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Reaching to sounds in virtual reality: A multisensory-motor approach to promote adaptation to altered auditory cues

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ABSTRACT

When localising sounds in space the brain relies on internal models that specify the correspondence between the auditory input reaching the ears, initial head-position and coordinates in external space. These models can be updated throughout life, setting the basis for re-learning spatial hearing abilities in adulthood. In addition, strategic behavioural adjustments allow people to quickly adapt to atypical listening situations. Until recently, the potential role of dynamic listening, involving head-movements or reaching to sounds, have remained largely overlooked. Here, we exploited visual virtual reality (VR) and real-time kinematic tracking, to study the role of active multisensory-motor interactions when hearing individuals adapt to altered binaural cues (one ear plugged and muffed). Participants were immersed in a VR scenario showing 17 virtual speakers at ear-level. In each trial, they heard a sound delivered from a real speaker aligned with one of the virtual ones and were instructed to either reach-to-touch the perceived sound source (Reaching group), or read the label associated with the speaker (Naming group). Participants were free to move their heads during the task and received audio-visual feedback on their performance. Most importantly, they performed the task under binaural or monaural listening. Results show that both groups adapt rapidly to monaural listening, improving sound localisation performance across trials and changing their head-movement behaviour. Reaching the sounds induced faster and larger sound localisation improvements, compared to just naming its position. This benefit was linked to progressively wider head-movements to explore auditory space, selectively in the Reaching group. In conclusion, reaching to sounds in an immersive visual VR context proved most effective for adapting to altered binaural listening. Head-movements played an important role in adaptation, pointing to the importance of dynamic listening when implementing training protocols for improving spatial hearing.

KEYWORDS

Dynamic listening, sound localisation, binaural cues, reaching to sounds, head movements.

HIGHLIGHTS

- We studied adaptation to monaural listening when listeners interact with sounds
- Reaching to sounds reduced errors more than just naming the sound sources
- Patterns of spontaneous head-movements changed during adaptation
- Exploration of a wider portion of space with the head was functional for adaptation
- Reaching to sounds promoted a more effective head-related behaviour

1. INTRODUCTION

Spatial hearing is a remarkable ability of the brain. To determine the spatial coordinates of sounds in the environment, the cognitive system exploits auditory cues resulting from the interactions between sound waves, the head and outer ears (Middlebrooks, 2015; Middlebrooks & Green, 1991; Wallach, 1940). Auditory cues are distinguished in binaural cues, which involve a combined computation of the signals reaching the two ears and are used for sound localisation in the horizontal dimension (Rayleigh, 1907), and monaural cues which involve the information available at each single ear and are crucial to localise sound in elevation, depth and anterior-posterior axis (Angell & Fite, 1901). In normal hearing listening condition, both monaural and binaural cues are weighted and combined to achieve optimal localisation of auditory events in the 3D space (Carlile, Martin & McAnally, 2005; see also Shinn-Cunningham, Santarelli, & Kopco, 2000). Auditory cues change during the life span, due anatomical modifications of one's own body during development (Clifton, Gwiazda, Bauer, Clarkson & Held, 1998) or changes in hearing threshold with ageing (Cranford, Andres, Piatz & Reissig, 1993; Dobрева, O'Neill & Paige, 2010). In addition, they change on a daily basis, due to the diversity of listening contexts to which we are all exposed (Majdak, Goupell & Laback, 2010). It is now clear that the brain remains capable to cope with these continuous changes in auditory cues throughout life (e.g., Carlile, Balachandar & Kelly 2014; Keating & King, 2015; Rabini, Altobelli & Pavani, 2019; Strelnikov, Rosito & Barone, 2011; Valzolgher, Campus, Rabini, Gori & Pavani, 2020; Van Wanrooij, John & Opstal, 2005). In the present work, we examined reaching to sounds in virtual reality as a multisensory-motor strategy for adapting sound localisation abilities in adulthood.

Updating of sound-space correspondences typically occurs in a multisensory environment. Whenever the other sensory systems (e.g., vision) provide reliable spatial information about auditory events, the brain exploits these additional sensory sources to calibrate and optimize internal models for spatial hearing (Keating & King, 2015). This notion emerged from studies that examined re-learning of sound-space correspondences when binaural auditory cues were temporarily altered using monaural ear-plugs (Rabini et al., 2019; Strelnikov et al., 2011; Trapeau & Schönwiesner, 2015; Valzolgher et al., 2020;), or monaural auditory cues were modified through ear molds (Van Wanrooij & Van Opstal, 2005) or non-individualised HRTFs (Head-Related Transfer Functions; Hendrickx, Stitt, Messonnier, Lyzwa, Katz & De Boishéraud, 2017; Honda, Shibata, Gyoba, Saitou, Iwaya & Suzuki, 2007; Parseihian, Jouffrais & Katz, 2014; Parseihian & Katz, 2012; Steadman, Kim, Lestang, Goodman & Picinali, 2019; Stitt, Picinali & Katz, 2019). In these

simulated altered-listening conditions, multisensory training procedures proved effective for adapting to novel auditory cues (for reviews see: Carlile, 2014; Keating & King, 2015; Knudsen & Knudsen, 1985; Mendonça, 2014; Irving & Moore, 2011). For instance, Strelnikov and colleagues (2011) studied the effects of audio-visual vs. auditory-only training on sound localisation in monaurally-plugged adults. They found that performance improvements were larger after a training that exploited spatially and temporally congruent audio-visual inputs, compared to a training based on auditory information alone. These findings complement other research in which participants received feedback after their sound localisation response, through audio-visual (Shinn-Cunningham, Durlach, & Held, 1998; Zahorik, Bangayan, Sundareswaran, Wang & Tam, 2006; see also Majdak, Walder & Laback, 2013) or visual cues (Bauer, Matuzsa, Blackmer & Glucksberg, 1966; Kumpik, Kacelnik & King, 2010; Mendonça, Campos, Dias & Santos, 2013). Finally, converging evidence in favour of multisensory-based training emerged from research in ferrets with unilateral and bilateral cochlear implants. Performance in early-deafened ferrets with bilateral cochlear implants improved consistently after a multisensory training that used interleaved auditory and visual stimuli (Isaiah, Vongpaisal, King, & Hartley, 2014).

In natural, off-laboratory conditions, spatial hearing is a dynamic and sensorimotor task. Listeners spontaneously orient their head, eyes and trunk to the auditory source (e.g., when turning to listen to a speaker behind us), or they move their body in the environment to approach the auditory source (e.g., when reaching to grasp the mobile phone ringing on the table). These dynamic and sensorimotor interactions with sound sources are almost ubiquitous in our everyday listening conditions. Head-orienting to sounds is a spontaneous behaviour: it is detected in infants 2-4 days after birth (Muir & Field, 1979) and it follows the shortest path to the sound already between 6 and 9 months of age (van der Meer, Ramstad, & van der Weel, 2008). Although adults have different propensities for head-movement (Fuller, 1992), they can easily orient their head to sounds when required by the task (Brimijoin, McShefferty, & Akeroyd, 2010). Experimental evidence shows that head-movements during listening improve sound localisation (Noble, 1981; Thurlow and Runge, 1967), and head-movement strategies change in altered hearing conditions in the attempt of coping with the hearing difficulty. For instance, Brimijoin and colleagues (2010) showed that people with hearing-impairment have more complex head-movements. Also, people with asymmetrical hearing impairment use head-orienting to maximize the level of a target sentence in their better ear when solving a speech-in-noise task (Brimijoin & Akeroyd, 2012). Yet, studies that examined adaptation to altered auditory cues have typically limited the possibilities for head-movements using a chinrest (Kumpik et al., 2010;

Strelnikov et al., 2011) or by instructing participants to refrain from head-movements during listening (Rabini et al., 2019; Van Wanrooij & Van Opstal, 2005; Zahorik et al., 2006).

However, notable exceptions to the static listening approach have emerged in the last decade. Using gamified scenarios, researchers have asked participants to use a hand-held tool to hit a moving sound presented in virtual auditory space (Honda et al., 2007; Honda et al., 2013; Ohunchi, Iwaya, Suzuki & Minekata, 2005), or to shoot audio-visual moving targets presented in virtual reality (Poirier-Quinot & Katz, 2020). In all these cases participants were free to move their heads and bodies. In more controlled conditions, Parseihian and Katz (2012) studied how people could adapt to non-individualized head-related transfer functions (HRTFs) when localizing virtual sound sources. They explored the effects of a multi-modal training platform in which participants were involved in an active game-like scenario. They actively searched for animal sounds, scanning the space around them (front and back), using a hand-held track-ball. Again, participants were free to move their heads and hands. This training improved vertical localisation performance and reduced front/back confusions, showing that people could rapidly adapt to novel monaural cues. Using an identical training approach, but with longer sessions and with perceptually worst-rated non-individualised HRTFs, Stitt and colleagues (2019) also found evidence for some degree of adaptation. Another recent study (Steadman et al., 2019) combined gamification, virtual reality and free head-movements in a training protocol aimed at ameliorating sound localisation with virtual sounds. These authors also trained participants to adapt to non-individualized HRTFs, hence to new monaural cues. They asked participants to listen to stationary virtual sounds, either with the head static or free to move. Compared to the static listening condition, when the head was free to move sound localisation improved even over a very short timescale, corroborating the importance of head movements when adapting to novel auditory cues.

Despite these studies provide initial evidence in support of a key role of dynamic and sensorimotor interactions with sounds when adapting to altered auditory cues, they did not investigate the qualitative and quantitative nature of the spontaneous head-movements during listening (e.g., head-movement number or amplitude, head-movement strategies). As such, they only provide limited evidence of the role of head-movements in adapting to novel listening conditions. Note that in the head-constrained context, researchers can only examine the cognitive mechanisms of adaptation, such as cue-remapping (i.e., changes in the internal models that specify the correspondence between auditory cues and spatial locations) or cue-reweighting (i.e., changes in the contributions each auditory cue in these internal models). By contrast, the conditions in which the head is free to move are informative about the strategies (implicit or explicit) that

participants use to cope with the altered listening conditions. In addition, although some of the previous literature point to a joint contribution of head-movements and reaching movements in improving sound localization with altered auditory cues (Honda et al., 2007; Honda et al., 2013; Ohunchi, Iwaya, Suzuki & Minekata, 2005; Parseihian & Katz, 2012), several questions remain open. Specifically, are reaching movements relevant in promoting the useful strategies for adapting to altered spatial hearing conditions? Could they trigger different head-movements during sounds compared to alternative and less-interacting responses (e.g., naming labels that identify the speaker position)? Finally, the vast majority of studies that examined the effects of dynamic and sensorimotor interactions with sounds when adapting to novel auditory cues focused on monaural cues. Thus, it remains an open question to what extent head-movements can also allow fast adaptation to altered listening when binaural rather than monaural cues are changed.

In the present study we addressed all these questions by asking two groups of participants to perform a sound localisation task in an interactive visual virtual reality scenario, with real sounds presented within reaching distance. Participants wore a Head-Mounted Display (HMD) and perceived themselves in the centre of an empty virtual room with visible virtual speakers. In each trial, a 3 seconds sound was emitted from a real speaker aligned with one of the visible virtual speakers. All participants were asked to identify from which virtual speaker the sound originated and were informed that they were free to move their head during sound emission to solve the task. Crucially, half of participants were instructed to stop sound emission by reaching to the correct source using a hand-held controller (Reaching group). If the participant reached to the correct speaker the sound stopped, promoting a sense of agency over the auditory change. If instead the participant reached towards the wrong speaker the sound continued playing and the correct speaker started flashing, providing multisensory cues to actual sound location until the participants gave the correct response (see Figure 1B). The other half of participants received identical stimulation and identical feedback but were instructed to stop sound emission by naming the number that identified the active speaker (Naming group).

To examine the role of these two response instructions when adapting to altered spatial hearing conditions we focused specifically on binaural cues alteration, using plugging and muffing of the right ear. Unlike previous related works (Honda et al., 2007; Honda et al., 2013; Ohunchi, Iwaya, Suzuki & Minekata, 2005; Parseihian & Katz, 2012; Stitt, Picinali & Katz, 2019), in our study monaural cues at the unplugged left ear remained unaltered. Instead, we aimed to simulate conductive hearing loss. In terms of auditory cues, our manipulation clearly affected inter-aural level differences (ILD). In addition, because we adopted a slowly

changing broad-band sound we made inter-aural time differences (ITD) largely ineffective (see Methods section).

If reaching to sounds play a role in adaptation to altered binaural cues, performance in the monaural listening condition should improve faster for the Reaching compared to the Naming group. The rationale for this hypothesis is linked to the fact that reaching to sounds requires a coordination of different effectors (eyes, head, hand) into a common reference frame (Cohen & Andersen, 2002). In turn, this may result in a more stable (or salient) spatial coding of sound source location and favour adaptation to altered spatial hearing conditions. In addition, reaching movement may help to direct attention towards the position occupied by the sound source, because of additional visual, proprioceptive and kinaesthetic cues resulting from the action.

2. MATERIAL AND METHODS

2.1. Participants

Twenty-eight participants (age: $M = 20.93$, $SD = 2.48$, range [18-30], 5 males, 14 right-handed in the Reaching Group, 13 right-handed in the Naming Group) were recruited to participate in the experiment, mostly among undergraduate students at the University of Trento. All participants signed an informed consent before starting the experiment, which was conducted according to the criteria of the Declaration of Helsinki (1964, amended in 2013) and approved by the ethical committee at the University of Trento (protocol: 2018-018). All had normal or corrected-to-normal vision, and reported no movement deficit. Hearing threshold was measured using an audiometer (Grason Stadler GSI 17 Audiometer) for all participants, testing different frequencies (250, 500, 1000, 2000, 4000 Hz), on the right and left ear separately. All participants had an average threshold below 11.7 dB HL.

2.2. Apparatus and stimuli

Visual virtual reality (VR) and kinematic tracking was implemented using an HTC Vive System, comprising one head-mounted display (HMD, resolution: 1080 x 1200 px, Field Of View (FOV): 110°, Refresh rate : 90 Hz), 1 controller (which was used by participants to interact with sounds), 1 tracker (which was placed above the speaker to track its position in real time) and 2 lighthouse base stations (which served for regular scanning of the position of the controller and the tracker). Tracking precision and accuracy of the HTC Vive System is adequate for behavioural research purposes, as recently measured by our research group (Verdelet et al., 2019; see also Gaveau et al., 2020). Specifically, the HTC Vive has submillimetre precision (0.237 mm) and near centimetre accuracy (9.0 mm when trackers are static; 9.4 mm when trackers are dynamic). The HMD was equipped with an SMI eye-tracking system (250 Hz). All stimuli were controlled and delivered using a LDLC ZALMAN PC (OS: Windows 10 (10.0.0) 64bit; Graphic card: NVIDIA GeForce GTX 1060 6GB; Processor: Intel Core i7-7700K, Quad-Core 4.2 GHz/4.5 GHz Turbo - Cache 8 Mo - TDP 95W) using Steam VR software and the development platform Unity.

The experiment was entirely run in a 4x3 meters ordinary room almost devoid of furniture, not treated for being anechoic and quiet. The subject sat in the centre of the room, with no constraints for her head (no chin-rest was used). The virtual environment in which participants were immersed was an ordinary squared room (grey wall), similar to the real experimental room. The room was empty and there were not objects on

the walls, except a door which was placed in the back wall. In front of participants 17 visible speakers were positioned at ear level. In each session, subjects wearing the HDM saw themselves in the virtual scenario, sitting 50 cm from the centre of a semicircle of 17 speakers, spanning about $\pm 80^\circ$ of visual angle. Each speaker was marked with a numeric label (from 1 to 17) that changed in each trial. Auditory stimuli were delivered by a real, unseen speaker (JBL GO Black), which was moved by the experimenter and whose position was tracked in space. The auditory stimulus was an amplitude-modulated (4 Hz) white noise bursts (about 60 dB SPL as measured by a Decibel Meter TES1350A placed at ears level).

This solution allowed us the possibility of tracking the position of the tracker (i.e., the real speaker), the controller (handled by the participant) and the Head Mounted Display, via sensors on the headset and VR controllers using IR led positioned on the base stations (frequency sample 250 Hz). We design the software to allow the experimenter to track and align the real loudspeaker (the sound source) with the desired position in the virtual environment (i.e., in correspondence of one of the visible loudspeakers). Specifically, in each experimental trial, the experimenter moved the loudspeaker to the desired position in 3D space, following visual instructions concerning the pre-determined speaker position. These instructions were visible only to the experimenter, and they were delivered using the stimulus visualization monitor placed in the testing room. The monitor provided a bird-eye view of the experimental room and conveyed the pre-determined position of the sound source for that trial and the actual real-time position of the speaker. Using these visual instructions, the experimenter reached for computer-determined position rapidly, keeping the speaker approximately at ear-level. The spanning of about $\pm 80^\circ$ permitted to the experimenter to stand still in front of the participant and move the speaker silently stretching her right or left arms. Although the noise produced by the experimenter were minimal, participants were explicitly informed to pay attention to the target sounds, as any other sound in the room could in fact be deceiving about target sound position. Before starting, the experimenter showed how she can stay to the right of participants while providing sound from the left of participants by stretching her arm of the hand with the speaker. This was a demonstration that background noise could provide erroneous cues and thus discourage their use by participants, which were invited to focus to the specific target sound. Most importantly, pilot work in our laboratory showed that participants cannot reliably point to the speaker if the same placement procedure is used but no target sound is delivered (Gaveau et al., 2020).

To simulate monaural hearing experience, the right ear of each participant was occluded using an ear-plug (3M PP 01 002; attenuation value for high frequencies = 30 dB SPL; attenuation value for medium

frequencies = 24 dB SPL; attenuation value for low frequencies = 22 dB SPL; Single Number Rating = 32 dB SPL; as reported by the manufacturer). In addition, a unilateral ear muff covered the right ear (3M 1445 modified to cover only the right ear; attenuation value for high frequencies = 32 dB SPL; attenuation value for medium frequencies = 29 dB SPL; attenuation value for low frequencies = 23 dB SPL; Single Number Rating = 28 dB SPL; as reported by the manufacturer). The combined use of an ear-plug and muff at the right ear clearly affected ILDs. In addition, by attenuating the intensity of our amplitude-modulated broadband signal to one ear we most likely reduced the available ITD cues. This because we reduced the possibility of comparing the fine structure at low frequency, as well as the amplitude modulation signals that reach the two ears. Thus, we altered both binaural cues while leaving intact the possibility of exploiting monaural cues at the unplugged left ear.

2.3. Procedure

We measured auditory performance during five different blocks, under two different listening conditions: binaural listening (B) and simulated monaural listening (M) in which the left ear was plugged (Figure 1A). In each block, participants performed 51 trials (3 trials for each source) of a sound localization task. First, participants were invited to sit down on a chair and wear the Head Mounted Display (HMD) and to perform an eye-tracker calibration (they had to follow a white dot moving on the screen with eyes). Then, they were immersed in the virtual scenario. Around them, the cylindrical speakers were located at the height of their ears. Participants were instructed that the starting position consisted in gazing at the central speaker (marked with a cross) and refrain from moving their head until the beginning of the sound. The system delivered the sound only when head (HMD) and eyes (tracked) were directed toward the centre. In such a way, we obtained replicable head and eyes posture across trials and participants. As soon as the sound started, participants were free to move their eyes and head as they wanted.

After each block, participants were given breaks and were asked to judge their performance (“How do you judge your performance?” from 1 = really bad to 9 = really good) and their perceived effort during the block (“How much effort (in terms of energy and cognitive resources) did the task require?” from 1 = none to 9 = many). At the end of 5 blocks, participants were invited to complete a questionnaire presented using Google Forms. The questionnaire comprised general questions about personal data (i.e., age, gender), questions to investigate their relationship with sound during life, specific questions to deepen the quality of our VR technology and its ergonomics, a question concerning their strategy to perform the task, two

questions concerning the feeling of being able to switch the sound off (Agency) and 15 items of 2 scales (Focus of Attention and Satisfaction), used typically to measure the engagement in video game-based environments (Figure 2). We adapted these items from the work of Wiebe and colleagues (2013) to make them more suitable for our VR experience. Participants indicated their agreement with each item using a 5-points Likert scale (from 1 = totally disagree to 5 = totally agree).

We divided participants in 2 groups: the Reaching group and the Naming group (Figure 1B). The Reaching group performed the task by moving a controller with their dominant hand to touch the speaker emitting the sound. The Naming group performed the same task by reading aloud the number located above the presumed source speaker (see Fig 1B). If the response was correct, the sound immediately stopped. If the response was wrong, the correct speaker produced a pulsing red light while the sound continued. This provided participants with audio-visual feedback about the correct position of the sound source. Participants either moved the controller in contact with the correct source or named the number of the correct speaker. When the correct speaker was reached (or named) the sound stopped. Importantly, participants were informed that they were free to exploit head-movements while listening to target sounds, without time pressure on their response. Both reaching and naming responses were followed by a brief vibration of the hand-held controller (which was kept in hand also during the naming task). *When participants in the Naming group were tested, a second experimenter in the room promptly registered the responses on the computer. Specifically, the second experimenter pressed a key on an additional VIVE controller to specify whether the response was correct or wrong, and at the end of the trial entered the spoken labels in the computer.*

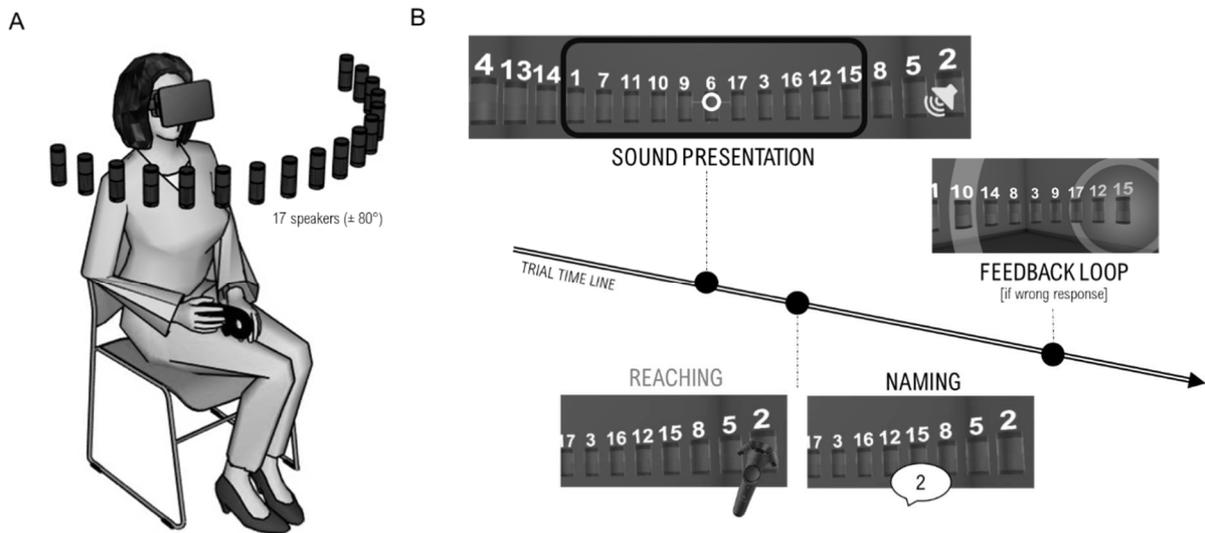


Figure 1. **EXPERIMENTAL PROCEDURE AND SETTING.** (A) Schematic representation of participant and speaker positions. (B) Schematic representation of 1 trial: participants saw the virtual room and part of the speakers' array (the black square represents participants starting view). They were allowed to turn their heads and move their eyes to see all speakers. In the Reaching group, participants stopped the sound by reaching and touching with the controller the virtual speaker emitting the sound. In the Naming group, the sound was stopped by the experimenter when participants read aloud the label above the speaker emitting the sound. If the answer was wrong, the correct source started to flash providing a visual feedback.

Head-movement pre-processing

To study head-movements, we calculated the tangential velocity on the x, y, z axis (expressed in degrees of rotation) using two-points central difference derivate algorithm (Bahill & McDonald, 1983) with 5 points for the half-window. The onset and the end of the movements were computed automatically using a velocity-based threshold (10°/s). Head-movements were checked manually by visualizing the spatial rotation changes of the head and its speed using a home-made tool box in MATLAB R2018b.

3. RESULTS

3.1. Sound localisation performance

3.1.1. Immediate ear-plug effect

To assess the immediate effects of monaural plugging, we compared absolute and signed errors before and after ear-plugging. Absolute and signed errors (calculated in each trial as the absolute or signed difference in degrees between actual and reported azimuth position of the sound, respectively) were entered into separate Analysis of Variance (ANOVA) with TARGET POSITION (17 positions, from -80° to $+80^\circ$) and LISTENING CONDITION (binaural B, monaural M1) as within-participants variables and GROUP (reaching, naming) as between-participants variable. All statistical analyses using the software JASP 0.9.1.0 and R-studio (version 1.0.143).

The analysis on absolute errors revealed a main effect of LISTENING CONDITION, $F(1,26) = 64.79$, $p < .001$, $\eta^2 = .71$, a main effect of TARGET POSITION, $F(3.95, 102.60) = 5.96$, $p < .001$, $\eta^2 = .18$, and the 2-way interaction between LISTENING CONDITION and TARGET POSITION, $F(3.9, 101.51) = 7.36$, $p < .001$, $\eta^2 = .22$. Sound localisation error increased significantly in M1 compared to the B listening condition (see black and light grey lines in Figures 2A and 2B), particularly for target delivered more towards the plugged ear (left). This effect emerged irrespective of GROUP (main effect and all interactions, p-values $> .27$). Likewise, the analysis on signed errors revealed a main effect of TARGET POSITION, $F(4.69, 121.90) = 9.42$, $p < .001$, $\eta^2 = .26$, and the 2-way interaction between LISTENING CONDITION and TARGET POSITION, $F(4.33, 112.64) = 8.08$, $p < .001$, $\eta^2 = .23$. Signed errors increased particularly for target delivered more towards the plugged ear (left). For signed errors we also found a main effect GROUP, $F(1,26) = 6.45$, $p = .02$, $\eta^2 = .20$ and the interaction between GROUP and LISTENING CONDITION ($F(1,26) = 4.36$, $p = .05$, $\eta^2 = .26$). Simple main effects revealed that the signed error of the Naming group was significantly impacted by listening condition ($F = 4.9$, $p = 0.05$), whereas this did not occur in the Reaching group ($F = 0.26$, $p = .62$). As shown in Figure 2B, during monaural listening the Naming group localised sound more to the unplugged side (Binaural: $M = -0.39$; $SD = 3.14$; Monaural: $M = 4.36$; $SD = 16.53$), whereas the Reaching group did not present this bias (Binaural: $M = -0.88$; $SD = 3.55$; Monaural: $M = -1.69$; $SD = 14.34$).

Participants were aware of their performance change after monaural plugging. Performance assessment scores (“How do you judge your performance?” from 1 = really bad to 9 = really good) were

lower in M1 (Reaching: $M = 3.29$; $DS = 1.90$; Naming: $M = 3.50$, $DS = 1.40$) compared to the B listening condition (Reaching: $M = 6.86$; $DS = 1.35$; Naming: $M = 6.57$, $DS = 0.85$; Chi-square = 24.14, $p < .001$, in non-parametric Friedman test), irrespective of GROUP. Participants also reported that monaural plugging required additional cognitive effort. Effort assessment scores (*“How much effort (in terms of energy and cognitive resourced used) did the task require?”* from 1 = none to 9 = many) were larger in M1 (Reaching: $M = 6.71$; $DS = 1.33$; Naming: $M = 6.21$, $DS = 1.72$) compared to the B listening condition (Reaching: $M = 3.29$; $DS = 1.49$; Naming: $M = 3.57$, $DS = 1.95$; Chi-square = 28, $p < .001$, in non-parametric Friedman test), again irrespective of GROUP.

3.1.2. *Adaptation to monaural listening*

To study *adaptation to monaural listening* across successive monaural blocks, we entered absolute and signed errors in separate ANOVAs with TARGET POSITION (17 positions, from -80° to $+80^\circ$) and MONAURAL BLOCKS NUMBER (M1, M2, M3 and M4) as within-participants variables, and GROUP (reaching, naming) as between-participants variable. The analysis on absolute errors revealed a main effect of MONAURAL BLOCK NUMBER, $F(3,78) = 8.51$, $p < .001$, $\eta^2 = .24$, a main effect of TARGET POSITION, $F(16, 416) = 8.89$, $p < .001$, $\eta^2 = .24$, and the 2-way interaction between MONAURAL BLOCK NUMBER and TARGET POSITION, $F(48, 1248) = 3.02$, $p < .001$, $\eta^2 = .10$. Participants improved across M blocks, especially for target positions more towards the plugged ear (left) (Figures 2A and 2B). No main effect or interaction involving the GROUP variable emerged (all p-values $> .18$), when considering overall performance in a block. A similar analysis on signed errors revealed a main effect of MONAURAL BLOCK NUMBER, $F(3,78) = 5.252$, $p = .002$, $\eta^2 = .16$, a main effect of TARGET POSITION, $F(16, 416) = 10.68$, $p < .001$, $\eta^2 = .28$, and the 2-way interaction between monaural block number and target position, $F(48, 1248) = 2.64$, $p < .001$, $\eta^2 = .09$. Participants bias changed across M blocks, especially for target positions on the plugged side (left) (Figures 2A and 2B). While participants perceived targets more toward the unplugged side at the beginning, repeating the task their started perceived the targets more toward the plugged side. Despite this pattern seems to differ in the 2 groups (the Naming group minimize the bias across blocks, while the Reaching group increased it toward the plugged side), no main effect or interaction involving the group variable emerged (all p-values $> .08$), when considering overall performance in a block.

To further investigate changes in localisation error as a function of practice in the two groups, we analysed performance changes across the 204 trials (51 trials in each of the 4 blocks) using a linear mixed

model (LMM). Specifically, we entered the absolute error in a model with GROUP (naming, reaching) and PRACTICE (as a continuous variable of 204 items). Participant and target position were considered as random effects in the model. This analysis revealed that absolute errors were influenced by PRACTICE ($t = -4.45$, $p < .001$), revealing that participants learned across monaural trials. Crucially, our model showed that error reduction was across trials was influenced by the type of task performed by participants. The Reaching group reduced localisation errors more rapidly and to a greater extent compared to the Naming group ($t = -3.09$, $p = .002$) as shown in Figure 3 A. A similar analysis on signed error revealed that signed errors was generally influenced by GROUP $t = -2.58$, $p = .01$). As shown in Figure 3B, the Reaching group in general perceived the sound as shifted toward the plugged side, while the Naming group perceived it more toward the unplugged. Interestingly, both groups modified their bias by repeating the task ($t = -6.73$, $p < .001$), but differently ($t = 2.71$, $p = .007$). While the Naming group changed the direction of the bias across trial repetition, the Reaching group increased the bias toward the plugged side.

Participants were aware that their performance improved across monaural blocks. Performance self-assessment scores increased across monaural blocks (M4: Reaching: $M = 4.29$; $DS = 1.38$; Naming: $M = 3.93$, $DS = 1.69$; Chi-square = 10.02, $p < .001$, in non-parametric Friedman test), irrespective of GROUP. Participants did not report any change in terms of energy and cognitive resources used to do the task across monaural blocks: effort assessment scores did not change across monaural blocks in either GROUP (all $ps > .23$).

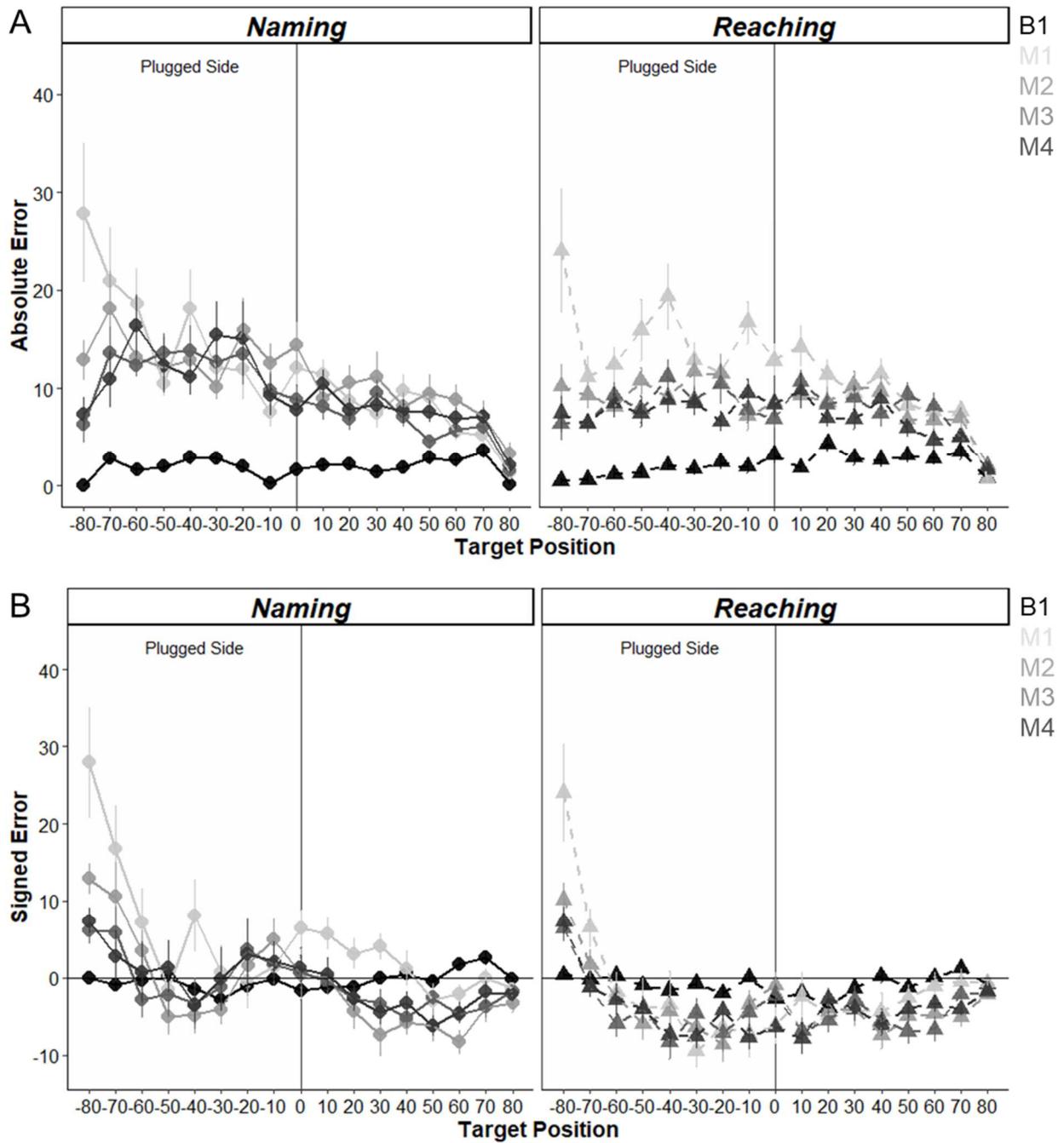


Figure 2. **SOUND LOCALISATION PERFORMANCE.** Absolute (A) and signed (B) errors (in degrees) as a function of Blocks (B = binaural block, M1 = first monaural block, M2 = second monaural block, M3 = third monaural block, M4 = fourth monaural block) and group (Naming: left panel, circles; Reaching: right panel, triangles). Error bars represent the standard error of the mean.

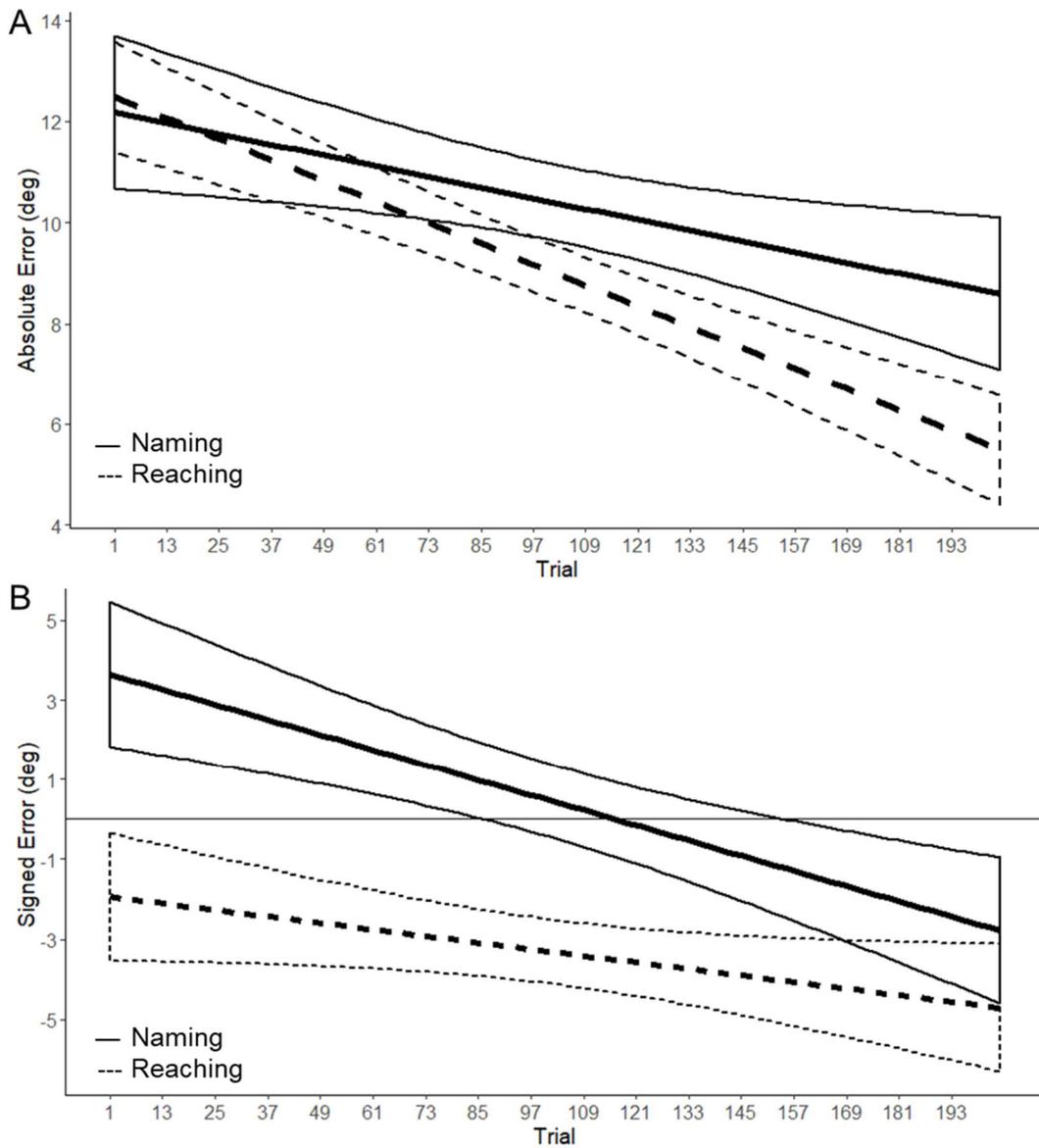


Figure 3. **SOUND LOCALISATION PERFORMANCE AS FUNCTION OF TRIAL.** Absolute (A) and signed (B) error as a function of trial for Naming (continuous line) and Reaching (dashed line) groups.

3.2. Head movements

To study head-movement behaviour, we measured the amplitude of the head rotation around the vertical axis for each detected movement. Next, we transformed the movement amplitude into a categorical variable with 10 bins (amplitude in each bin = 15,8 degrees; bins: 1 = 1.0° - 16.8°; 2 = 16.8° - 32.7°; 3 = 32.7°- 48.5°; 4 = 48.5° - 64.3°; 5 = 64.3°- 80.1°; 6 = 80.2° - 96.0°; 7 = 96.3° - 111.9°; 8 = 113.9° - 126.8°; 9 = 126.8° - 143.2°; 10 = 143.2° - 159.3°) and counted the number of head movements in each amplitude bin, separately for each group and experimental block.

Furthermore, we considered two additional variables computed across all trials: head-rotation around vertical axis as a function of target position and overall head-direction bias during an entire block. The latter two indices were extracted by linear fitting of the changes in head-rotation extent as a function target position (see example in Figure 3). Head-rotation extent was calculated as the average between the leftmost and rightmost head-rotation, for any given target position. The slope of the fitting line captures head-rotation around the vertical axis: the larger the slope the more participants rotated their head as a function of target eccentricity. In the representative participant (ID=21) shown in Figure 4, the slope remained stable from B to M1 (0.24 vs. 0.22) but increased from M1 to M4 (0.22 vs. 0.40), indicating a larger propensions to rotate the head towards peripheral targets in M4 compared to M1. The intercept of the fitting line captures the overall head-direction bias during an entire block, with negative values indicating a bias towards the left (plugged) side. In the same representative participant, the intercept became progressively more negative from B to M1 to M4 (-0.22, -1.73, -17.14, respectively) revealing the bias of this participant to rotate the head further to the plugged side, thus bringing the unplugged ear towards the target.

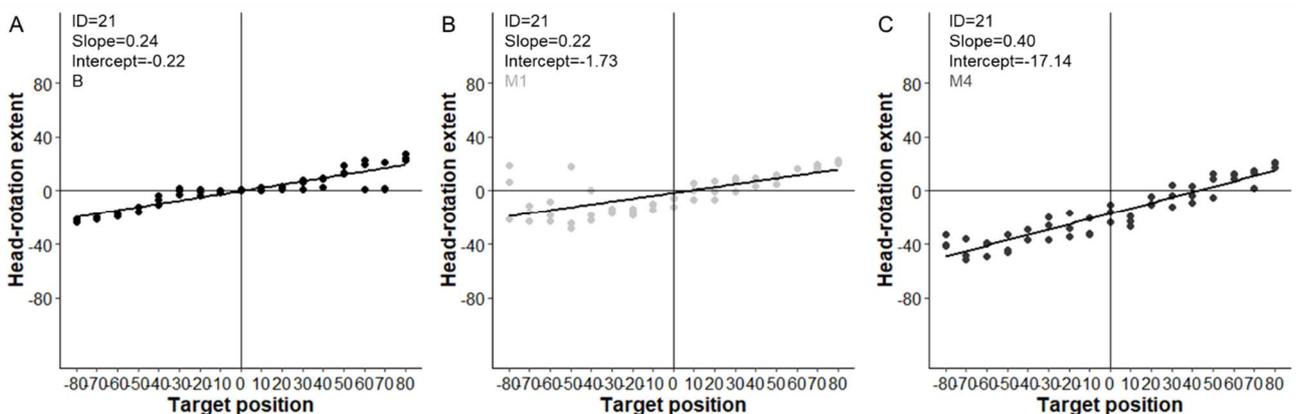


Figure 4. **SLOPE AND INTERCEPT INDICES CALCULATION** Head-rotation extent as a function of target position of participants 21 during first binaural block B (A), the first monaural block M1 (B) and the last monaural block M4 (C).

3.2.1. Immediate ear-plug effect

We started by studying the immediate effect of monaural plugging on the number of head movements in the two groups, as a function of head-movement amplitude. To this aim, a Poisson regression model was fitted on the observed number of movements using `AMPLITUDE BIN` (covariate), `GROUP` (Naming, Reaching), `LISTENING CONDITION` (Binaural, Monaural), and all interaction terms. The participant was included as random effect. The deviance table¹ for this model revealed a significant effect of `AMPLITUDE BIN` ($\chi^2(1) = 157.1710$, $p < 0.001$). Number of movements was inversely related with amplitude, as evident from the corresponding negative Poisson parameter estimate ($\beta_{\text{Amplitude}} = -0.58333$, $z = -12.537$, $p < 0.001$). Number of movements also increased significantly from the binaural (B1) to the first monaural (M1) listening block ($\beta_{m1} = 0.67464$, $z = 6.647$, $p < 0.001$) for both groups (main effect of Block, $\chi^2(1) = 44.1786$, $p < 0.001$). This increase concerned primarily head-movements of smaller amplitude (Amplitude by Block, $\chi^2(1) = 15.861$, $p < 0.001$). All the other effects were not statistically significant ($ps > 0.05$) (Figure 5A).

Next, we examined how participants explored auditory space with their head during sound emission, in the binaural and in the first monaural block. To this aim we focused on (1) head-rotation around vertical axis as a function of target position (slope of the fitting line, as specified above) and (2) overall head-direction bias during an entire block (intercept of the fitting line). Both measures were entered separately into an ANOVAs with `LISTENING CONDITION` (B, M1) as within-participants variable and `GROUP` (reaching, naming) as between-participants variable. The analyses on head-rotation around vertical axis revealed that participants in the Reaching group turned their head as a function of target position to a greater extent compared to those in the Naming group (main effect of group, $F(1,26) = 5.29$, $p = .03$, $\eta^2 = .17$). In other words, they explored auditory space with their head to a greater extent (compare B and M1 in Figures 6A). No main effect or interaction involving `LISTENING CONDITION` emerged, indicating that this group difference was already present in the binaural listening condition.

The analysis on the overall head-direction bias revealed instead a main effect of `LISTENING CONDITION`, $F(1,26) = 19.09$, $p < .001$, $\eta^2 = .42$. Intercepts became negative in M1 (Naming: $M = -3.41$, $SD = 6.20$; Reaching: $M = -3.39$, $SD = 4.31$) compared to the B listening condition (Naming: $M = 0.56$, $SD = 1.25$; Reaching: $M = 0.90$, $SD = 1.50$). This means that, when listening with the left ear plugged, all participants

¹ Deviance decomposition table for the Poisson model derived using the `Anova` function in the `Car` package by John Fox. We adopted the `glmer` function in the `lme4` package for parameter estimates and the `lmerTest` package for the computation of the corresponding p-values.

turned their head leftward, to approach the sound with their unplugged (right) ear (compare B and M1 in Figure 6B).

3.2.2. *Adaptation to monaural listening*

To study the effect of the adaptation to monaural listening on head-movements, we started by examining the number of head movements in the two groups, as a function of head-movement amplitude, in the first and in the last monaural block. As before, a Poisson regression model was fitted on observed number of movements as a function of AMPLITUDE BIN (covariate), GROUP (Naming, Reaching), BLOCK (M1, M4) with all interaction terms. Participant number was included as random effect. The deviance table revealed a significant effect of AMPLITUDE BIN ($\chi^2(1) = 584.4407$, $p < 0.001$). Number of movements was inversely related with amplitude as evident from the corresponding negative Poisson parameter estimate ($\beta_{\text{Amplitude}} = -0.50891$, $z = -24.175$, $p < 0.001$). Number of movements also increased significantly from the first (M1) to the fourth (M4) monaural listening block, for larger amplitude levels ($\beta_{\text{Amplitude,M4}} = 0.11675$, $z = 4.321$, $p < 0.001$). This was also reflected from the significant interaction effect BLOCK by AMPLITUDE BIN ($\chi^2(1) = 18.6691$, $p < 0.001$). We also observed a significant effect for GROUP ($\chi^2(1) = 5.5511$, $p < 0.05$). The Reaching group was associated with a lower number of movements ($\beta_{\text{Reaching}} = -0.33190$, $z = -2.356$, $p < 0.05$). All the other effects were not statistically significant ($ps > 0.05$) (Figure 5B).

Finally, we examined how participants explored auditory space with their head across monaural blocks. Slopes and intercepts across participants were entered into separate ANOVAs with MONAURAL BLOCK NUMBER (M1, M2, M3 and M4), as within-participants variable and GROUP (reaching, naming) as between-participants variable. Both analyses revealed only a main effect of MONAURAL BLOCK NUMBER (slope: $F(3,78) = 12.67$, $p < .001$, $\eta^2 = .32$; intercept: $F(1.57,40.86) = 9.47$, $p < .001$, $\eta^2 = .27$). As monaural blocks progressed, participants in both groups increased their exploration of auditory space and turned their head more to approach sounds with their unplugged (right) ear (Figure 6A and 6B).

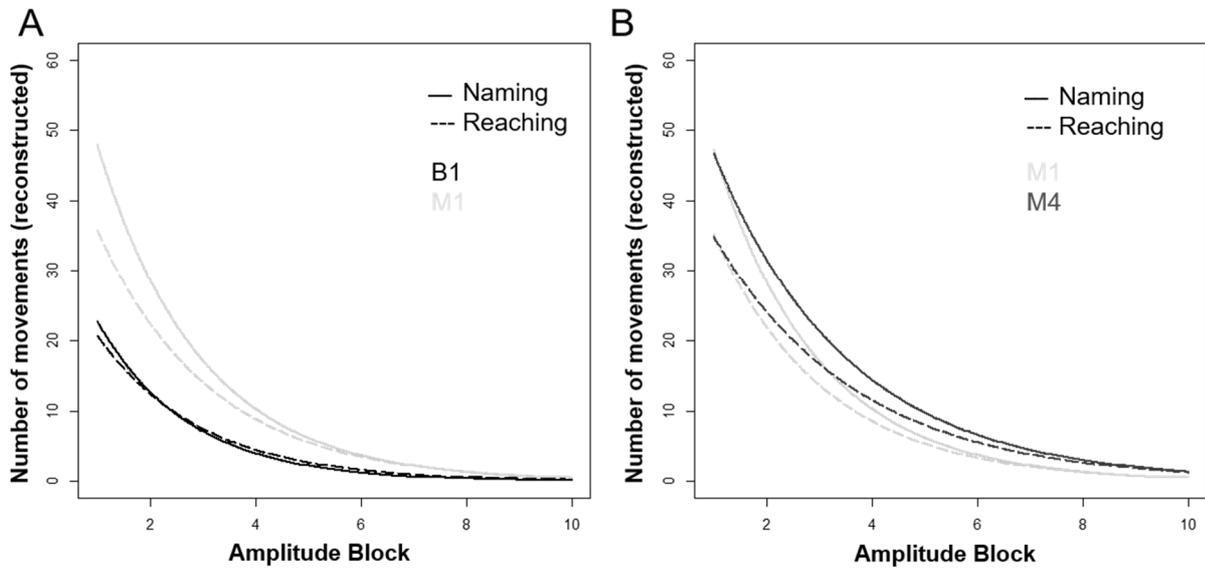


Figure 5. **NUMBER OF MOVEMENT AND AMPLITUDE** A) Poisson model representation. N° of movements as a function of Amplitude block (data binning: 10 bins: 1 = 1.0° - 16.8°; 2 = 16.8° - 32.7°; 3 = 32.7° - 48.5°; 4 = 48.5° - 64.3°; 5 = 64.3° - 80.1°; 6 = 80.2° - 96.0°; 7 = 96.3° - 111.9°; 8 = 113.9° - 126.8°; 9 = 126.8° - 143.2°; 10 = 143.2° - 159.3°); Black patterns correspond to binaural listening condition (B1) and light grey pattern correspond to monaural listening condition (M1). The continuous patterns represent the Naming group while dashed one the Reaching group. B) Poisson model representation. N° of movements as a function of Amplitude block. Light grey patterns correspond to the first monaural block (M1) and dark grey pattern correspond to the fourth monaural listening condition (M4). The continuous patterns represent the Naming group while dashed one the Reaching group.

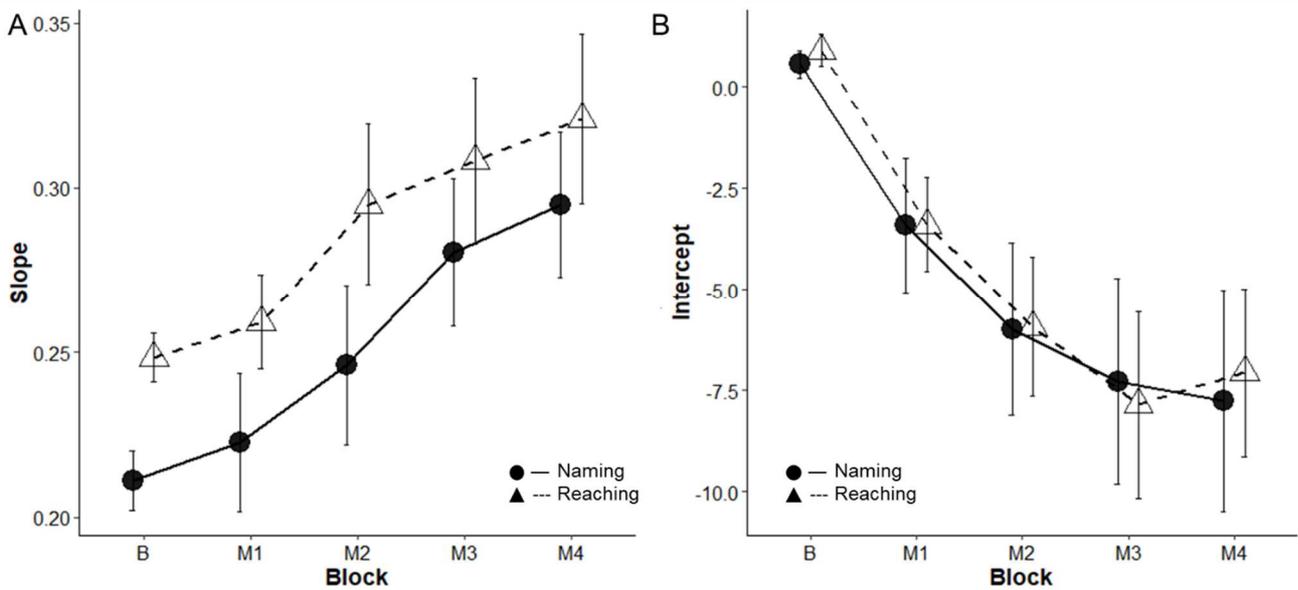


Figure 6. **SPACE EXPLORED.** Slope (A) and intercept (B) values as a function of block B1 M1 M2 M3 M4. Naming group (black circles) and Reaching group (white triangles).

3.3. Relation between changes in sound localisation performance and head-movements

3.3.1. Immediate ear-plug effect and head-movements

We first examined if the immediate ear-plug effect (i.e., changes in absolute localisation error between M1 and B; with positive values indicating larger plug-effect) correlated with changes in the number of head movements (i.e., changes between M1 and B). When studied separately for each group, using Pearson correlation with Bonferroni correction, a significant relation emerged only for the Naming group (naming: $r = 0.57$, $p = 0.04$; reaching: $r = 0.12$, $p = 0.68$). However, this correlation was driven by a single participant ($r = 0.22$, $p = 0.46$ with the participant 18 was removed).

Next, we examined if the immediate ear-plug effect (i.e., changes in absolute localisation error between M1 and B; positive values indicate larger plug-effect) correlated with changes in the space explored with the head (i.e., changes in slope between M1 and B). Unlike the case for number of head-movements described above, this correlation was reliable in each group (Pearson correlation with Bonferroni correction: reaching, $r = -0.66$, $p = 0.01$; naming, $r = -0.79$, $p < 0.001$; see Figure 7A). Irrespective of group, the more participants increased explored space between B and M1 blocks, the less the cost of ear plugging on their sound localisation performance.

3.3.2. Adaptation to monaural listening and head-movements

The number of head movements also increased between M1 and M4 block (see section 3.2.2). We examined if adaptation (i.e., changes in absolute localisation error between M4 and M1; positive values indicate larger improvement after trials repetition) correlated with the changes in the number of head movements (i.e., changes between M4 and M1). We did not find any relations for both groups (all $ps > 0.31$).

The portion of space explored with the head also changed across monaural blocks (comparison between M1-M4 blocks, see section 3.2.2). We examined if adaptation (i.e., changes in absolute localisation error between M4 and M1; positive values indicate larger improvement after trials repetition) correlated with changes in the space explored with the head (i.e., changes in slope between M4 and M1). This correlation is shown in Figure 7B, separately for each group (Pearson correlation with Bonferroni correction: reaching, $r = 0.60$, $p = 0.02$; naming, $r = 0.01$, $p = 0.97$). A positive relation emerged for the Reaching group, but not for the Naming group. Comparing correlations across group (as in Eld, Gollwitzer and Schmidt, 2011) produced a marginally significant between-group difference ($z = -1.602$, $p = 0.055$). This suggests that compensatory head-movement behaviour may relate with adaptation more for participants in the Reaching group.

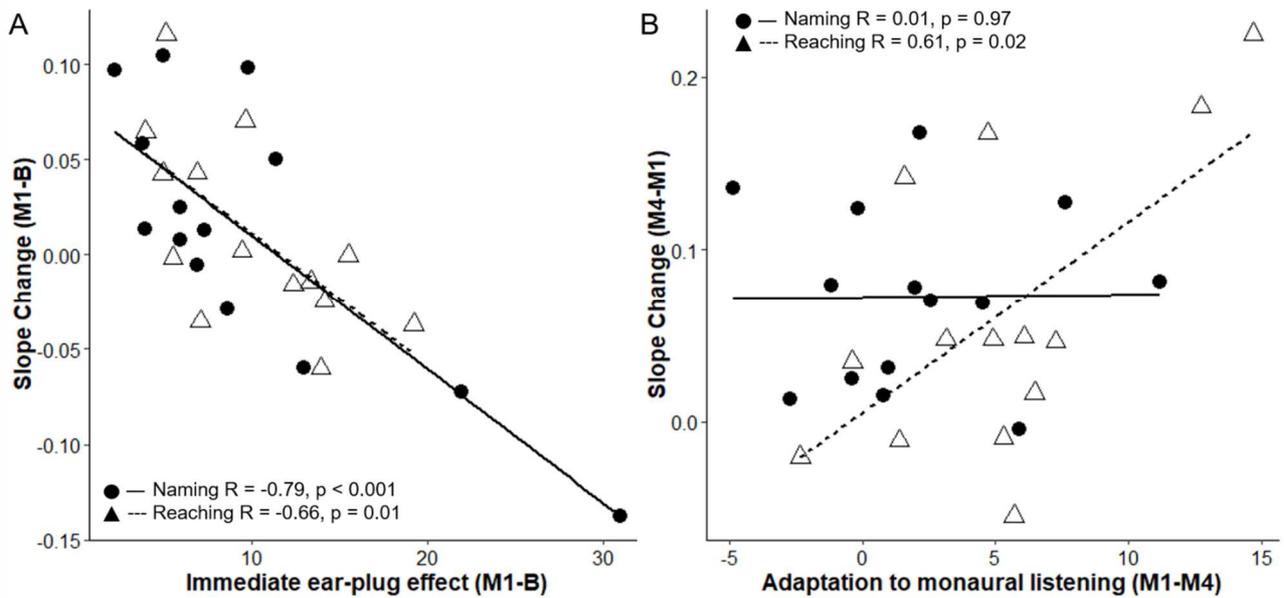


Figure 7. **CORRELATION BETWEEN SPACE EXPLORED ROTATING THE HEAD AND PERFORMANCE** A) Correlation between Ear-plug effect and Slope Change, B) Correlation between Slope Change and Adaptation to monaural listening. In both graphs participants in the Reaching group are indicated with white triangles (regression line shown as dashed) and those in the Naming group are indicated with black circles (regression line shown as continuous).

3.4. VR experience

At the end of the experiment, participant replied to questions about their experience using VR system, to assess also the feasibility of our approach. They judged that the overall experience with virtual reality was positive ($M = 7.86, SD = 1.15$, using a scale from 1 =negative to 9 =positive), that the scene appeared realistic ($M = 6.61, SD = 1.47$, using a scale from 1 = unrealistic to 9 = very realistic) and reported no feeling of losing balance ($M = 1.53, SD = 1.07$, using a scale from 1 = not at all to 9 = completely) or being annoyed ($M = 2.61, SD = 1.81$, using a scale from 1 = not at all to 9 = completely).

Participants were also queried about the sense of agency and the perceived gaming experience when performing the two tasks (i.e., reaching or naming).

Sense of agency

Participants indicated their agreement with 2 items (“I felt that I can turn off the sound”, “I felt that I can act on the sound”) using a 5-points Likert scale (from 1 = totally disagree to 5 = totally agree). Participants in both groups felt equally that they could act on sounds (reaching: $M = 2.29, SD = 0.99$; naming: $M = 1.71, SD = 0.99$; $W = 64, p = .14$ on Mann Whitney). However, the Reaching group reported the experience of turn off

the sound strongly ($M = 4.43$, $SD = 0.51$) compared to the Naming group ($M = 1.21$, $SD = 0.58$), $W = 0.00$, $p < 0.001$ (Mann Whitney).

Gaming experience

To investigate their gaming task-related experience, we proposed 15 items of 2 scale of the User Engagement Scale (UES) questionnaire, typically used to measure engagement during video-game playing (Wiebe, Lamb, Hardy & Sharek, 2014): focus of attention scale and satisfaction scale (Figure 8). We compared responses of the two groups for each item of the 2 scales, as well as the cumulative indices (average of the respective items, Cronbach's α : 0.8; 0.89) in t-test analyses. Overall, our virtual reality scenario was an effective method to create a game-like situation, capable of actively involving participants. The satisfaction scale items revealed a difference between tasks: participants of the Reaching group ($M = 3.71$, $SD = 0.83$) perceived the experience more rewarding compared to the Naming group ($M = 2.93$, $SD = 0.83$; $W = 47.50$, $p = .015$). Moreover, they expressed more interest in doing the task (Reaching: $M = 4.71$, $SD = 0.47$; Naming: $M = 4.07$, $SD = 0.92$, $W = 60$, $p = .05$).

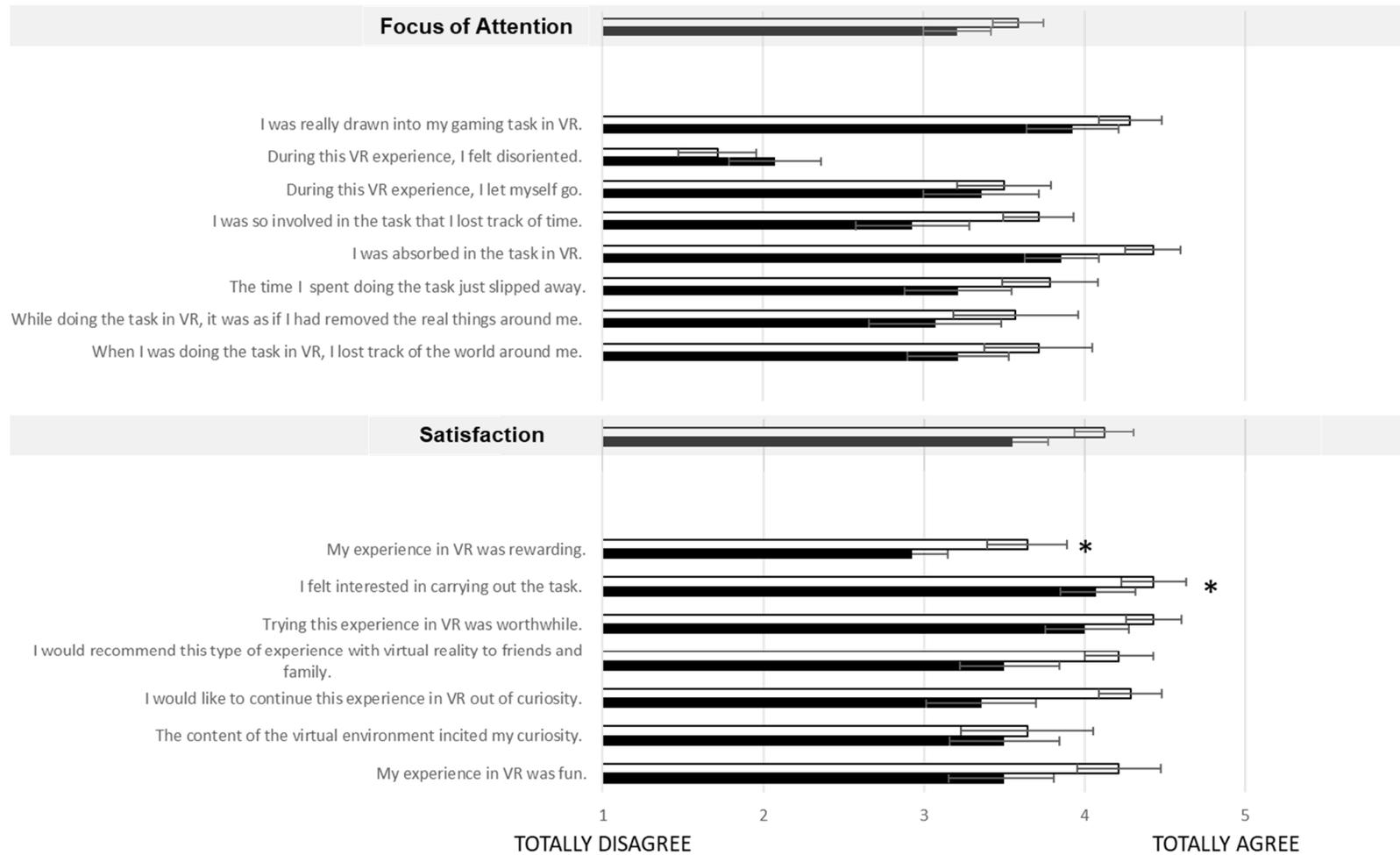


Figure 8. **VR EXPERIENCE.** Mean ratings for the Reaching (white bars) or Naming (black bars) group. Cumulative scores for focus of attention and satisfaction are highlighted in grey. The error bars represent the standard error of the mean.

4. DISCUSSION

The cognitive ability to localise sounds relies on internal models that specify the correspondences between the auditory input reaching the ears, initial head-position and coordinates in external space. It is now well established that these correspondences can be updated throughout life (Carlile, 2014; Keating & King, 2015; Rabini et al., 2019; Strelnikov et al., 2011; Van Wanrooij et al., 2005), setting the basis for re-learning spatial hearing abilities in adulthood. In addition, whenever auditory cues are altered, humans can exploit active perception strategies to adapt to the novel listening situations. For instance, people with hearing-impairment use head-movements to cope with their hearing difficulties (Brimijoin et al., 2010; see also Brimijoin & Akeroyd, 2012). Understanding the cognitive adjustments of internal models for spatial hearing, as well as the behavioural strategies adopted when localising sounds in novel listening conditions, is particularly important for individuals who experience long-term auditory alterations (e.g., hearing loss, hearing aids, cochlear implants). In addition, it may provide useful indications for training normal hearing individuals who must adapt to novel auditory cues (e.g., when listening with non-individualised HRTFs in virtual auditory environments).

Until now, however, several methodological constraints have limited our understanding of the mechanisms involved in adapting spatial hearing skills when exposed to novel listening situations. Specifically, the potential role of dynamic and sensorimotor interactions with the sounds have remained largely overlooked. These interactions include head-movements performed during sound, as well as reaching actions towards the sounds themselves. Using a novel methodology, based on virtual reality and real-time kinematic tracking of the participant's head and hand, we examined the contribution of reaching movements and head movements when adapting to monaural listening. Our experimental approach is based on a new apparatus (SPHERE; Pavani et al., 2017; Gaveau et al., 2020) that allows to present free-field sounds from a real loudspeaker, placed at pre-determined locations and aligned with a virtual reality scenario. This allows full control over visual cues about the visual environment (here, an empty room), cues to sound position (here, a visible array of virtual loudspeakers) and feedback (here, the flashing speaker that appeared in case of mistaken responses). Most importantly, our approach allows full monitoring of head position. This ensured identical straight-ahead initial posture for all trials and participants, but also permitted tracking of spontaneous head-movements during the response phase. Finally, precise kinematic of the hand response was measured in real-time. This allowed measuring of end-pointing positions in the Reaching group and ensured compliance with the instructions in the Naming group.

Four novel findings emerged. First, we documented that **adaptation to monaural listening** can occur over a relatively short period of time (about 200 trials, completed in approximately 50 minutes). Second, we showed that monaural plugging affected both sound localisation performance and spontaneous head-movements. Third, in line with our main prediction, we found that reaching to sounds proved more effective than naming sound position when adapting to **altered binaural cues**. Fourth, we document that **head-movements played an important role in this fast adaptation: reduction in localisation errors was accompanied by wider portions of space explored with the head**. Notably, performance improvements correlated with changes in head-movement extension selectively in the Reaching group, providing initial evidence for an interaction between reaching to sounds and head-movements when adapting spatial hearing abilities to monaural listening conditions.

4.1. Sound localisation improves rapidly during monaural listening

The present study demonstrates that normal hearing adults, listening with one ear plugged and muffled, can improve their sound localisation abilities over a short period of time. Both group of participants (Reaching and Naming) progressively reduced their error over trials, within a single testing session. We promoted adaptation to altered binaural cues through a combination of audio-visual feedback (Strelnikov et al., 2011; Rabini et al., 2019; **Valzolgher et al., 2020**) and dynamic sensorimotor interactions with the sounds (spontaneous head-movements, agency over the sound). **Despite most of the participants were naïve to virtual reality, they easily understood the instructions, were engaged by the task, and gave a positive assessment to the VR experience overall**. This confirms the feasibility of our novel approach, which represents an important pre-requisite for the use of similar VR applications in auditory perception research and clinical rehabilitation (see 3.4).

While adaptation to altered auditory cues has been documented in several previous reports (Carlile, 2014; Kacelnik, Nodal, Parsons & King, 2006; Keating & King, 2015; Nawaz, McNeill & Greenberg, 2014; Steadman et al., 2019), to the best of our knowledge, improvements on a trial-by-trial basis have not been **studied and described before**. Traditionally, spatial hearing adaptation has been examined in paradigms which comprised pre- and post-testing phases separated by training sessions which occurred over several days (e.g., 5 days in Strelnikov et al., 2011 and in Irving & Moore, 2011; 10 days in Ohuchi et al., 2005). Thus, even when adaptation of spatial hearing abilities occurred after a small number of short training session (3 sessions, lasting 15 minutes as in Steadman et al., 2019), they were performed across multiple

days. Although in our study we did not test the generalisation of the observed adaptation of spatial hearing abilities, we investigated the improvements occurring over the course of 204 trials administered in a single session.

Two mechanisms may subtend the fast adaptation we have documented. On the one hand, it is possible that participants learned to adjust the contribution of the different auditory cues to sound localisation. Re-weighting of the auditory cues, with increased reliance on monaural cues at the unplugged ear for localization, is one of the mechanisms by which sound localization in azimuth can improve during monaural listening (see Kumpik & King, 2019). We designed the experiment to selectively impact on binaural cues (both interaural-level differences and inter-aural time differences) while leaving monaural cues at the unplugged ear intact. Hence, participants may have learned to exploit monaural cues to a greater extent during the session. On the other hand, because participants were free to move their head during sound emission, it is possible that strategic (rather than cognitive) adaptation mechanisms could account for the observed fast improvements in sound localisation. Cognitive and strategic contributions to sound localisation improvements are clearly not mutually exclusive, and our study cannot determine their relative contributions to the observed performance changes. Yet, as described in the next section, we suggest a key role of compensatory behavioural strategies related to head-movements.

4.2. Monaural listening triggered compensatory head-movements

The role of head-movements in sound localisation has been emphasised since the 1940's (Wallach, 1940), but it has been studied sporadically until recent years (Iwaya, Suzuki & Kimura, 2003; Morikawa & Hirahara, 2013; Perrett & Noble, 1997; Toyoda, Morikawa & Hirahara, 2011). Here, we characterised head-movements with different variables (number and amplitude of head-movements, head-rotation around vertical axis, and overall head-direction bias during an entire block). Our results show that head-movements changed immediately when passing from binaural to monaural listening conditions. In the first monaural listening block, the number of head movements increased, specifically for movements of smaller amplitude. In addition, participants turned their heads to approach sounds with their unplugged ear (as evidenced by immediate changes in the intercept). Our results also show that participants adapt their head-movements across the monaural blocks to adapt to the altered listening condition. Specifically, the number of head-movement continued to increase, but this time for movements of larger amplitude (compare Figure 5B and 5A). Moreover, participants increased their exploration of auditory space by turning their head to more

eccentric positions (as evidenced by changes in slope; see Figure 6A) and turned their head even more to approach the sounds with their unplugged ear (see Figure 6b).

Many previous works showed that head-orientation and head-movements improve sound localisation performance in azimuth and elevation (Morikawa & Hirahara, 2013; Perret & Noble, 1997; Thurlow & Runge, 1967) and facilitate disambiguation of front/back confusions (Brimijoin et al., 2012; Kim, Barnett-Cowan, & Macpherson, 2013; McAnally & Martin, 2014; Perret & Noble, 1997; Wightman & Kistler, 1999; Pöntynen & Salminen, 2019). This document the well-known effect of head-movements on spatial hearing. However, much less work has described the actual changes in head-movements that occur in difficult or altered listening conditions – as here. In a task that required head orienting to spoken sentences, Brimijoin and colleagues (2010) observed that normal hearing listeners performed smoother and more sigmoidal head-movement trajectories compared to hearing-impaired listeners. In the latter group, abrupt velocity changes, reversal of directions and frequent corrections tended to prevail. Note however, that this study described the kinematic of head-movements when participants were explicitly instructed to point to the sound, whereas we reported the head-movement pattern observed in the spontaneous movements produced while the sound was playing and before the response. Although other works have examined spontaneous head-movements in novel and challenging listening conditions (as here), they did so when participants were not explicitly instructed to localise sounds. For instance, Brimijoin and colleagues (2012) has shown that participants use head-movements to increase the level of the signal in their better ear, or to increase the difference in level between the signal and the noise, when listening in complex auditory scenes. Remarkably, this type of head movement differs compared to those performed in more typical hearing situations (i.e., binaural hearing), whereby participants rather tend to face the speaker frontally when performing a sounds localisation task (Iwaya et al., 2003; Thurlow, Mangels & Runge, 1967). A recent study by Hadley and colleagues (Hadley, Brimijoin & Whitmer, 2019) has shown that, as noise increases, people move closer to the target rather than make use of the potentially beneficial effects of head-orientations.

In our study, participants appear to have moved their head during monaural listening to achieve two goals: (1) orienting of their unplugged ear to the sound; (2) exploring auditory space to a greater extent. The need to cope with monaural listening was fulfilled by increasing the frequency and extent of head-turns to favour perception with the unplugged ear. This peculiar type of movement could have allowed greater exploitation of monaural cues. Specifically, listeners could have rapidly made use of changes in spectral monaural cues across the blocks, or – perhaps more likely – they could have exploited the attenuating

effects of the head to identify the azimuthal position of sounds (for discussion of the different use of monaural cues in actual or simulated unilateral hearing loss see Kumpik & King, 2019). Along a similar line of reasoning, greater exploration of auditory space may have permitted participants to ‘search’ for the region of maximal sound intensity. A third possibility is that participants learned to use their asymmetric binaural cues to localise sounds in azimuth (as proposed by Agterberg, Snik, Hol, Van Wanrooij & Van Opstal, 2012, albeit for listeners with acquired unilateral conductive hearing loss who had much longer experience with the asymmetrical binaural cues). In particular, it is possible that they learned to determine the head-orientation that brought the target sound on their medial plane (i.e., 0 ITD orientation). In future works, it would be important to assess the relative contribution of spectral and intensity monaural information, by affecting the spectral information at the unplugged ear using an ear-mould.

4.3. Reaching to sounds promote adaptation to monaural listening more than naming

One clear result that emerged from our study is that the instructions on how to perform the task (Reaching vs. Naming) impacted on sound localization performance, head-movements during sounds and adaptation to monaural listening in general. In the first monaural listening condition (M1), the Naming group perceived sounds more toward the unplugged side, whereas the Reaching group did not present this bias (Figure 2B). In addition, across trial repetitions, participants of the Reaching group reduced localisation errors faster compared to those who interacted with sounds simply by reading labels (the Naming group). This result revealed that Reaching to sound was effective in promoting faster adaptation to monaural listening. Across monaural trials, the error changed differently. As indicated by the signed error (which refers to the lateralized bias of the response), the Naming group reduced the bias toward the unplugged side across trials, while the Reaching group developed a slight bias towards the plugged side (Figure 3B).

Response type also affected head-movements during sound emission. Participants in the Reaching group turned their head as a function of target position to a greater extent compared to the Naming group, irrespective of listening condition (binaural vs. first monaural block; see 3.2.1). Interestingly, when considering the progressive adaptation to monaural listening blocks, only the Reaching group showed a correlation between head-movement extension (slope) and performance (Figure 7). Thus, although participants in both groups were free to move the head during the task, only participants in the Reaching group appeared to have developed effective dynamic listening strategies involving head-movements, which in turn impacted on adaptation to monaural listening.

Why the response type (Reaching vs. Naming) influenced adaptation to monaural listening? As anticipated in the introduction, reaching to sounds requires a coordination of different effectors (eyes, head, hand) into a common reference frame (Cohen & Andersen, 2002). In turn, this may result in a more stable (or salient) spatial coding of sound source location and favour re-learning of sound-space correspondences. In addition, reaching movement may have helped directing attention towards the position occupied by the sound source, because of additional visual, proprioceptive and kinaesthetic cues resulting from the action. The analysis of spontaneous head-movements, however, revealed a more complex scenario than expected. Reaching participants explored a wider portion of space with the head compared to Naming participants, and this was functional for adaptation selectively for the Reaching group. Movements of smaller amplitudes, appeared to have played a less important role for adaptation: they were more numerous for Naming than Reaching participants, but only in the first monaural block. At present we can only speculate about the origin of this different head-movement behaviour (and consequent change in performance) in the Reaching group. One possibility, is that head-movements were more functional to the key task (sound localisation) for the Reaching group than the Naming group. Specifically, it could be argued that participants in the Naming group used head-movements also to explore the labels that identified the speakers (recall that labels changed randomly between trials and thus they had to be read anew every time). In turn, this could have resulted in head-movements that could have interfered with the ones needed to optimally adapt to the monaural listening condition. Another possibility is that Reaching was a more engaging task for participants than Naming. In the questionnaires, the Reaching participants reported a stronger feeling of agency on the sound sources. In turn, this could have led to a stronger motivation when performing the task (Aarhus, Grönvall, Larsen, & Wollsen, 2011). The Reaching group also perceived the experience as more rewarding overall, and expressed more interest in the task compared the Naming group. Recall that the participants in the Naming group did not directly interrupted the sound, as it was the experimenter that entered the response. Future works should make this aspect more comparable between groups, and assess to what extent motivation and sense of agency per se could be at the origin of the different head-movement behaviour.

4.4. Conclusions

In this article we show that reaching to sounds can promote fast adaptation to altered binaural cues, more than naming sounds. In addition, we document that listening with one ear plugged triggers compensatory head-movement behaviour, which in turn can modulate sound localization performance. The head-

movement behaviour we observed can be interpreted as a strategic (rather than cognitive) adaptation mechanism to altered spatial hearing. However, cognitive and strategic contributions to sound localisation improvements are clearly not mutually exclusive and, in fact, it is plausible that head-related behavioural strategies may trigger cognitive changes. The implications of these results are two-fold. First, they show the importance of considering dynamic listening behaviour (reaching to sounds and head-movements) when studying how humans adapt to altered auditory cues. This is now increasingly possible thanks to virtual reality and kinematic tracking approaches, like the one we adopted in the present study and other recent works (Parseihian, Jouffrais & Katz, 2014; Parseihian & Katz, 2012; Steadman, Kim, Lestang, Goodman & Picinali, 2019; Stitt, Picinali & Katz, 2019). More generally, researchers should pursue the novel opportunity to study spatial hearing in more realistic and ecological environments (see Hadley et al., 2019). Second, our findings could pave the way for new approaches to the rehabilitation of spatial hearing difficulties in people suffering from hearing loss or using hearing-enabling devices such as hearing aids or cochlear implants.

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All figures will be black and white.

REFERENCES

- Aarhus, R., Grönvall, E., Larsen, S. B., & Wollsen, S. (2011). Turning training into play: Embodied gaming, seniors, physical training and motivation. *Gerontechnology*, 10(2), 110-120. <https://doi.org/10.4017/gt.2011.10.2.005.00>;
- Agterberg, M.J., Snik, A.F., Hol, M.K., Van Wanrooij, M.M., Van Opstal, A.J., 2012. Contribution of monaural and binaural cues to sound localization in listeners with acquired unilateral conductive hearing loss: improved directional hearing with a bone-conduction device. *Hear. Res.* 286, 9e18. <https://doi.org/10.1016/j.heares.2012.02.012>;
- Angell, J. R., & Fite, W. (1901). From the Psychological Laboratory of the University of Chicago: The monaural localization of sound. *Psychological Review*, 8(3), 225–246. <https://doi.org/10.1037/h0073690>
- Bahill, A. T., & McDonald, J. D. (1983). Frequency limitations and optimal step size for the two-point central difference derivative algorithm with applications to human eye movement data. *IEEE Transactions on Biomedical Engineering*, (3), 191-194. <https://doi.org/10.1109/TBME.1983.325108>;
- Bauer, R. W., Matuzsa, J. L., Blackmer, R. F., & Glucksberg, S. (1966). Noise Localisation after Unilateral Attenuation. *The Journal of the Acoustical Society of America*, 40(2), 441–444. <https://doi.org/10.1121/1.1910093>;
- Biguer, B., Prablanc, C., & Jeannerod, M. (1984). The contribution of coordinated eye and head movements in hand pointing accuracy. *Experimental brain research*, 55(3), 462-469. <https://doi.org/10.1007/BF00235277>;
- Brimijoin, W. O., & Akeroyd, M. A. (2012). The role of head movements and signal spectrum in an auditory front/back illusion. *i-Perception*, 3(3), 179-182. <https://doi.org/10.1068/i7173sas>;
- Brimijoin, W. O., McShefferty, D., & Akeroyd, M. A. (2010). Auditory and visual orienting responses in listeners with and without hearing-impairment. *The Journal of the Acoustical Society of America*, 127(6), 3678-3688. <https://doi.org/10.1121/1.3409488>;
- Carlile, S. (2014). The plastic ear and perceptual relearning in auditory spatial perception. *Frontiers in neuroscience*, 8, 237. <https://doi.org/10.3389/fnins.2014.00237>;
- Carlile, S., Balachandar, K., & Kelly, H. (2014). Accommodating to new ears: The effects of sensory and sensory-motor feedback. *The Journal of the Acoustical Society of America*, 135(4), 2002–2011. <https://doi.org/10.1121/1.4868369>;
- Carlile, S., Martin, R., & McAnally, K. (2005). Spectral Information in Sound Localization. *International Review of Neurobiology*, 70, 399–434. [https://doi.org/10.1016/S0074-7742\(05\)70012-X](https://doi.org/10.1016/S0074-7742(05)70012-X)
- Clifton, R. K., Gwiazda, J., Bauer, J. A., Clarkson, M. G., & Held, R. M. (1988). Growth in head size during infancy: Implications for sound localisation. *Developmental Psychology*, 24(4), 477. <http://dx.doi.org/10.1037/0012-1649.24.4.477>;
- Cohen, Y. E., & Andersen, R. A. (2002). A common reference frame for movement plans in the posterior parietal cortex. *Nature Reviews Neuroscience*, 3(7), 553. <https://doi.org/10.1038/nrn873>;
- Cranford, J. L., Andres, M. A., Piatz, K. K., & Reissig, K. L. (1993). Influences of age and hearing loss on the precedence effect in sound localisation. *Journal of Speech, Language, and Hearing Research*, 36(2), 437-441. <https://doi.org/10.1044/jshr.3602.437>;

- Dobrev, M. S., O'Neill, W. E., & Paige, G. D. (2011). Influence of aging on human sound localisation. *Journal of neurophysiology*, 105(5), 2471-2486. <https://doi.org/10.1152/jn.00951.2010>;
- Eid, M., Gollwitzer, M., & Schmitt, M. (2011). Statistik und Forschungsmethoden. Lehrbuch (2., korr. Aufl.). *Grundlagen Psychologie*;
- Fogt, N., Uhlig, R., Thach, D. P., & Liu, A. (2002). The influence of head movement on the accuracy of a rapid pointing task. *Optometry (St. Louis, Mo.)*, 73(11), 665-673;
- Francesco Pavani, Valerie Gaveau, Anael Belle, Eric Koun, Romeo Salemme, Clement Desoche, Eric Truy, Alessandro Farnè (2017). Active sound localisation in 3D space in unilateral and bilateral cochlear implant users: a new approach to spatial hearing assessment through immersive virtual reality. *International Federation of ORL Societies (IFOS)*, Paris, June 24-27th;
- Fuller, J. H. (1992). Head movement propensity. *Experimental Brain Research*, 92(1), 152-164. <https://doi.org/10.1007/BF00230391>;
- Gaveau, V., Coudert, A., Salemme, R., Koun, E., Desoche, C., Truy, E., ... & Pavani, F. (2020). SPHERE: A novel approach to 3D and active sound localization. *bioRxiv*.
- Hadley, L. V., Brimijoin, W. O., & Whitmer, W. M. (2019). Speech, movement, and gaze behaviours during dyadic conversation in noise. *Scientific reports*, 9(1), 1-8. <https://doi.org/10.1038/s41598-019-46416-0>;
- Hendrickx, E., Stitt, P., Messonnier, J. C., Lyzwa, J. M., Katz, B. F., & De Boishéraud, C. (2017). Influence of head tracking on the externalization of speech stimuli for non-individualized binaural synthesis. *The Journal of the Acoustical Society of America*, 141(3), 2011-2023. <https://doi.org/10.1121/1.4978612>
- Honda, A., Shibata, H., Gyoba, J., Saitou, K., Iwaya, Y., & Suzuki, Y. (2007). Transfer effects on sound localisation performances from playing a virtual three-dimensional auditory game. *Applied Acoustics*, 68(8), 885–896. <https://doi.org/10.1016/J.APACOUST.2006.08.007>;
- Honda, A., Shibata, H., Hidaka, S., Gyoba, J., Iwaya, Y., & Suzuki, Y. (2013). Effects of head movement and proprioceptive feedback in training of sound localization. *i-Perception*, 4(4), 253-264. <https://doi.org/10.1068/i0522>;
- Irving, S., & Moore, D. R. (2011). Training sound localisation in normal hearing listeners with and without a unilateral ear plug. *Hearing Research*, 280(1–2), 100–108. <https://doi.org/10.1016/J.HEARES.2011.04.020>;
- Isaiah, A., Vongpaisal, T., King, A. J., & Hartley, D. E. (2014). Multisensory training improves auditory spatial processing following bilateral cochlear implantation. *Journal of Neuroscience*, 34(33), 11119-11130. <https://doi.org/10.1523/JNEUROSCI.4767-13.2014>;
- Iwaya, Y., Suzuki, Y., & Kimura, D. (2003). Effects of head movement on front-back error in sound localisation. *Acoustical science and technology*, 24(5), 322-324. <https://doi.org/10.1250/ast.24.322>;
- Kacelnik, O., Nodal, F. R., Parsons, C. H., & King, A. J. (2006). Training-induced plasticity of auditory localisation in adult mammals. *PLoS biology*, 4(4), e71. <https://doi.org/10.1371/journal.pbio.0040071>;
- Keating, P., & King, A. J. (2015). Sound localisation in a changing world. *Current opinion in neurobiology*, 35, 35-43. <https://doi.org/10.1016/j.conb.2015.06.005>;
- Kim, J., Barnett-Cowan, M., & Macpherson, E. A. (2013). Integration of auditory input with vestibular and neck proprioceptive information in the interpretation of dynamic sound localisation cues.

- In *Proceedings of meetings on acoustics ICA2013*, 19, (1), 050142). ASA. <https://doi.org/10.1121/1.4799748>;
- Knudsen, E. I., & Knudsen, P. F. (1985). Vision guides the adjustment of auditory localisation in young barn owls. *Science*, 230(4725), 545-548. <https://doi.org/10.1126/science.4048948>;
- Kumpik, D. P., Kacelnik, O., & King, A. J. (2010). Adaptive reweighting of auditory localisation cues in response to chronic unilateral earplugging in humans. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, 30(14), 4883–4894. <https://doi.org/10.1523/JNEUROSCI.5488-09.2010>;
- Kumpik, D. P., & King, A. J. (2019). A review of the effects of unilateral hearing loss on spatial hearing. *Hearing research*, 372, 17-28. <https://doi.org/10.1016/j.heares.2018.08.003>
- Majdak, P., Goupell, M. J., & Laback, B. (2010). 3-D localisation of virtual sound sources: effects of visual environment, pointing method, and training. *Attention, perception, & psychophysics*, 72(2), 454-469.; <https://doi.org/10.3758/APP.72.2.454>;
- Majdak, P., Walder, T., & Laback, B. (2013). Effect of long-term training on sound localisation performance with spectrally warped and band-limited head-related transfer functions. *The Journal of the Acoustical Society of America*, 134(3), 2148–2159. <http://asa.scitation.org/doi/10.1121/1.4816543>;
- McAnally, K. I., & Martin, R. L. (2014). Sound localisation with head movement: implications for 3-d audio displays. *Frontiers in neuroscience*, 8, 210. <https://doi.org/10.3389/fnins.2014.00210>;
- Mendonça, C. (2014). A review on auditory space adaptations to altered head-related cues. *Frontiers in neuroscience*, 8, 219. <https://doi.org/10.3389/fnins.2014.00219>;
- Mendonça, C., Campos, G., Dias, P., & Santos, J. A. (2013). Learning auditory space: Generalization and long-term effects. *PloS one*, 8(10), e77900. <https://doi.org/10.1371/journal.pone.0077900>;
- Middlebrooks, J. C. (2015b). Sound localisation. *Handbook of Clinical Neurology* (1st ed., Vol. 129). Elsevier B.V. <https://doi.org/10.1016/B978-0-444-62630-1.00006-8>;
- Middlebrooks, J. C., & Green, D. M. (1991). Sound localisation by human listeners. *Annual review of psychology*, 42(1), 135-159. <https://doi.org/10.1146/annurev.ps.42.020191.001031>;
- Morikawa, D., & Hirahara, T. (2013). Effect of head rotation on horizontal and median sound localisation of band-limited noise. *Acoustical Science and Technology*, 34(1), 56-58. <https://doi.org/10.1250/ast.34.56>;
- Morikawa, D., Toyoda, Y., & Hirahara, T. (2011, July). Impact of head movement on sound localization with band-limited noise. In *INTER-NOISE and NOISE-CON Congress and Conference Proceedings* (Vol. 2011, No. 6, pp. 1963-1968). Institute of Noise Control Engineering;
- Muir, D., & Field, J. (1979). Newborn infants orient to sounds. *Child development*, 431-436;
- Nawaz, S., McNeill, C., & Greenberg, S. L. (2014). Improving sound localisation after cochlear implantation and auditory training for the management of single-sided deafness. *Otology & Neurotology*, 35(2), 271-276. <https://doi.org/10.1097/MAO.0000000000000257>;
- Noble, W. G. (1981). Earmuffs, exploratory head movements, and horizontal and vertical sound localisation. *Journal of Auditory Research*;

- Ohuchi, M., Iwaya, Y., Suzuki, Y., & Munekata, T. (2005). Training effect of a virtual auditory game on sound localisation ability of the visually impaired. Georgia Institute of Technology; <http://hdl.handle.net/1853/50191>;
- Parseihian, G., Jouffrais, C., & Katz, B. F. (2014). Reaching nearby sources: comparison between real and virtual sound and visual targets. *Frontiers in neuroscience*, 8, 269. doi: 10.3389/fnins.2014.00269;
- Parseihian, G., & Katz, B. F. G. (2012). Rapid head-related transfer function adaptation using a virtual auditory environment. *The Journal of the Acoustical Society of America*, 131(4), 2948–2957. <https://doi.org/10.1121/1.3687448>;
- Perrett, S., & Noble, W. (1997). The contribution of head motion cues to localisation of low-pass noise. *Perception & Psychophysics*, 59(7), 1018–1026. <https://doi.org/10.3758/BF03205517>;
- Poirier-Quinot, D., & Katz, B. F. (2018, August). Impact of HRTF individualization on player performance in a VR shooter game II. In *Audio Engineering Society Conference: 2018 AES International Conference on Audio for Virtual and Augmented Reality*. Audio Engineering Society.
- Rabini, G., Altobelli, E., & Pavani, F. (2019). Interactions between egocentric and allocentric spatial coding of sounds revealed by a multisensory learning paradigm. *Scientific reports*, 9(1), 7892. <https://doi.org/10.1038/s41598-019-44267-3>;
- Rayleigh, Lord. (1907). On our perception of sound direction. *The London, Edinburgh, and Dublin Philosophical Magazine and Journal of Science*, 13(74), 214–232. <https://doi.org/10.1080/14786440709463595>
- Shinn-Cunningham, B. G., Durlach, N. I., & Held, R. M. (1998). Adapting to supernormal auditory localisation cues. I. Bias and resolution. *The Journal of the Acoustical Society of America*, 103(6), 3656. <https://doi.org/10.1121/1.423088>;
- Shinn-Cunningham, B. G., Santarelli, S., & Kopco, N. (2000). Tori of confusion: Binaural localization cues for sources within reach of a listener. *The Journal of the Acoustical Society of America*, 107(3), 1627. <https://doi.org/10.1121/1.428447>
- Steadman, M. A., Kim, C., Lestang, J. H., Goodman, D. F., & Picinali, L. (2019). Short-term effects of sound localisation training in virtual reality. *Scientific Reports*, 9(1), 1-17. <https://doi.org/10.1038/s41598-019-54811-w>;
- Stitt, P., Picinali, L., & Katz, B. F. (2019). Auditory accommodation to poorly matched non-individual spectral localization cues through active learning. *Scientific Reports*, 9(1), 1-14, <https://doi.org/10.1038/s41598-018-37873-0>.
- Strelnikov, K., Rosito, M., & Barone, P. (2011). Effect of audiovisual training on monaural spatial hearing in horizontal plane. *PLoS one*, 6(3), e18344. <https://doi.org/10.1371/journal.pone.0018344>;
- Thurlow, W. R., & Runge, P. S. (1967). Effect of Induced Head Movements on Localisation of Direction of Sounds. *The Journal of the Acoustical Society of America*, 42(2), 480–488. <https://doi.org/10.1121/1.1910604>;
- Thurlow, W. R., Mangels, J. W., & Runge, P. S. (1967). Head movements during sound localization. *The Journal of the Acoustical society of America*, 42(2), 489-493. <https://doi.org/10.1121/1.1910605>;

- Trapeau, R., & Schönwiesner, M. (2015). Adaptation to shifted interaural time differences changes encoding of sound location in human auditory cortex. *NeuroImage*, 118, 26–38. <https://doi.org/10.1016/J.NEUROIMAGE.2015.06.006>;
- Valzolgher, C., Campus, C., Rabini, G., Gori, M. & Pavani, F. (accepted for publication). Updating spatial hearing abilities through multisensory and motor cues. *Cognition*;
- van der Meer, A. L., Ramstad, M., & van der Weel, F. R. (2008). Choosing the shortest way to mum: Auditory guided rotation in 6-to 9-month-old infants. *Infant Behavior and Development*, 31(2), 207-216. <https://doi.org/10.1016/j.infbeh.2007.10.007>;
- van Wanrooij, M. M., John, A., & Opstal, V. (2005). Relearning Sound Localisation with a New Ear. *The Journal of Neuroscience*, 25(22), 5413–5424. <https://doi.org/10.1523/JNEUROSCI.0850-05.2005>;
- Vercher, J. L., Magenes, G., Prablanc, C., & Gauthier, G. M. (1994). Eye-head-hand coordination in pointing at visual targets: spatial and temporal analysis. *Experimental brain research*, 99(3), 507-523. <https://doi.org/10.1007/BF00228987>;
- Verdelet, G., Desoche, C., Volland, F., Farnè, A., Coudert, A., Hermann, R., ... & Salemme, R. (2019, December). Assessing spatial and temporal reliability of the vive System as a tool for naturalistic behavioural research. In 2019 International Conference on 3D Immersion (IC3D) (pp. 1-8). IEEE.
- Wallach, H. (1940). The role of head movements and vestibular and visual cues in sound localisation. *Journal of Experimental Psychology*, 27(4), 339. <https://doi.org/10.1037/h0054629>;
- Wiebe, E. N., Lamb, A., Hardy, M., & Sharek, D. (2014). Measuring engagement in video game-based environments: Investigation of the User Engagement Scale. *Computers in Human Behavior*, 32, 123-132. <https://doi.org/10.1016/j.chb.2013.12.001>;
- Wightman, F. L., & Kistler, D. J. (1999). Resolution of front–back ambiguity in spatial hearing by listener and source movement. *The Journal of the Acoustical Society of America*, 105(5), 2841-2853. <https://doi.org/10.1121/1.426899>;
- World Medical Association. (2013). *WMA declaration of Helsinki: Ethical principles for medical research involving human subjects*. Retrieved from <https://www.wma.net/policies-post/wma-declaration-of-helsinki-ethical-principles-for-medical-research-involving-human-subjects/>;
- Zahorik, P., Bangayan, P., Sundareswaran, V., Wang, K., & Tam, C. (2006). Perceptual recalibration in human sound localisation: learning to remediate front-back reversals. *The Journal of the Acoustical Society of America*, 120(1), 343–359. <https://doi.org/10.1121/1.2208429>