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Crocodiles use both interaural level differences and interaural time differences to locate a sound source

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Abstract: To explore how crocodilians locate a sound source, two Nile crocodiles (*Crocodylus niloticus*) were trained to swim towards an acoustic target. Using filtered versions of synthesized stimuli, the respective roles of interaural level differences (ILDs) and interaural time differences (ITDs), which are the two main cues providing information on sound source position, were tested. This study shows that crocodiles rely on both ILDs and ITDs to locate the spatial direction of a sound source and that their performance is lower when one of the cues is lacking. © 2020 Acoustical Society of America. <https://doi.org/10.1121/10.0001979>

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1. Introduction

The ability to locate the spatial position of a sound source is of paramount importance for animals that communicate acoustically as well as to escape predators or to find prey (Klump, 2000; Klump *et al.*, 2004; Popper *et al.*, 2005). Previous research has shown that receivers assess the direction to a source using acoustic cues provided by the sound signal (Moore, 2013). Spatial acoustic cues arise from two main phenomena. First, sounds experience spectral modifications during their propagation around the receiver's head, leading to an "acoustic shadow" whose characteristics depend on the position of the source (De Mey *et al.*, 2008; Knudsen and Konishi, 1979; Middlebrooks and Green, 1990). This shadow may result in a difference in sound level intensity between both ears [interaural level differences (ILDs)]. Additionally, the sound waves may arrive with a fixed time delay between ears depending on the direction of the sound source [interaural time differences (ITDs)] (Carr and Christensen-Dalsgaard, 2015; Middlebrooks and Green, 1990).

Previous studies have shown differences among animals in the use of these localization cues. Many species use both ITDs and ILDs [e.g., humans, Rayleigh (1909); Japanese macaques *Macaca fuscata*, Brown *et al.* (1978); and common vampire bats *Desmodus rotundus*, Heffner *et al.* (2015)]. Conversely, some animals rely only on ILDs [e.g., big brown bat *Eptesicus fuscus*, Norway rat *Rattus norvegicus*; Heffner and Heffner (2016), Koay *et al.* (1998), and Wesolek *et al.* (2010)], whereas others rely only on ITDs [e.g., cattle, horse; Heffner and Heffner (1984) and Heffner and Heffner (1992)]. This diversity may be explained by the fact that the acoustic characteristics of the signal to be located would favor either ILDs or ITDs, and/or by physiological constraints which could hinder the perception of one or the other cue. Thus, high frequency sounds are more likely to be filtered by the receiver's head, leading to more salient ILDs (Feddersen *et al.*, 1957), while the perception of ITDs requires neuronal temporal coding which is more accurate for low frequency sounds (Moore, 2013).

The hearing of crocodilians is highly developed, a trait correlated with their predator and social life (Vergne *et al.*, 2009). Crocodilians are very vocal and they use the acoustic

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channel throughout all their life. For example, they use sound to find prey when hunting or precisely locate their calling young within the environment. Their auditory sensitivity peaks around 1000 Hz, and although their hearing is most sensitive in the 100–3000 Hz range, they are able to detect frequencies up to 8000 Hz. (Bierman *et al.*, 2014; Higgs *et al.*, 2002; Manley, 1970; Vergne *et al.*, 2009; Wever and Vernon, 1957). Previous investigations demonstrated that both ILDs and ITDs are available to a crocodylian cruising at the interface between air and water, with only the upper part of the head—including the nostrils, eyes, and ears—above the surface (Bierman *et al.*, 2014; Papet *et al.*, 2019). Measurements of head-related-transfer functions (HRTFs) on specimens from different crocodylian species show that ILDs start to be available above 2000 Hz (Bierman *et al.*, 2014; Papet *et al.*, 2019), while results from biophysical studies combined with neurophysiological investigations suggest that ITDs prevail up to 1000 Hz in these animals (Bierman *et al.*, 2014; Carr *et al.*, 2009; Papet *et al.*, 2019). These data are in line with the “duplex theory” proposed by Lord Rayleigh at the beginning of the 20th century to explain how humans find the direction to a sound source (Rayleigh, 1909). Rayleigh’s theory emphasizes the “frequency of ambiguity” (f_a) that separates the two frequency domains where either ILDs or ITDs predominate. Although authors have debated the specific value of this frequency (Hartmann *et al.*, 2016), the general consensus is that ILDs predominate at high frequencies (above around 1500 Hz in humans) while ITDs predominate at lower frequencies (Hartmann *et al.*, 2016; Macpherson and Middlebrooks, 2002).

The available data from crocodylians suggest that their frequency of ambiguity might lie between 1000 and 2000 Hz (i.e., ITD below 1000 Hz and ILD above 2000 Hz). However, there is currently no experimental evidence that these animals could use both ILDs and ITDs cues or preferentially rely on one of them to find the direction of a sound source. Since crocodylian auditory sensitivity is centered around low frequencies, one could expect that these animals may rely more on ITDs and largely ignore ILDs cues. Here we test this hypothesis through a practical method for inferring the use of ILD and ITD, based on behavioral experiments, with the Nile crocodile *Crocodylus niloticus*.

2. Methods

2.1 Animals

The subjects were two 2-year-old Nile crocodiles belonging to the zoo “La Ferme aux crocodiles” (Pierrelatte, France). Both animals had joined the ENES lab when they were 6 months old and had never been included in any experimental protocol and had never been exposed to ototoxic drugs. At the time of the experiment, they were 60.0 and 55.5 cm long (including tail) and their interaural distances were 3.3 and 3.2 cm, respectively. Both individuals showed a normal development, they were fed with [50,100] g of meat per week. The study was conducted under the ethical agreement of the ENES Lab (No. D 42–218-0901).

2.2 Apparatus

The experiments were conducted in a square pool (1.75 m wide) placed inside a $1.8 \times 2.3 \times 2.2$ m acoustic booth [background noise measured in the center of the pool: broadband, unweighted sound pressure level (SPL) below 40 dB re 20 μ Pa—reverberation time = 0.44 s, volume = 9.11 m³, see Fig. 1, left panel and Mm. 1], with a water level of 15 cm allowing the animal to swim freely. All trials were run in the dark and filmed with an infrared camera (ABUS TVCC34010) enabling real-time monitoring by the experimenter. As crocodylians are not sensitive to infra-red light (Grigg and Kirshner, 2015; Nagloo *et al.*, 2016), no visual cues were available. Two loudspeakers (Audiopro Bravo Allroom Sat; frequency response and directivity pattern can be found in the supplementary material¹) were placed on the edge of the pool, 5 cm from above the water surface (Fig. 1, left panel). The loudspeakers can be placed anywhere on the edge of the pool and their position was chosen randomly for each experimental session, with a minimal distance between both of loudspeakers of 50 cm. Sound playback was driven by the experimenter from outside of the booth using a computer delivering the signals to an amplifier (Yamaha AX-397) connected to the loudspeakers.

Mm. 1. Video example of a playback experiment as described in Sec. 2 and illustrated in Fig. 1. The solid and dashed lines correspond, respectively, to the head and neck trajectory. The pink circles illustrate the emission of a buzz. This is a file of type “mp4” (4.5 Mb).

2.3 Experimental stimuli

The stimuli were 500 ms harmonic complex tones (“buzz”) at three different fundamental frequencies (207, 220, and 233 Hz; Fig. 1, top-right panel). These tones were generated at 44 100 Hz sampling frequency by adding all the harmonics from f_0 to 10 kHz. To avoid clicks, they were faded in and out using 50 sample-long half Hann windows and filtered with a third order band-

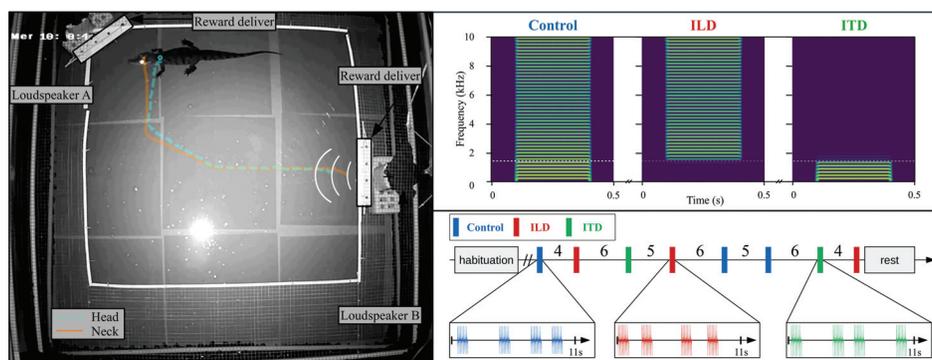


Fig. 1. Left panel: Experimental pool (screenshot of the video [Mm. 1](#)). The subject's behavioral response to stimuli was tracked using the following points: the head (solid line) and the neck (dashed line). Top-right panel: Spectrographic representations of the experimental signals before being played back (from left to right: control, ILD and ITD stimuli; sample frequency = 44 100 Hz; length of the Hann window = 1024; overlap = 90%). Bottom-right panel: Timeline of the experiment and examples of the unit stimuli (total length: 11 s, one stimulus is made of four 500 ms buzzes) played back to the animal. The habituation phase lasts at least 30 min (until the crocodile stopped exploring the pool); the rest duration was 30 min after the last stimulus. The numbers between each stimulus correspond to an example of the length of the silent periods in minutes.

pass filter (cut-off frequencies equal to 70 Hz and 10 kHz). Before starting the experiments, they were normalized in RMS levels in order to measure at 1 m from the loudspeakers (5 cm from above the water surface) inside the pool a sound level of 60 dB SPL re 20 μ Pa (sonometer RION NL52—as a guide, the sound level was constant ± 1 dB inside the pool area).

Because of a lack of phase-locking, crocodilians are not able to use the ITDs at frequencies above 1000 Hz ([Carr et al., 2009](#)). Conversely, their external morphology does not induce ILDs for frequencies below 2000 Hz ([Bierman et al., 2014](#); [Papet et al., 2019](#)). To test the respective effect of ILDs and ITDs, we built three families of experimental stimuli from the original buzzes, assuming a “frequency of ambiguity” f_a of 1500 Hz ([Bierman et al., 2014](#); [Carr et al., 2009](#); [Papet et al., 2019](#)): 1/ control buzzes: original signals (bandwidth = [70, 10 000] Hz); 2/ ILD buzzes: high-pass filtered signals (bandwidth = [1500, 10 000] Hz); 3/ ITD buzzes: low-pass filtered signals (bandwidth = [70, 1500] Hz). We assume that ITD cues predominate in the ITD while the ILD cues predominate in the ILD stimuli.

2.4 Testing procedure

Prior to the experimental trials, both crocodiles were separately trained to swim toward a sound source emitting control buzzes using food reward (one portion of [5,10] g of meat) as positive reinforcement [“conditioning experiment,” [Grap et al. \(2020\)](#), [Holt et al. \(2004\)](#), and [Kastak et al. \(2005\)](#)]. A response was considered as successful when the crocodile arrived within 15 cm off the target loudspeaker. Both animals reached 100% success after 7 weeks of training.

Prior to a testing session, one of the two crocodiles was taken from its vivarium and placed in the pool at least 30 min before the test to limit the influence of the stress induced by the capture. After several minutes without showing any movement, the individual started to swim all around the pool for around 10 min and then stopped. No trial started before the animal stopped exploring the pool (Fig. 1, bottom-right panel). After 2–3 min of immobility, the three types of signals were then played back (control, ILD, and ITD buzzes) in a random order, from a randomly selected loudspeaker. The subsequent trial was launched after the first 10 s period of immobility (after [4,6] min of rest), ensuring that the animal is staying at 50 cm minimum from the playing loudspeaker (Fig. 1, bottom-right). Each stimulus consisted of four repetition of identical buzzes, with a pseudo-random rhythm (2 ± 0.2 s of silence between each buzz, total duration: 11 s). The crocodile's behavior was assessed during the two minutes following the onset of a trial. In response to a stimulus, if the subject swam within 15 cm of the target loudspeaker, it was rewarded instantaneously with a portion of food ([5,10] g of meat). The reward was distributed by the experimenter from outside the booth, using a manual wired system delivering one piece of meat at a time in front of the loudspeaker (5 cm from the membrane of the speaker). The reward was delivered at the end of the trajectory, i.e., the moment the crocodile crossed the limit of 15 cm from the speaker.

We emitted a maximum of eight stimuli during a given session (Fig. 1). After the last trial, the animal was left in the pool for at least 30 min before returning to its vivarium. During the testing period (17 weeks), the crocodiles were only fed during the experimental trials. The quantity of their food intake was continuously monitored to ensure that they received a sufficient

amount ([50,100] g per week). By coding a successful trial with a value of 1 and a failed trial with a value of 0, the global success rate, corresponding to the average value within all the trials, is 81.0%. At the end of the experiments, one subject had been tested with 23 control, 11 ILD, and 13 ITD stimuli, while the other subject had been tested with 22 control, 22 ILD, and 20 ITD stimuli.

2.5 Data processing

We assessed the tested subject's behavioral response through video analysis (Kinovea software). For each experimental trial, three types of variables were taken into account: (1) the reaction time to the first sound stimulus, (2) the dynamics of the orientation angles from the onset to the end of the trial, and (3) the minimum audible angle (MAA) (estimated from the final orientation angle, see below).

Because the animals were always motionless before a stimulus was played, the reaction time was measured as the time delay between the onset of the first sound stimulus and the first noticeable movement of the animal (in any direction).

The orientation angles θ were measured continuously during the whole duration of each trial. To assess the orientation angles, we characterized the crocodile swimming trajectory using the coordinates of two points of reference, one on the neck and the other between the ears. The virtual line passing through these two points defined the "pointing direction" of the animal. The orientation angle was the angle between the pointing direction and the direction defined by the line going from the neck point to the edge of the loudspeaker. In fact, the loudspeaker could not be considered as a single point but rather as a surface (diameter = 4.7 cm). When the pointing direction of the animal was in between the two edges of the loudspeaker, the orientation angle θ was thus set to 0°. If the animal was pointing outside the loudspeaker surface, the orientation angle was defined as the angle between the pointing direction and the line going from the neck point to the closest edge of the loudspeaker (see supplementary material¹). Once we determined orientation angles for each trial, we put all trials on the same temporal scale by normalizing their durations. On average, the crocodiles reached their final position after 11.32 ± 5.54 s (mean value and standard deviation, $n = 111$). This process gave normalized dynamics of angles variation $\theta(\tilde{t})$. The beginning of a trial ($\tilde{t} = 0$) was defined as the onset of the first buzz, and the end of a trial as the moment when the animal crossed the 15 cm limit from the loudspeaker ($\tilde{t} = 1$). For each trial, variations in the orientation angle according to the normalized time \tilde{t} were fitted to a simple exponential model as follows: $\theta(\tilde{t}) = a \times e^{b\tilde{t}}$. This model was fitted to the raw data using a least-mean square method, resulting an average error of $1.02 \pm 0.68^\circ$. The horizontal asymptote is a , and $a \times b$ corresponds to the slope of the exponential model at $\tilde{t} = 0$. The temporal constant τ was then computed as $\tau = 1/b$ for each trial. We then computed the averaged temporal constant τ for each of the three stimuli types (control, ILD, and ITD), and further compared these three averaged temporal constants using an analysis of variance (ANOVA) model testing the influence of the subject identity, the stimulus condition and the interaction between both previous factors.

The MAA is a classical indicator to quantify sound localization ability (Feinstein, 1973; Holt *et al.*, 2004; Mills, 1958). Traditionally, the MAA is defined as the smallest angular separation allowing the detection and location of a sound source. In their study about sound localization in cats, Moore *et al.* provide evidence that MAAs are also comparable to the absolute sound localization acuity as measured in the present study (Hartmann and Raked, 1989; Moore *et al.*, 2008). Based on that study, the MAA is computed as 50% of the standard deviation of the distribution of final angles of orientation across trials of a given stimulus condition. The final orientation angle is considered as the orientation angle when the crocodile has crossed the limit of 15 cm from the speaker. To compare the localization accuracy between conditions, we tested the final orientation angles θ_C differences using an ANOVA model (JASP software) testing the influence of the subject identity, stimulus condition, and interaction.

3. Results

The reaction times measured in the control and the ITD conditions were not statistically different ($RT_C = 1.29$ s and $RT_{ITD} = 1.15$ s, respectively; *post hoc* test: mean difference = 0.170 s, $p = 0.877$). Conversely, the ILD condition was characterized by a significantly longer reaction time ($RT_{ILD} = 1.95$ s) compared both to control (mean difference = -0.860 s, $p = 0.046$) and ITD condition (mean difference = 1.031 s, $p = 0.023$).

During the testing, the crocodiles were still but changed their body orientation intermittently, mainly after renditions of the sound stimuli (see supplementary material¹). Figure 2 illustrates the temporal dynamics of the orientation angles $\theta(t)$ during all trials for the three experimental conditions. Comparison between the averaged temporal constants τ across

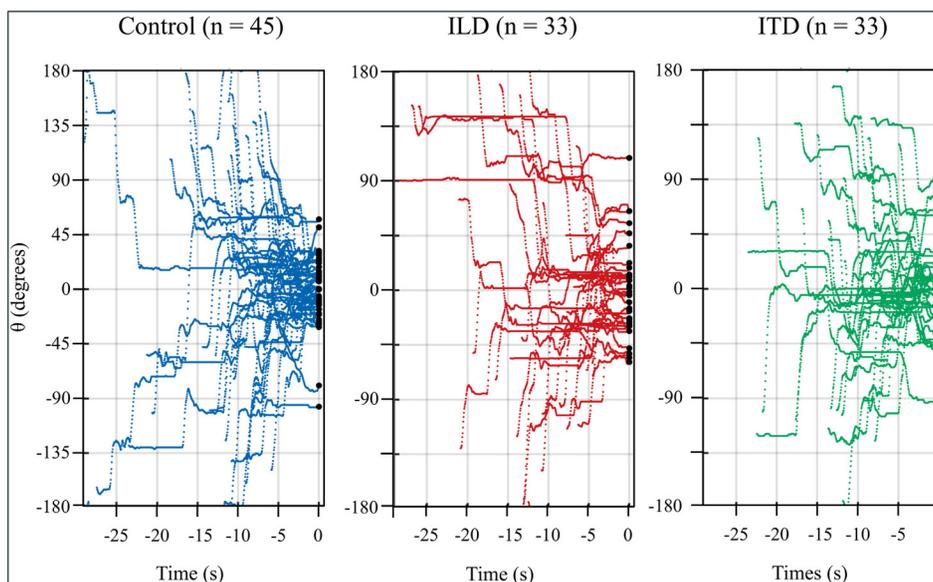


Fig. 2. (Color online) Variation of the crocodiles' orientation angles $\theta(t)$ during the playback experiment [all trials are plotted relative to time (s)]. The points at $t = 0$ s correspond to the final orientation angles (before the animal was rewarded).

conditions revealed a significantly higher value in the ILD condition ($\tau_{ILD} = 0.717$) compared to the control condition ($\tau_C = 0.476$; *post hoc* test: mean difference = -0.238 , $p = 0.007$). The same trend, although not significant, was observed when comparing the ILD condition to the ITD condition ($\tau_{ITD} = 0.563$; mean difference = 0.138 , $p = 0.218$). There was no significant difference between control and ITD conditions (mean difference = -0.099 , $p = 0.379$).

The three final orientation angles θ_C distributions (Fig. 3, control, ILD, and ITD) showed slight differences between each other. The average final orientation angles were $1.1 \pm 26.6^\circ$, $-9.6 \pm 47.7^\circ$, and $2.1 \pm 45.4^\circ$, respectively, in the control, ILD, and ITD conditions (average \pm standard deviation; Fig. 3). However, the resulting MAAs vary appreciably (13.3° , 23.9° , and 22.7° in the control, ILD, and ITD conditions, respectively) but these differences are not significant.

4. Discussion

Our results demonstrate that crocodiles are able to use both ILD and ITD when they locate the spatial position of a source emitting a broadband sound. However, crocodiles still manage to locate the source fairly well when one of these cues is lacking. ILD stimuli lead to a longer reaction time to sound stimuli and to a slower effort to locate the source. Conversely, crocodiles react to sound stimuli including ITD cues as quickly as to a control sound containing both ILD and ITD cues.

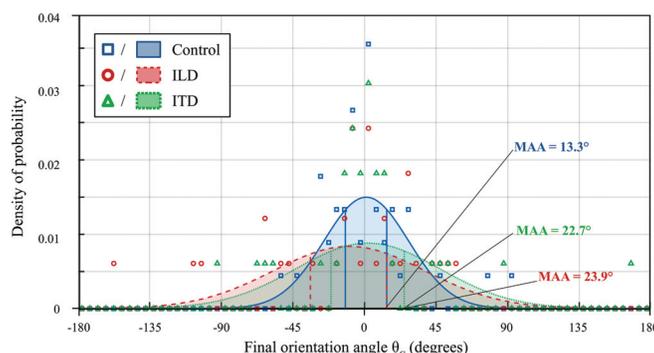


Fig. 3. Density of probability of the final orientation angles θ_C . The points correspond to the raw densities in the control (squares), ILD (circles), and ITD (triangles) condition. The filled lines are the Gaussian fitting to the raw densities of probability (control condition: solid line; ILD condition: dashed line; ITD condition: dotted line). The shaded areas represent 50% of the final orientation angles and the vertical lines are plotted for $\theta_C = \pm$ MAA in each condition. The average final orientation angles are $1.1 \pm 26.6^\circ$, $-9.6 \pm 47.7^\circ$, and $2.1 \pm 45.4^\circ$, respectively, in the control, ILD and ITD conditions (average \pm standard deviation).

These data suggest that ITDs are likely the predominant cues for sound source localization in crocodiles. The relative supremacy of ITDs compared to ILDs might be explained by the auditory sensibility of crocodilians. As these animals are tuned toward low frequencies (around 1 kHz), the ITD stimuli used in our experiments may have been perceived louder than ILD stimuli. This potential difference in salience could have contributed to the difference in reaction time observed across signal conditions; however, in humans, it has been reported that localization in the horizontal plane is independent of global loudness (Myers, 1914). Furthermore, potential difference in perceived salience of the ITD stimuli could also have play a part in the difference of reaction time between signal conditions.

The value of 13.3° as the MAA obtained in the control condition looks like a poor performance for these top predators compared to other species. Humans show far better sound localization performances, with very small MAAs ($\approx 1^\circ$) (Heffner and Heffner, 1988) and Pinnipeds (northern elephant seal *Mirounga angustirostris*, harbor seal *Phoca vitulina*, and California sea lion *Zalophus californianus*) also appear very accurate with MAAs between 3° and 6° (Holt *et al.*, 2004). Conversely, horses and cows show MAAs between 25° and 30° (Heffner and Heffner, 1984, 1992), underlying poor localization abilities. In birds, one species of raptor, the Marsh hawk (*Circus cyaneus hudsonius*), has a MAA of only 2° (Rice, 1982). In our opinion, the MAA values provided here have to be interpreted with respect to the acoustic context of an experimental booth. From our extensive field work experience with crocodilians, we assume that these animals perform better in natural conditions [e.g., a crocodile mother is able to precisely locate a calling offspring at more than 20 m (personal observation)] mainly because of the acoustic properties of their environment. Here, the subjects were tested in a small (9.11 m³) non-anechoic enclosure (reverberation time = 0.44 s). Because reverberation may influence sound localization (Hartmann, 1983), our set-up may lead to an overestimation of the MAA experienced by crocodilians in their natural, semi-anechoic, habitat.

In conclusion, our study reports the first experimental investigation testing the relative importance of ILDs and ITDs cues for sound spatial localization in crocodilians. The most original result is that ILD cues brought by frequencies above 1500 Hz can facilitate the localization process. This ability to rely on ILD cues may be important in the real life of crocodilians since social calls of both offspring and adults, as well as noise and vocalizations produced by potential preys are mostly broadband signals. Moreover, external noise such as the one induced by water falls or rivers may mask the low frequency part of these signals, enhancing the importance of high frequencies and thus of ILDs. In these environments, which are common for crocodiles, the ability for a croc mother to rely on ILD cues to locate her crying newborn may improve offspring survival. Being able to rely on all cues provided by a broadband signal appears to be adaptive for crocodilians.

The data set used in this study is available online (Papet, 2020). The data include the coordinates of the different points tracked on the animal's body, the coordinates of the target, and the sound emission according to time.

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References and links

¹See supplementary material at <https://doi.org/10.1121/10.0001979> for frequency response and directivity pattern of the loudspeakers, a graphical representation of the different angles, and a graphical representation of the different metrics measured on a typical trial.

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