma_A^2 + \sigma_H^2}$. In the upright task, the standard deviations of auditory and head posture signals are minimal, and total response variability is expected to be smallest. In the tilted world-centred task, the standard deviations of both signals increase, and therefore variability is highest for that task, with the tilted head-centred task yielding intermediate results.

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