# Spatial Representation in Body Coordinates: Evidence From Errors in Remembering Positions of Visual and Auditory Targets After Active Eye, Head, and Body Movements

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**Abstract** Eight participants were presented with auditory or visual targets and then indicated the target's remembered positions relative to their head eight seconds after actively moving their eyes, head or body to pull apart head, retinal, body, and external space reference frames. Remembered target position was indicated by repositioning sounds or lights. Localization errors were found related to head-on-body position but not of eye-in-head or body-in-space for both auditory (0.023 dB/deg in the direction of head displacement) and visual targets (0.068 deg/deg in the direction opposite to head displacement). The results indicate that both auditory and visual localization use head-on-body information, suggesting a common coding into body coordinates – the only conversion that requires this information.

**Résumé** On a présenté à huit participants des cibles auditives ou visuelles, puis on leur a demandé d'indiquer la position des cibles mémorisée par rapport à la position de leur tête, après qu'ils eurent bougé vigoureusement les yeux, la tête ou le corps dans le but de séparer les cadres de référence spatiale externe, de la tête, rétinien et du corps. La position mémorisée de la cible était indiquée par le biais du repositionnement des sons ou de la cible lumineuse. Des erreurs de localisation ont été notées en ce qui concerne la position de la tête par rapport au corps, mais ce ne fut pas le cas de l'œil par rapport à la tête et du corps par rapport à l'espace, ni pour les cibles auditives (0,023 dB/deg dans le cas de l'orientation du déplacement de la tête) ni pour les cibles visuelles (0,068 deg/deg dans le cas de l'orientation opposée au déplacement de la tête). Les résultats indiquent que la localisation de cibles à la fois auditive et visuelle fait appel à l'information provenant de la position de la tête par rapport au corps, ce qui suggère l'existence d'un codage commun dans la coordination corporelle – la seule conversion qui exige cette information.

Determining the location of real-world objects requires the integration of sensory information concerning not only the location of the stimulus relative to the sense organs but also of the sense organs relative to some reference system common to all the senses. The retina, head, body, or external space could theoretically provide such a reference frame. A series of conversions is then needed to move information from its initial coding in the frame of a particular sense organ into such a frame. Since eye, head, body, and space reference frames move relative to each other every time the eye, head, or body move, knowledge of the position of each frame relative to the others is needed when converting information from one to another (Harris, 1997; Pöppel, 1973). Any errors in coding the relative position of the frames could therefore lead to corresponding errors in the stored location.

Our experiments looked for reference frame conversion errors that would betray which conversions had been done and thus reveal which frame was used to code the information. After viewing a target, participants were asked to reproduce its position relative to the head after changing eye, head, or body position. If the location of a sound were stored in head coordinates, for example, then no conversions would be necessary to solve the reproduction task and no errors would be expected related to movements of the eyes in the head or head on the body. If location were stored in visual coordinates then eye-in-head information would be required both to store and retrieve the location, and systematic errors might be found related to the position of the eye in the head. Similarly, if sound location were stored in body coordinates then head-on-body information would be required for storing and retrieving, and errors might be found related to head position. Visual location is originally in eye coordinates and therefore eye-in-head information is always required for a head-based task. But if visual information were stored in body coordinates then head-on-body information would also be required, and errors might be found related to head position.

If no systematic errors are found related to the relative positioning of these frames it does not necessarily indicate that a particular conversion is not done. It could be that it was done perfectly and left no errors. However, if systematic errors are found they are strong indications of particular conversions taking place.

Possible neural substrates exist that could support any of these frames. Reports of auditory receptive fields moving in the superior colliculus tend to remain aligned with their visual counterparts during eye movements (Jay & Sparks, 1984), support the visual frame as a feasible candidate. Modulation of visual fields in the parietal cortex in response to eye position could represent a neural basis for a head-centred coding system (Bremmer, Distler, & Hoffman, 1997). Head position related cells in the parietal (Brotchie, Andersen, Snyder, & Goodman, 1995) could support body-centred localization. Using spatial coordinates is initially appealing in its directness (Mergner, Nasios, Maurer, & Becker, 2001) but since such coding is not related to any part of the organism, the representation would be unaffected by any movements of any extent or direction. Hippocampal cells show some of the required properties (Georgesfrancois, Rolls, & Robertson, 1999).

Effects of eye position on the perception of sound direction have been studied extensively (Bohlander, 1984; Goldstein & Rosenthal-Viet, 1926; Lackner, 1973a; Lewald, 1997, 1998; Lewald & Ehrenstein, 1996, 1998a; Pierce, 1901; Ryan & Schehr, 1941; Weerts & Thurlow, 1971) with inconclusive results. We have investigated eye position effects using a novel approach: using intracranial auditory targets and measuring their remembered positions always with respect to the head. With our design, participants could use a clearly defined head frame of reference for localization: The auditory targets were heard "inside the head" (lateralized) and the task was to move another sound heard "inside the head" to the remembered location. With this design, an effect of eye position on the remembered position of a sound would suggest auditory information being transferred into retinal frame of reference.

Effects of head and body position on the perception of auditory space have been reported (Goossens & Van Opstal, 1999; Karrer & Davidon, 1967; Lackner, 1973a; Lewald & Ehrenstein, 1998b; Lewald et al., 1999; 2000) but they have been difficult to compare to perceptual shifts related to eye or body position changes. In our experiments, we have investigated the influence of eye, head, and body position using the same design. We have examined the influence of eye, head, and body shifts on both auditory and visual stimulus localization in comparable circumstances in the same participants. We find consistent errors predominantly related to the position of the head on the body. These results are compatible with the conclusion that the locations of visual and auditory targets are coded relative to the body.

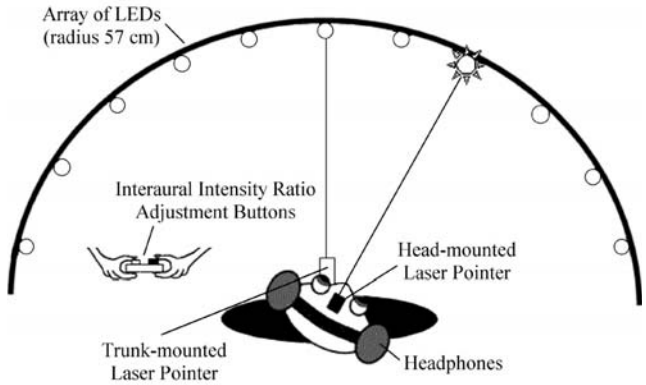


*Figure 1.* Auditory experimental setup. Participants adjusted the interaural sound pressure level differences of a sound played through headphones using a button box (insert) until its perceived position matched the position of targets, either actual or remembered. Eye position was controlled approximately by fixation lights, shown as circles. Head position was controlled by having participants position a head-mounted laser pointer (Experiment 1b). Body position was controlled by having participants position a trunk-mounted laser pointer (Experiment 1c & 1d).

## Experiment 1: Auditory Lateralization

METHOD

*Overview.* Participants were presented with a sound through headphones and were asked to remember its position relative to the head. They were then asked to move their eyes (Experiment 1a), head, and eyes (Experiment 1b), body beneath a stationary head (Experiment 1c) or entire body and eyes (Experiment 1d) before repositioning the sound to its previously heard location in the head.

*Participants.* Eight participants (aged 21-42 years) took part in the auditory experiments. None of them knew the scientific background of the study and they were given only general information about the purpose of the study. All subjects were paid for their participation. All experiments were conducted in accordance with the ethics procedures of York University.

*Auditory stimulus presentation apparatus.* The auditory experiments were performed using headphones in a dark and quiet room. The experimental setup is illustrated in Figure 1.

Waveforms were generated on a PC and downloaded to a 1401 Cambridge Electronics Design interface from which they were played out through two DACs and through appropriate impedance-matching circuits into the left and right channels of an audio

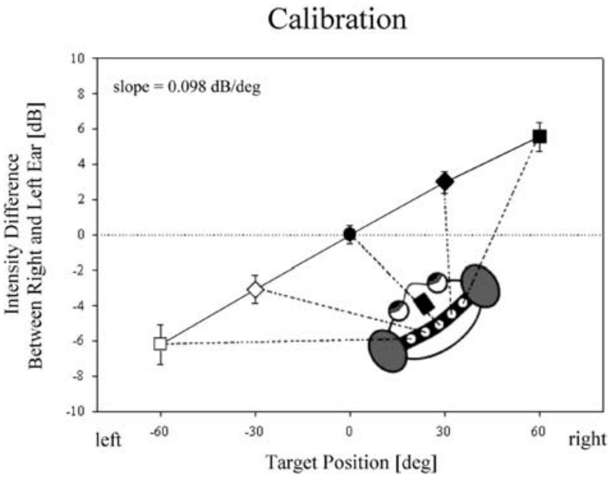


*Figure 2.* Calibration. Participants adjusted the interaural sound pressure level difference of dichotically presented sounds to align their perceived position with lights presented at 0° (filled circle), 30° (open diamond), and 60° (open square) to their left or 30° (filled diamond) and 60° (filled square) to their right. Convention: target position, negative corresponds to left of the participant's straight ahead; intensity difference, negative corresponds to higher sound pressure level in the left ear. A linear regression line through the data provides a calibration number of 0.098dB/deg. Although participants were highly reliable in their judgments (see standard error bars), the task of lining up sounds heard within the head with external lights involves some assumptions (see text).

amplifier (Nikko STA-8080) and presented through stereo headphones (Pioneer SE 80A). The auditory stimulus was a series of square-wave windowed 1 kHz, 15-ms sounds separated by 150 ms during target presentation and 230 ms during adjustment. When the sound pressure level was equal in the two ears, the sound played at 58 dB. To move the apparent position of the sound, the left-to-right sound pressure ratio was adjusted by pressing left or right buttons. The sound pressure level was increased in the left or right ear, respectively, in 0.1-dB steps and simultaneously decreased in the other ear by the same amount.

This dichotic auditory stimulus in which the only difference in the sounds to the two ears is the sound pressure level, is heard as a sound *inside* the head (lateralized). We were anxious to use headphones to present our stimuli so that we could be sure that any changes we found were not due to changes in position between the head and any external sound source and reflective surfaces.

Auditory target eccentricities were calibrated by adjusting the interaural sound pressure difference expressed in dB [(-20 log (sound pressure level $_{\text{Left Ear}}$ /sound pressure level $_{\text{Right Ear}}$)] to align sounds with lights presented at 0°, 30° and 60° to the left or right. Participants were instructed to "move the sound until it best aligns with the target light." The calibration is presented in Figure 2. The average slope between interaural sound pressure level difference and target position was 0.1 dB/deg ($p < 0.0001$).

Even though the participants could consistently perform these matches, as indicated by the small standard errors, the calibration values should be interpreted with caution because participants were asked to associate a sound that was heard "inside the head" with position in external space. Auditory directions obtained this way might not exactly correspond to the specified external directions and therefore the results of these experiments have been reported only in dB.

*Controlling eye, head, and body position.* Participants were asked to look at fixation points that remained on for the duration of the trial. Fixation can be kept within 2 degrees of a target position in the dark (Skavenski, 1971), and with much higher accuracy when the target is visible (Barlow, 1952; Steinman & Haddad, 1973). Since preliminary experiments found no effect of even large changes of eye position on sound localization (see Figure 4), we deemed it unnecessary to measure eye position. Even if participants had been highly inaccurate with their fixation, it would have had no effect on their ability to do the task.

Head position was controlled by having participants point a laser that was firmly attached to the brim of a tightly fitting baseball hat, at a target. Participants could see both the target and the laser spot, and their task was merely to line them up. This they were able to do within the diameter of the LED target (about 0.25°).

Body position was controlled in a manner similar to the head by having participants point a laser that was attached to their trunk, at a target. The laser was mounted on an angled plate that was snugly strapped around the participant's chest. To move their body, participants sat on a rotating chair and pushed themselves round with their feet with their head kept either earth or body stable. To keep it earth stable, the head was strapped to an earth-stationary headrest by means of a tightly fitting band around the forehead. To keep the head body stable, participants wore a modified cranial collar.

Targets for the eyes, head, and body were LEDs mounted on a metal half-hoop of radius 57 cm at eye level in the azimuthal plane. Thirteen yellow LEDs were arranged at 15°, 30°, 40°, 60°, 80°, and 90° to the left and right of a central yellow LED straight ahead of the participant. Two additional red LEDs were mounted 7.5° to the left and right of the centre. They were used to indicate the direction when large head or body displacements were required where the target LED might be too far eccentric to be detected comfortably.

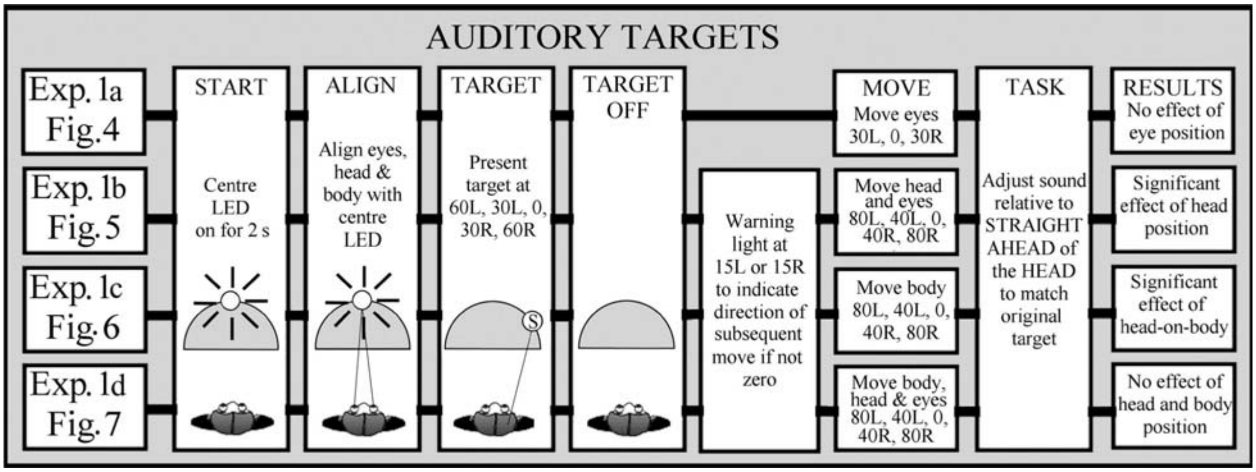


*Figure 3.* Timelines for the procedures for auditory experiments. Time goes from left to right. The auditory target (S) was presented through headphones and was heard as a sound INSIDE the head (lateralized). The numbers represent degrees of eccentricity defined relative to the central LED.

*Experimental procedure.* The experimental procedure was similar for all the experiments presented in this paper and is summarized in Figure 3. To start the trials, the centre LED was illuminated for two seconds and participants aligned their eyes, head, and body with this light. The laser was then extinguished and, while the eye, head, and body were thus aligned, participants were presented with an auditory lateralized stimulus. Intracranial auditory targets were chosen that had interaural sound intensity differences that had previously been judged as corresponding to 60° left, 30° left, central, 30° right or 60° right (see calibration). The target was turned off by the participants when they felt that they had determined its position, which usually took about 4 s. Participants then moved their eyes (Experiment 1a), eyes and head (Experiment 1b), body (Experiment 1c) or eyes, head, and body (Experiment 1d) to particular eccentricities guided by LEDs (eyes: 30° left to 30° right; head and body: 80° left to 80° right; see Figure 3). They were allowed 6 s to position their eyes, head, and body, and then another auditory stimulus was turned on at a random position either to the left or right of the original target position. Participants moved this stimulus to the perceived position *relative to their head* of the original stimulus using the button box described above (see Appendix 1).

There were 60 trials in Experiment 1a: three eye positions, five target positions, two starting positions, and each condition was repeated, in a separate session, with a reversed button box. Experiments 1b, 1c, and 1d had 100 trials each comprising five head or body positions. Each experiment lasted approximately 20-30 minutes and participants completed all the experiments in two experimental sessions run on different days. The experiments were presented in random order.

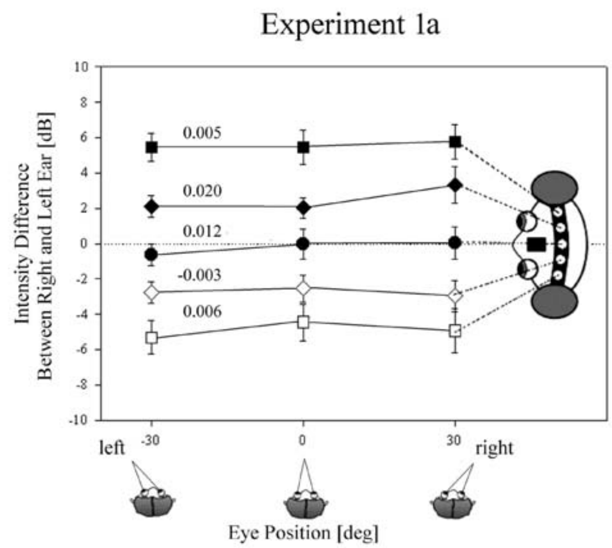


*Figure 4.* No effect of eye position on auditory localization. Graphs show means and standard errors of interaural sound pressure level differences (vertical axis) between right and left ear (+ve = right louder) as a function of eye position (horizontal axis) when participants were asked to adjust the sound until its perceived position matched the position of a remembered sound. Eyes were positioned straight ahead during target presentation, and eccentrically during sound adjustment. Symbols as in Figure 3. Numbers by each graph are the slopes of the regression line in dB/deg; none was significantly different from a horizontal line (see text).

RESULTS

*Experiment 1a. The effect of eye position on auditory localization.* While looking straight ahead, participants were presented with an auditory lateralized stimulus at one of five interaural sound pressure level differences. They then moved their eyes to fixate an LED at either

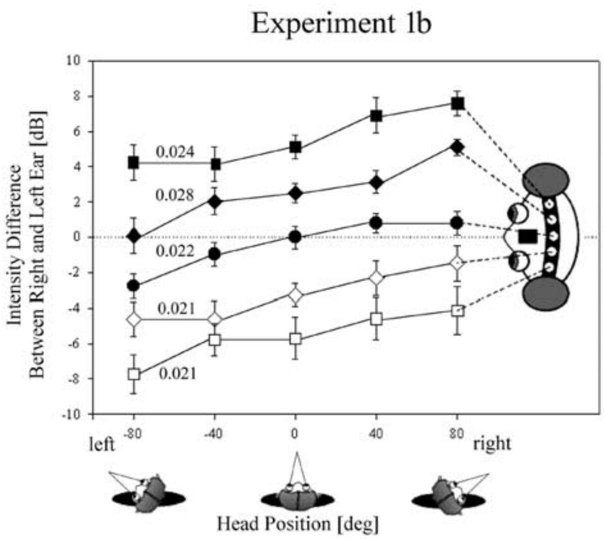


*Figure 5.* The effect of head position on auditory localization. Graphs show means and standard errors of interaural sound pressure level differences between right and left ear as a function of head position when participants were asked to adjust the sound to match the position of a remembered sound. Head pointed straight ahead during target presentation and eccentrically, guided by LEDs, during sound adjustment. Conventions as for Figure 4. Numbers by each graph are the slopes of the regression line in dB/deg. They are all significantly different from zero (see text). The average slope of these graphs is 0.023 dB/deg.

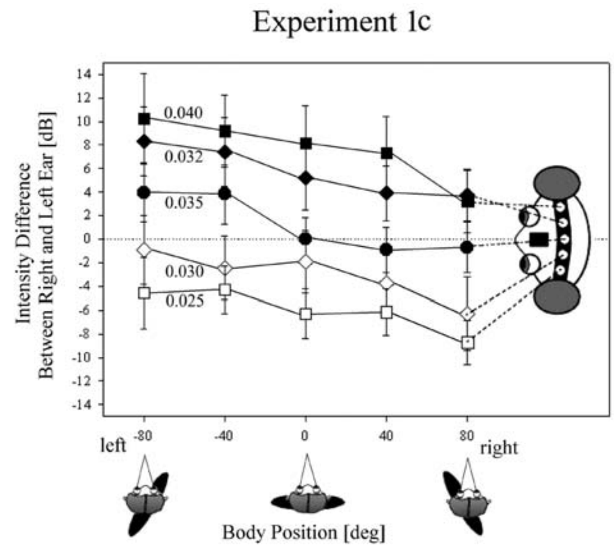


*Figure 6.* The effect of body-under-head position on auditory localization. Graphs show means and standard errors of the interaural sound pressure level differences between right and left ear as a function of body position when participants were asked to adjust the sound to match position of a remembered sound. Body was straight during target presentation and eccentric during sound adjustment. Head was always fixed with respect to space. The average slope of these graphs is 0.032 dB/deg. Conventions as for Figure 4. Numbers by each graph are the slopes of the regression line in dB/deg.

30° to the left or to the right. In the control condition they remained looking straight ahead. Participants then adjusted the interaural sound pressure level difference of a sound to match the original target position. Figure 4 shows that participants' performance was not affected by eye position, $F(2, 14) = 1.60$, nonsignificant. The slopes between eye position and interaural sound pressure level ratios were not different from zero. The interaction effect of eye and target position was also not significant, $F(8, 56) = 1.18$, nonsignificant. Since we did not measure eye position, it is possible that fixations were not accurate.

*Experiment 1b. The effect of head-on-body position on auditory localization: Body stable in space, head eccentric.* The effect of an intervening head-on-body displacement on the perceived location of the same remembered auditory lateralized targets as were used in Experiment 1a, is shown in Figure 5. There was a systematic error in the remembered sound position relative to the head (60° left to 60° right) related to the head displacement (80° left to 80° right), $F(4, 28) = 28.41$, $p < 0.0001$. The interaction effect of head and target position was not significant, $F(16, 112) = 1.77$, nonsignificant.

Slopes for each auditory target are shown in Figure 5. As indicated by t-tests for regression slope being different from zero, all of the slopes were significant ($p < 0.05$) confirming a systematic effect of head position. The overall average slope was 0.023 dB/deg ($p < 0.0001$).

It is important to interpret the direction of this slope correctly. If participants were performing ideally then there would be no effect of head position at all, since they were supposed to line up the targets to the same position relative to the head. However, when the head was rotated to the left, for example, participants needed to adjust the sound level higher in their left ears (ipsilateral to the head displacement) than they did when the head was not moved in order to match the position of the remembered targets. A sound with an interaural sound pressure level difference that was previously judged equivalent to the remembered target when the head was aligned on the trunk would now suffer an illusory shift to the right of that position when the head was to the left and thus require a nulling shift to the left. The difference between the sound pressure level differences required when the head was straight ahead and the difference needed when the head was displaced represents the sound pressure level difference needed to null the illusory shift.

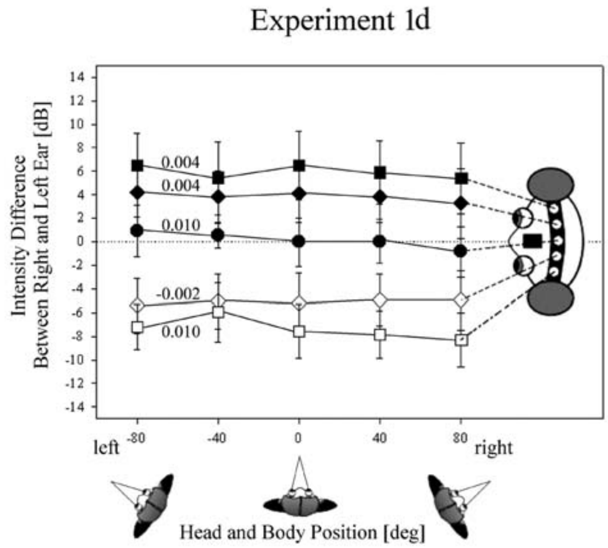


*Figure 7.* No effect of whole body position on auditory localization. Graphs show means and standard errors of interaural sound pressure level differences between right and left ear as a function of body position (with the head fixed on the body) when participants were asked to adjust the sound to match position of a remembered sound. The body was straight during target presentation and eccentric during sound adjustment. Head was fixed with respect to the body. Conventions as for Figure 4. Numbers by each graph are the slopes in dB/deg.

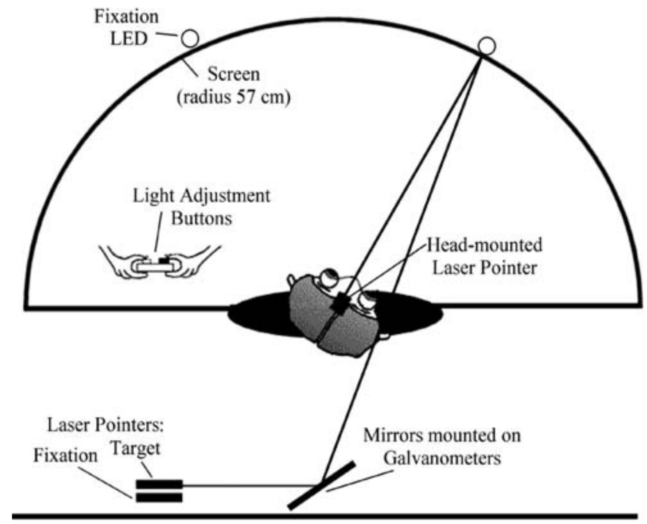


*Figure 8.* Visual experimental setup. By means on buttons, participants adjusted the angle of a mirror mounted on a galvanometer to direct a laser beam to point at a remembered light position. Eye and head position were controlled as for the auditory experiments.

*Experiment 1c. The effect of head-on-body position on auditory localization: Head stable in space, body eccentric.* When the head moved on the trunk in Experiment 1b, it changed position relative both to the body and to external space. Experiment 1c measured which aspect of the movement was significant by keeping the head movement relative to the body the same, while removing the head's displacement in space. In-between the presentation of the target and aligning a new sound with the remembered position, participants kept their heads still (restrained as described in the methods) and rotated only their bodies. Thus the relative position of body and head were the same as in Experiment 1b but head position in space was unchanged. The task was defined in a head reference frame: Participants were asked to adjust the sound to match the remembered sound with respect to their heads.

The effect of eccentric head position on the body while maintaining a constant head position in space is plotted in Figure 6.

There was a systematic error in the sound adjustments to the remembered target-sound position, $F(4, 28) = 0.032$, $p < 0.0005$, related now to the eccentricity of the body-under-the-head position. The interaction effect of body and target position was not significant, $F(16, 112) = 0.259$, nonsignificant. Slopes for each auditory lateralized target are shown in Figure 6. As indicated by t-tests for regression slopes being different from zero, all of these slopes were significant ($p < 0.05$). The overall slope was 0.032 dB/deg ($p < 0.005$).

These data show that when the body was rotated to the right side (corresponding to a leftward displacement of the head relative to the body), there was a perceived shift of auditory target location (judged with respect to the head) to the right, requiring a nulling shift to the left. This perceptual shift is thus in the same direction, relative to the head, as for the head-on-trunk movements of Experiment 1b.

*Experiment 1d. The effect of body position on auditory localization: Head fixed with respect to body, both eccentric.* To see whether shifts of the body-in-space contributed to the perceived shifts of auditory target locations found in Experiments 1b and 1c, we measured the location of remembered auditory targets after the head and body both moved together relative to space. The head was stabilized with respect to the body as described in the Method. The task was defined in a head reference frame: Participants were asked to adjust the sound to match the remembered sound with respect to their heads.

The effect of rotating the body and head together in space are shown in Figure 7. For each of the five auditory targets presented, there was no consistent effect of body position on the interaural sound pressure level difference that was matched with the remembered target position, $F(4, 28) = 0.59$, nonsignificant. The interaction effect of body and target position was also not significant, $F(16, 112) = 0.53$, nonsignificant).

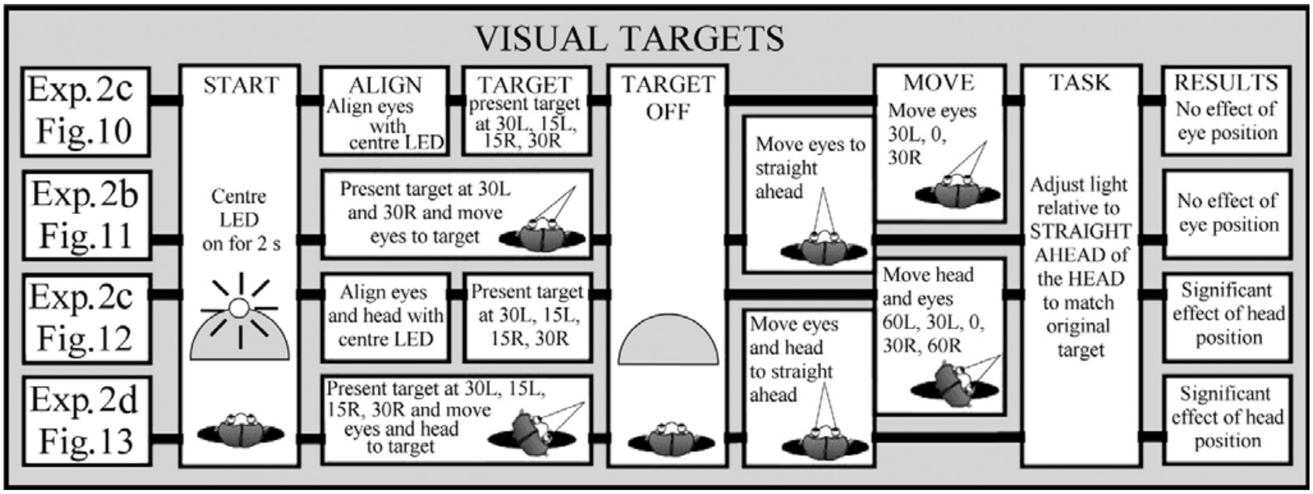


*Figure 9.* Timelines for the procedures for visual experiments. Time goes from left to right. The numbers represent degrees of eccentricity defined relative to the central LED.

### Experiment 2: Visual Localization

METHOD

*Overview.* Experiment 2 used the same principles as Experiment 1 but for visual targets. Participants were presented with a reflected laser beam light target (eyes centred, target in periphery) and were asked to remember its position. They were then asked to move their eyes (Experiment 2a), or head and eyes (Experiment 2c) before repositioning the light to its previously seen location relative to the head. To control for the effects of eccentric viewing, these experiments were repeated with the participant looking at the target during the initial presentation (eyes eccentric, target on fovea) and then returned their eyes (Experiment 2b) or eyes and head (Experiment 2d) to the centre before adjusting the pointing light.

*Participants.* Eight participants (aged 21-42 years) took part in Experiments 2a and 2c, and 10 in Experiments 2b and 2d.

*Visual stimulus presentation apparatus.* The visual stimuli were 0.08° radius dots from laser pointers reflected off mirrors mounted on galvanometers onto a 57-cm-radius hemispherical screen, illustrated in Figure 8. The laser beams were dimmed for safety reasons by passing the laser light through layers of exposed film. Participants sat with their eyes at the geometric centre of the hemisphere. Two 0.18° radius LEDs positioned at 30° to the left and right from the centre, viewed through the translucent screen, served as fixation points (Experiment 2a).

The laser dots could be moved incrementally in 0.3° steps by pressing left and right buttons. When a button was held down continuously, the dot moved at 3 deg/s; if it was held down for more than 0.3 s, the dot speeded up to 30 deg/s.

*Controlling eye and head position.* Eye and head position were controlled as in Experiment 1.

*Experimental procedure.* The experimental procedure was similar for visual and auditory experiments (see Figure 9). Each trial was initiated by a 2 s presentation of the "laser dot" straight in front of the participant. Participants were instructed to align their eyes and heads with the straight-ahead light by pointing the laser-on-hat at the light. The laser dot was then extinguished and participants were then presented with the target. Visual targets were at 60°L, 30°L, 15°L, 0°, 15°R, 30°R, 60°R but not all targets were used for all experiments. The targets were presented for 6 s while the eye and head were aligned straight ahead (Experiments 2a and 2c) or with the eyes (Experiment 2b) or eyes and heads (Experiment 2d) pointing at the targets. The targets were then extinguished and the participants moved their eyes (Experiment 2a) or their eyes and head (Experiment 2c) to particular eccentricities (eyes: 30°L-30°R; head: 60°L-60°R; see Figure 9) as indicated by the lights presented for 6 s. For Experiments 2b and 2d, they returned to the straight-ahead position during this phase. Participants then aligned a visual stimulus to the position of the original stimulus making their alignments so that the target was in the same position relative to the head (not space). The instructions given to the participants are listed in Appendix 2. There were 64 trials in Experiments 2a, 2c, and 2d and 32 in Experiment 2b. Each experiment lasted approximately 20-30 minutes, and participants completed all the experiments in two experimental sessions run on dif-

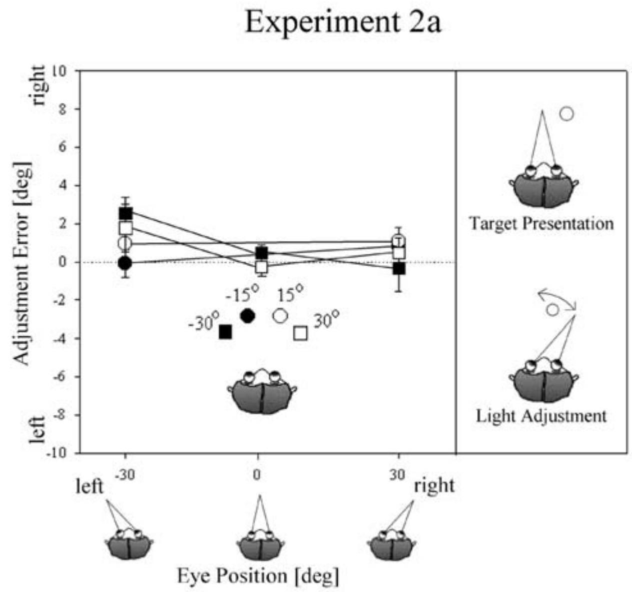


*Figure 10.* No effect of eye position on visual localization. Graphs show means and standard errors of light adjustment errors as a function of eye position when participants were asked to adjust the light to match the position of a remembered light. Eyes were straight ahead during target presentation (illustrated in the top insert on right) and eccentric during light adjustment (bottom insert on right). Target lights were presented at 15° (open circles), and 30° (open squares) to the left and right (filled symbols) with respect to the participants' straight ahead.

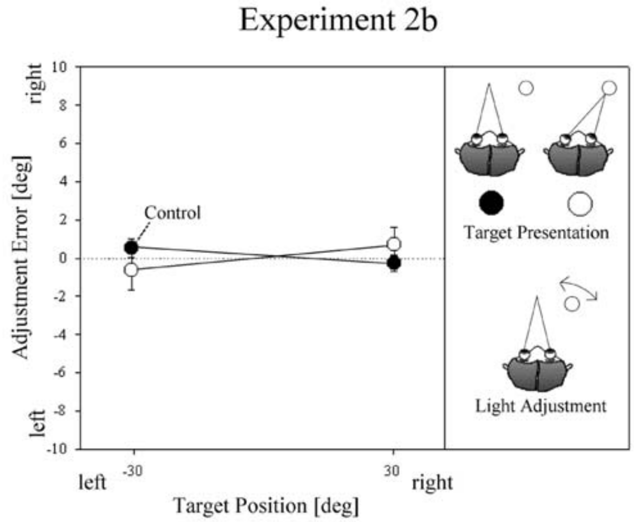


*Figure 11.* No effect of eye position on visual localization: controlling for target eccentricity. Graphs show means and standard errors of light adjustment errors as a function of target position when participants were asked to position a light to match the position of a remembered light. Eyes were either straight ahead during target presentation (filled circles; control condition) or eccentric (open circles; illustrated in top insert on the right) and straight ahead during light adjustment (bottom insert). Target lights were presented at 30° to the left or right with respect to the participants' straight ahead.

ferent days. The experiments were presented in random order.

RESULTS

*Experiment 2a and 2b: The effect of eye position on visual localization.* Experiments 2a and 2b measured how well participants took into account eye eccentricity in judging the localization of a visual target. In Experiment 2a, participants looked straight ahead while targets were presented at various eccentricities (15 and 30° to the left or right from straight ahead). They then moved their eyes and positioned a laser spot at the remembered location. This experiment therefore exactly matches Experiment 1a. In Experiment 2b, participants looked at the eccentric target whose location they were trying to remember and returned their eyes to the straight-ahead position before aligning a laser to the remembered location. Thus they needed to use ocular eccentricity to represent the position of the target in space, or relative to the head, correctly. Control trials measured the ability to localize a remembered light without an intervening eye movement.

Adjustment errors (the difference between actual visual target positions and the position indicated by the participant) are plotted in Figure 10 as a function of the amount the eye moved in-between viewing the target (straight ahead) and setting the pointer light to match its remembered position. Eye movement estimates are approximate since we did not measure eye movement but only asked participants to fixate the position. Figure 11 plots adjustment errors against target position when participants looked at the initial target and then moved their eyes to the centre before setting the pointer light to indicate its previous position. No consistent errors were seen in any of the tested conditions: Eye position was taken accurately into account and there were no significant effects of eye position on the accuracy of the visual location adjustments (Experiment 2a: $F(1, 7) = .45$, nonsignificant; Experiment 2b: $F(1, 9) = 1.82$, nonsignificant).

*Experiments 2c and 2d: The effect of head position on visual localization.* Experiments 2c and 2d measured the effect of different eccentricities of head position on the perceived location of remembered visual targets. Experiments 2c and 2d were divided as in Experiments 2a and 2b, with the targets delivered while the eyes and head were straight ahead in Experiment 2c and with the eyes and head aligned with the target in Experiment 2d. For Experiment 2c, they moved their

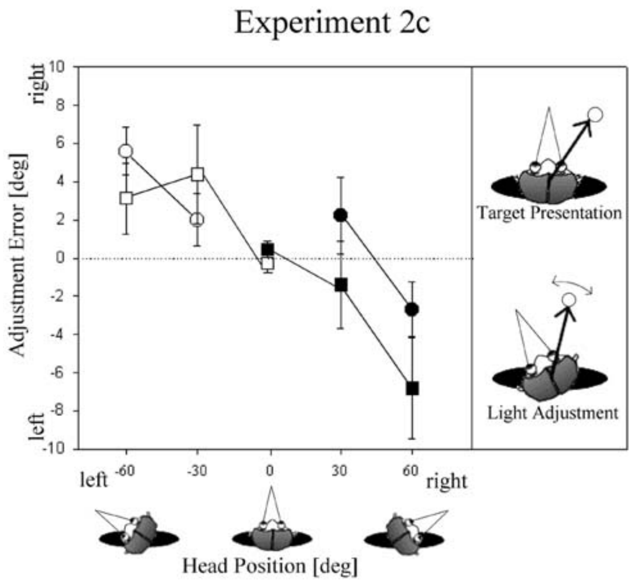


*Figure 12.* The effect of head position on visual localization. Graphs show means and standard errors of light adjustment errors as a function of head position when participants were asked to adjust the light to match the position of a remembered light with respect to their heads. Head was straight during target presentation (top insert on right), and eccentric during light adjustment (bottom insert). Target lights were presented at 15° (circles) and 30° (squares) to the left (open symbols) and right (filled symbols) with respect to the participants' straight ahead. The average slope was 0.068 deg/deg.

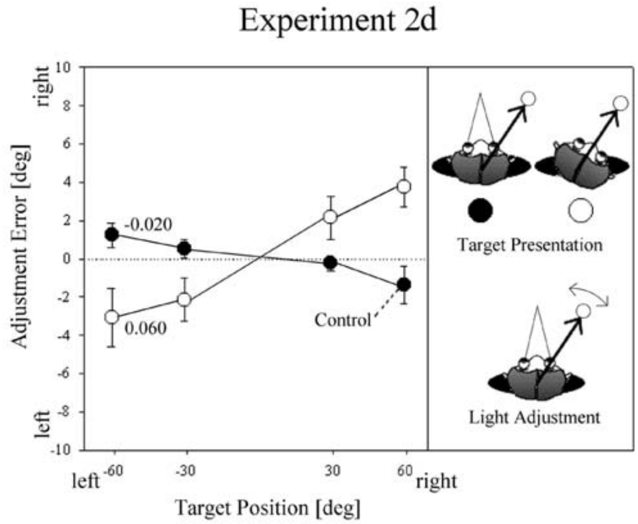


*Figure 13.* The effect of head position on visual localization: controlling for target eccentricity. Graphs show means and standard errors of light adjustment errors as a function of target position when participants were asked to adjust the light to match the position of a remembered light. Head was either straight (filled circles) or eccentric (open circles) during target presentation (top insert on right) and straight ahead with respect to the body during light adjustment (bottom insert). Target lights were presented at 30° and 60° to the left and right with respect to the participants' straight ahead. Numbers by each graph are the slopes of the regression line in deg/deg; the average slope was 0.06 deg/degs.

eyes and head to eccentric positions before moving a laser to indicate the remembered location whereas in Experiment 2d, they returned to straight ahead. In Experiment 2c, the correct strategy was to ignore head position completely throughout the experiments since participants were always asked to position the lights at the same place relative to the head. Thus a light that had been presented 15° left should be positioned after a 15° leftward head movement at 30° left on the screen, keeping its original 15° eccentricity relative to the head.

Far from being able to ignore their head position, Figure 12 shows that participants made localization errors as a function of head eccentricity when they remembered the target location relative to their heads (Experiment 2c).

There was a significant effect of head position on the accuracy of where participants positioned the indicator light, $F(2, 14) = 4.91$, $p < .025$. The slope between the relocation error and head position was -0.068 deg/deg. Head displacement was associated with participants displacing the laser in the opposite direction. If the head was displaced, for example, to the left, visual targets suffered an illusory shift to the left and required participants to add a shift to the right to compensate. This is opposite to the perceptual shift of dichotically presented sounds with head displacement found in Experiment 1.

Localizing the visual targets in Experiment 2d required participants to know about their head eccentricity since they viewed the target with their head pointing straight at it (confirmed by the laser pointer mounted on participants' heads). They then returned their head and eyes to the straight-ahead position before indicating where the target had been. Thus a light that had been presented 15° left and associated with a 15° leftward head movement should be positioned at 15° left (relative to both head and space) after the head and eyes have been returned to straight ahead. In a control condition, visual targets were presented eccentrically and participants aligned the laser to their remembered location with no intervening head movement (Figure 13; filled circles). Figure 13 (open circles) shows the error in participants' ability to do this task as a function of head eccentricity (and thus target eccentricity). There was a significant effect of head position on the accuracy of the light adjustments, $F(3, 27) = 8.77$, $p < .0001$. The slope between adjustment error and target position was 0.060 deg/deg ($p < 0.0001$).

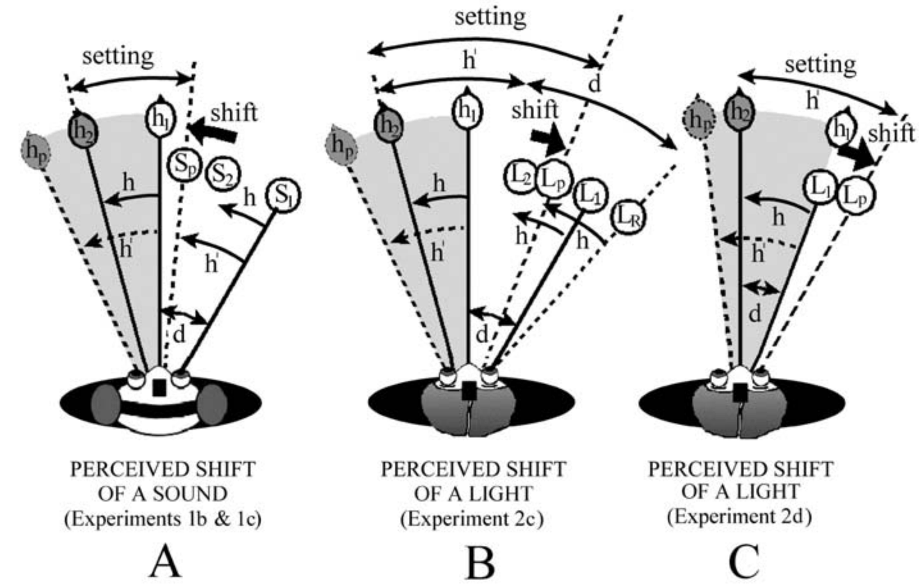


*Figure 14.* Explanation of perceived shifts of lights and sounds based on an overestimation of the intervening head shift. When the head moves from $h_1$ to $h_2$ by amount h we hypothesize that the internal representation $h^I$ is larger than the actual movement (shaded area; see text for details of this hypothesis) even though the head is perceived to have moved the correct amount (h). (**A**) An internal representation of a sound ($S_1$) is moved by this too-large amount $h^I$ to a position $S_p$ beyond its veridical position $S_2$. Settings are therefore displaced in the direction of head movement. (**B**) Constructing the remembered position ($L_R$) of a light ($L_1$) relative to the body requires adding the internal representation of head movement ($h^I$) to the original displacement (d). If the internal representation ($h^I$) is larger than the actual movement (h) then the remembered position of the target ($L_R$) will be further away than the correct position ($L_1$), i.e. displaced in the opposite direction to the head movement. Displacing this remembered location by the perceived amount of the head movement (h) to the perceived position of the target ($L_p$) thus results in a shift opposite to the head movement relative to the correct position ($L_2$). (**C**) To estimate the perceived position of a target ($L_p$) that was presented with the head eccentric and aligned with the target ($h_1$= $L_1$), after the head has returned to the central position, requires an internal representation of the magnitude of the returning head movement ($h^I$). If the internal representation of this head movement ($h^I$) is larger than the actual value (h) then the perceived position of the target ($L_p$) will be shifted accordingly.

When the head was displaced when viewing the target and then returned (rightwards) to the centre before judging its position, errors were made in the same direction (Figure 13; open circles). This shift is in the same direction as seen in Experiment 2c and is opposite to the shifts in auditory localization found in Experiment 1.

Curiously, when no head movement at all intervened between target presentation, indicating its location, a small but significant shift was also seen (Figure 13; filled circles; -0.020 deg/deg ($p < 0.005$) but in the opposite direction. That is, a target on the left was judged as being to the right of where it had actually appeared. These measurements taken with no intervening head movement suggest that between the presentation and relocalizing of a target (about 8 s), the memory of the target location drifted by about 2% towards the straight ahead (cf. Sheth & Shimojo, 2001).

## Discussion

This study has shown that the remembered location of lateralized sounds and visual targets are displaced from their correct angular directions relative to the head as a result of the head being in eccentric position with respect to the body but not when the eyes move in the head or the body moves in space.

When the head was actively turned to one side in the dark, the perceived location of remembered auditory lateralized targets shifted in the same direction by approximately 23% (0.023 dB/deg) of the head turn

(Figure 6). The percentage was obtained using the calibration procedure described in the methods for converting internally heard sounds to external directions. This shift related to head-on-body position indicates that participants were using head-on-body information in their judgments. Head-on-body information is needed to convert information from a head frame to a body frame, a reference frame conversion which is not required if the location of the sound were stored relative to the head since all judgments were made relative to the head. Furthermore, the head-on-body information that the participants were using was inaccurate: The amount of head displacement was overestimated. When the same displacement of the head on the shoulders was achieved by keeping the head still in space and moving the body (under the participants' control), the error was even larger: 32% (0.032 dB/deg; Figure 7). The amplitude of an active head turn is accompanied by vestibular and neck sensory cues and a sense of effort (efference copy). Moving the body beneath an earth-stationary head by pushing a rotating chair around with the feet is accompanied by sensory cues from the neck but no vestibular cues and the sense of effort is associated with the feet rather than the neck. Greater errors in knowledge of head-on-body position were found when the head's position was monitored by this combination of cues.

The remembered location of visual targets was also displaced during a head movement but by a smaller amount (6%, 0.06 degs/deg; Figures 12 & 13) and in the same direction as the head movement.

### FRAMES OF REFERENCE

We postulate an explanation for these findings based on the creation of an internal representation of target locations relative to the body using inaccurately processed head-on-body information. When the head moves under the conditions of these experiments, we hypothesize that the internal representation of the displacement is larger than the actual movement even though the head is perceived to have moved through the correct amount specified in this case by the distance between LEDs. This suggestion is supported by direct measures of perceived head position (Becker & Saglam, 2001), which find an overestimation of head position of between 6 and 18%. Thus if the head is requested to move through 15°, participants can do this and know that they have done it accurately because of feedback – they can see the position of their head-mounted laser. However, the movement feels curiously unnatural. Normal gaze shifts are only partly achieved by a head movement, the short-fall being made up by an eccentric eye position of about 10-15% of the total shift (Becker & Saglam, 2001; Biguer et al., 1984; Gresty, 1974; Kopinska & Harris, 1998; Stahl, 1999; Zambarbieri et al., 1997). When the gaze change is made up entirely by a head movement – leaving the eyes centred in their orbits – we postulate that this results in too large an internal estimate of the head movements' magnitude connected to this unusual situation. When making spatial judgments, the internal representation of a sound is then moved by this too-large amount to a position that is beyond its veridical position. Settings are therefore displaced in the direction of head movement. This is illustrated diagrammatically in Figure 14a. The larger shift found when the head was stationary in space (Experiment 1c, 32%) compared to when it was moving (Experiment 1b, 23%) suggests that vestibular information might contribute to registering the head displacement. If the neck muscles are stimulated alone, illusory motion of a visual target is created (Biguer et al., 1988; Roll et al., 1991; Taylor & McCloskey, 1991), suggesting that vestibular and neck cues combine to create the normal veridical perception of head position in space (see also Mergner et al., 2001). However, when the head and body were moved together in space (Experiment 1d) no perceptual shift was seen (Figure 9).

When storing the remembered position of a visual target in a body frame of reference, an internal representation of the head's position ($h^I$) has to be added to the eccentricity of the target (Figure 14b). If the added internal representation is larger than the actual head displacement then the target will be remembered as being at a larger eccentricity that its correct position (i.e., displaced in the opposite direction to the head movement; Figure 14b and 14c). Our task needed judgments relative to the position of the head. Therefore the internal representation of the target needed to be displaced by the perceived distance of the head movement. Any error in the original target's representation would thus persist when judging the target relative to the head.

The lack of eye-position related errors during the sound and light adjustments does not on its own allow us to exclude the possibility that eye position information is used in the coding of visual and auditory location. Eye position information must be used to make any visual judgments relative to any nonvisual reference such as the head or body. However, if eye position were accurately taken into account no errors would be expected. Accurate eye position knowledge has been confirmed by experiments judging the position of objects in space after eye movements (Mergner et al., 2001), and by our Experiment 2b in which the target location could only be calculated from a knowledge of eye position since targets were always presented on the fovea.

The existence of head-on-body related errors during both visual and auditory localization suggests that head-on-body information is needed for coding spatial location, and implies either a body- or space-centred frame of reference since head-on-body information is not required to perform our tasks if stimuli were coded in retinal or head coordinates. We found no errors in auditory localization related to head-in-space position when the head was stabilized with respect to the body (Figure 9) which suggests a body-centred rather than space-centred frame for coding auditory and visual space. The suggestion that auditory and visual space is coded relative to the body is compatible with emerging studies in object localization (Goossens & Van Opstal, 1999) and philosophy (Thompson & Varela, 2001) stressing the role of the body as a reference.

### HEAD POSITION AND AUDITORY LATERALIZATION

The dependence of auditory localization on perceived head position has been reported before (e.g., Goossens & Van Opstal, 1999; Karrer & Davidon, 1967; Lackner, 1973a; Lewald & Ehrenstein, 1998b; Lewald et al., 1999; Lewald et al., 2000). Although the direction of our shifts is the same, the magnitude of the shift of the remembered location of auditory targets during head displacement that we report here is rather larger than the 3-5% shift reported by Lackner (1973a) or the 3.6% reported by Lewald et al. (2000). Caution must be used comparing our intracranial perceptual shifts to external magnitudes. A difference between these experiments and ours is that in our study remembered positions of target locations were indicated relative to the head whereas Lackner (1973a) and Lewald et al. (2000) measured the perceived location only of the auditory midline. When we used our auditory stimulus to indicate the location of the perceived auditory midline, the magnitude of the shift was in the same direction as reported here but approximately 8% of the head shift (Harris et al., 1997; Harris et al., 1998; Kopinska & Harris, 1998; Lackner, 1973a). Comalli and Altshuler (1973) found no shift but their resolution was too low even to see effects of the magnitude we report here.

### HEAD POSITION AND VISUAL LOCALIZATION

In our study, participants underestimated target eccentricity by between 6 and 7% of the head eccentricity when judgments were made with respect to the head. Similar shifts have been described using hand pointing (Lewald & Ehrenstein, 2000) or gaze changes (Zambarbieri et al., 1997) to the remembered spatial locations of visual targets. These reported shifts contrast with accurate performance when the position of remembered visual targets is indicated by relocating targets in space (Mergner et al., 2001). All these observations are compatible with a body-referenced memory of visual locations that does not need a head-on-body signal to transform information from a body to a spatial position.

### EYE POSITION AND AUDITORY LATERALIZATION

If the head-related errors we found arise from a reference frame conversion of auditory information into a body-centred reference system, it is not surprising that we found no errors associated with eye position. Eye-position related errors imply conversion into a retinal reference frame. It seems unlikely that localization information would be stored in both retinal and body frames for this perceptual task.

The search for errors in auditory localization related to eye position has had a long and inconclusive history. Early reports (Goldstein & Rosenthal-Viet, 1926; Pierce, 1901) are largely anecdotal. Studies are often hard to interpret because of the multiple steps involved in assessing perceived auditory location, each one of which can potentially by affected by eye position (Rossetti et al., 1994) and many or all of which are vulnerable to adaptation. Pointing with a hand or laser to a location in space (Lewald & Ehrenstein, 1998a), for example, involves different steps from moving a sound to a position relative to the head. Using headphones Lewald and Ehrenstein (1996) reported a perceived shift of the auditory midline in the direction of eye displacement but Lackner (1973b) found no such effect. Free-field sound studies (Bohlander, 1984; Lewald, 1997; Ryan & Schehr, 1941) have shown substantial variability with some participants showing a shift of perceived sounds in the direction of eye eccentricity, others in the opposite direction, and still others showing no effect of eye position at all.

We postulate that apparent eye position effects could be secondary to a perceived change of head-on-body (or even contribute to it; Lewald & Ehrenstein, 2000) even in the absence of overt head movement. There is emerging evidence that gaze rather than the individual eye and head components is coded by the nervous system (Galiana & Guitton, 1992; Goossens & Van Opstal, 1997). We suggest that maintaining eccentric gaze might, under some circumstances, be interpreted as comprising “normal” eye and head components even in the absence of an actual head displacement (see also Goossens & Van Opstal, 1999). Thus effects might sometimes be seen related to the expected head component of the gaze angle. In the present experiments, the position of the head was entirely under participant control with the participants controlling the head position by aligning their laser even for the eye position experiments.

EYE POSITION AND VISUAL LOCALIZATION

Like Mergner et al. (2001) we found no visual localization effects related to eye position. At first glance this seems strange since many studies have demonstrated eye position information being inaccurately taken into account when performing visual localization tasks (Biguer et al., 1984; Bock, 1986, 1993; Hill, 1972; Lewald, 1998; Morgan, 1978; Prablanc et al., 1979; Rossetti et al., 1994). Interpreting these errors depends critically on the measuring technique (e.g., pointers, Lewald & Ehrenstein, 2000) and whether that is influenced by eye position (which pointing certainly is; O'Regan, 1984; Osaka, 1977; Rossetti et al., 1994) and adaptation effects involving shifts of the perceived midline towards the current gaze position (Lackner, 1973a; Paap & Ebenholtz, 1976). These data, however, when taken in the context of the head position related error in visual localization, are compatible with a body-referenced coding system for visual localization.

CONCLUSION

The systematic errors introduced by moving the head while remembering the location of sounds and lights suggests that head-on-body information is used as part of the localization process. This in turn suggests that sounds and lights are localized with respect to the body, rather than to the head or eyes.

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## Appendix 1

The instructions that were given to the subjects for each of the auditory experiments were as follows. Each consisted of a standard first and last part, with additional instructions, specific to each experiment, in-between.

First part (all)
"Please look at the central yellow LED. After 2 secs the light will go out and you will be played a sound; please remember its location relative to the centre of your head. The sound will repeat until you press either button to stop it and continue. Then.."

Experiment 1a
"...move your eyes to the position indicated by the green LED that comes on."

Experiment 1b
"...the laser on your hat will come on. Please align it (by moving your head) with the green LED that comes on. The red LEDs indicate which way you should go. Continue to look at the green LED."

Experiment 1c
"...the laser on your body will come on. Please align this laser (by moving your body) with the green LED. Move your body by shuffling the chair on which you are seated around with your feet. The red LEDs indicate which way you should go. Return your gaze to the central yellow LED while keeping your body in this orientation."

Experiment 1d
"... the lasers on your hat and body will both come on. Please align them (by moving your head and body) with the green LED that comes on. The red LEDs indicate which way you should go. Rotate your body by shuffling the chair on which you are seated around with your feet. Continue to look at the green LED."

Last part (all)
"While you are looking at this point, please adjust the position of the sound that you will hear so that it has the same position relative to your head as before. Use the buttons. Pressing the left button moves the sound left, pressing the right button moves the sound right. Indicate that you are happy with your positioning by pressing both buttons together, which will start the next trial."

## Appendix 2

The instructions that were given to the subjects for each of the visual experiments were as follows. Each consisted of a standard first and last part, with additional instructions, specific to each experiment, in-between.

First part (all)
"Please look at the central LED. After 2 s the light will go out and you will be shown a red spot; please remember its location relative to the centre of your head. The target light will be on for 6 s."

Experiment 2a
"When it goes out move your eyes to the position indicated by the laser spot that comes on."

Experiment 2b
"Move your eyes to the target light immediately and keep looking at it until it goes out. Then return your gaze to the central LED."

Experiment 2c
"When it goes out, move the laser on your cap to align with a new spot that will come on. Keep looking at this spot."

Experiment 2d
"Your hat laser will be on at the same time. Move the laser on your hat to point at the target. Continue also to look at the target light."

Last part (all)
"While you are looking at this point, please adjust the position of the red target spot so that it has the same position relative to your head as before. Use the buttons. Pressing the left button moves the light left, pressing the right button moves it right. Indicate that you are happy with your positioning by pressing both buttons together, which will start the next trial."