



Where did that noise come from? Memory for sound locations is exceedingly eccentric both in front and in rear space

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Received: 10 January 2019 / Accepted: 3 June 2019 / Published online: 13 June 2019
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Abstract

Few studies have examined the stability of the representation of the position of sound sources in spatial working memory. The goal of this study was to verify whether the memory of sound position declines as maintenance time increases. In two experiments, we tested the influence of the delay between stimulus and response in a sound localization task. In Experiment 1, blindfolded participants listened to bursts of white noise originating from 16 loudspeakers equally spaced in a 360-degree circular space around the listener in such a way that the nose was aligned to the zero-degree coordinate. Their task was to indicate sounds' position using a digital pointer when prompted at varying delays: 0, 3, and 6 s after stimulus offset. In Experiment 2, the task was analogous to Exp. 1 with stimulus–response delays of 0 or 10 s. Results of the two experiments show that increasing stimulus–response delays up to 10 s do not impair sound localization. Participants systematically overestimated the eccentricity of the auditory stimulus by shifting their responses either toward the 90-degree coordinate, in alignment with the right ear, or toward the 270-degree coordinate, in alignment with the left ear. Such bias was analogous in the front and in the rear azimuthal space and was only marginally influenced by the delay conditions. We conclude that the representation of auditory space in working memory is stable, but directionally biased with systematic overestimation of eccentricity.

Keywords Eccentricity · Sound localization · Oblique effect · Spatial working memory · Directional bias

Introduction

Imagine you move to a small village in an Alpine valley. As soon as you arrive, you decide to go to the woods to pick mushrooms even if the surroundings are unknown to you. After a while, however, you realize that you are lost and cannot find your way back. Suddenly you hear church bells ring, and you immediately sprint toward the direction of the sound. After nine rings, however, the bells stop. Would you be able to find your way back following the memory of the sound's location, or are you going to spend your first night stuck in the woods?

This story illustrates the contrast between sound localization in perception and memory. When the bells are still ringing, you rely on auditory localization mechanisms to follow the direction of the sound. Humans utilize interaural differences in intensity, spectrum, and time to calculate the position of sounds in their surroundings (see Phillips 2008; Middlebrooks and Green 1991 for reviews). But what happens when the bells stop ringing? Only a few studies have analyzed the persistence and stability of auditory spatial information in working memory, the most notable being Lewald and Ehrenstein's (2001).

A great number of studies have been conducted on sound location in humans and other animals. There is evidence supporting that barn owls localize sound topographically (Knudsen and Konishi 1978; see Konishi 2003 for a review), which means that the cortical space used to represent the perceptual space is isomorphic to the represented perceptual space. Other birds, such as the chicken, also use topographic maps (Overholt et al. 1992). The discovery of topographic maps in birds led to the hypothesis that mammals may also use similar mechanisms for sound localization. Bats, for example, use spatio-topic maps to localize sound (Razak

Handling editor: Marta Olivetti Belardinelli (Sapienza University of Rome).

Reviewers: two researchers who prefer to remain anonymous.

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2011). In small-headed mammals and in humans, however, little evidence has surfaced supporting a topographic organization (Brunetti et al. 2005; Leaver and Rauschecker 2016), and recent studies have found opposing evidence favoring an opponent-channel model, in which intertemporal distances (ITDs) between stimuli are coded non-topographically (Salminen et al. 2010; Briley et al. 2012). In the opponent-channel model, two opposing sets of neurons are clustered in the left and right hemifields, and their response magnitudes increase as ITDs increase toward the left or right (Colburn and Latimer 1978; Harper and McAlpine 2004; McAlpine et al. 2001; van Bergeijk 1962; Von Békésy and Wever 1960; for review see McAlpine 2005). A sound's ITD is the relative activity balance between the two channels. This model develops and adjusts the Jeffress model (1948), in which neurons are assumed to be distributed in a linear array across both hemifields.

Sound localization accuracy varies according to the technique used to measure performance (Makous and Middlebrooks 1990). Relative localization thresholds (Mills 1958; Molino 1974; Perrott 1984) provide a measure of the ability to determine whether a stimulus has changed location. Relative thresholds provide measures of smaller minimal audible angle (MAA) than absolute thresholds, which assess the ability to determine the location of a single stimulus (Stevens and Newman 1936; Newton 1983; Butler 1986; Perrott et al. 1987; Middlebrooks 1992; Butler and Musicant 1993; Good and Gilkey 1996; for a review, see Recanzone et al. 1998). In this study, we will use an absolute localization task.

The cone of confusion (and its particular instance of front/back confusion) is a perceptual phenomenon in which a listener is not able to determine whether a sound originated either from the location in which the sound source is actually located or from a mirror location which shares identical phase delays transient disparities with the sound source. Such phenomenon is often observed in absolute localization tasks (Oldfield and Parker 1984; Wightman and Kistler 1989; Wenzel et al. 1993). After controlling for front-back confusion and cone of confusion, the signed angular azimuthal error is at its lowest magnitude at locations presented in front of subjects. Error magnitude increases as a function of eccentricity and is the worst at locations behind the subjects' heads (Makous and Middlebrooks 1990).

Performance is also influenced by the method used to measure the pointing response (Gilkey et al. 1995). Different types of pointing, such as head pointing (Makous and Middlebrooks 1990), gun pointing (Oldfield and Parker 1984), laser pointing (Lewald and Ehrenstein 1998), stylus pointing (Gilkey and Anderson 1994), and gaze pointing (Populin 2008), have been used to allow participants to indicate sound position in azimuthal space. Head pointing is the most accurate method of response (Middlebrooks and

Green 1991). Pollack and Rose (1967) compared localization with restricted-head motion and allowed-head motion and found that average errors were 10–15% less when head movement was allowed. Populin (2008) showed that gaze pointing allows smaller angular error than head pointing when stimuli are located in the frontal field, while no differences between methods are found for more eccentric positions. In general, these findings suggest that the method of response can significantly affect localization accuracy in a given spatial area. Such evidence begs the question whether different response methods can not only modulate response accuracy but also produce or prevent the emergence of systematic response biases.

As mentioned above, very few studies have investigated the stability of the memory for sound position. Lewald and Ehrenstein (2001) investigated sound localization in perception and working memory. The task was to indicate the position of sound source through a laser pointer arranged on the subjects' heads. Participants were asked to keep the laser pointer aligned with an illuminated "target square", which was located in front of their mid-sagittal body line, and to move their head and gaze toward the sound position when prompted. The purpose of the target square was to keep the head position constant before stimuli were presented to subjects. The target square provided both spatial and temporal cues. Spatially, it signaled the position of the zero-degree speaker. Temporally, it provided the prompt to move the head toward the sound. Participants had to wait for 0, 4, 8, or 12 s before responding. The authors found a systematic bias toward the direction of the ears. Interestingly, such systematic bias was progressively larger when the stimulus–response delay increases.

Lewald and Ehrenstein (2001) results seem to indicate that, when estimating the azimuthal position of sounds, human listeners tend to systematically overestimate the eccentricity of the sound source. Also, such eccentricity overestimation worsens as a function of the delay between stimulus and response. The overestimated eccentricity effect was previously reported in the literature (e.g., Matsumoto and Scripture 1897; Pierce 1901; Preibisch-Effenberger 1966; Oldfield and Parker 1984; Lewald and Ehrenstein 1998) and more recently by Garcia et al. (2017), but only in the front field. For example, the observation that the effect worsens as a function of delay is possibly associated with the use of visual cues. There is evidence that reorienting attention in space can be modulated by cross-modal influences, from vision to hearing (Slutsky and Recanzone 2001), from hearing to vision (Botta et al. 2011), and bidirectionally (Alais and Burr 2004, Ferlazzo et al. 2002). In particular, the role of non-informative vision in auditory spatial cognition (Kennett et al. 2001) and the dominance of visual perception in cross-modal localization tasks (Pick et al. 1969) support

the idea that, by using visual cues, auditory localization can be cross-modally biased by visual perception. Clarke et al. (1998) observed that visual interference significantly decreased sound localization. Goossens and van Opstal (1999) studied non-auditory influences in sound localization in humans. They systematically manipulated eye and head positions before asking participants to perform a saccade toward an auditory stimulus in darkness. They found that subjects were able to reconstruct the position of the auditory source despite these manipulations. The authors concluded that humans use a body-centered frame of reference to represent auditory space in both azimuth and elevation.

Moreover, there is also direct evidence that spatial references affect sound localization (Goossens and van Opstal 1999; Populin 2008). We argue that the association of a prompt with specific external location (like the visual target square with the mid-sagittal in Lewald and colleagues' study) can provide a cross-modal spatial cue. Consequently, it is not sure whether the eccentricity overestimation effect observed in Lewald and Ehrenstein is due to the cross-modal integration of auditory and visual signals or if it can be also obtained in absence of visual cues.

The second limitation is that their study and the other above-mentioned studies reporting an eccentricity effect only included sound sources located in the front field of azimuthal space. Consequently, it is not possible to conclude from their data that what they observed is a general eccentric overestimation effect valid for all the circular azimuthal space around the listener. The goal of our study is to confirm that the eccentricity overestimation effect occurs in working memory even in absence of visuospatial cues and to generalize it to all azimuthal coordinates by including sounds originating from sources equally distributed across all positions in a 360-degree azimuthal auditory field.

In this study, we designed an experimental procedure where blindfolded participants were asked to provide a localization response after a LED light prompt was presented directly inside the blindfold while their eyes were closed. Such signal is perceived as a diffuse, non-directional variation of illumination, instead as of a spatial cue. We believe that by providing a dissociation between the prompt (temporal) and visual reference (spatial), we were able to prevent the intervention of visual spatial reference as a modulating factor in the spatial representation of the auditory space.

The goal of this study was to investigate whether or not the accuracy of the memory for sound position decays as a function of the delay between stimulus (sound) and response (localization of the source in the azimuthal plane). We also wanted to verify whether the presence of systematic directional distortions in the representation of the auditory space, if any, would be influenced by the delay between stimulus and response.

Experiment 1

Methods

Ethics statement

The experiment was conducted in agreement with the ethics and safety guidelines of Utrecht University, which are based on the Declaration of Helsinki. A written informed consent was obtained from all participants. Under the advice of the WMO Advisory Committee of the Faculty of Social and Behavioral Sciences at Utrecht University, we decided not to submit our study for approval to the Medical Review Committee (METC) of the Utrecht Medical Center (UMC), as an explicit approval was not necessary for studies of this kind.

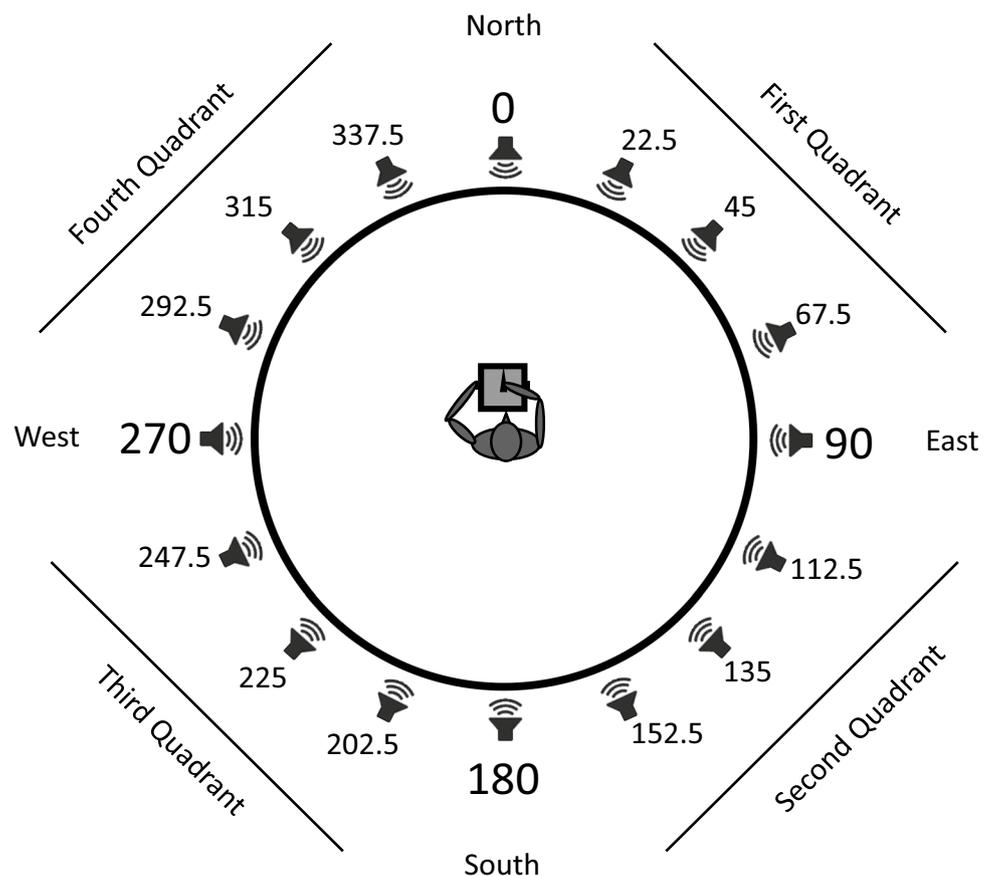
Apparatus

The experimental setting included sixteen loudspeakers lined around a sound-attenuated circular chamber (see Fig. 1), a master workstation computer, an input/output 24-channel sound card (Motu 24 I/O), a digital pointer, and a blindfold with embedded LED lights. All loudspeakers were arranged on wooden supports attached to the walls of the circular chamber at the elevation of 1.20 meters from the ground. The circular chamber was built using medium-density fiberboard (MDF) panels entirely covered with acoustic foam egg crate 48" × 24" × 2.5" panels for sound absorption. The average background noise in the listening chamber was 38.5 dBA, with no peaks above 42 dBA.

The chamber had a diameter of 3.10 meters. The loudspeakers were equidistant from one another with an azimuthal separation of 22.5 degrees and equidistant from the center of the chamber. The distance between the center of the chamber and the centroid of each speaker was 1.55 meters.

A digital pointer with an arrow capable of rotating 360 degrees in each azimuthal direction was used by participants to indicate sound locations. The device was made of a square-shaped metal box (height 15 cm, length 25 cm, and width 25 cm) to which a metal pointer (16 cm long). The pointer was able to rotate 360 degrees in both directions (see Fig. 2). The box was aligned to the north–south and east–west axis of the chamber and firmly taped to a table fixed to the ground through screws that prevented the table to move off position. The metal box with the pointer was located exactly in the middle of the circular chamber, with the rotation point of the pointer equidistant from each of the 16 loudspeakers. The resolution of the digital pointer was 0.5 degrees.

Fig. 1 Spatial arrangement of loudspeakers around the listener in both experiments



Directional responses were digitally recorded and sent to the master computer via an analog port input. Head-pointing devices are often preferred to rotating pointing devices because they are more accurate (Pollack and Rose 1967; Haber et al. 1993), but in our case we preferred to use a rotating digital pointer because we needed listeners to be able to localize sound sources located in the rear space. Participants wore a blindfold equipped with two small LED lights positioned near the eye sockets. The LED lights never had direct physical contact with the participants' eyes, and the intensity of the light was soft enough not to cause any eye damage or discomfort. Participants were recommended to keep their eyes closed during the experiment. The blindfold's LEDs were used to prompt the participant to respond by moving the pointer toward the direction of the auditory stimulus. To ensure the participants' heads remained in a fixed position throughout the duration of the experiment, a chin rest was used. The experiment was designed and executed using MATLAB®.

Participants

Twelve students from Utrecht University (8 women) with an average age of 25.5 (SD=4.2) participated in the study in exchange of a small amount of money or course credits.

All participants reported normal hearing and normal or corrected-to-normal vision.

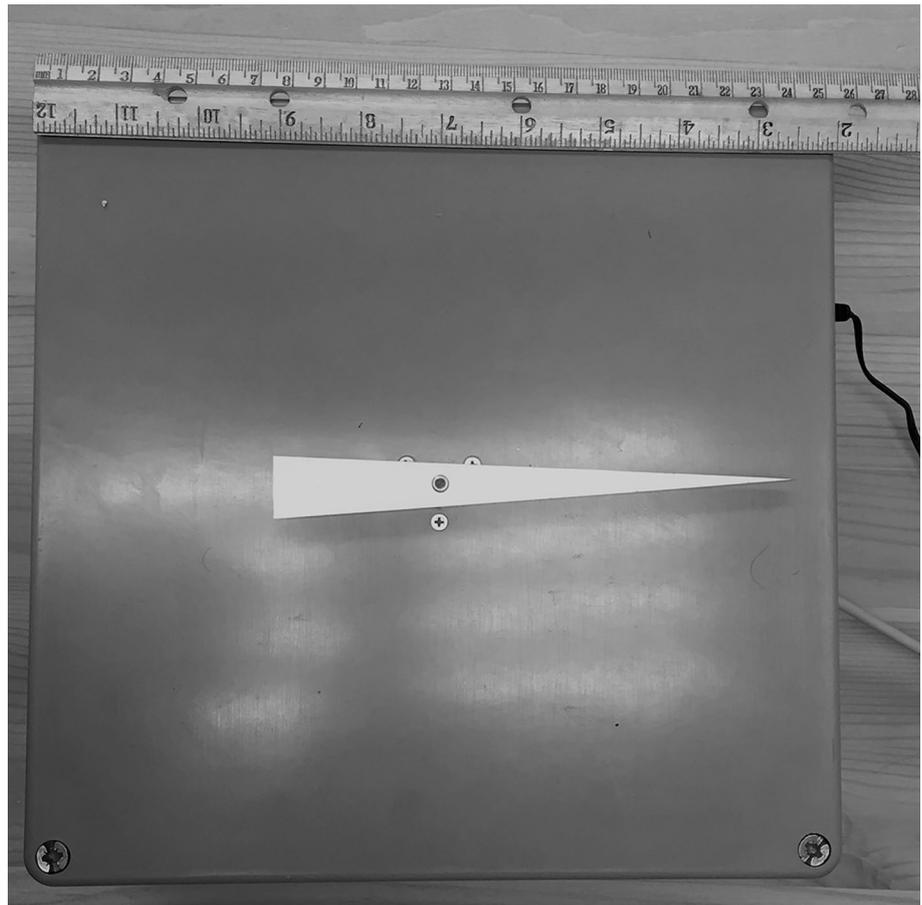
Materials

The stimuli were bursts of Gaussian noise with 5 ms linear rise and fall generated in MATLAB. Stimuli were played at 70 dBA for a duration of 500 ms.

Procedure

During the experiment, participants listened to sounds emitted in a random order from the sixteen loudspeakers. In order to avoid influences of visual cues, participants were blindfolded before entering the experimental room and remained blindfolded throughout the entire duration of the experiment. Participants were neither aware of the number nor of the locations of the loudspeakers within the room. Before the experiment, the experimenter guided the blindfolded participants inside the experimental room, helped her/him sit in a chair in front of a table placed in the middle of the circular room, and let her/him familiarize with the pointing device. The pointing device had a button on each side allowing participants to log in the chosen position of the arrow and initiate the next sound. The participant could

Fig. 2 Top-view picture of the pointer device used in experiments 1 and 2



choose his preferred hand to respond with because buttons were on both sides of the pointer. Participants sat erect on the chair and placed their heads on a chin rest, aligning their nose with the zero-degree speaker, their left ear with the speaker located at the 270 degrees and the right ear aligned with the speaker at 90 degrees. Participants did not report any problems in understanding how to use the pointer to indicate the origin of the sounds. When the participant was ready to start, the experimenter left the chamber and, after prompting the participant, started the experiment.

Three blocks of trials were administered to each participant, each block with a different condition of delay. The order of conditions was counterbalanced between participants. In between blocks of trials, participants rested for a few minutes in the adjacent room.

Angular responses were recorded by the digital pointer. When the blindfolded participants heard the emitted sound, they aimed the pointer to indicate what direction the sound came from. The LED flash from their blindfold prompted them to use the pointer. Participants could not use the pointer before they saw the LED flash. The pointer recorded their answers in degrees, and their answers were compared with the loudspeakers' actual positions in the room to determine the accuracy of the participant. The response delay had three

delay conditions: 0, 3, and 6 s from the offset of the noise burst. In the (very rare) case that participants did not provide a response within 10 s after the LED light flash, the experiment automatically proceeded to the next trial. There were 128 trials of each delay condition (384 total trials). Each speaker was used 8 times per condition. Each session had an average duration of about 40 min.

Spatial coordinates, types of errors, data processing, and statistical analysis

Sixteen different locations in the horizontal plane were used in this experiment. The choice of sixteen locations was made to have four cardinal points and several intermediate locations in each of the four quadrants. Each quadrant, in particular, has one source that is closer to one of the two cardinal points, a source that is intermediate between cardinal points, and a third source that is closer to the other cardinal point. Localization errors were calculated as the azimuthal difference between the stimulus and the response location (response location minus stimulus location). Unsigned errors were obtained by calculating the absolute value of the errors and were used as a measure of accuracy (magnitude of the error irrespective of direction). Signed errors indicate bias

toward a direction and keep the direction of the error. A negative error (undershooting) is a localization response that has fewer degrees than the actual target position (for example, if the target position is 22.5 degrees and the response is 15 degrees), while a positive error (overshooting) is a response that has more degrees than the actual target position (for example, if the target position is 22.5 degrees and the response is 30 degrees). A significant signed error in the averaged responses of a participant for a specific location indicates the presence of systematic directional bias.

To test accuracy and directionality of the angular error across the 16 locations, we ran a series of single sample *t* tests in which we compared responses for each speaker position with a reference value. For accuracy, we contrasted the unsigned localization errors with the grand average of localization errors. We used the above-mentioned *t* tests to verify whether accuracy at a particular position was significantly smaller or greater than the average. To prevent the risk of inflated type 1 error, we corrected the *p* values of each *t* test with the procedure introduced by Benjamini and Hochberg (1995). The corrected *p* values are included in the tables of results for each series of *t* tests.

We also analyzed with ANOVA the difference in accuracy between loudspeakers located in cardinal points: north (0 degree), east (90 degree), south (180 degree), west (270 degree) and in intermediate positions, which we defined quadrants. Quadrant data were obtained by averaging the unsigned and signed errors produced by each participant when localizing sounds from loudspeakers at 22.5, 45, and 67.5 degrees (first quadrant), at 112.5, 135, and 157.5 degrees (second quadrant), at 202.5, 225.5, and 247.5 degrees (third quadrant), and at 292.5, 315, and 337.5 degrees (fourth quadrant). Accuracy at cardinal points and at quadrants in the three delay conditions was compared in an 8X3 ANOVA analysis with *location* (north, east, south, west, first quadrant, second quadrant, third quadrant, and fourth quadrant) and *delay* (0 s, 3 s, 6 s) as independent variables and the unsigned error as dependent variable.

For the directional bias, we contrasted the averaged signed localization errors with the reference value of zero (absence of bias). If the signed error at a particular position was significantly different from zero, then the directionality of the error was also significant, indicating the presence of a systematic directional bias for that particular location. This test produced two kinds of possible distortions: undershooting and overshooting. Errors at cardinal points and at quadrants in the three delay conditions were compared in an 8X3 ANOVA analysis with *location* (north, east, south, west, first quadrant, second quadrant, third quadrant, and fourth quadrant) and *delay* (0 s, 3 s, 6 s) as independent variables and the signed error as dependent variable.

Before analysis, data were processed to exclude responses generated by well-known biases like the cone of confusion

and the front–back confusion (see, for example, Oldfield and Parker 1984). All errors greater than 45 degrees were excluded from analysis. We chose a 45-degree threshold value because the angular separation between two consecutive loudspeakers is 22.5 degrees. In our setup, 45 degree is the minimal error that the cone-of-confusion phenomenon can produce ($22.5 \times 2 = 45$). Cone-of-confusion errors and front–back confusions accounted for 10.06% of the total trials from 16 subjects. Filtering them from the final analysis did not significantly skew the results. Errors from four participants exceed two standard errors from the mean and therefore were excluded from final analysis, lowering the final sample size to 12.

Results

The mean unsigned error in the sound localization task was $M = 14.66$ ($SD = 5.96$). Concerning the influence of speaker's location in localization accuracy, cardinal points (0, 90, 180, and 270 degrees) tended to elicit better performances. A *t* test on the mean error for each speaker showed that all four cardinal location loudspeakers, and also at the 112.5- and 247.5-degree loudspeakers, elicited significantly lower angular errors than the grand mean of errors in all loudspeakers (see Table 1). On the contrary, loudspeakers placed at 135, 157.5, and 202.5 degrees elicited significantly higher errors than the grand mean.

To confirm that cardinal points elicited more accurate localizations than loudspeakers within quadrants, we performed a 8X3 ANOVA analysis with *location* (north, first quadrant, east, second quadrant, south, third quadrant, west, fourth quadrant, see Fig. 1 for a graphical representation of the eight levels) and *delay* as independent within-subject variables and the unsigned angular error as the dependent variable. Results show an effect of the loudspeaker position, $F(7, 77) = 10.58$, $p < .0001$, $\eta^2 = 0.49$ which indicate a significant difference in accuracy response between loudspeakers. Specifically, the post hoc analysis (Fisher LSD) showed a systematic superior accuracy of loudspeakers located in all four cardinal points over loudspeakers located within the four quadrants. The unsigned errors in all cardinal points were not different from each other (all *p* values > 0.05) and were all significantly smaller than the unsigned errors of all four quadrants. Similarly, all quadrants were not different from each other. (All comparisons have *p* values greater than $p = 0.05$.) There was no effect of *delay*, $F(2, 22) = .94$, $p = .40$, indicating that localization accuracy was not affected by the amount of time in between auditory stimulation and localization response. The interaction between *delay* and *location* was also not significant, $F(14, 70) = .62$, $p = .85$

Concerning directional errors, we ran a *t* test on the mean signed error for each loudspeaker comparing it to a reference value of zero (absence of directional error). Results showed

Table 1 Results of one-sample *t* test and descriptive statistics for the unsigned error in the 16 speakers

Speaker # (deg.)	Mean error	SD	<i>n</i>	Comparison value (err. grand mean)	<i>t</i>	<i>p</i>	Benjamini–Hochberg <i>p</i> value
1 (0 deg.)	7.14	4.50	12	14.66	–5.779*	< 0.0001	0.001
2 (22.5 deg.)	15.38	8.69	12	14.66	0.290	0.776	0.828
3 (45 deg.)	16.38	6.88	12	14.66	0.867	0.404	0.497
4 (67.5 deg.)	17.11	5.70	12	14.66	1.488	0.164	0.239
5 (90 deg.)	8.20	5.17	12	14.66	–4.322*	0.001	0.003
6 (112.5 deg.)	9.71	1.55	12	14.66	–3.185*	0.008	0.021
7 (135 deg.)	27.77	2.19	12	14.66	5.969*	< 0.0001	0.001
8 (157.5 deg.)	18.14	1.32	12	14.66	2.632*	0.023	0.046
9 (180 deg.)	7.11	1.18	12	14.66	–6.356*	< 0.0001	0.001
10 (202.5 deg.)	20.09	2.15	12	14.66	2.519*	0.028	0.050
11 (225 deg.)	14.97	1.47	12	14.66	0.215	0.833	0.833
12 (247.5 deg.)	10.08	1.06	12	14.66	–4.286*	0.001	0.003
13 (270 deg.)	10.36	1.58	12	14.66	–2.713*	0.020	0.046
14 (292.5 deg.)	17.53	2.23	12	14.66	1.287	0.224	0.299
15 (315 deg.)	19.01	2.33	12	14.66	1.867	0.088	0.141
16 (337.5 deg.)	15.55	1.47	12	14.66	0.606	0.556	0.635

**p* < .05 after Benjamini–Hochberg correction

that the four loudspeakers located at the cardinal points were never significantly different from zero, in none of the three delay conditions (see Table 2), while in all the other conditions, but two, there was always a significant undershooting (negative error) or overshooting (positive error). Interestingly, from the *t* test analysis it emerges that the direction of the error, which is indicated by its sign in the signed error measure, reverses systematically at each cardinal point crossing (see Fig. 3).

To verify the presence of systematic biases in localization, we performed a 8X3 ANOVA analysis with *location* (north, first quadrant, east, second quadrant, south, third quadrant, west, fourth quadrant) and *delay* as independent within-subject variables and the signed angular error as the dependent variable. Results show an effect of the loudspeaker position, $F(7, 35) = 19.203$, $p < .0001$, $\eta^2 = 0.52$ which indicate that directional bias varies in strength, direction, and statistical significance according to the position of the loudspeaker. In terms of magnitude, the signed error in cardinal loudspeakers was always smaller than ± 5 , while the signed error in quadrants was always greater than ± 10 . The post hoc analysis (Fisher LSD) showed that the signed errors in all cardinal points were smaller than the errors in the quadrants (all *p* values < 0.05), indicating a greater directional bias for loudspeakers located in the four quadrants than for loudspeakers located in cardinal points. The signed error in loudspeakers located in cardinal points did not differ from each other (all *p* values > 0.05). Most importantly, the signed errors in adjacent quadrants (first with second, second with third, third with fourth) were always

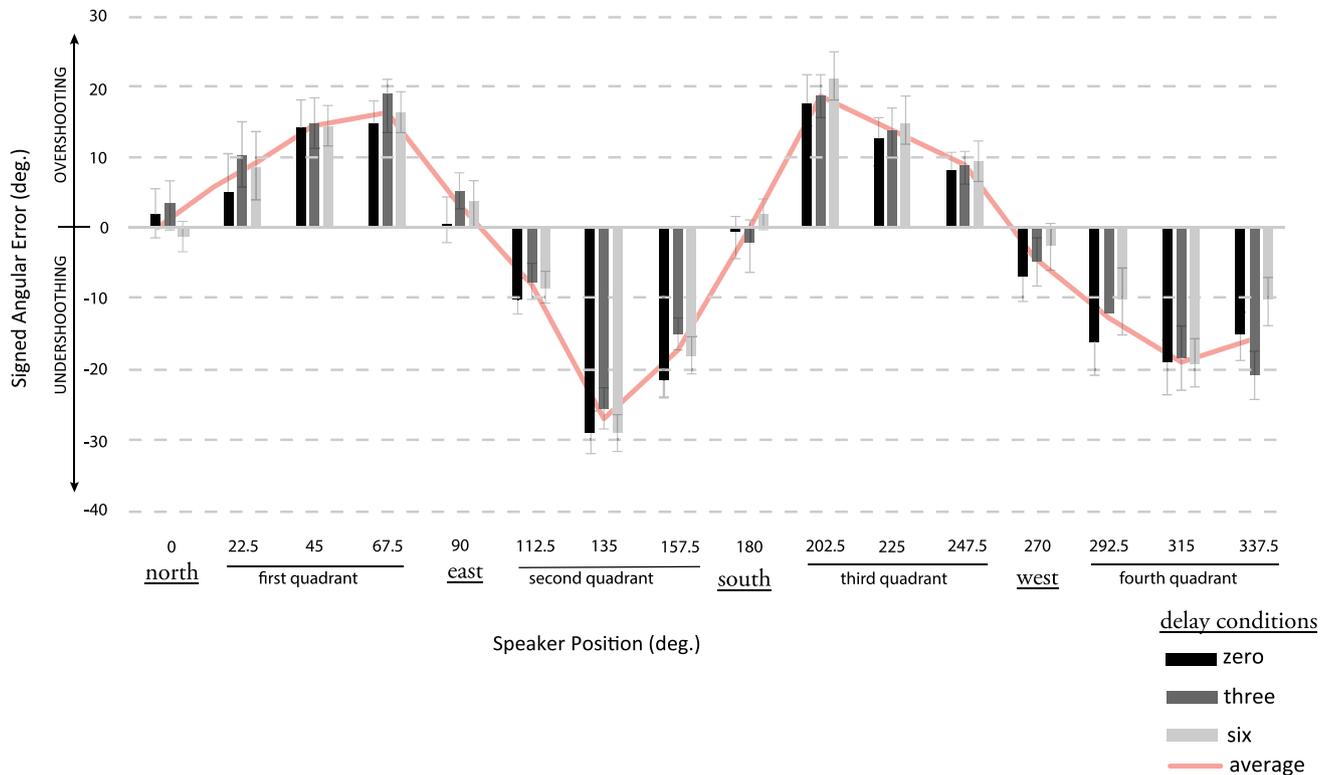
of opposite sign and their difference always significant (all *p* values < 0.0001). On the contrary, in opposing quadrant, the signed errors were always of the same sign and their difference was always not significant (all *p* values < 0.05). This pattern is clearly evident in all *delay* conditions (see Fig. 2).

There was also a significant effect of *delay*, $F(2, 10) = 5.44$, $p = .025$, $\eta^2 = 0.16$. In particular, post hoc analysis (Fisher LSD) showed that the signed errors in the six-second delay (Mean = 1.16) was significantly different ($p = 0.008$) from errors in the zero-second delay condition (Mean = –4.49), while the difference between the three-second conditions was not different from the zero-second one ($p = 0.19$) or the six-second one ($p = 0.132$). It is important to note that, as the main factor *delay* averages positive and negative errors in eight different locations (four quadrants and four cardinal points), the significant difference in delay between zero and six conditions does not indicate that the performance in the six-second condition was any worse (or any better) than in the other delay conditions. Such inference could only be derived from the analysis of the interaction between *location* and *delay*. Interestingly, the interaction between *delay* and *location* was not significant, $F(14, 70) = 0.38$, $p = .975$ indicating that the amount of delay did not significantly influence the error in specific locations of the azimuthal plane.

Two main observations emerge from the results. First, stimuli originating from loudspeakers at cardinal points do not elicit any significant directional bias. Second, the direction of the error, which is indicated by its sign in the signed error measure, reverses systematically at each cardinal point

Table 2 Results of one-sample *t* test and descriptive statistics for the signed error in the 16 speakers in Exp. 1

Speaker # (location)	Delay (s)	Mean signed error	SD	<i>n</i>	Comparison value	<i>T</i>	Directional bias	<i>df</i>	<i>p</i>	Benjamini–Hochberg <i>p</i> value
1 (0 deg.)	0	1.97	12.33	12	0.00	0.55	None	11	0.59	0.62933
2 (22.5 deg.)	0	5.23	18.86	12	0.00	0.96	None	11	0.35	0.40976
3 (45 deg.)	0	14.30	13.33	12	0.00	3.71*	Overshooting	11	<<0.0011	< 0.001
4 (67.5 deg.)	0	14.90	10.85	12	0.00	4.76*	Overshooting	11	<<0.0011	< 0.001
5 (90 deg.)	0	0.66	12.45	12	0.00	0.18	None	11	0.85	0.85
6 (112.5 deg.)	0	−9.86	10.23	12	0.00	−3.34*	Undershooting	11	< 0.001	< 0.001
7 (135 deg.)	0	−28.82	10.50	12	0.00	−9.51*	Undershooting	11	< 0.001	< 0.001
8 (157.5 deg.)	0	−21.48	6.46	12	0.00	−11.52*	Undershooting	11	< 0.001	< 0.001
9 (180 deg.)	0	−0.80	8.62	12	0.00	−0.32	None	11	0.75	0.76596
10 (202.5 deg.)	0	17.75	14.51	12	0.00	4.24*	Overshooting	11	< 0.001	< 0.001
11 (225 deg.)	0	12.54	11.01	12	0.00	3.94*	Overshooting	11	< 0.001	< 0.001
12 (247.5 deg.)	0	8.36	9.13	12	0.00	3.17*	Overshooting	11	< 0.001	< 0.001
13 (270 deg.)	0	−6.91	12.02	12	0.00	−1.99	None	11	0.07	0.09333
14 (292.5 deg.)	0	−15.94	17.13	12	0.00	−3.22*	Undershooting	11	< 0.001	< 0.001
15 (315 deg.)	0	−18.95	11.51	12	0.00	−5.70*	Undershooting	11	< 0.001	< 0.001
16 (337.5 deg.)	0	−15.23	11.83	12	0.00	−4.46*	Undershooting	11	< 0.001	< 0.001
1 (0 deg.)	3	3.58	10.86	12	0.00	1.14	None	11	0.27	0.324
2 (22.5 deg.)	3	10.41	16.47	12	0.00	2.19	None	11	0.05	0.06857
3 (45 deg.)	3	14.82	12.48	12	0.00	4.11*	Overshooting	11	< 0.001	< 0.001
4 (67.5 deg.)	3	19.11	7.01	12	0.00	9.44*	Overshooting	11	< 0.001	< 0.001
5 (90 deg.)	3	5.41	8.80	12	0.00	2.13	None	11	0.05	0.06857
6 (112.5 deg.)	3	−7.72	8.12	12	0.00	−3.29*	Undershooting	11	< 0.001	< 0.001
7 (135 deg.)	3	−25.48	9.97	12	0.00	−8.85*	Undershooting	11	< 0.001	< 0.001
8 (157.5 deg.)	3	−14.96	7.48	12	0.00	−6.93*	Undershooting	11	< 0.001	< 0.001
9 (180 deg.)	3	−2.47	12.59	12	0.00	−0.68	None	11	0.51	0.55636
10 (202.5 deg.)	3	18.86	10.69	12	0.00	6.11*	Overshooting	11	< 0.001	< 0.001
11 (225 deg.)	3	13.82	10.99	12	0.00	4.35*	Overshooting	11	< 0.001	< 0.001
12 (247.5 deg.)	3	8.74	7.71	12	0.00	3.92*	Overshooting	11	< 0.001	< 0.001
13 (270 deg.)	3	−4.67	11.85	12	0.00	−1.36	None	11	0.19	0.24
14 (292.5 deg.)	3	−12.06	16.72	12	0.00	−2.50*	Undershooting	11	0.02	0.03
15 (315 deg.)	3	−18.40	15.05	12	0.00	−4.24*	Undershooting	11	< 0.001	< 0.001
16 (337.5 deg.)	3	−20.68	11.51	12	0.00	−6.22*	Undershooting	11	< 0.001	< 0.001
1 (0 deg.)	6	−1.10	7.39	12	0.00	−0.51	None	11	0.61	0.63652
2 (22.5 deg.)	6	8.93	16.85	12	0.00	1.84	None	11	0.09	0.11676
3 (45 deg.)	6	14.61	10.24	12	0.00	4.94*	Overshooting	11	< 0.001	< 0.001
4 (67.5 deg.)	6	16.46	9.41	12	0.00	6.06*	Overshooting	11	< 0.001	< 0.001
5 (90 deg.)	6	3.69	10.50	12	0.00	1.22	None	11	0.24	0.29538
6 (112.5 deg.)	6	−8.45	7.38	12	0.00	−3.96*	Undershooting	11	< 0.001	< 0.001
7 (135 deg.)	6	−29.03	8.78	12	0.00	−11.45*	Undershooting	11	< 0.001	< 0.001
8 (157.5 deg.)	6	−18.00	8.82	12	0.00	−7.07*	Undershooting	11	< 0.001	< 0.001
9 (180 deg.)	6	1.93	7.86	12	0.00	0.85	None	11	0.41	0.46857
10 (202.5 deg.)	6	21.38	11.41	12	0.00	6.49*	Overshooting	11	< 0.001	< 0.001
11 (225 deg.)	6	15.33	11.74	12	0.00	4.52*	Overshooting	11	< 0.001	< 0.001
12 (247.5 deg.)	6	9.62	9.30	12	0.00	3.58*	Overshooting	11	< 0.001	< 0.001
13 (270 deg.)	6	−2.50	11.07	12	0.00	−0.78	None	11	0.45	0.50233
14 (292.5 deg.)	6	−9.99	15.12	12	0.00	−2.29*	Undershooting	11	0.04	0.05818
15 (315 deg.)	6	−19.01	11.80	12	0.00	−5.58*	Undershooting	11	< 0.001	< 0.001
16 (337.5 deg.)	6	−10.09	10.68	12	0.00	−3.27*	Undershooting	11	< 0.001	< 0.001

Table 2 (continued)* $p < .05$ after Benjamini–Hochberg correction**Fig. 3** Signed angular error as a function of loudspeaker position and stimulus–response delay in Exp. 1

crossing. Specifically, there was always overshooting in all loudspeakers within the first quadrant (between 2 and 89 degrees), undershooting in loudspeakers within the second quadrant (between 91 and 179 degrees), overshooting in loudspeakers between the third quadrant (between 181 and 269 degrees), and undershooting in loudspeakers of the fourth quadrant (between 271 and 359 degrees) (see Fig. 1).

Discussion

In Experiment 1, we asked blindfolded participant to localize sounds originating from 16 different sources in a 360-degree azimuthal space. The goal was to verify whether the magnitude and the direction of the localization error were influenced by the position of the sound source and by the amount of delay between stimulation and localization response.

Localization accuracy was relatively low compared to previous findings (see, for example, Recanzone et al. 1998; Makous and Middlebrooks 1990). The greater magnitude of errors is probably due to the fact that the above-mentioned studies used head movements to indicate sound positions, which generally leads to greater accuracy (Populin 2008).

Moreover, we found that sounds were easier to localize in certain locations: sounds originating from cardinal points elicited more precise localization responses than sounds originating from loudspeakers located in intermediate (non-cardinal) positions. These results are consistent with previous findings (Recanzone et al. 1998; Makous and Middlebrooks 1990). This was not the case in McCarthy and Olsen (2017), where participants were more accurate in non-cardinal positions in front of the listeners than in the left and right cardinal positions.

Interestingly, results indicate the presence of a systematic overestimation of the eccentricity of the sound source which is manifested in significant localization shift toward the direction of the ear nearest to the loudspeaker in the azimuthal plane. This effect is present in all loudspeakers except for the ones placed at cardinal points. Participants systematically overshoot (responses placed on the right of the actual location) in response of stimuli placed within quadrants 1 and 3, while they systematically undershot (responses placed on the left of the actual location) in response to stimuli placed within quadrants 2 and 4. Our results generalize to different techniques of response (absence of vision) and to the entire azimuthal

auditory field, what shown in Lewald and Ehrenstein's study (2001) in which participants had to localize sounds originating from 6 positions with different degrees of eccentricity (0° , $\pm 20^\circ$, $\pm 40^\circ$, $\pm 60^\circ$). It seems that such systematic shifts were not caused by head movements as participants were not allowed to orient their heads to the sound source, and their heads, unlike in the Lewald and Ehrenstein procedure, remained in a fixed position during both sound perception and localization response.

The amount of delay between stimulus and response did not affect neither the accuracy, nor the directionality of the error in any specific location. In fact, while localization accuracy in the three-second delay and six-second delay was analogous to the no-delay condition, and the amount of directional bias did not increase with delay. The accuracy results are consistent with Lewald and Ehrenstein (2001), who found that the unsigned error does not increase as a function of delay. However, our results are not consistent with theirs about the influence of delay. In fact, they found that the amount of directional error increase with the delay, while we did not find any influence of delay on the amount of signed error for specific locations.

Experiment 2

In Experiment 1, we manipulated the delay between stimulus and responses including three conditions of delay (zero, three seconds, six seconds). We found that delays up to 6 s had no influence on the directional bias and no effect on accuracy. In Experiment 2, we wanted to test whether the hypothesis of delaying response had no effect in the accuracy and the directionality of the error with greater delays. We decided to test two delay conditions with the same experimental design of Experiment 1: a ten-second delay condition and a zero-delay condition. There were 128 trials of each delay condition (256 total trials). Each speaker was used 8 times per condition. Each session had an average duration of about 40 min.

Also, it should be noted that Experiment 2 took place in different laboratories (Multisensory Laboratory, Lawrence Technological University), and while all the experimental settings and procedures were analogous to those used in Experiment 1, the physical experimental rooms in the two experiments were different. Experiment 2, therefore, allows for retesting the zero-delay condition of Experiment 1 in a different physical setting with a different sample.

Methods

Ethics statement

The experiment was conducted in agreement with the ethics and safety guidelines of Lawrence Technological University,

which are based on the Declaration of Helsinki. A written informed consent was obtained from all participants. The study was reviewed and approved by the IRB of Lawrence Technological University.

Apparatus

The apparatus for Experiment 2 was the same as in Experiment 1.

Participants

The participants included fifteen healthy students (ages 18–25; 3 females) from Lawrence Technological University which had not taken part in Experiment 1. They were compensated for their participation with a small amount of money or course credits. All participants reported to have normal hearing.

Materials

Same as in Experiment 1.

Procedure

The procedure was identical as in Experiment 1 except for stimulus–response delays, which were 0 and 10 s.

Results

Before analysis, trials with errors exceeding 45 degrees were excluded from the final data to avoid the influence of the cone-of-confusion phenomenon and front–back inversion. Such trials were less than 1% of the total trials. Concerning accuracy, the mean unsigned error in the sound localization task was $E = 11.70$ ($SD = 8.6$).

Concerning the magnitude of the angular error, a t test on the mean error for each loudspeaker showed that all but one loudspeaker at the cardinal points (the exception is loudspeaker at 270 degrees), elicited angular errors that were significantly inferior to the grand mean of errors in all loudspeakers (see Table 3).

The error at the 157.5 loudspeaker was significantly inferior to the grand mean. To confirm that cardinal points elicited more accurate localizations than loudspeakers within quadrants, we performed a 8X3 ANOVA with *location* (north, first quadrant, east, second quadrant, south, third quadrant, west, fourth quadrant,) and *delay* (zero- and 10 seconds) as independent within-subject variables and the unsigned angular error as the dependent variable. Results show a significant effect of *location*, $F(7, 98) = 7.17$, $p < .0001$, $\eta^2 = 0.34$ which indicate that the sound was more difficult to localize when originating from certain locations.

Table 3 Results of one-sample *t* test and descriptive statistics for the unsigned error in the 16 speakers in Exp. 2

Speaker # (location)	Mean error	SD	<i>n</i>	Comparison value	<i>t</i>	<i>df</i>	<i>p</i>	Benjamini–Hochberg <i>p</i> value
1 (0 deg.)	6.54	5.52	15	11.70	−3.621*	14	0.004	0.021
2 (22.5 deg.)	8.46	7.37	15	11.70	−1.698	14	0.124	0.248
3 (45 deg.)	13.44	10.24	15	11.70	0.671	14	0.559	0.561
4 (67.5 deg.)	14.01	7.76	15	11.70	1.114	14	0.303	0.404
5 (90 deg.)	5.51	4.88	15	11.70	−5.263*	14	0.001	0.008
6 (112.5 deg.)	9.96	7.41	15	11.70	−0.905	14	0.441	0.543
7 (135 deg.)	16.10	8.46	15	11.70	1.976	14	0.070	0.192
8 (157.5 deg.)	18.31	8.37	15	11.70	3.067	14	0.016	0.064
9 (180 deg.)	6.00	4.42	15	11.70	−5.003*	14	0.000	0.000
10 (202.5 deg.)	14.86	8.59	15	11.70	1.588	14	0.285	0.404
11 (225 deg.)	12.47	7.31	15	11.70	0.433	14	0.282	0.404
12 (247.5 deg.)	9.92	5.88	15	11.70	−1.195	14	0.266	0.404
13 (270 deg.)	8.01	7.62	15	11.70	−1.880	14	0.084	0.192
14 (292.5 deg.)	17.56	11.75	15	11.70	1.946	14	0.074	0.192
15 (315 deg.)	13.56	9.58	14	11.70	0.729	13	0.488	0.558
16 (337.5 deg.)	12.99	6.85	14	11.70	0.759	13	0.561	0.561

**p* < .05 after Benjamini–Hochberg correction

Specifically, the post hoc analysis (Fisher LSD) showed a systematic superior accuracy of loudspeakers located in all four cardinal points over loudspeakers located within the 4 quadrants. The unsigned errors in all cardinal points were not different from each other (all *p* values > 0.05) and were all significantly smaller than the unsigned errors of all four quadrants. Similarly, all quadrants were not different from each other (all comparisons have *p* values greater than *p* = 0.05). Importantly, there was no effect of *delay*, $F(1, 14) = .008$, $p = .93$, indicating that localization accuracy was not affected by the amount of time in between auditory stimulation and localization response. The interaction between *delay* and *location* was also not significant, $F(7, 98) = .87$, $p = .52$.

Concerning the directional bias, a *t* test comparing all the loudspeaker values to zero showed that three of the four cardinal points were not significantly different from 0 in both the zero-second and in the ten-second delay conditions. The loudspeaker at the west coordinate (270 degrees) was significantly higher than zero in both conditions; see Table 4).

To verify the presence of systematic biases in localization, we performed a 8X3 ANOVA analysis with *location* (north, first quadrant, east, second quadrant, south, third quadrant, west, fourth quadrant) and *delay* as independent within-subject variables and the signed angular error as the dependent variable. Results show an effect of *location*, $F(7, 98) = 24.86$, $p < .0001$, $\eta^2 = 0.63$ which indicate that directional bias varies in strength, direction, and statistical significance according to the position of the loudspeaker. The post hoc analysis (Fisher LSD) showed that the signed

errors in all cardinal points were smaller than the errors in the quadrants (all *p* values < 0.01) indicating a greater directional bias for loudspeakers located in the four quadrants than for loudspeakers located in cardinal points. The signed error in loudspeakers located in cardinal points did not differ from each other (all *p* values > 0.05) with the exception of northeast comparison ($p = 0.044$), east–west ($p = 0.016$) and west–southwest ($p = 0.017$). Most importantly, the signed errors in adjacent quadrants (first with second, second with third, third with fourth) were always of opposite sign and their difference always significant (all *p* values < 0.0001). On the contrary, in opposing quadrant, the signed errors were always of the same sign and their difference was always not significant (all *p* values < 0.05). This pattern is evident both in the zero- and in the ten-second delay conditions (see Fig. 4).

There was no main effect of *delay*, $F(1, 14) = .002$, $p = .96$, but the interaction between *delay* and *location* was marginally significant, $F(7, 98) = 2.32$, $p = .031$, $\eta^2 = 0.14$. Post hoc analysis showed that, in the south cardinal point loudspeaker, the signed error in the zero-second delay condition ($E = 2.12$) was significantly different ($p = 0.007$) from the ten-second delay condition ($E = -2.23$). Also the signed error in the fourth quadrant in the zero-second delay condition ($E = -16.91$) was significantly different ($p = 0.016$) from the ten-second delay condition ($E = -13.05$). All the other comparisons of errors at specific locations in two different delay conditions showed no significant differences (Fig. 4).

Concerning reaction times, we ran an ANOVA with *loudspeaker* and *delay* as factors and response time as the

Table 4 Results of one-sample *t* test and descriptive statistics for the signed error in the 16 speakers in Exp. 2

Speaker # (location)	Delay (s)	Mean signed error	SD	<i>N</i>	Comparison value	<i>t</i>	Directional bias	<i>df</i>	<i>p</i>	Benjamini–Hochberg <i>p</i> value
1 (0 deg.)	0	−3.22	8.65	15	0.00	−1.44	None	14	0.17	0.20148
2 (22.5 deg.)	0	4.20	10.13	15	0.00	1.61	None	14	0.13	0.1664
3 (45 deg.)	0	10.04	11.90	15	0.00	3.26*	Overshooting	14	0.01	0.01524
4 (67.5 deg.)	0	11.81	9.02	15	0.00	5.07*	Overshooting	14	0.00	0
5 (90 deg.)	0	1.80	6.78	15	0.00	1.03	None	14	0.32	0.32
6 (112.5 deg.)	0	−8.99	9.79	15	0.00	−3.56*	Undershooting	14	0.00	< 0.001
7 (135 deg.)	0	−15.68	8.43	15	0.00	−7.21*	Undershooting	14	0.00	< 0.001
8 (157.5 deg.)	0	−19.57	8.24	15	0.00	−9.19*	Undershooting	14	0.00	< 0.001
9 (180 deg.)	0	2.12	6.51	15	0.00	1.26	None	14	0.23	0.25379
10 (202.5 deg.)	0	11.99	11.64	15	0.00	3.99*	Overshooting	14	0.00	< 0.001
11 (225 deg.)	0	13.96	8.70	15	0.00	6.22*	Overshooting	14	0.00	< 0.001
12 (247.5 deg.)	0	3.53	10.77	15	0.00	1.27	None	14	0.23	0.25379
13 (270 deg.)	0	−6.03	8.99	15	0.00	−2.60*	Undershooting	14	0.02	0.02909
14 (292.5 deg.)	0	−16.98	14.14	15	0.00	−4.65*	Undershooting	14	0.00	< 0.001
15 (315 deg.)	0	−14.03	9.04	13	0.00	−5.60*	Undershooting	12	0.00	< 0.001
16 (337.5 deg.)	0	−13.67	7.20	13	0.00	−6.85*	Undershooting	12	0.00	< 0.001
1 (0 deg.)	10	−3.60	7.33	15	0.00	−1.90	None	14	0.08	0.10667
2 (22.5 deg.)	10	5.35	10.52	15	0.00	1.97	None	14	0.07	0.09739
3 (45 deg.)	10	12.13	14.06	15	0.00	3.34*	Overshooting	14	0.00	< 0.001
4 (67.5 deg.)	10	13.36	11.08	15	0.00	4.67*	Overshooting	14	0.00	< 0.001
5 (90 deg.)	10	2.27	7.88	15	0.00	1.12	None	14	0.28	0.29867
6 (112.5 deg.)	10	−8.35	8.20	15	0.00	−3.94*	Undershooting	14	0.00	< 0.001
7 (135 deg.)	10	−16.44	8.63	14	0.00	−7.13*	Undershooting	13	0.00	< 0.001
8 (157.5 deg.)	10	−17.05	8.49	15	0.00	−7.77*	Undershooting	14	0.00	< 0.001
9 (180 deg.)	10	−2.22	8.09	15	0.00	−1.07	None	14	0.30	0.30968
10 (202.5 deg.)	10	11.08	14.47	15	0.00	2.97*	Overshooting	14	0.01	0.01524
11 (225 deg.)	10	9.44	8.44	15	0.00	4.33*	Overshooting	14	0.00	< 0.001
12 (247.5 deg.)	10	4.62	11.32	15	0.00	1.58	Overshooting	14	0.14	0.17231
13 (270 deg.)	10	−7.06	8.97	15	0.00	−3.05*	Undershooting	14	0.01	0.01524
14 (292.5 deg.)	10	−16.72	11.50	15	0.00	−5.63*	Undershooting	14	0.00	< 0.001
15 (315 deg.)	10	−12.68	10.66	15	0.00	−4.61*	Undershooting	14	0.00	< 0.001
16 (337.5 deg.)	10	−9.76	10.28	15	0.00	−3.68*	Undershooting	14	0.00	< 0.001

**p* < .05 after Benjamini–Hochberg correction

dependent variable. Results show that the effect of *delay* is significant, $F(1, 14) = 34.4$, $p < .0001$, $\eta^2 = 0.63$, indicating that participants were faster in the zero-delay condition (average response time = 2.9 s., $SE = 0.69$) than in the ten-second delay condition (average response time = 3.7 s., $SE = 0.35$). *Loudspeaker* was not significant, $F(15, 195) = .58$, $p = .88$. The delay–loudspeaker interaction was also not significant, $F(15, 195) = 1.05$, $p < .40$.

Discussion

The purpose of Experiment 2 was to test whether increased stimulus–response delays were able to influence localization

accuracy and the directionality of the error. Concerning accuracy, results show that localization tended to be more accurate at cardinal points (with the exception of cardinal point at 270 degree) than at locations between them (with the exception of loudspeaker at 167.5 degree) and that there is no influence of delay on localization accuracy. Concerning directional bias, systematic undershoots and overshoots were observed at intermediate locations (non-cardinal points) with a clear and consistent tendency to overshooting in quadrants 1 and 3 and to undershoot in quadrants 2 and 4. As in Experiment 1, no influence of delay was observed as main factor, while a significant interaction between *location* and *delay* indicates a selective influence of stimulus–response

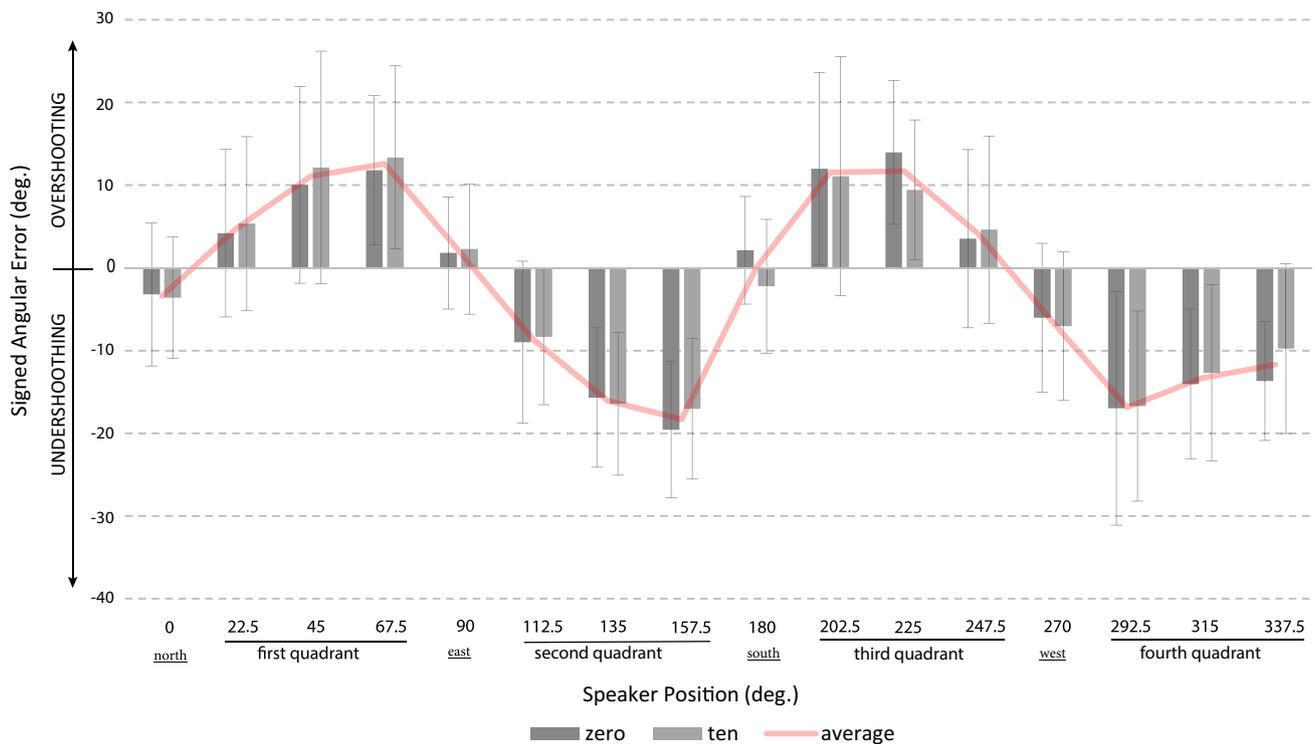


Fig. 4 Signed angular error as a function of loudspeaker position and stimulus–response delay in Exp. 2

delay for certain loudspeakers. Specifically, we observed a significant difference between zero- and ten-second delay conditions in the 180-degree loudspeaker (south). Specifically the zero-second condition elicited a positive error, while the ten-second delay condition a negative one. This result pertains directional error in a cardinal point and does not provide information about the influence of delay in the systematic overestimation of eccentricity in quadrants. More interesting in such respect is the influence of delay we found in the fourth quadrant. In particular, we found that a delay of 10 s significantly diminished, from -16 to -13 degrees, the amount of undershooting when compared with the zero-delay condition. This result is in contrast with what found by Lewald and Ehrenstein (2001), when reporting that delay increases the overestimation of eccentricity. We are going to discuss this contrast in the general discussion.

Experiment 2 results confirmed that an effect of overestimation of eccentricity is valid for all the azimuthal perceptual field and without the influence of visual cues. We also confirmed that overestimation of eccentricity in the quadrants does not increase with longer delays.

Response time was faster in the zero-delay condition than in the ten-second delay condition. This effect is probably due to the long waiting time before the response prompt, which could be distracting for participants. It is interesting that longer response time is not associated with impaired accuracy in the ten-second delay condition.

General discussion

In this study, we used an absolute localization task to test the influence of stimulus–response delays on sound localization in azimuthal space. In two experiments, blindfolded participants listened to bursts of white noise originating from 16 loudspeakers equally spaced in a 360-degree circular space. The task was to indicate sounds' position in the different conditions of delays between sound and localization response: 0, 3, and 6 s (Experiment 1) and 0 and 10 s (Experiment 2).

Results indicate that localization accuracy is not affected by stimulus–response delays. In particular, delays up to 10 s did not significantly impair accuracy in the pointing task with the exception of few specific loudspeakers in Experiment 2. It is important to mention that limiting the delay to a maximum of 10 s can limit the generalizability of the results. Testing longer delay conditions would extend the external validity of the results and better represent the dynamics of working memory. Our rationale for our limited delay choice was linked to the logistic of the experiment. The experimental sessions in both experiments 1 and 2 lasted about 40 min. With longer delays, let's say, 20 s, the length of the experiment increases sensibly, making tiredness a possible intervening factor or forcing the experiments to important changes in the paradigm. Testing longer delays in future studies can be useful to increase the external validity of

our results. These results indicate that working memory for sound location tends to be stable in time, at least for retention times up to ten seconds. Our findings extend to the entire 360-degree azimuthal space what was previously found by Lewald and Ehrenstein (2001) in the frontal (± 60 degrees) field.

Considering the lack of evidence for specific spatio-topic maps in the human brain (Leaver and Rauschecker 2016), sound location is likely to be represented in a non-auditory coordinate system. For example, it could be that the acoustic input is combined with information about the position of the body in a body-centered frame of reference (Goossens and van Opstal 1999; Lewald et al. 2000). In such a theoretical framework, the stability of the localization performance over time can be explained by the use of an effective, sound-independent system of coordinates during rehearsal. From our data, it is not possible to make inferences about whether such a system is visual (Clarke et al. 1998), proprioceptive (Aytekin et al. 2008), or supramodal (Lehnert and Zimmer 2008) and whether the coordinates are centered to the body (Goossens and van Opstal 1999), or if they are referred to the external environment. It would be interesting to test what kind of interference (acoustic, visuospatial, verbal) is more effective in disrupting auditory localization to have further indication on the nature of the representation of sound location in working memory.

The most relevant result of the study is that sound localization response was systematically biased in azimuth toward the direction of the closest ear, which corresponds to a systematic overestimation of eccentricity in the whole 360-degree azimuthal space. The tendency to shift sound location toward the ears was previously reported, but limitedly to the frontal auditory field. For example, Recanzone and colleagues observed that their subjects shifted their estimates toward the right for targets located toward the right (up to 48 degrees), but they did not further discuss this result because they did not find any significant correlation between loudspeaker position and loudspeaker eccentricity (Recanzone et al. 1998). Lewald and Ehrenstein (2001) found that localization of sounds located in the front quadrants (± 60 deg.) was exceedingly eccentric. The results of both above-mentioned studies are consistent with our findings, but they are whether restricted to a limited range of degrees in front of the listeners (Lewald and Ehrenstein 2001) or to one side of the acoustic field (Recanzone et al. 1998). Moreover, in both above-mentioned studies, participants received visual inputs and had the possibility to build up a visual frame of reference in which to integrate auditory information. Considering that visual stimulation was systematically reported to directionally bias auditory localization (see Recanzone 2009 for a review), these previous studies could not disentangle the eccentricity effect from a possible cross-modal influence.

We believe that our study solves both the above-mentioned limitations. In fact, we found that the tendency to overestimate eccentricity is significant also for sounds originating in the posterior quadrants and in the complete absence of a visual frame of reference. This finding suggests that localization of sounds originating from all the azimuthal coordinates is systematically biased toward the interaural axis, with an overestimation of the perceived eccentricity of sound sources.

As auditory source localization is influenced by the method used to measure the pointing response (Gilkey et al. 1995), it would be useful to run the experiment with an alternative method to measure the localization response in order to verify whether the nature and the strength of the bias are independent from the methods of response.

How to explain such systematic bias? Previous accounts suggested that the effect is likely based on physical factors such the directional properties of the external ears rather than on the central nervous system (Lewald and Ehrenstein 1998). As our findings show that the effect is also present in the rear space, we tend to exclude a crucial role of the directional properties of the pinna in the nature of the effect.

We argue that eccentricity overestimation can be the effect of a distorted representation of the sound space. We speculate that the mechanisms at the basis of the distortion can be similar to the ones found in spatial anisotropy in other sensory modalities. Previous findings show anisotropy in the representation of space in vision (Appelle 1972) and haptics (Lechelt et al. 1976). Such anisotropy, which is referred to as the *oblique effect*, is defined as better performances when stimuli are horizontal or vertical as opposed to oblique (Appelle 1972). The systematic shift that we observed can be interpreted as a perceptual regularization of intermediate positions. In fact, our findings showed that the localization is more precise at regular positions while responses at intermediate, non-cardinal positions are the only ones to be significantly biased toward more eccentric positions. In more general terms, it is possible that perceptual regularization is needed when perceptual uncertainty increases. This line of interpretation is consistent with recent results Garcia et al. (2017) who observed that eccentricity effect increases with sensory uncertainty. Such perpetual phenomena are often linked with neurophysiological evidence of fewer neural units devoted to process oblique stimuli. In vision, for example, cardinal orientation elicits a greater response in the primary visual cortex of non-human primates (Celebrini et al. 1993; De Valois et al. 1982) and humans (Furmanski and Engel 2000). Further research is needed to determine the mechanisms that generate and modulate the eccentricity effect. In particular, neurophysiology studies can determine whether sounds originating from non-cardinal position elicit weaker neural responses than the ones originating from cardinal points.

Concerning the temporal dynamics of the bias, we compared localization performances at zero, 3, 6, and 10 s delays. These delays are in the same range and complementary with the delays tested by Lewald and Ehrenstein (zero, 4, 8 and 12 s). This way, considering the two works in conjunction we can have a sharper resolution of the temporal dynamics within the 0–12-s interval. While Lewald and Ehrenstein (2001), found that the distortion increased, even if not linearly for all angular conditions) as a function of the delay time, in our study we did not observed effects of longer delay conditions on the eccentricity bias with the only exception of the fourth quadrant in Experiment 2, in which actually the systematic distortion decreased with the longer delay instead of increasing, as in Lewald's study. These contrasting results may be associated with the use of different procedures. Considering that auditory azimuthal localization is influenced by cross-modal interactions in perception (e.g., Bertelson and Radeau 1981) and attention (e.g., Olivetti Belardinelli and Santangelo 2005; Olivetti et al. 2007), the linear increase of the eccentricity bias in Lewald's study may be related to the use of visual cues during the delay time. In fact, in their study the temporal triggers of the trial are associated with a particular location in space. The go-signal, which is visually presented for different amounts of time in different delay conditions, has a precise location in participants' visual fields, which is the north coordinate. This could have induced a visual recalibration of auditory signals that may bias auditory localization responses. In their procedure, the longer the presentation of the visual cue, the greater the directional bias. In contrast, the absence of visuospatial cueing in our procedure could have limited the visual influence and the recalibration. As we did not directly contrast the two paradigms within the same study, our interpretations over the role of visual cuing and over the differences between Lewald's and our results are still speculative. More research needs to be conducted in order to test our speculations.

Conclusions

This research included two experiments aimed at testing some properties of the representation of sound localization in working memory. We found that working memory representation of auditory source location is biased toward the interaural axis, with a systematic overestimation of sound eccentricity originating from loudspeakers located in non-cardinal points. Importantly, such overestimation of eccentricity is observed both in the front and in the rear azimuthal space, which makes explanations in terms of directional properties of the external ears unlikely. Both the sound localization accuracy and the systematic bias are stable within a time frame of ten seconds after the auditory stimulation. We argue that the directional bias might be

caused by a cortical over representation of sound locations aligned with the interaural axis. Analogous with the oblique effect in vision and haptics, we speculate that the bias could have the function of stabilizing the perception and the spatial representation of surrounding space. We believe that further research should be conducted to clarify whether the eccentricity effect is primarily perceptual or representational and to understand its neurophysiological basis.

Compliance with ethical standards

Conflict of interest The authors declare that there is no conflict of interest regarding the publication of this article.

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