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„Reweighting of Binaural Cues: Generalizability and
Applications in Cochlear Implant Listening“

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Abstract

Normal-hearing (NH) listeners rely on both interaural time (ITDs) and level (ILDs) differences for azimuthal sound localization. These two cues are weighted mainly based on the sound's frequency content with ITDs dominating for low and ILDs dominating for high frequencies. Localization with cochlear implants (CIs), however, is mainly based on ILDs. Since current envelope-based stimulation strategies do not encode salient ITD cues, CI listeners may learn to rely on ILDs based on their experience in day-to-day life.

A series of experiments was performed to study such ITD/ILD reweighting. In NH listeners, we measured binaural-cue weights for various noise bands presented via headphones and employed two different multi-day training paradigms (a lateralization and a discrimination task) to induce a change in these binaural-cue weights. In CI listeners, we measured binaural-cue thresholds as well as binaural-cue weights for 100-pps and 300-pps pulse trains (associated with high and low ITD sensitivity, respectively) presented at a single interaurally place-matched electrode pair and used a lateralization task to induce an increase in ITD weights.

NH listeners' binaural-cue weighting gradually changed from ITD-dominant to ILD-dominant as the stimulus' frequency region increased. For broadband sounds or if the frequency band is wide enough to include ITD-dominant frequency regions, ITDs dominated the percept. This binaural-cue weighting could be changed in NH listeners via both lateralization and discrimination training under certain stimulus conditions: To induce an increase in ILD weighting, the frequency region needed to be sufficiently high while to induce an increase in ITD weighting, it needed to be sufficiently low without providing fine-structure ITD cues. Finally, ITD weights could be increased in CI listeners for 100-pps but not for 300-pps pulse trains, suggesting that basic sensitivity is needed for binaural-cue reweighting. This change in weights was not associated with a corresponding change in binaural-cue sensitivity, suggesting that reweighting happened on a supra-threshold level. The results are promising in terms of making ITD information better usable with future CI systems that reliably and saliently convey ITD cues.

1. General Introduction

Spatial hearing enables us to determine the location of sound sources, to orient in space, and to understand speech in complex environments. It is, therefore, a vital part of our everyday lives. To complete the above-mentioned tasks, we make use of several acoustical cues (for a review on sound localization cues, see, e.g., Middlebrooks and Green 1991). The degree to which each of these cues contributes depends on the specific setting, such as the sound source location (e.g., horizontal plane, vertical plane, distance) or the sound reaching the ears itself (e.g., frequency content, reverberation). This thesis focusses on sound localization in the horizontal plane and on the two cues most important for it, namely interaural differences in time and level. Specifically, we investigate the flexibility with which these two cues are integrated into a percept when the lateral location of a sound source is determined.

1.1. Spatial hearing in the horizontal plane

For spatial hearing within the horizontal plane, humans primarily rely on two binaural cues, i.e., cues that arise when the input at the two ears is compared. These two cues are the interaural level difference (ILD), which is the difference in sound pressure level at the two ears, arising because the head attenuates the sound reaching the far ear, and the interaural time difference (ITD), which is the difference in the arrival time of the sound to each ear. ITDs can be detected in the fine-scale temporal features of the stimulus waveform (fine-structure ITDs) in the lower frequency region or in the slower fluctuations in the stimulus amplitude (envelope ITDs) in the higher frequency region. The sensitivity to fine-structure ITDs is best between 700-1000 Hz and becomes unmeasurable from approximately 1400 Hz onwards (e.g., Brughera, Dunai, & Hartmann, 2013). For stimuli with higher carrier frequencies, envelope ITD sensitivity decreases for modulation rates above approximately 300 Hz (Bernstein & Trahiotis, 2002). Compared to ITDs, the sensitivity to ILDs is relatively unaffected by the frequency region, although it is slightly worse around 1000 Hz (Brown & Tollin, 2021; Goupell & Stakhovskaya,

2018). This is interesting given that for real-life stimuli, ILDs are highly frequency dependent and physically negligible at low frequencies (Xie, 2013).

The two binaural cues provide information about the azimuth, which is, relative to the listener, the lateral angle of the sound source location (e.g., Middlebrooks and Green 1991). Determining the azimuth of a sound source is termed lateralization. When sound sources are lateralized via headphone presentation based on ITDs and/or ILDs alone, they are often perceived to originate from inside the head on a line between the two ears (Plenge, 1974). Nevertheless, reliable judgements of in-head lateralization can be obtained via head-pointing (i.e., an intuitive response measurement for real-life stimuli), without training participants to externalize the sound (Jeffress & Taylor, 1961; Stecker, 2010).

1.2. Weighting of ITD and ILD

When normal-hearing (NH) listeners lateralize sounds, ITD and ILD cues contribute to varying amounts to the azimuthal percept, mainly based on the frequency content of the sound. According to the well-known duplex theory of sound localization (Strutt, 1907), the ITD is the dominant localization cue for low-, and the ILD is the dominant cue for high-frequency pure tones. This is in line with the decline in ITD sensitivity with increasing frequency and with ILDs being physically negligible at low frequencies as discussed above. More recently, it has been shown that this finding can be extended to complex sounds: ITD weights are large and ILD weights are small for low-pass stimuli (0.5-2 kHz), whereas the opposite pattern is observed for high-pass stimuli (4-16 kHz), although the ITD weight for these stimuli could be increased by introducing amplitude modulation (i.e., salient envelope cues). For wideband stimuli (0.5-16 kHz), ITDs tend to dominate (Macpherson & Middlebrooks, 2002). Additionally, Ahrens, Joshi, and Epp (2020) observed divergence in the binaural-cue weighting for the lowest and highest frequency bands of a multiband stimulus (i.e., stronger ITD weights for the lowest and stronger ILD weights for the highest band) but constant weights for in-between frequency bands. This simultaneous presentation may, however, not show the weighting of each frequency band individually and instead be affected by simultaneous grouping effects such as binaural interference (Ahrens et al.,

2020). The diverging weights for the lowest and highest bands appear to reflect an “edge effect” (i.e., stronger weighting of information at the edges), because the same pattern was observed when only intermediate frequency bands were presented (“removed” condition, Ahrens et al., 2020). Therefore, it is still unclear whether binaural-cue weights gradually change with increasing frequency or whether they abruptly switch from being ITD dominant to being ILD dominant.

The relative weight with which ITDs and ILDs contribute to a spatial percept has traditionally been measured using ITD/ILD trading ratios, estimated by presenting one cue at a fixed value and instructing the participants to adjust the other cue until the sound is perceived centrally (Durlach & Colburn, 1978). Trading ratios are usually reported in units of $\mu\text{s}/\text{dB}$ (i.e., it takes an ITD of $x \mu\text{s}$ to counteract a 1 dB ILD favoring the opposite ear) with smaller values indicating ITD dominance. While trading ratios depend primarily on the frequency content of the stimulus, they are also influenced by other stimulus factors such as overall intensity (David, Guttman, & van Bergeijk, 1959; Deatherage & Hirsh, 1959) or the rate of clicks in click trains (Stecker, 2010). Additionally, contextual or environmental factors influence the binaural-cue weighting. Rakerd and Hartmann (2010) observed that in reverberant environments, participants’ responses follow ILDs when localizing 500 Hz pure tones, a stimulus for which localization is based on ITDs in anechoic environments. Moreover, ITD/ILD trading ratios depend on which cue is adjusted. Namely, the to-be-adjusted cue receives greater weight, presumably because attention is shifted towards it (Lang & Buchner, 2008) or due to cue-specific adaptation (Moore, Picou, Hornsby, Gallun, & Stecker, 2020).

Another method to measure binaural-cue weighting, which is not subject to the bias described by Lang and Buchner (2008), is to ask participants to lateralize stimuli with conflicting ITD and ILD cues (Macpherson & Middlebrooks, 2002; Stecker, 2010, “open loop” procedure). The binaural-cue weight can then be inferred based on the distance between the response azimuth and the azimuth corresponding to either of the two cues (i.e., if the response azimuth is closer to the ITD azimuth than the ILD azimuth, the ITD dominated the percept and vice versa).

1.3. Learning and adaptation to sound localization cues

There is evidence that normal-hearing listeners can improve their performance on sound localization and discrimination of sound localization cues with training, although contradictory results have been reported (see Wright & Zhang, 2006, for a review). With respect to the two cues of interest for this thesis, learning is generally shown for ILD discrimination (Gao, Yan, Huang, Li, & Zhang, 2020; Wright & Fitzgerald, 2001; Zhang & Wright, 2007; Zhang & Wright, 2009), whereas results for ITD discrimination are mixed with some studies showing learning (Ortiz & Wright, 2009; Ortiz & Wright, 2010; Rowan & Lutman, 2006; Rowan & Lutman, 2007) while others do not (Gao et al., 2020; Wright & Fitzgerald, 2001; Zhang & Wright, 2007).

It should also be noted that the relationship of sound localization cues to corresponding locations in space may change during one's life. Increasing head size during development (Clifton, Gwiazda, Bauer, Clarkson, & Held, 1988) or temporary physiological changes due to middle ear infections (Morrongiello, 1989), for example, affect sound localization cues reaching the cochleae. Consequently, adaptation to altered spatial cues has been extensively studied (see Carlile, 2014; King et al., 2011; and Wright & Zhang, 2006, for reviews), highlighting the plasticity of the auditory system. Observed adaptation can either result from the establishment of a new spatial map of the altered cues (i.e., a modified relationship between sound localization cues and corresponding locations in space; Keating, Dahmen, & King, 2015; Knudsen, 2002; Shinn-Cunningham, Durlach, & Held, 1998; Trapeau & Schönwiesner, 2015) or from a stronger relative weighting of unaltered compared to altered spatial cues, referred to as reweighting (Keating, Dahmen, & King, 2013; Kumpik, Kacelnik, & King, 2010; Kumpik, Campbell, Schnupp, & King, 2019; van Wanrooij & van Opstal, 2007). While several studies observed an increase in weighting for monaural, spectral-shape cues (i.e., the filter characteristics of the pinnae mainly used for vertical-plane localization) compared to binaural cues for horizontal-plane localization (Keating et al., 2013; Kumpik et al., 2010; van Wanrooij & van Opstal, 2007), studies attempting to induce purely binaural-cue reweighting produced inconclusive results (Jeffress & McFadden, 1971; Kumpik et al., 2019). This thesis aims to shed further light on the phenomenon of purely binaural-cue reweighting.

1.4. Spatial hearing with cochlear implants (CIs)

Hearing impairment at one or both ears often causes deterioration or even total loss of spatial hearing ability, which in turn leads to severe difficulties in the daily listening situations mentioned at the beginning. In cases of profound hearing loss or complete deafness while the auditory nerve is still intact, cochlear implants (CIs) have been shown to be successful in restoring auditory sensation. CIs are auditory prostheses that stimulate the auditory nerve electrically. While state-of-the-art CIs enable listeners to understand speech in quiet, they allow only relatively poor performance in horizontal sound localization and speech-understanding in noise, even when they are implanted bilaterally (Nopp, Schleich, & D'Haese, 2004; Schleich, Nopp, & D'Haese, 2004; van Hoesel & Tyler, 2003). It has been shown that localization in the horizontal plane with present-day CI systems is almost entirely based on ILDs, while ITDs contribute only little or not at all (Grantham, Ashmead, Ricketts, Haynes, & Labadie, 2008; Seeber & Fastl, 2008).

On the one hand, this is due to the properties of present-day envelope-based CI systems, which do not encode ITDs via the pulse timing (pulse ITDs) and whose envelope ITD cues for practically-relevant low modulation rates may not be sufficiently salient (Grantham et al., 2008; Laback, Pok, Baumgartner, Deutsch, & Schmid, 2004; Laback, Zimmermann, Majdak, Baumgartner, & Pok, 2011). On the other hand, the sensitivity of CI listeners to optimally presented ITDs (i.e., pulse ITDs presented via a research system to a single electrode pair, bypassing the sound processor of the CI), is lower and much more variable across listeners compared to NH listeners (Laback, Majdak, & Baumgartner, 2007; Majdak, Laback, & Baumgartner 2006; van Hoesel, 2007). So, even if ITD information is optimally conveyed, CI listeners perform worse on average than NH listeners.

Considering the adaptation to altered sound localization cues in NH listeners as discussed above, the low contributions of ITDs in CI listeners even in situations where pulse ITDs are saliently conveyed by a research system might be explained or intensified by reweighting of binaural cues. Specifically, CI listeners using present-day envelope-based clinical systems may learn to put greater weight

on ILDs than on ITDs since ILDs consistently indicate the visually perceived source location while reliable and salient ITD information is not conveyed.

1.5. Research questions

This thesis aims to shed further light on the phenomenon of binaural-cue reweighting. Since the only two studies that explicitly attempted to achieve ITD/ILD reweighting produced inconclusive results (Jeffress & McFadden, 1971; Kumpik et al., 2019), we first establish that the two binaural cues can indeed be reweighted. We further explore different training methods to induce binaural-cue reweighting to develop a training tool that is easily accessible for a wide range of people. Moreover, it is of interest whether binaural-cue reweighting can be achieved for different frequency regions (e.g., regions for which either ITDs or ILDs are known to dominate), and whether binaural-cue reweighting generalizes to untrained frequency regions. In this context, an open question regarding the transition of binaural cue weights from low to high frequency regions (i.e., whether they change gradually or switch abruptly) is also addressed. Finally, we investigate whether the ITD weighting can be increased in CI listeners (i.e., whether the assumed maladaptive weighting can be reversed) and whether binaural-cue weighting simply reflects binaural-cue sensitivity or whether it is a supra-threshold mechanism.

2. Empirical Work

2.1 Reweighting of binaural localization cues induced by lateralization training

The following manuscript was published in the Journal of the Association for Research in Otolaryngology:

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Research Article

Reweighting of Binaural Localization Cues Induced by Lateralization Training

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ABSTRACT

Normal-hearing listeners adapt to alterations in sound localization cues. This adaptation can result from the establishment of a new spatial map of the altered cues or from a stronger relative weighting of unaltered compared to altered cues. Such reweighting has been shown for monaural vs. binaural cues. However, studies attempting to reweight the two binaural cues, interaural differences in time (ITD) and level (ILD), yielded inconclusive results. This study investigated whether binaural-cue reweighting can be induced by lateralization training in a virtual audio-visual environment. Twenty normal-hearing participants, divided into two groups, completed the experiment consisting of 7 days of lateralization training, preceded and followed by a test measuring the binaural-cue weights. Participants' task was to lateralize 500-ms bandpass-filtered (2–4 kHz) noise bursts containing various combinations of spatially consistent and inconsistent binaural cues. During training, additional visual cues reinforced the azimuth corresponding to ITDs in one group and ILDs in the other group and the azimuthal ranges of the binaural cues were manipulated group-specifically. Both groups showed a significant increase of the reinforced-cue weight from pre- to posttest, suggesting that participants reweighted the binaural cues in the expected direction. This reweighting occurred within the first training session. The results are relevant as binaural-cue reweighting likely occurs when normal-hearing listeners adapt to

new acoustic environments. Reweighting might also be a factor underlying the low contribution of ITDs to sound localization of cochlear-implant listeners as they typically do not experience reliable ITD cues with clinical devices.

Keywords: Spatial hearing, Interaural time difference, Interaural level difference, Plasticity, Adaptation, Trading ratio

INTRODUCTION

Spatial hearing mechanisms allow us to determine the location of a sound source and are important for understanding speech in complex environments as well as orienting in space. For vertical-plane localization, we rely primarily on monaural spectral-shape cues, while for azimuthal sound localization the binaural cues of interaural time difference (ITD) and interaural level difference (ILD) are most important (for a review on localization cues, see, e.g., Middlebrooks and Green 1991). This study investigates the flexibility with which the two binaural cues are integrated to form an azimuthal percept.

The extent to which each binaural cue contributes to azimuthal sound localization mainly depends on the frequency content of the sound. ITDs are dominant at low frequencies whereas ILDs are dominant at higher frequencies (Macpherson and Middlebrooks 2002; Strutt 1907; Wightman and Kistler 1992). The relative weight with which ITDs and ILDs contribute to a spatial percept has traditionally been measured using ITD/ILD trading ratios, estimated by presenting one cue at a fixed

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value and instructing the participants to adjust the other cue until the sound is perceived centrally (Durlach and Colburn 1978).

While trading ratios depend primarily on the frequency content of the stimulus, they are also influenced by other stimulus factors such as overall intensity (David et al. 1959; Deatherage and Hirsh 1959) or the inter-click interval of click trains (Stecker 2010). Contextual or environmental factors also influence the ITD/ILD weighting. Rakerd and Hartmann (2010) observed that in reverberant environments, participants' responses follow ILDs while localizing 500 Hz sine tones, a stimulus for which ITDs are dominant in anechoic environments. Moreover, ITD/ILD trading ratios depend on which cue is adjusted. Namely, the to-be-adjusted cue receives greater weight, presumably because attention is shifted toward it (Lang and Buchner 2008) or due to cue-specific adaptation (Moore et al. 2020).

Trading ratios are usually only measured at a single point in time. However, the relationship of sound localization cues to corresponding locations in space may change during one's life. Therefore, adaptation to altered spatial cues has been extensively studied (see Carlile 2014, and King et al. 2011, for reviews), highlighting the plasticity of the auditory system. Observed adaptation can either result from the establishment of a new spatial map of the altered cues (i.e., a modified relationship between sound localization cues and corresponding locations in space; Keating et al. 2015; Knudsen 2002; Shinn-Cunningham et al. 1998; Trapeau and Schönwiesner 2015) or from a stronger relative weighting of unaltered compared to altered spatial cues, referred to as reweighting (Keating et al. 2013; Kumpik et al. 2010; van Wanrooij and van Opstal 2007). In these latter studies, participants learned to increase the relative weight of monaural compared to binaural cues for azimuthal sound localization.

The current study examines whether not only monaural vs. binaural but also the two binaural cues ITD and ILD can be reweighted. Only two previous studies explicitly attempted to achieve binaural-cue reweighting, yielding inconclusive results. Jeffress and McFadden (1971) used a left/right discrimination task with ITDs and ILDs favoring opposite ears and presented feedback consistent with only one of the cues but did not find any changes in the ITD/ILD weighting after training. Potential reasons for their null result are that (1) the training regimen (i.e., left/right discrimination) was not sufficiently intuitive, (2) the stimuli were noise bands centered at 500 Hz and thus in a frequency range where only ITDs but not ILDs arise naturally (except for sound sources near the head), (3) the binaural cues used were not sufficiently salient as they were close to the binaural-cue threshold, and (4) auditory and visual stimuli were not presented simultaneously, preventing bottom-up multisensory integration that may be required to induce reweighting. Kumpik et al. (2019)

presented auditory stimuli with either randomized ITDs (and stable ILDs) or randomized ILDs (and stable ITDs) while participants completed a visual oddball task. They observed an increase in ILD weighting after ITDs were randomized, but no increase in ITD weighting after ILDs were randomized. Since the auditory stimuli were task irrelevant, they might not have received enough attention to induce an effect in both directions. Additionally, the potential to increase the ITD weighting may have been restricted due to applying reverberation, presumably making the ITDs less reliable. This is in line with Rakerd and Hartmann's (2010) observation that responses follow ILDs in reverberant environments. Furthermore, Kumpik et al. (2019) found an even stronger increase in ILD weighting for a condition in which no cue was randomized (i.e., spatially consistent ITDs and ILDs were presented), making it difficult to draw strong conclusions. Considering the changing relative contributions of ITD and ILD depending on stimulus and contextual factors as discussed above, binaural-cue reweighting likely plays a role in adapting to variable acoustic environments. Therefore, these inconclusive results are rather surprising and worthy of further consideration.

Here, we reexamined the question of whether the auditory system can adjust the binaural-cue weights via training. We trained participants using a lateralization task in a well-controlled virtual environment involving auditory, visual, and proprioceptive information based on the procedure used in Majdak et al. (2013). A schematic illustration of the visual environment and the task is shown in Fig. 1. The training used two forms of visually guided auditory spatial calibration: (1) visual stimuli presented after the auditory stimuli to serve as top-down feedback (see red square in panel 3 in Fig. 1) comparable to the "feedback" experiments of Shinn-Cunningham et al. (1998), and (2) simultaneously presented auditory and visual stimuli to encourage multisensory bottom-up processes (see panel 5 in Fig. 1) equivalent to those evoked in the ventriloquism aftereffect paradigm (Reccanzone 1998). In contrast to Kumpik's et al. (2019) study, the auditory stimuli were critical to perform the task and unlike Jeffress and McFadden (1971), we used a stimulus spectrally focused at an intermediate frequency region, to ensure that neither ITDs nor ILDs are used by default. Since the sensitivity to binaural cues can be modified based on the statistics of the sound (Dahmen et al. 2010), we additionally manipulated the across-trial stability of the two binaural cues during training by varying one of the cues over a larger range than the other. Finally, a variety of combinations of ITDs and ILDs were presented to facilitate generalization of reweighting across spatial configurations and to minimize chances for strategic responding (i.e., memorizing specific stimuli or azimuths and responding accordingly).

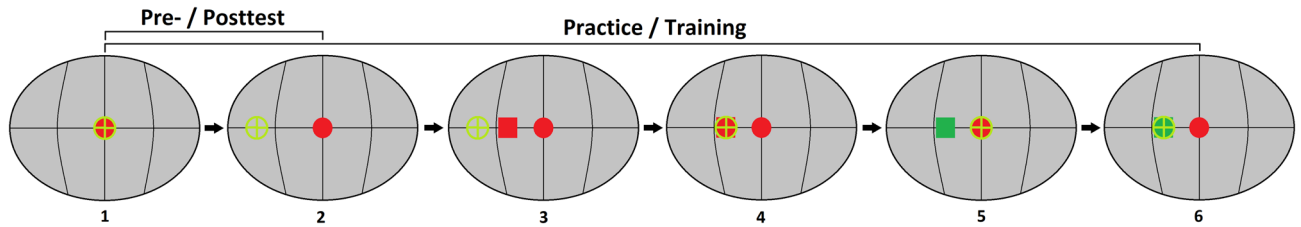


FIG. 1 Time course of a trial during testing (panels 1–2), practice (panels 1–6), and training (panels 1–6). (1) Participants oriented towards the reference position straight ahead (indicated by a red sphere) by turning their head (guiding a green crosshair) toward it and pressed a button to elicit the sound presentation. (2) Participants turned their head to the perceived azimuth and pressed a button at the end of the head turn to record the response azimuth (in this example, they performed a head-turn to the left). During testing, the next trial was initiated after the button press while during practice and training, the trial continued with steps 3–6. (3) Visual

reinforcement (a rotating red cube) appeared at the reinforced-cue azimuth. (4) The participants confirmed the reinforced-cue azimuth via a head turn to the reinforced-cue azimuth and a button press. (5) The visual reinforcement turned green, and participants returned to the reference position. After another button press, the auditory stimulus was presented again while the visual reinforcement was still visible. (6) Participants performed another head turn to the reinforced-cue azimuth and pressed the button. In steps 4 and 6, the button-press was accepted only if the head-orientation (green cross-hair) was within $\pm 5^\circ$ of the reinforced-cue azimuth

METHODS

Participants

Twenty-six normal-hearing adult participants took part in the study. All participants gave informed consent before participating and received monetary compensation for their participation. Basic lateralization ability as well as sensitivity to both ITDs and ILDs were assessed in a practice session (see “[Procedure](#)” for details) and served as an inclusion criterion. Of these 26 participants, three had to be excluded because they experienced dizziness induced by the head-mounted display used for the presentation of the visual environment. Another two participants exercised their right to terminate the experiment prematurely and were therefore excluded. In addition, one participant was excluded due to poor ITD sensitivity (i.e., the percentage of responses at the correct side in practice trials with ILDs fixed at zero was at chance level). Twenty participants (10 female, mean age 26.9 years, $SD = 4.13$, range 21–40 years) therefore completed the experiment. We used two experimental groups: ITDs were reinforced for the ITD group and ILDs were reinforced for the ILD group. Participants were pseudo-randomly assigned to one of the groups, ensuring balanced age, sex, and basic lateralization ability. Ten participants (five female, mean age: 27 years, $SD = 5.27$), were assigned to the ITD group. The other ten participants (five female, mean age: 26.8 years, $SD = 2.86$), were assigned to the ILD group. The research protocol was submitted to the acoustics research institute’s ethics committee for consideration, comments, guidance, and approval. After taking ethical issues, local laws and regulations into account, the ethical committee approved the protocol.

Apparatus and Stimuli

Participants stood on a platform surrounded by a circular railing inside a sound booth. The experiment was controlled by custom-written software routines that were run on two communicating personal computers (via UDP protocol), that shared the tasks of acquiring head tracking data, creating and presenting acoustic stimuli, and rendering the visual environment. Binaural auditory stimuli were generated using a computer and output via a digital audio interface (ADI-8, RME) at a 96-kHz sampling rate and presented via headphones (HD 580, Sennheiser). Visual stimuli were presented binocularly via a head-mounted display (Oculus Rift DK1). Participants’ head position and orientation were tracked with a head-mounted tracking sensor (Flock of Birds, Ascension), and the visual environment was rendered accordingly in real time (the latency between head movements and the updated visual information was less than 37.3 ms). The rendering of the visual environment using Pure Data (with GEM, IEM, Graz) was based on the left/right rotation information from the tracking sensor while the up/down information was ignored to force participants to respond only in the horizontal plane. The virtual visual environment consisted of a reference position straight ahead, a crosshair in the direction of the head orientation, a single horizontal line at eye level, and vertical lines every 15° in azimuth for guidance (Fig. 1).

Auditory source stimuli were white noise bursts, randomly generated on each trial, which were filtered with a 2–4 kHz¹ Butterworth band-pass filter (roll-off outside the passband: approximately 30 dB/oct; Fig. 2a), on which ITDs ranging from -662 to $+662$ μ s and ILDs ranging from -19.4 to $+19.4$ dB were imposed. These cues correspond to an azimuthal range from -70.2° to $+70.2^\circ$

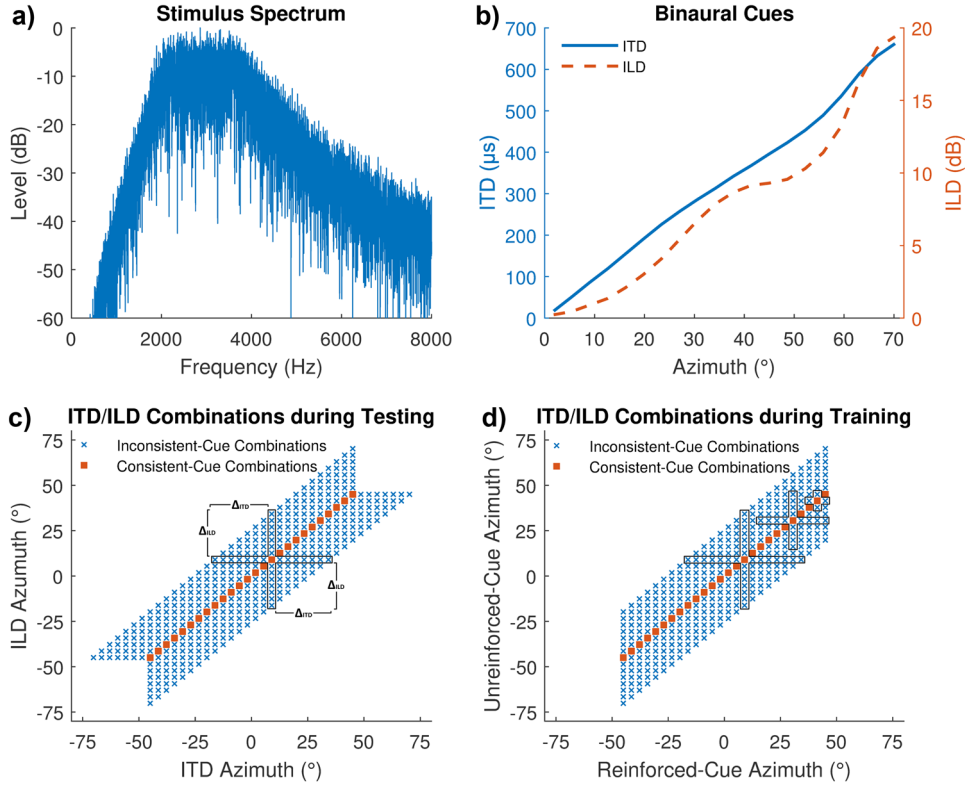


FIG. 2 Experimental setup and stimuli. **a** Spectrum of the auditory stimuli used. **b** Functional relation between the azimuth and the binaural cues as derived by Xie (2013) from the KEMAR head-related impulse responses (HRIRs), with ITDs (solid line) referring to the left ordinate and ILDs (dashed line) referring to the right ordinate. ITDs are based on broadband cross-correlation of the left and right ear HRIRs. ILDs are based on HRTF magnitudes at 2.8 kHz. **c** ITD/ILD-azimuth combinations used in the pre- and posttest. The frame indicates the azimuthal offsets Δ_{ITD} and Δ_{ILD} that were used to estimate the parameters of the regression analysis for the pre-/

posttest data at one example azimuth (9°). **d** All cue combinations used in the training. For the ITD group, reinforced and unreinforced cues were ITD and ILD, respectively, and for the ILD group, reinforced and unreinforced cues were ILD and ITD, respectively. The frames indicate the data that were used to estimate the parameters of the regression analysis for the training data at example azimuths of 9° (large frame), 30.6° (medium frame), and 41.4° (small frame). The reduction of frame size towards the edge was required to ensure symmetric distributions (see text)

(Fig. 2b), as estimated by Xie (2013) using the head-related transfer functions (HRTFs) of the KEMAR head with DB-61 small pinna at a source distance of 1.4 m. In Xie (2013), the ITD values were obtained via broadband cross-correlation of the left and right ear head-related impulse responses (HRIRs) and the ILD values were based on the HRTF magnitudes at 2.8 kHz (i.e., the center frequency of the auditory stimuli used in the present study). The stimuli were not HRTF filtered to ensure that they did not convey monaural spectral localization cues that are potentially informative about the azimuth of the stimulus, to reveal purely binaural-cue reweighting. The choice of the stimulus center frequency of 2.8 kHz was guided by the requirement of monotonically increasing ILDs

with increasing azimuth at the center frequency within the desired stimulus azimuthal range of $\pm 70.2^\circ$ to avoid ambiguous ILDs which would occur if the same cue value corresponded to multiple azimuths. Additionally, the chosen frequency range of 2–4 kHz lies in between frequency ranges that are typically either ITD- or ILD-dominant. It was therefore assumed that neither of the two binaural cues would be weighted particularly strongly and each binaural cue weight would thus have the potential to be increased. For frequencies above 1.4 kHz, thresholds for ITDs conveyed by the carrier signal (the so-called temporal fine structure) become unmeasurable (Brughera et al. 2013), and therefore, ITD cues are conveyed only via the stimulus’ temporal envelope. Bernstein and Trahiotis

(1982), however, showed that low-frequency residual energy far below the nominal pass band of a stimulus can provide salient ITD cues, even if those cues are transmitted at a low sensation level. We therefore cannot rule out some contribution of fine-structure ITD cues. Note that the particular contribution of envelope or fine-structure ITD cues was not the focus of this study. The stimulus duration was 500 ms, including 50-ms raised-cosine on/off ramps. The mean overall sound pressure level (SPL) across ears was 65 dB. To discourage participants from using differences in the absolute level rather than ILDs for lateralization, the overall level was randomly roved from trial to trial within a ± 2.5 dB range.

Our study included stimuli with spatially consistent or inconsistent binaural cues. For consistent-cue conditions, the ITD and ILD cues corresponded to the same azimuth (squares in Fig. 2c, d), whereas for inconsistent-cue conditions, the ITD and ILD cues corresponded to disparate azimuths (“x” symbols in Fig. 2c, d). In the training sessions, 26 reinforced-cue azimuths (i.e., azimuths corresponding to the visually reinforced binaural cue) were distributed between -45° (left) and $+45^\circ$ (right) with a spacing of 3.6° (x-axis in Fig. 2d). This range corresponds to the field of view of the head-mounted display. In conditions with inconsistent ITD/ILD-combinations, the unreinforced-cue azimuths (i.e., azimuths corresponding to the unreinforced cue) were uniformly distributed $\pm 25.2^\circ$ around each reinforced-cue azimuth (columns in Fig. 2d), also with an azimuthal spacing of 3.6° , resulting in a total range of unreinforced-cue azimuths from -70.2° to $+70.2^\circ$. The disparity between ITD and ILD azimuths was intentionally limited (maximum of 25.2°) with the goal of avoiding the perception of split images (e.g., Hafer and Jeffress 1968). Based on Gaik’s (1993) results, we did not expect split-image perception to occur for the frequency range and binaural cue disparities used in this study. In the pre- and posttest, in which no cue was reinforced, all combinations of ITD and ILD azimuths used for either group during training were included (Fig. 2c). The rationale behind using so many different spatial configurations

of ITD and ILD was to prevent the possibility of identifying individual stimulus azimuths and then responding strategically.

Procedure

The general task involved indicating the perceived azimuth of an intracranial sound source via head turn. Because stimuli were relatively narrowband and contained no HRTF filtering, they were likely not externalized by the participants. Thus, participants had to map the perceived intracranial image to the visual response field. Moore et al. (2020) argue that head-pointing in a virtual audio-visual environment can be used to obtain reliable in-head lateralization judgments without training participants to externalize the auditory stimuli. The paradigm for estimating binaural cue weights was based on Stecker’s (2010) “open loop” and Macpherson and Middlebrooks’ (2002) methods. Namely, by asking participants to lateralize stimuli containing spatially inconsistent ITD and ILD, we inferred how much each cue contributed to the azimuthal percept by comparing the response azimuth to the azimuths of the binaural cues (the measure of interest). This method is not subject to the bias of traditional trading ratio measurements (e.g., Deatherage and Hirsh 1959), because no cue is actively manipulated by the participants (see Lang and Buchner 2008) and single stimuli are presented (see Moore et al. 2020).

The experimental phases are shown in Table 1. The experiment started with a *practice session* to get participants accustomed to the task and to check their lateralization ability and sensitivity to both binaural cues. It continued with a *pretest* to measure the initial ITD and ILD weights, a 7-day *training* (completed within a 2-week interval) in which one of the cues was reinforced, and a *posttest* to remeasure the weights after the training. The approximate duration of the sessions was 2 h on the first day and 1.5 h per day on days 2 to 7. The choice of the number of training sessions and their duration was guided by the training regimen used in Kumpik et al. (2010).

TABLE 1

Time course (top to bottom and left to right) of experimental phases. On day 1, participants completed the practice session, followed by the pretest, followed by half a training session. On days 2–6, participants completed one training session each. On day 7, participants completed half a training session followed by the posttest. The seven testing sessions were completed within a 2-week interval

Day 1	Day 2	Day 3	Day 4	Day 5	Day 6	Day 7
Practice (130 trials)						
Pretest (446 trials)						
Training (195 trials)	Training (390 trials)	Training (390 trials)	Training (390 trials)	Training (390 trials)	Training (390 trials)	Training (195 trials)
						Posttest (446 trials)

Practice. The practice session (performed at the beginning of the experiment) consisted of 130 trials that differed from training trials (see training procedure below) only in the stimuli they used. The practice stimuli had either consistent ITD/ILD combinations (to measure basic lateralization ability) or they had either the ITD or the ILD fixed at zero while the other cue corresponded to a reinforced-cue azimuth (to test for sensitivity to the cues in isolation). Of the 130 practice trials, 78 (3 per reinforced-cue azimuth) contained consistent-cue stimuli, 26 (each reinforced-cue azimuth once) contained stimuli with ILD fixed at zero, and 26 (again each reinforced-cue azimuth once) contained stimuli with ITD fixed at zero. The trials were presented in random order while ensuring that the first 26 trials were consistent-cue combinations. Visual reinforcement was provided in each trial, as in the training (described below).

Testing. The pretest and the posttest were identical for the two groups and did not include visual reinforcement (see steps 1 and 2 of Fig. 1). On each trial, participants listened to the auditory stimulus while facing straight ahead (the reference position) and then indicated the perceived azimuth of the auditory stimulus via head turn and a button press (i.e., the azimuth indicated by the head turn at the time of the button press was recorded as the response azimuth). When they returned to the reference position, the session continued with the next trial. A total of 446 trials were presented, namely each ITD/ILD combination shown in Fig. 2c was presented once. These comprised all ITD/ILD combinations included in the training phase for both groups. The trials were presented in random order and after each 150 trials, participants took a short break.

Training. For training, we used a lateralization procedure based on the procedure used in Majdak et al. (2013). We adapted it by restricting it to the horizontal (azimuthal) dimension and by using the head-pointing technique. The training procedure consisted of 6 steps (shown in Fig. 1): (1) listening to the auditory stimulus while at the reference position straight ahead (initiated by pressing the button at the reference position), (2) indicating the perceived azimuth via head turn and button press, (3) receiving visual reinforcement (a rotating cube) at the reinforced-cue azimuth, (4) finding and confirming the reinforced-cue azimuth via head turn and button press, (5) returning to the reference position and listening to the same auditory stimulus again (initiated with a button press) while the visual reinforcement is still visible, and (6) confirming the reinforced-cue azimuth again via head turn and button press after which the visual reinforcement disappears. Participants were instructed to remain at the reference position for the duration of the auditory stimulus (500 ms) and reminded to do so throughout the experiment. However, participants were not physically

prevented from initiating head turns during sound presentation. Nevertheless, even if they did start to turn their heads before the stimulus ended, there is no reason to expect that this would confound the experimental variables under investigation. After every 65 training trials, participants took a short break.

Auditory stimuli included both inconsistent and consistent ITD/ILD-combinations, as shown in Fig. 2d. The training procedure was the same for the two groups except for which cue was visually reinforced and presented in a limited azimuth range. Thus, for the ITD group, ITD azimuths did not exceed $\pm 45^\circ$ and for the ILD group, ILD azimuths did not exceed $\pm 45^\circ$. This ensured that the visual reinforcement was visible while at the reference position, as $\pm 45^\circ$ was the field of view of the head-mounted display. A full training session consisted of 390 trials presented in random order. On days 1 and 7, participants completed only half sessions (195 trials each, created by splitting a randomized item list for a full session) to prevent fatigue because the pre- and posttest were also completed on these days. On days 2 to 6, participants completed full training sessions.

Analysis

The data were analyzed using MATLAB R2018b (The MathWorks, Natick, MA). Statistical analyses of results were performed using SPSS Statistics 20 (IBM, Armonk, NY). We estimated pre- and posttest binaural cue weights separately for each participant based on a regression analysis fitted separately for each azimuth α (between 1.8° and 45° with a 3.6° spacing between azimuths) after mirroring the data across the midline to get more reliable estimates (assuming left/right symmetry). The regression model equation is as follows:

$$R_{ITD}(\alpha, \Delta_{ITD}) = k_{ITD}(\alpha) * \Delta_{ITD} + Q_{ITD}(\alpha)$$

$$R_{ILD}(\alpha, \Delta_{ILD}) = k_{ILD}(\alpha) * \Delta_{ILD} + Q_{ILD}(\alpha)$$

$$w_{ILD}(\alpha) = \frac{\text{atan}\left(\frac{k_{ILD}(\alpha)}{k_{ITD}(\alpha)}\right)}{\frac{\pi}{2}}$$

$$Q(\alpha) = \frac{Q_{ILD}(\alpha) + Q_{ITD}(\alpha)}{2} \quad (1)$$

where R_{ITD} (R_{ILD}) is the participant's response azimuth in a trial with ITD (ILD) corresponding to the azimuth $\alpha + \Delta_{ITD}$ ($\alpha + \Delta_{ILD}$) and ILD (ITD) corresponding to α . The parameters k_{ITD} and k_{ILD} are the estimated linear regression slopes at azimuth α (determining the individual binaural cue weight contributions), and Q is the estimated response azimuth for consistent cues corresponding to

azimuth α . Parameter k_{ITD} (k_{ILD}) was estimated at each azimuth by considering various azimuthal offsets (from -25.2° to $+25.2^\circ$ in 3.6° steps) of the cue, Δ_{ITD} (Δ_{ILD}), while setting the offset of the other cue, Δ_{ILD} (Δ_{ITD}), to zero. Thus, referring to Fig. 2c, the model was fitted for each azimuth α , indicated by a square, by considering only items of the row (for k_{ITD}) and column (for k_{ILD}) that included that square (an example set of data used for the estimation of parameters at α of 9° is indicated by the black frame in Fig. 2c). These estimates of k_{ITD} and k_{ILD} , representing orthogonal vectors, were then combined to derive the ILD weight w_{ILD} (note that $w_{ITD} = 1 - w_{ILD}$). Finally, parameter Q was estimated as the average of the constants obtained in the regressions for ITD and ILD.

In addition to the estimation of pre- and posttest binaural cue weights, we sought to determine binaural-cue weights across the course of the training. This required, however, a modification of the procedure. The pre- and posttest data fulfilled the requirement of the regression analysis of a balanced distribution (specifically $\pm 25.2^\circ$) of ITD azimuths around ILD azimuths and vice versa. During training, this balanced distribution was available only for azimuths up to 19.8° , as reinforced-cue azimuths were limited to $\pm 45^\circ$. When analyzing the training data, we therefore gradually limited the range of Δ_{ITD} and Δ_{ILD} with increasing azimuth for azimuths more lateral than 19.8° , always ensuring a balanced, albeit reduced distribution (for example, at 41.4° , only the two neighboring azimuths as well as the consistent-cue condition were considered, see Fig. 2d). For the training data, responses were averaged across azimuths before running the regression analysis, since the model could not be fitted for all azimuths and time points separately, as in training sessions one and seven, only half of the items were presented. To compare weights estimated from the training data with weights estimated from the pre- and posttest data, this limited-range regression analysis was applied also to the pre- and posttest data (in addition to the main regression analysis using the full range).

RESULTS

Lateralization Responses

To evaluate the overall lateralization performance in our experiment, we calculated a basic, widely used measure, the root-mean-square error (RMSE) between response and stimulus azimuth for the consistent-cue items. The RMSE contains errors due to both systematic bias and response variability. In the pretest, the mean across all participants was 13.04° ($SD = 4.94$). Using a head pointing method in a virtual environment including individual HRTF filtering, Middlebrooks (1999) reported a mean lateral RMSE of 14.5° ($SD = 2.2$) and Majdak et al. (2010) a mean lateral RMSE of 14.4° for untrained participants.

Note that the sources in these studies also varied in elevation. However, restricting the range of polar source angles in Majdak et al. (2010), solely including sources close to the horizontal plane, only marginally decreased the lateral RMSE. We assume a similar dependency for the data of Middlebrooks (1999). Our lateralization method using binaural stimuli without HRTF filtering therefore shows comparable accuracy to virtual acoustics studies using a similar response paradigm.

Figure 3 provides a descriptive overview of the overall results pattern. Statistical analyses of the data are provided in later sections. It plots the mean response azimuth across participants as a function of either the reinforced-cue azimuth (panels a–d, left-hand side) or the unreinforced-cue azimuth (panels e–h, right-hand side). The data are parameterized by the offset of one cue (the cue that is not shown on the x -axis) from the other cue (the cue that is shown on the x -axis), pooling across three offset ranges: central offsets (-3.6° , 0° , and 3.6° , cyan circles), leftward offsets ($\leq 14.4^\circ$, blue downward-pointing triangles) or rightward offsets ($\geq 14.4^\circ$, red upward-pointing triangles). The cyan response curves (showing consistent-cue conditions and conditions with very small cue disparities) are fairly linear and close to the diagonal, showing that participants were able to extract the binaural cues and responded accurately using the employed setup. The separation of the three lines in each panel shows that both cues contributed to the perceived azimuth (e.g., response azimuths are further right for rightward offsets compared to central offsets, independent of which cue is parameterized as shown by the red lines falling above the cyan lines). In the posttest, response slopes were generally shallower compared to the pretest, suggesting an overall compression of response azimuths (reduced range of response azimuths relative to presented azimuths) which is further explored below. The distance between the three curves is indicative of binaural cue weighting. It is larger in conditions where the ITD offset is shown as the parameter (panels c–f), suggesting a larger ITD weight in both groups, which is particularly prominent in the pretest data (panel c versus a and panel e versus g). For panels showing the unreinforced-cue offset as the parameter (a–d), the distance between curves is expected to be smaller in the post- compared to the pretest, assuming a reduction of the unreinforced-cue weight and thus an increase of the reinforced-cue weight. This indeed seems to be the case for both groups (mean vertical separation between downward and upward triangles decreases from 16.1 to 11.6° for the ITD group and from 23.6 to 18.3° for the ILD group). Note, however, that compression also contributes to a reduced distance between curves. In contrast, for panels showing the reinforced-cue offset as the parameter (e–h), binaural cue reweighting would result in increasing distance between curves from pre- to posttest. In this case, however, compression counteracts cue reweighting. Consistent with these assumptions, the distance between curves

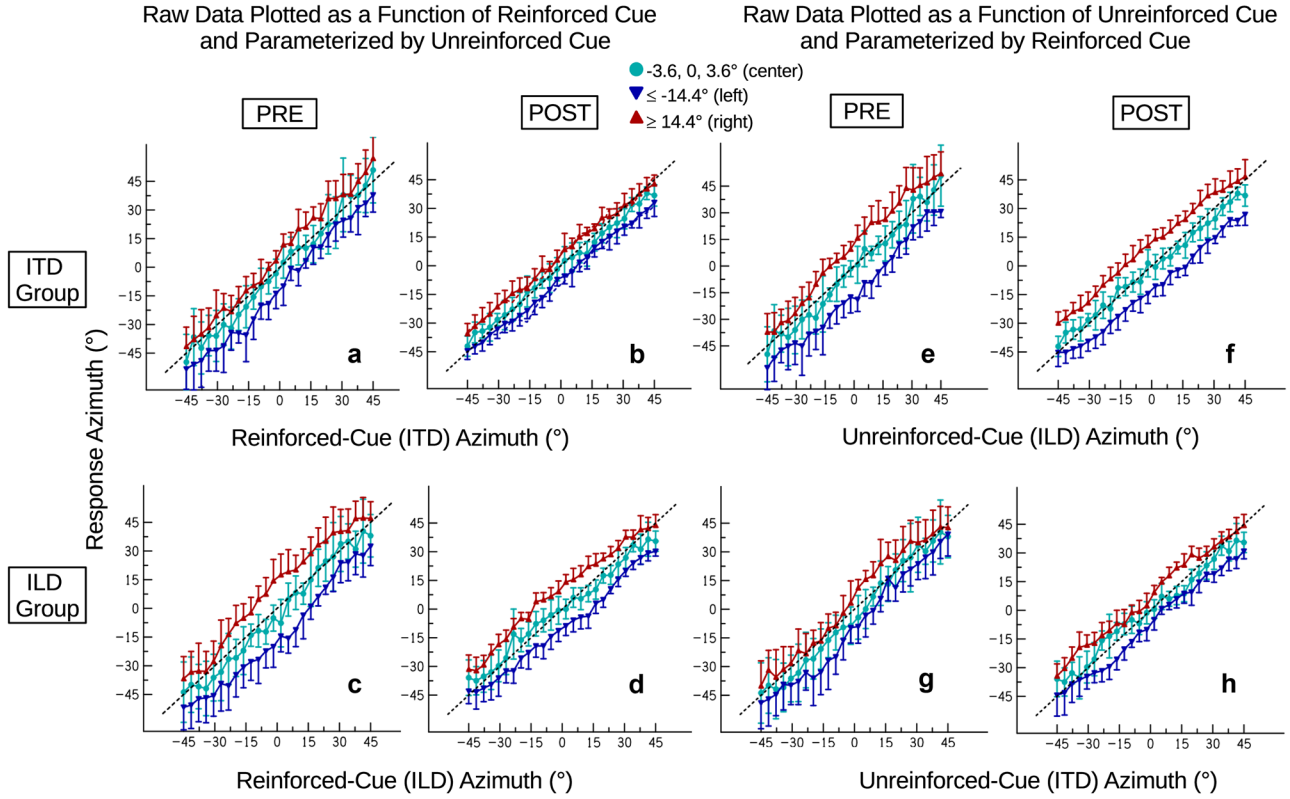


FIG. 3 An overview of mean response azimuths across participants as a function of either reinforced-cue azimuth (ITD azimuth for the ITD group, ILD azimuth for the ILD group; panels **a–d**, left-hand side) or unreinforced-cue azimuth (ILD azimuth for ITD group, ITD azimuth for ILD group; panels **e–h**, right-hand side). The data are parameterized by the offset of the cue not shown on the x-axis from

the cue shown on the x-axis, pooling across three offset ranges: central offsets (-3.6° , 0° , and 3.6° , cyan circles), leftward offsets ($\leq -14.4^\circ$, blue downward-pointing triangles) or rightward offsets ($\geq 14.4^\circ$, red upward-pointing triangles). In each panel pair, the panel on the left shows the pretest and the panel on the right shows the posttest. Error bars indicate standard deviations

appears to be more similar in pre- and posttest (mean vertical separation changes only marginally from 23.8 to 22.1° for the ITD group and even increases slightly from 13.2 to 14.5° for the ILD group).

Binaural-Cue Weights

Figure 4 shows the ILD weights (w_{ILD}) as determined by the regression analysis at each azimuth separately for the two groups. Posttest ILD weights (red squares) *decreased* for the ITD group and *increased* for the ILD group compared to pretest ILD weights (blue circles). A $2 \times 13 \times 2$ mixed-design ANOVA with the within-participants factors *time* (pre- vs. posttest) and *azimuth* and the between-participants factor *group* (ITD vs. ILD group) yielded no significant main effects, but a significant *time* $\times$ *group* interaction ($F(1,18) = 20.44$, $p < 0.001$, $\eta_p^2 = 0.532$). All other interactions were non-significant. The lack of a significant main effect of *time* was expected, assuming opposing effects of time on the ILD weights for the two groups. Simple main effect analyses showed that the *time* $\times$ *group* interaction was driven by a significant difference between

the pre- and posttest in the ITD group ($F(1,18) = 7.44$, $p = 0.028$, $\eta_p^2 = 0.293$, Bonferroni-corrected), with larger ILD weights in the pretest ($M = 0.40$, $SD = 0.13$) compared to the posttest ($M = 0.31$, $SD = 0.09$), as well as a significant difference between the pre- and posttest in the ILD group ($F(1,18) = 13.43$, $p = 0.004$, $\eta_p^2 = 0.427$, Bonferroni-corrected), with smaller ILD weights in the pre- ($M = 0.31$, $SD = 0.09$) compared to the posttest ($M = 0.43$, $SD = 0.10$). They further showed that the groups did not differ significantly in the pretest ($F(1,18) = 3.17$, $p = 0.184$, $\eta_p^2 = 0.150$, Bonferroni-corrected), but there was a significant group difference in the posttest ($F(1,18) = 8.04$, $p = 0.022$, $\eta_p^2 = 0.309$, Bonferroni-corrected). Figure 5 plots the reinforced-cue weights averaged across azimuths of each participant. Consistent with the significant pre- vs posttest difference in both groups, the weight given to the reinforced cue increased from pre- to posttest for 16 out of 20 participants. Note that the estimates of w_{ILD} are independent of response compression under the assumption that compression affects both cues equally, so its effect on the slopes k_{ITD} and k_{ILD} cancels out in the final weight estimation (Eq. 1). This assumption was tested using a modeling approach,

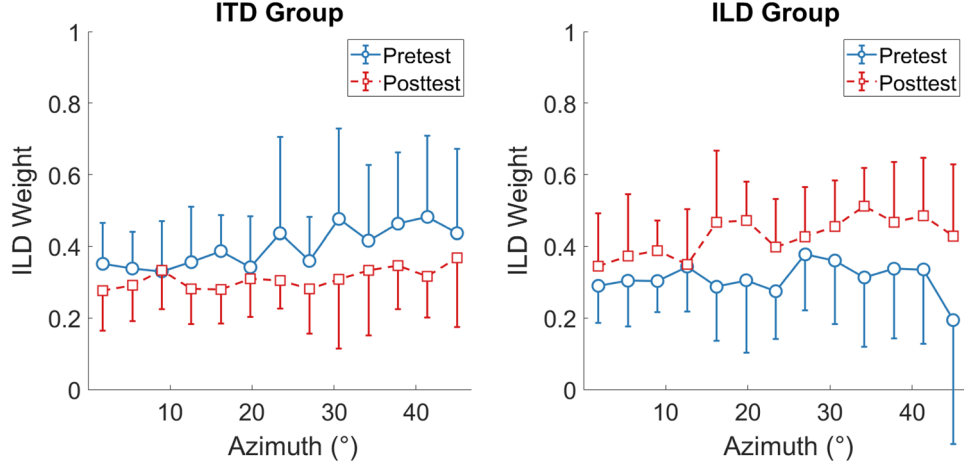


FIG. 4 ILD weights as a function of azimuth (after collapsing data across left and right azimuths) derived using a regression analysis. Blue circles show the pretest results and red squares the posttest results, separately for the ITD and ILD groups (individual panels). Note that, by definition, ITD weight = $1 - \text{ILD weight}$. Error bars show standard deviations

which yielded a better account of the data for a model version assuming reweighting combined with cue-independent compression than a model version assuming cue-specific compression of the unreinforced cue (see Appendix for details). Taken together, these results suggest that the training induced an azimuth-independent increase in the reinforced-cue weights for both groups.

Next, we addressed the potential implication of apparently asymmetric binaural cue weights (i.e., an overall stronger weighting of ITD cues). Since azimuth had no significant effect on the ILD weights, the weights were averaged across azimuths. The mean ILD weights were significantly smaller than 0.5 (a weight of 0.5 means equal weighting of the two binaural cues) in both the pretest ($M = 0.35$, $SD = 0.12$, $T(19) = -5.59$, $p < 0.001$, $d_z = -1.25$)

and the posttest ($M = 0.37$, $SD = 0.11$, $T(19) = -5.37$, $p < 0.001$, $d_z = -1.20$), showing an overall dominance of ITD cues. Because a higher baseline (pretest) weight for the reinforced cue potentially limits the room for training-induced reweighting towards the reinforced cue, we first checked if the amount of reweighting, quantified as the post- versus pretest difference in reinforced-cue weights, differed between groups. The amount of reweighting (ITD group 0.09; ILD group 0.12) did not differ significantly between groups ($T(18) = -0.66$, $p = 0.516$, $d = -0.31$), providing no evidence that such ceiling effects might have affected the ITD group. As the distribution of pre- and posttest weights across participants might provide further hints, we examined the posttest reinforced-cue weight as a function of the pretest reinforced-cue weight (see

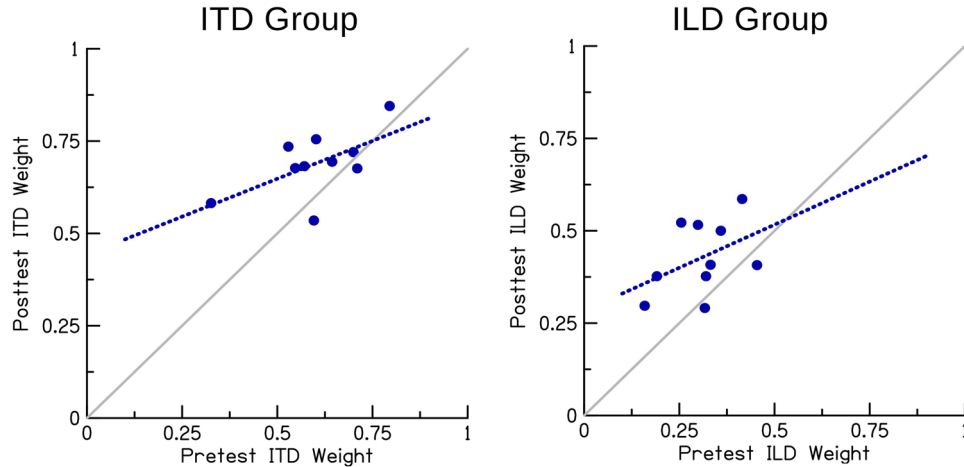


FIG. 5 Posttest reinforced-cue weight as a function of pretest reinforced-cue weight including the slopes of linear regressions fitted to the data. The symbols show individual participants

Fig. 5). For the ITD group (left panel), the data points accumulate more towards the upper right quadrant of the plot and the pattern appears to be shallower than the diagonal. Accordingly, the 95 % confidence interval (CI) for the slope of a linear regression fitted to the data did not include 1 (slope 0.41; 95 % CI = $-0.03, 0.85$). We therefore cannot completely rule out that participants with a high pretest ITD weight were somewhat affected by ceiling effects. For the ILD group (right panel), the data accumulate more toward the lower left quadrant of the plot and the pattern is, compared to the ITD group, more parallel to the diagonal. Consistently, the 95 % CI for the slope of a linear regression fitted to the data did include 1 (slope 0.47; 95 % CI = $-0.34, 1.27$). Thus, there is no hint for ceiling effects in the ILD group, which is expected given the low pretest ILD weight of all participants.

Time Course of Cue Reweighting

We further sought to investigate the time course of cue reweighting across training sessions. Figure 6 shows the training progress for a data subset (see “Methods” section for details) for the two groups. For comparison, the pre- and posttest weights calculated using all data, replotted from the means across azimuth in Fig. 4, are added as separate filled symbols at the far left and far right of the figure. For both groups, the training effect

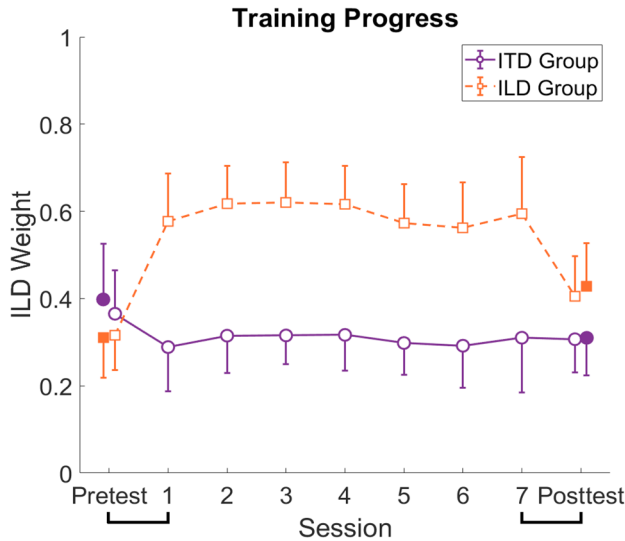


FIG. 6 Training progress. ILD weights calculated by limiting the combinations considered for azimuths more lateral than 19.8° to ensure balanced distributions are shown for the pretest, the seven training sessions and the posttest. Purple circles show the results for the ITD group, orange squares for the ILD group. For comparison, the pre- and posttest weights calculated using all data are shown as separate symbols at the far left and far right of the figure. Error bars show standard deviations

seems to have been induced within the first training session and there appears to be no further change over the course of training. In the ITD group, the relatively small effect appears to have persisted after training, while in the ILD group the initially larger effect appears to have partly dissipated in the posttest. Two repeated-measures ANOVAs (separate for the groups) using the seven training sessions as the within-subjects factor confirmed that there were no significant differences across training sessions. We therefore averaged across training sessions to further explore the relationship between the pre-/posttest and the training. We ran two repeated-measures ANOVAs (one for each group) with the within-subjects factor *time* (pretest–averaged training sessions–posttest) including post-hoc pairwise comparisons. For the ITD group, the main effect of *time* failed to reach significance after correcting for a sphericity violation ($F(1.27, 11.44) = 3.72, p = 0.072, \eta_p^2 = 0.292$, Greenhouse–Geisser-corrected). The post-hoc pairwise comparisons also did not yield any significant differences (all $p > 0.191$, Bonferroni-corrected). For the ILD group, the repeated-measures ANOVA yielded a significant main effect of *time* ($F(1, 18) = 19.55, p < 0.001, \eta_p^2 = 0.685$). The post hoc pairwise comparisons showed significant differences between the pretest and the training ($p = 0.001$, Bonferroni-corrected) with smaller ILD weights in the pretest ($M = 0.315, SD = 0.079$) compared to the training ($M = 0.594, SD = 0.089$), the training and the posttest ($p = 0.022$, Bonferroni-corrected) with larger ILD weights in the training compared to the posttest ($M = 0.405, SD = 0.092$) as well as the pre- and the posttest ($p = 0.048$, Bonferroni-corrected) with smaller ILD weights in the pretest compared to the posttest. Hence, the ITD group showed a modest, albeit non-significant decrease in the ILD weight from the pretest to the first training session and no change afterwards. In contrast, the ILD group showed a larger, significant increase in the ILD weight during the first training session and a significant reduction of the ILD weight from the last training session to the posttest. Note that these training results should be interpreted with caution, given that only a subset of data could be analyzed, given the requirement to estimate binaural cue weights independent of response bias.

Response Compression

Next, we examined the response compression (i.e., overall shallower lateralization slopes in the posttest) from pre- to posttest observed for both groups (see description of Fig. 3). Figure 7 shows the estimated response azimuths for consistent cues based on the regression analysis (i.e., the estimated values of Q from Eq. 1), pooled across groups. Lateralization in the pretest was fairly accurate, since the estimated response azimuths are similar to the cue azimuths

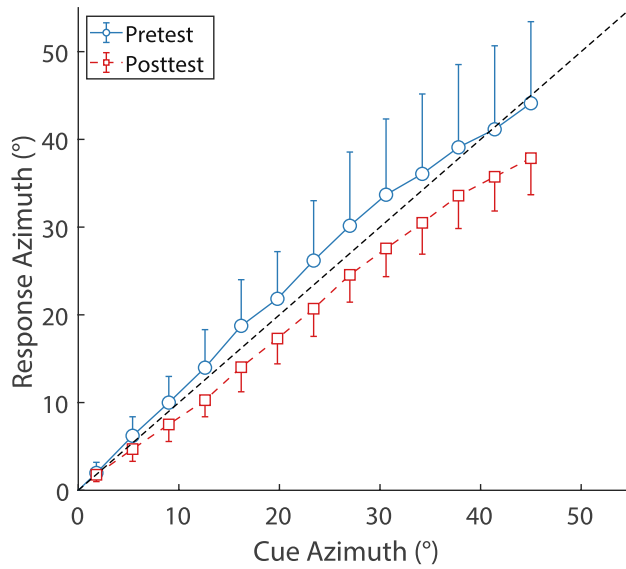


Fig. 7 Estimated response azimuths for the consistent items (i.e., the parameter Q from the regression analysis) as a function of cue azimuth, pooled across the groups. Blue circles show the pretest results and red squares the posttest results. Error bars show standard deviations

(i.e., close to the diagonal) and pretest slopes of estimated response vs. cue azimuths were not significantly different from 1 ($M=1.04$, $SD=0.25$, $T(19)=0.81$, $p=0.431$, $d_z=0.18$). Posttest slopes, however, were shallower than pretest slopes and significantly different from 1 ($M=0.87$,

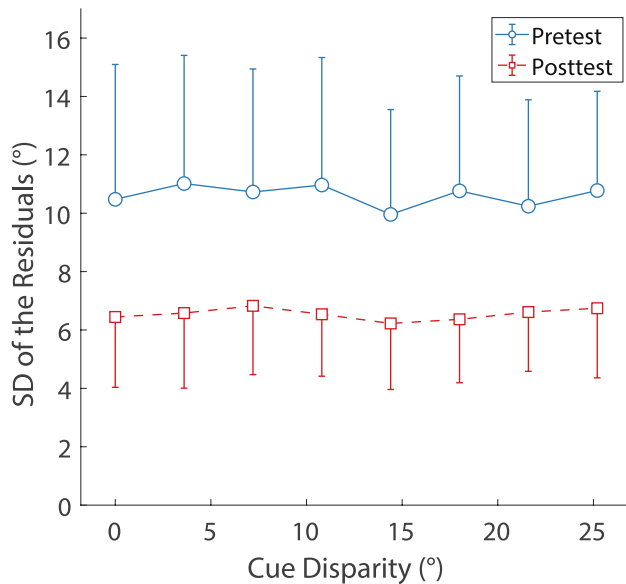


Fig. 8 Response variability (defined here as the standard deviation of the residuals of the regression analysis) as a function of cue disparity in the pre- and posttest pooled across groups. Blue circles show the pretest results and red squares the posttest results. Error bars show standard deviations

$SD=0.10$, $T(19)=-5.90$, $p<0.001$, $d_z=-1.32$), suggesting a systematic and apparently linear compression of responses. Subjecting the ratio of estimated responses/cue azimuths to a 2 (*time*) $\times$ 13 (*azimuth*) $\times$ 2 (*group*) mixed-design ANOVA yielded a significant main effect of *time* ($F(1,18)=18.19$, $p<0.001$, $\eta_p^2=0.503$), but neither the main effects (*azimuth* and *group*) nor the interactions were significant, suggesting that this compression of responses from pre- to posttest is indeed linear and similar in both groups.

Change in Lateralization Precision and Split-Image Perception

Finally, we attempted to quantify the training-induced change in overall lateralization precision (i.e., the consistency in lateralization responses; see Heffner and Heffner 2005) and confirm that the participants did not perceive split images (Haft and Jeffress 1968) when stimuli with inconsistent cues were presented. To that end, response variability was calculated by computing the residuals (where, for each response, the residual is defined as the deviation of the actual response azimuth from the response azimuth predicted by the regression analysis from Eq. (1) and then computing the standard deviation of these residuals. Figure 8 shows the results as a function of cue disparity, averaged across groups. The response variability was systematically lower in the posttest than in the pretest, while there seems to be no systematic effect of cue disparity. The mean variability across groups and all binaural cue disparities decreased from 10.62 ($SD=3.90$) in the pretest to 6.54 ($SD=2.17$) in the posttest. A 2 (*time*) $\times$ 8 (*cue disparity*) $\times$ 2 (*group*) mixed-design ANOVA showed significant main effects of the factors *time* ($F(1,18)=27.24$, $p<0.001$, $\eta_p^2=0.602$) and *cue disparity* ($F(4.18,75.26)=2.51$, $p=0.046$, $\eta_p^2=0.123$, Greenhouse–Geisser-corrected) but no significant effect of the factor *group* and no significant interactions. Post hoc pairwise comparisons revealed that the main effect of *cue disparity* was driven by a significant difference between cue disparities of 14.4° and 25.2° ($p=0.008$, Bonferroni-corrected). However, variability did not systematically increase with increasing cue disparity nor adopt an inverted u-shape. Either of these two patterns might be expected if larger cue disparities had evoked the perception of split images. As a further check for the possibility of split image perception, we inspected the response distributions as a function of binaural cue disparity for each participant and found no systematic indications for distributions being bimodal or centered close to one cue azimuth only, as may be expected in the case of split image perception. Thus, these results provide no indication for split image perception and instead suggest that participants perceived a single compact auditory image for all cue disparities included in this study.

DISCUSSION

This study is, to our knowledge, the first one to provide evidence that it is possible to selectively increase the relative weighting of either ITD or ILD cues. This binaural-cue reweighting was induced through lateralization training in a virtual audio-visual environment, employing visual reinforcement as well as symmetric azimuthal variation of unreinforced cues around reinforced cues. The results demonstrate that the auditory system flexibly adjusts the contribution of each of the two binaural cues to the perceived lateral position of an auditory object based on previous experience.

Factors Contributing to Binaural-Cue Reweighting

While several studies have addressed the plasticity of the spatial auditory system to spatial cue modifications (e.g., Kumpik et al. 2010; Shinn-Cunningham et al. 1998), the only two published studies we are aware of explicitly addressing binaural-cue reweighting (Jeffress and McFadden 1971; Kumpik et al. 2019) produced inconclusive results. Jeffress and McFadden observed no reweighting effect and while Kumpik et al. report an increase in ILD weighting after ITDs were randomized, they did not observe an increase in ITD weighting when ILDs were randomized and observed an even stronger increase in ILD weighting when spatially consistent ITDs and ILDs were presented. These different results (both regarding previous literature as well as the present study) can likely be attributed to differences in the methodology, as discussed in the introduction, suggesting that factors necessary to induce binaural-cue reweighting may include active listening, intuitive responding, bottom-up multisensory integration, and auditory stimuli that contain salient ITDs as well as salient ILDs.

Our study employed five key manipulations during training to maximize chances for inducing binaural-cue reweighting: (1) presenting visual stimuli at the reinforced-cue azimuth after the response as top-down feedback, (2) presenting visual stimuli simultaneously with the second sound presentation to tap into multisensory bottom-up processes, (3) requiring responses via head-turn, therefore also involving proprioceptive information, (4) using narrow-band noise at a frequency range for which neither ITDs nor ILDs are known to dominate, and (5) manipulating the stability of the cues by varying the unreinforced cue over a larger range than the reinforced cue. Trapeau and Schönwiesner (2015) observed that, when participants wear earplugs consistently delaying the sound at one ear, they remap their auditory space based on that delay instead of increasing the weight given to preserved ILD cues. Therefore, cue variation as opposed to a predictable cue manipulation might also be an important factor contributing to cue reweighting.

Time Course of Cue Reweighting

Although our data are not optimally suited for studying the time course of reweighting (e.g., not all ITD/ILD combinations included in the pre- and posttest were included in the training), the current analysis of the training data suggests that reweighting occurred predominantly within the first training session. This is consistent with Kumpik et al. (2019), who reported binaural cue reweighting to occur within less than 1 h of training. Kumpik et al. (2010) on the other hand did not observe adaptation (reweighting towards monaural cues in this case) when all training trials were performed in one day, but rather found continuous improvement across all 7 or 8 training days. A plausible explanation could be that the participants in their study needed to learn to exploit monaural spectral cues for azimuthal localization when the binaural cues were disrupted, while such learning was not required in our study given that both binaural cues are used by default.

It should also be noted that the time course seems to differ between the two groups in the current study. While the ITD group showed less reweighting from the pretest to the training which then remained stable through the posttest, the ILD group showed stronger reweighting from the pretest to the training, part of which then got lost from the last training session to the posttest. Wright and Fitzgerald (2001) also reported different time scales for ITD vs. ILD discrimination learning. However, these time scales differ from the current observations. Namely, they report an initial rapid improvement for both cues that generalizes across conditions followed by a slower improvement for ILD discrimination only. Another possibility to consider is that the adaptation occurs on multiple time scales, as, for example, observed in the ventriloquism aftereffect (Bosen et al. 2018). Specifically, the reweighting of the ILD group might consist of a quick strong component that is spontaneously reversed when the visual feedback stops, combined with a weaker, also quick, but more sustained reweighting. In comparison, the ITD group might only show the more sustained component. This would be interesting to explore in future studies.

Conscious vs. Unconscious Reweighting

An important question is whether the current results could have been mediated by conscious or strategic listening. We consider strategic reweighting very unlikely given the myriad of reinforced- and unreinforced-cue azimuths spread across a wide range. Moreover, the disparity between ITD and ILD azimuths was intentionally limited (maximum of 25.2°) with the goal to avoid the perception of split images (e.g., Hafer and Jeffress 1968) which could theoretically allow for strategic listening, if the two binaural cues could be distinguished. In fact, all participants (as well as the authors during informal piloting) reported perceiving compact auditory images, with no indication of split images.

Consistent with these subjective reports, we observed similar response variability across cue disparities and no indications for response distributions being bimodal or centered close to the azimuth of one binaural cue only. The observation that there was no improvement after the first training session (especially in the ILD group whose ILD weights were still far from 1) further makes conscious reweighting unlikely. Taken together, these results suggest that binaural-cue reweighting occurs at a more low-level, unconscious processing stage.

Response Compression

We found a systematic compression of the response azimuth range from pre- to posttest. This can at least partly be attributed to limiting the azimuth range of the reinforced cue to $\pm 45^\circ$ during training. While the unreinforced cues ranged up to $\pm 70.2^\circ$ and auditory stimuli were certainly perceived beyond $\pm 45^\circ$, reinforced-cue azimuths and therefore also the visual reinforcement were restricted to $\pm 45^\circ$, likely triggering a mapping to this azimuth range. Interestingly, the resulting response compression occurred not only at the edges, but across the entire azimuth range, and followed a linear function. This result is consistent with an earlier study showing that various nonlinear mapping functions between auditory and visual azimuth space resulted in response azimuths following a linear approximation of these functions (Shinn-Cunningham et al. 1998). Furthermore, fatigue or decreased willingness by the participants to exploit the whole azimuthal response range in the post-test might have contributed to response compression.

We considered the possibility that response compression was specific to the unreinforced cue, given that it was varied over a larger range than the reinforced cue during training. However, the results of a simple modelling approach indicate that the compression is cue-independent, suggesting that it occurs after the information of the two binaural cues is integrated (see [Appendix](#)).

Pretest ITD Weights

The dominance of ITD cues observed in the present study is consistent with the literature (Macpherson and Middlebrook 2002; Wightman and Kistler 1992). Macpherson and Middlebrooks observed that for their wideband stimulus condition, participants either weighted ITDs and ILDs equally or weighted ITDs more. Since our passband lies in between Macpherson and Middlebrooks' low-pass and high-pass stimulus conditions and some low- and high-frequency energy was present due to the roll-off of our band-pass filter, Macpherson and Middlebrooks' wideband stimuli appear most comparable to the stimuli used in the present study.

Implications of the Particular Auditory Stimuli Used

The passband of our stimuli lies in a frequency region where ITDs are conveyed only via the temporal envelope. Bernstein and Trahiotis (1982), however, observed that residual energy below the stimulus passband, comparable to our study, can provide access to salient low-frequency (likely fine-structure based) ITD cues. Some influence of fine-structure ITDs in the present study is in fact suggested by the overall stronger weighting for ITDs, like in Macpherson and Middlebrooks' (2002) wideband condition.

We intentionally chose a frequency range for our stimuli that lies in between typically ITD- or ILD-dominant regions so that both ITD and ILD weighting had the potential to be increased. Future studies may investigate whether reweighting also occurs for more natural broadband stimuli including low- and high-frequency regions where ITDs and ILDs, respectively, are known to dominate perceptually. Additionally, it is unclear whether the training-induced reweighting generalizes to non-trained frequency regions. Wright and Fitzgerald (2001), for example, observed different generalization patterns of ITD and ILD sensitivity training.

Furthermore, we presented auditory stimuli via headphones using constant binaural cues across the stimulus spectrum rather than HRTF filtering. This was done to ensure that the stimuli did not convey monaural spectral localization cues that are potentially informative about the azimuth of the stimulus, to reveal purely binaural-cue reweighting. Kumpik et al. (2010), for example, observed an increased weighting of monaural cues and no adaptation to changed binaural cues when monaural spectral cues were preserved at one ear. As monaural and binaural localization cues interact in everyday life, the effect of binaural-cue reweighting on more realistic stimuli is an interesting topic for future studies.

Applications

Binaural-cue reweighting might be useful for situations in which one of the cues is particularly informative while the other cue is less reliable or even misleading. For example, since listeners benefit from the presence of both ILD and ITD cues in spatial release from speech masking (e.g., Ellinger et al. 2017; Kidd et al. 2010), binaural-cue reweighting may be a means to cope with the changing reliability of binaural cues in speech in multi-talker or differing acoustically complex environments. Consistent with this suggestion, Rakerd and Hartmann (2010) observed that ILDs were increasingly favored as the binaural waveform coherence decreased after introducing reverberation.

Similarly, our results might have implications for listeners with cochlear implants (CIs). It has been shown that localization in the horizontal plane with current CI systems is almost entirely based on ILDs, while ITDs contribute only very little or not at all (Grantham et al. 2008; Seeber and Fastl 2008). On one hand, this is due to the properties of current envelope-based CI systems, which encode no useful ITDs in the pulse carriers and whose envelope ITD cues for real-life stimuli are not very salient (Grantham et al. 2008; Laback et al. 2004, 2011). On the other hand, even when presenting pulse carrier ITDs highly controlled via a research system at a single interaural electrode pair, CI listeners' sensitivity is greatly reduced and much more variable across listeners compared to normal-hearing listeners' carrier ITD sensitivity (Laback et al. 2007; Majdak et al. 2006; van Hoesel 2007). Several explanations have been proposed for this perceptual deficit in electric hearing (see, e.g., Laback et al. 2015). Considering our current results, it might partly be a result of reweighting of the binaural cues over time. Specifically, it is possible that binaural cue reweighting takes place after CI implantation, resulting in a stronger weighting of the ILDs which consistently indicate sound source locations, and a decreased weighting of the ITDs which are not reliably and saliently provided by the CI listeners' clinical devices.

Summary and Overall Conclusions

In conclusion, our results suggest that reweighting of auditory localization cues is not limited to monaural vs. binaural cues, which has been shown in previous studies, but that reweighting of the two binaural cues ITDs and ILDs is also possible. Specifically, we show that the weighting of both ITDs and ILDs can be selectively increased by reinforcing the respective cue through lateralization training. This could play a role in adapting to variable acoustic environments, be a factor contributing to the low contribution of ITDs to sound localization in CI listeners, and have potential applications, for example, in training for unfamiliar audio-visual environments or with hearing devices that impede one of the two binaural cues.

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Appendix

The estimate of w_{ILD} is independent of response compression under the assumption that compression affects both cues equally, so that its effect on the slopes k_{ITD} and k_{ILD} cancels out in the final weight estimation (Eq. 1). However, as unreinforced-cue azimuths were varied over a wider range ($\pm 70.2^\circ$) than reinforced-cue azimuths ($\pm 45^\circ$) during training, it is conceivable that the training led to a specific compression of the unreinforced cue while the reinforced cue was not affected by compression. Such a scenario could be an alternative interpretation of the results because it would reduce the relative contribution of the unreinforced cue, similar to the effect of cue reweighting. In this Appendix, we describe the results of a simple modeling approach to determine which of these two scenarios quantitatively better characterizes the current data. To that end, we predicted lateralization responses based on weighted averages of the cue azimuths under different compression assumptions and compared those predictions to the actual posttest data. The mean posttest data of each group from Fig. 3 were used, for which either the unreinforced cue was varied around the reinforced cue (panels b and d) or the reinforced cue was varied around the unreinforced cue (panels f and h), categorized by cue offsets “center,” “left,” or “right” (see caption of Fig. 3). Predictions were made separately for each azimuth.

For a given condition with a certain combination of binaural-cue values, corresponding cue azimuths were first multiplied by a compression factor, C ($C = 1$: no compression; $C < 1$: compression), which was either the same (cue-independent) or different (cue-specific) for the two cues (see model versions below). The resulting values were then subjected to weighted averages as determined by the parameter w_{ILD} (see description of regression analysis in the “Methods” section) to form the predicted response azimuth. Depending on the model version, either or both parameters C and w_{ILD} were freely varied (in steps of 0.01) and the parameter(s) resulting in the highest prediction accuracy were determined. Prediction

TABLE 2

Results of modeling the posttest data for the ITD group (upper two rows) and ILD group (lower two rows) using two model versions, the cue-specific compression (CSC) model and the reweighting and cue-independent compression (RCIC) model. RMSE refers to the RMS deviation between observed and predicted response azimuths, C to the compression factor, and w_{ILD} to the ILD weight

Model version	Compression	Cue weight	Mean RMSE across azimuths	SD	C	SD	w_{ILD}	SD
Cue-specific compression (CSC)	Varied	Pretest	1.54	0.55	0.70	0.10	-	-
Reweighting and cue-independent compression (RCIC)	Varied	Varied	1.09	0.36	0.89	0.03	0.35	0.03
Cue-specific compression (CSC)	Varied	Fixed (pretest)	2.37	0.85	0.79	0.03	-	-
Reweighting and cue-independent compression (RCIC)	Varied	Varied	1.96	0.60	0.87	0.03	0.45	0.06

accuracy was determined by means of the RMS deviation between observed and predicted response azimuths (referred to as RMSE). All conditions fulfilled the requirements for convex optimization.

We compared the performance of two model versions. In the *cue-specific-compression* (CSC) model, C was freely varied for the unreinforced cue while it was fixed for the reinforced cue. Specifically, for the reinforced cue, C was based on the consistent-cue pretest data (1.070 and 1.024 for the ITD and ILD groups, respectively). Parameter w_{ILD} was fixed and taken from the regression analysis of the pretest data, where C is very close to 1 and, thus, weight estimation is very unlikely to be confounded by cue-specific compression. In the *reweighting-and-cue-independent-compression* (RCIC) model, both C and w_{ILD} were freely varied, i.e., all combinations of the two parameters were evaluated.

The results are summarized in Table 2. The RCIC model resulted in a lower RMSE (1.09°) than the CSC model (1.54°). This difference was significant for both the ITD group ($T(12) = 3.57$, $p = .004$, $d_z = 0.99$) and the ILD group ($T(12) = 3.09$, $p = .006$, $d_z = 0.86$) when comparing the means across azimuths. Moreover, the estimates of w_{ILD} across azimuths by the RCIC model correspond very well to the respective posttest estimates by the regression analysis ($r^2 = 0.9$ and 0.94 for the ITD and ILD groups, respectively). Also, mean C estimates by the RCIC model (0.89 and 0.87 for ITD and ILD groups, respectively) correspond very well to the bias estimates of the regression model (0.87 and 0.87 for ITD and ILD groups, respectively). In summary, the model results suggest that the training effect observed in the posttest was more likely induced by cue reweighting combined with cue-independent compression than by cue-specific compression of the unreinforced cue.

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2.2 Reweighting of binaural localization cues induced by discrimination training

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REWEIGHTING OF BINAURAL LOCALIZATION CUES INDUCED BY DISCRIMINATION TRAINING

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ABSTRACT

Normal-hearing listeners weight binaural localization cues depending on the sound's frequency content. Interaural time differences (ITDs) dominate at low frequencies and interaural level difference (ILDs) dominate at high frequencies. The contribution of each cue to an azimuthal localization percept also depends on environmental factors such as room acoustics. Furthermore, ITD/ILD weighting was shown to change for stable sound conditions through a lateralization training in virtual reality (VR) using visual feedback. This study aims to induce similar reweighting using a simple left/right discrimination task without VR.

Participants were divided into two groups, a group trained to increase their ILD weighting and a no-training control group. Both groups completed an identical pre and post assessment involving a relative discrimination task without feedback, using various combinations of spatially inconsistent ITD and ILD. The training group additionally completed three sessions of an adaptive relative discrimination training including feedback (correct/incorrect) always consistent with the ILD azimuth. After each incorrect response, the auditory stimulus was repeated with the correct response shown on screen.

Responses followed the ILD azimuth significantly more often in the posttest than in the pretest for the training group but not for the control group, suggesting that binaural cue reweighting can be achieved by a simple discrimination task.

1. INTRODUCTION

Normal-hearing listeners primarily rely on two binaural cues for sound localization in the horizontal plane, the interaural time difference (ITD) and the interaural level difference (ILD) [1]. They apply frequency-dependent weights when combining these cues to determine the perceived azimuth of a sound source. While ITDs dominate at low frequencies (up to approximately 1.5 kHz), ILDs are dominant for high-frequency stimuli, which is known as the duplex theory of sound localization [2-3]. However, binaural cue weighting is not only determined by the sound's frequency content. For instance, it also depends on the overall level of the sound [4], whether the listener actively manipulates one of the cues [5], and on room acoustics [6].

Furthermore, listeners adapt to manipulated sound localization cues by changing the perceptual weights given to these cues. Several studies report a stronger weighting of monaural spectral cues compared to binaural localization cues for horizontal sound localization after wearing unilateral earplugs [7-9]. In another study, listeners were observed to increase their ILD weighting when ITDs were randomized, even though the auditory stimuli were irrelevant to the task [10]. Finally, normal-hearing listeners were shown to increase the relative weight given to either ITD or ILD, depending on which cue was visually reinforced during a lateralization training in a virtual audio-visual environment [11].

While the latter study [11] successfully induced reweighting, it was rather complex and required sophisticated equipment (e.g., virtual reality glasses). In addition, a compression of the lateralization responses from pre- to posttest was observed that might complicate the interpretation of the results. Therefore, we now seek to develop a simpler method to induce reweighting of the two binaural cues, which is not susceptible to response compression and which does not require sophisticated equipment. A left/right discrimination task matches these criteria. However, an early study attempting to reweight ITD and ILD through left/right discrimination training was not successful [12]. The stimuli used in that study were noise bands centered at 500 Hz, the binaural cues were close to the binaural cue threshold, and feedback was given after participants had responded. Therefore, potential reasons for the null result are that (1) the stimulus was in a frequency range where only ITDs but not ILDs arise naturally, (2) the binaural cues were not sufficiently salient, and (3) no corrective measures were taken if the participant responded "incorrectly". Based on the methods used in [11], we address these points in the present study by (1) using a noise band centered at 2.8 kHz to ensure that neither of the two cues are weighted predominantly strongly, (2) using a two-interval, relative discrimination task instead of a one-interval task, which allows us to test many spatial configurations as we are not restricted to azimuths close to the midline, and (3), in addition to giving feedback (correct/incorrect) after each response, repeating the auditory stimuli after each "incorrect" response with the "correct" response shown on the screen.

2. METHODS

2.1 Participants

21 participants completed the experiment, 10 of which were assigned to a training group and trained to increase their ILD weighting. The remaining 11 participants were assigned to a no-training control group. All but two participants had normal hearing (≤ 20 dB HL threshold at frequencies between 250 and 8000 Hz) as tested with an audiometer. The remaining two participants had thresholds ≤ 30 dB HL. The participants received monetary compensation for their participation. All procedures were approved by the UPJS Ethics Committee.

2.2 Apparatus and Stimuli

The experiment was controlled by Psychtoolbox-3 for MATLAB (The MathWorks, Natick, MA), running on a personal computer. Auditory stimuli were generated by an external sound card (RME Fireface 400) and presented via headphones (Sennheiser HD 800 S). Participants were seated in front of a monitor inside a soundproof booth and responded with the left and right arrow keys of a keyboard.

The same auditory stimuli as in [11] were used, namely 500-ms (including 50-ms raised-cosine on/off ramps) narrow-band white noise bursts with a bandwidth of one octave, geometrically centered at 2.8 kHz. Combinations of ITDs (ranging from -662 to $+662$ μ s) and ILDs (ranging from -19.4 to $+19.4$ dB) were imposed on these stimuli. We used a set of ITDs and ILDs corresponding to azimuths between -70.2° (left) and $+70.2^\circ$ (right) with a spacing of 3.6° between azimuths based on the calculations of Xie [13], who used the head related transfer functions (HRTFs) of the KEMAR dummy head with DB-61 small pinna at a source distance of 1.4 m. The stimulus choice ensured that both ITD and ILD increased monotonically with increasing azimuth. To discourage listeners from using absolute levels rather than ILD cues for determining the azimuth of a stimulus, the presentation level of each noise burst was independently roved by ± 2.5 dB.

2.3 Procedure

The experiment was conducted on three consecutive days. On the first day, all participants completed a pre-training to get accustomed to the task, the first assessment (pretest), and, if they were assigned to the training group, the first training session. On the second day, only participants assigned to the training group came in and completed their second training session. On the third day, participants assigned to the training group performed the third training session and all participants completed the second assessment (posttest).

All tasks were two-interval, two-alternative-forced-choice tasks. The inter-stimulus-interval was 0 ms, however, due to the 50-ms on/off ramps a small gap was perceived between the two stimuli.

2.3.1 Pre-Training

The procedure of the pre-training was the same as of the training (see below), except for the auditory stimuli used. In the pre-training, only consistent-cue stimuli were used, meaning that the ITD and ILD of a stimulus always corresponded to the same azimuth. On each trial, one azimuth between $\pm 59.4^\circ$ with a 3.6° spacing between azimuths was chosen randomly and both the ITD and ILD of the first stimulus corresponded to that azimuth. The ITD and ILD of the second stimulus then corresponded to the azimuth either 10.8° to the left or 10.8° to the right (also chosen randomly) of the first stimulus' azimuth. Participants completed one block of 50 trials. We then checked their accuracy and if it was below 0.75, the pre-training was repeated until the criterion was reached or the participant was asked not to continue his/her participation in the study.

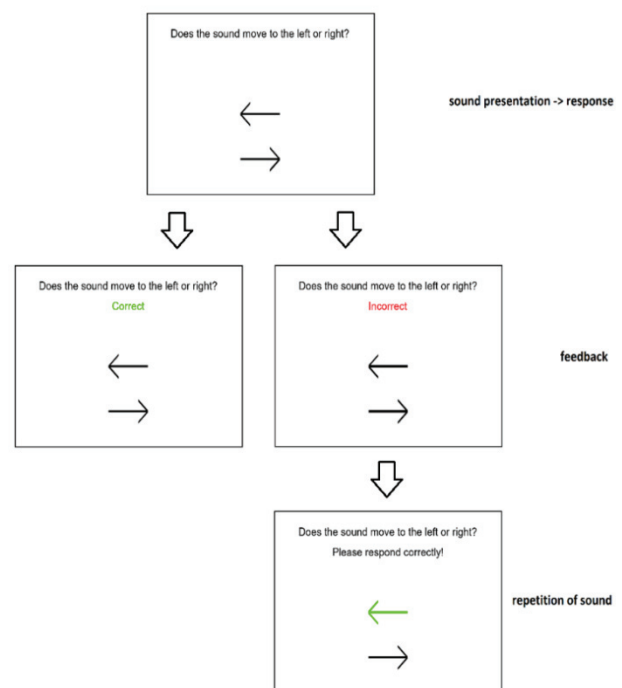


Figure 1. Experimental procedure. During the assessments, only the first screen was shown and no feedback was given. During the pre-training and training, feedback was given after each response and if the response was “incorrect” the stimulus pair was repeated with the “correct” response shown on screen (green arrow), requiring the subject to respond “correctly”.

2.3.2 Assessment

During the assessments, participants did not receive feedback. They only listened to the two consecutive stimuli and responded on what side of the first stimulus they perceived the second stimulus (top panel of Figure 1).

The same inconsistent ITD/ILD combinations as in [11] were used. Each stimulus pair used two azimuths, $az1$ and $az2$, such that the first stimulus contained an ITD corresponding to $az1$ and an ILD corresponding to $az2$ and the second stimulus contained an ILD corresponding to $az1$ and an ITD corresponding to $az2$, or vice versa. The $az1$

was located between $\pm 45^\circ$ (uniformly distributed, 3.6° spacing between azimuths) and the az2 was located $\pm 25.2^\circ$ re. az1 (also with a uniform distribution and 3.6° spacing between azimuths). Therefore, one of the cues always moved to the right while the other cue moved to the left by the same amount. It was assumed that the perceived direction of motion is indicative of which cue contributed more to the azimuthal percept. There were 4 repetitions of each az1/az2 combination. We additionally included 52 catch trials that consisted of consistent-cue combinations to check, if participants are doing the task correctly. In the catch trials, the first stimulus corresponded to an azimuth between $\pm 45^\circ$ (uniformly distributed, 3.6° spacing) and the second stimulus corresponded to an azimuth shifted by 10.8° either to the left or right re. the first stimulus. That is in the catch trials, both ITD and ILD moved either to the left or to the right.

Each assessment consisted of 892 trials in a randomized order with a short break after each 100 trials. It took about 50 min to complete.

2.3.3 Training

During training, participants received feedback after each response (Figure 1). The feedback was always consistent with the ILD. That is, if the second stimulus ILD was smaller than the first stimulus ILD and the participant responded left, they would receive the positive feedback “correct”, otherwise the response was “incorrect”. After each “incorrect” response, the stimulus pair was repeated with the “correct” response shown on the screen and participants had to press the “correct” button to move on.

A two-down-one-up adaptive procedure was used for training. Three staircases were adapted in parallel, one using a cue disparity of 25.2° , one using 21.6° , and one using 18° (i.e., the three largest cue disparities used in the assessments). On each trial, one of the three staircases was chosen randomly. For the first stimulus of each trial, one azimuth between $\pm 30.6^\circ$ with a 3.6° spacing was chosen randomly and both the ITD and ILD corresponded to that azimuth. The ILD azimuth of the second stimulus was shifted either to the left or right (chosen randomly) of the first stimulus’ azimuth. The amount of this shift depended on the adaptive staircase: At the beginning of each session, the ILD azimuth was shifted by 32.4° and with each staircase adaptation, this shift was reduced by 3.6° . The ITD azimuth of the second stimulus was shifted from the ILD azimuth of the second stimulus in the direction towards the first stimulus by the cue disparity linked to the chosen staircase. This ensured that at the beginning of each training session, both cues of the second stimulus were shifted to the same side of the first stimulus, making the task solvable independent of the binaural cue weights. As the staircases progressed, the second stimulus’ ITD and ILD would point to opposite directions *re.* the first stimulus. For a cue disparity of 25.2° , the ITD azimuth was on the opposite side of the first stimulus’ azimuth after the third staircase adjustment, for a cue disparity of 21.6° after the fourth staircase adjustment and for a cue disparity of 18° after the fifth staircase adjustment.

In each training session, participants completed 500 trials with a short break after each 100 trials. Each training session took about 30 min to complete.

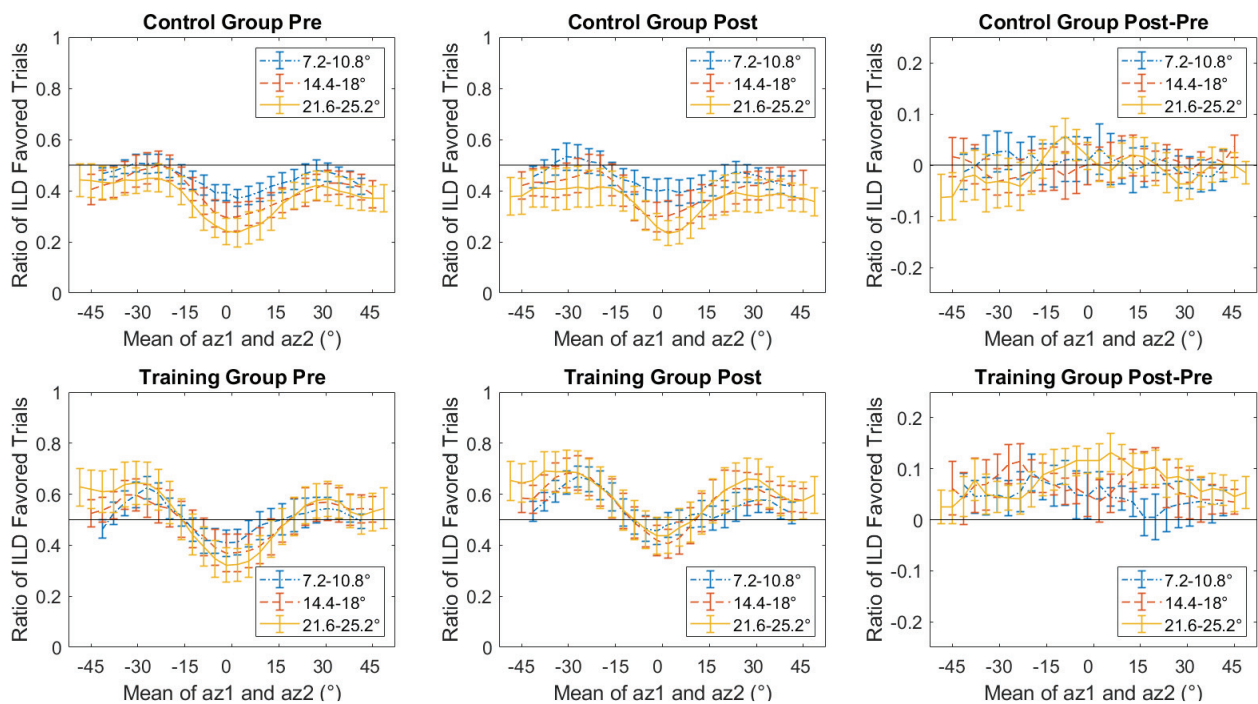


Figure 2. Ratio of trials in which responses followed the ILD azimuth as a function of the mean of az1 and az2 plotted separately for different az1-az2 cue disparities. Data are smoothed across cue disparity pairs (separate lines; disparity 3.6° is omitted) and azimuths (smoothing window with width of $\pm 7.2^\circ$). The error bars show the standard error of the mean.

2.4 Analysis

The data were analyzed using MATLAB R2018b (The MathWorks, Natick, MA). For the assessments, we calculated the ratio of inconsistent-cue trials in which responses followed the ILD azimuth. Statistical analyses were performed using SPSS Statistics 20 (IBM, Armonk, NY).

3. RESULTS

Figure 2 shows the ratio of inconsistent-cue trials in which responses followed the ILD as a function of the az1/az2 mean and separately for different az1-az2 disparities. The top row shows the no-training control group, the bottom row shows the ILD training group. The first column shows the pretest data, the second column the posttest data, and the third column shows the posttest-pretest difference. The plotted data were smoothed across azimuths by using a rectangular smoothing window with a width of $\pm 7.2^\circ$ and averaged across neighboring az1-az2 disparities (the smallest disparity of 3.6° is omitted).

We ran a mixed-design ANOVA with the data shown in Figure 2. To ensure independent data points despite smoothing, only azimuths -32.4° , -16.2° , 0° , 16.2° , and 32.4° were included, leading to a 2 (*pre- vs. posttest*) $\times 3$ (*mean azimuth disparities of 9° , 16.2° , and 23.4°*) $\times 5$ (*azimuth*) $\times 2$ (*control group vs. training group*) ANOVA. The ANOVA yielded significant main effects of *testing time* ($F(1,19) = 6.80$, $p = .017$, $\eta_p^2 = .263$) and *azimuth* ($F(2,28,43.39) = 17.56$, $p < .000$, $\eta_p^2 = .480$, Greenhouse-Geisser corrected) as well as several significant interactions. A significant interaction of *testing time* $\times$ *group* ($F(1,19) = 6.61$, $p = .019$, $\eta_p^2 = .258$) confirmed a significant increase in responses following the ILD for the training group while there was no significant change between the two assessments for the control group. A significant *azimuth disparity* $\times$ *group* interaction ($F(2,38) = 4.72$, $p = .015$, $\eta_p^2 = .199$) suggests that there were no significant differences between the azimuth disparities for the training group while the ratio of ILD-following responses decreased with increasing disparity for the control group. Finally, a significant *azimuth disparity* $\times$ *azimuth* interaction ($F(8,152) = 4.25$, $p < .000$, $\eta_p^2 = .183$) indicates that the cue weighting at different azimuth disparities varies with stimulus azimuth. Specifically, the ratio of ILD-following responses decreased with increasing disparity for stimuli near the midline and it increased at the lateral azimuths, especially for larger disparities. Confirming this observation, follow-up ANOVAs showed no significant difference between azimuths and cue disparities when 0° azimuth was excluded while at 0° azimuth, responses followed the ILD azimuth less often, particularly the larger the cue disparity.

Figure 3 shows the change in the ratio of inconsistent-cue trials in which responses followed the ILD azimuth in the posttest vs pretest, separately for each participant. It shows that the individual participants' ILD weight (defined here as the ratio of ILD-following responses) varied across a wide range of values. For 9 out of 10 training

group participants, responses followed the ILD more often in the post- than in the pretest, while the ratio of ILD-following responses increased or decreased for approximately the same number of control-group participants.

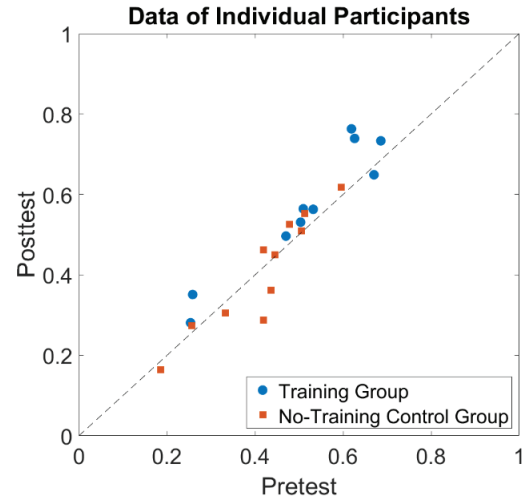


Figure 3. Posttest-to-pretest scatterplot of the ratio of inconsistent-cue trials in which responses followed the ILD azimuth for each participant.

4. DISCUSSION

The present results suggest that binaural cue reweighting can be achieved not only through lateralization training but also by a simple left/right discrimination task.

It has previously been shown that both ITD and ILD weighting can be increased through a lateralization training in a virtual audio-visual environment, depending on which of the two cues is visually reinforced [11]. However, the methods used in that study were rather complex and required a VR setup. Furthermore, a compression of responses from pre- to posttest was observed, potentially complicating the interpretation of the results. Another recent study observed an increase in ILD weighting when ITDs were randomized during a simple visual oddball task, even though the auditory stimuli accompanying the visual stimuli were not needed to perform the training task [10]. However, in that latter study, no increase in ITD weighting was observed when ILDs were randomized, and an increase in ILD weighting was also found for a condition in which ITDs were not randomized, making it difficult to draw strong conclusions. In comparison, the present study used a simple left/right discrimination task which does not require VR equipment and is not susceptible to response compression. Also, it included a no-training control group which did not show binaural cue reweighting, confirming that the difference in ILD weighting observed in the training group were indeed induced by the training.

Although an early study attempting to reweight the binaural cues with a left/right discrimination training did not yield significant results [12], in the present study, training-group responses followed the ILD azimuth significantly more often in the post- compared to the pretest. These inconsistent results might be explained by differences in the

experimental design. The current study used auditory stimuli for which neither of the two cues is weighted predominantly strongly, it involved a variety of spatial configurations instead of only using cues close to the binaural cue threshold, and it provided multi-modal feedback while requiring a corrective response after “incorrect” responses.

We observed the ILD weights to be lower for central azimuths. This is consistent with the previous lateralization study [11], which also showed a trend for this pattern, although it did not reach significance. Furthermore, we observed the ILD weights at the midline to be lower the larger the azimuth disparity. This makes sense given the experimental design: For an ILD weight $\neq 0.5$, the amount of perceived movement is expected to grow with the azimuth disparity, as the difference between the ILD azimuths of the first and second stimulus equals the azimuth disparity of each stimulus.

The current study also introduced a new method for measuring binaural cue weights. Traditionally, ITD/ILD trading ratios were measured by fixing one of the cues and letting the participant adjust the other cue until the auditory image is centered [4]. However, this leads to a stronger weighting of the to-be-adjusted cue, probably because attention is shifted towards it [5]. Estimating binaural cue weights based on the lateralization of stimuli with spatially inconsistent ITD and ILD [2,11] is not susceptible to this bias, but requires sophisticated equipment (e.g., head tracking, if responses are given with the head pointing method). The method used here is also not susceptible to an attentional bias as no cue is actively manipulated and it only requires a simple left/right response, therefore not needing a head tracking device.

Importantly, the current study only included one type of stimulus. Therefore, future studies need to examine how effective the training will be for stimuli with different spectral content, for ITD training, and how well the training generalizes to different frequencies and stimuli.

In conclusion, binaural cue reweighting can be induced with a simple left/right discrimination task, which might make a training more easily accessible for a wide range of listeners, e.g. after introducing a previously impeded cue to hearing devices such as cochlear implants.

5. ACKNOWLEDGEMENTS

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2.3 Binaural-cue weighting and training-induced reweighting across frequencies

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Author contributions: Both authors developed the study concept and the experimental design. MK developed the experimental software in collaboration with Michael Mihocic and collected as well as analyzed the data. MK drafted the manuscript, BL added to it and provided critical revisions. Both authors approved the final version of the manuscript for submission.

Binaural-cue Weighting and Training-Induced Reweighting Across Frequencies

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Abstract

During sound lateralization, the information provided by interaural differences in time (ITD) and level (ILD) is weighted, with ITDs and ILDs dominating for low and high frequencies, respectively. For mid frequencies, the weighting between these binaural cues can be changed via training. The present study investigated whether binaural-cue weights change gradually with increasing frequency region, whether they can be changed in various frequency regions, and whether such binaural-cue reweighting generalizes to untrained frequencies. In two experiments, a total of 39 participants lateralized 500-ms, 1/3-octave-wide noise bursts containing various ITD/ILD combinations in a virtual audio-visual environment. Binaural-cue weights were measured before and after a 2-session training in which, depending on the group, either ITDs or ILDs were visually reinforced. In experiment 1, four frequency bands (centered at 1000, 1587, 2520, and 4000 Hz) and a multiband stimulus comprising all four bands were presented during weight measurements. During training, only the 1000-, 2520-, and 4000-Hz bands were presented. In experiment 2, the weight measurements only included the two mid-frequency bands, while the training only included the 1587-Hz band. ILD weights increased gradually from low- to high-frequency bands. When ILDs were reinforced during training, they increased for the 4000- (experiment 1) and 2520-Hz band (experiment 2). When ITDs were reinforced, ITD weights increased only for the 1587-Hz band (at specific azimuths). This suggests that ILD reweighting requires high, and ITD reweighting requires low frequencies without including frequency regions providing fine-structure ITD cues. The changes in binaural-cue weights were independent of the trained bands, suggesting some generalization of binaural-cue reweighting.

Keywords

spatial hearing, interaural time difference, interaural level difference, plasticity, adaptation

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Introduction

Spatial hearing is an important ability of the auditory system, as it allows the localization of sound sources and improves speech understanding in complex environments. This ability relies on the integration of information provided by different auditory cues (for a recent review on sound localization cues, see Stecker & Gallun, 2012). For azimuthal sound localization (i.e., in the horizontal dimension, referred to as lateralization for in-head localization judgements), which is the focus of this study, humans rely primarily on two binaural cues, namely interaural differences in time (ITD) and level (ILD).

Psychophysical and physiological studies (e.g., Grothe et al., 2010; Henning, 1980) have revealed that ITD cues are available in the temporal fine structure at low carrier frequencies (up to approx. 1.4 kHz) and in the temporal envelope at higher carrier frequencies. ILD cues, on the other hand, are much more pronounced at high frequencies, due

to the frequency dependence of the head shadow (e.g., Middlebrooks & Green, 1991). Consequently, there are disparate cues available at low (mainly ITDs) and high (mainly ILDs) frequencies, a phenomenon known as the duplex theory of sound localization (Strutt, 1907). To establish the perceived azimuth of a sound source, the auditory system weights the information provided by the binaural cues. Given that the information carried by ITD and ILD cues varies with frequency, it is an important question to

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what extent these binaural-cue weights depend on the sound's frequency content. In fact, studies have shown that ITDs dominate for broadband sounds and at low frequencies, while ILDs dominate at higher frequencies (Ahrens et al., 2020; Macpherson & Middlebrooks, 2002; Wightman & Kistler, 1992). It is unclear, however, whether this binaural-cue weighting gradually changes with increasing frequency or whether it abruptly switches from being ITD dominant to being ILD dominant. Macpherson and Middlebrooks (2002) investigated the effect of delaying or attenuating the signal at one ear (while keeping the other localization cues intact) on localization of low-pass (0.5–2 kHz), high-pass (4–16 kHz), or wideband (0.5–16 kHz) stimuli, but did not test intermediate frequency bands. Ahrens et al. (2020) presented multiband stimuli consisting of up to 11 frequency bands which varied independently in either ITD or ILD while fixing the other cue at zero. They observed divergence for the lowest and highest frequency bands (i.e., stronger ITD weights for the lowest and stronger ILD weights for the highest band) but constant weights for in-between bands. This simultaneous presentation may, however, not show the weighting of each frequency band individually and instead be affected by simultaneous grouping effects, particularly binaural interference (Ahrens et al., 2020). The diverging weights for the lowest and highest bands appear to reflect an “edge effect” (i.e., stronger weighting of information at the edges), because the same pattern was observed in different edge bands when only intermediate frequency bands were presented (“removed” condition, Ahrens et al., 2020). Therefore, we were interested in whether binaural-cue weights measured similarly to Macpherson and Middlebrooks (2002) methods (i.e., by presenting each frequency band in isolation) show a comparable pattern to Ahrens et al. (2020) or whether they gradually change with increasing frequency. Such a gradual change would be more in line with the information carried by the binaural cues as discussed above as well as with previous literature on the basic sensitivity to ITD and ILD cues, assuming higher sensitivity (i.e., a lower detection threshold) correlates with stronger weighting of the respective cue. ILD thresholds tend to gradually improve between 1000 and 4000 Hz with increasing center frequency of narrow-band noise stimuli (Gabriel et al., 1992; Goupell & Stakhovskaya, 2018). In contrast, ITD thresholds worsen in a similar frequency range with increasing center frequency (Buchholz et al., 2018; Gabriel et al., 1992; Klumpp & Eady, 1956; Smoski & Trahiotis, 1986; Trahiotis & Bernstein, 1990). Note that the noise bands provide temporal fine-structure ITDs at lower frequencies and temporal envelope ITDs at higher frequencies. Therefore, if binaural cue weights are related to binaural cue thresholds, one would expect a gradual change in binaural-cue weighting with increasing frequency.

In addition to frequency, the binaural-cue weighting is influenced by other stimulus properties such as the overall intensity (David et al., 1959; Deatherage & Hirsh, 1959),

the inter-click interval of click trains (Stecker, 2010), or the presence of reverberation (Rakerd & Hartmann, 2010) and shows substantial variation across listeners (Klingel et al., 2021; Klingel et al., 2020; Macpherson & Middlebrooks, 2002). Such a dependence on stimulus, environmental, and personal properties is not surprising, given that listeners adapt their processing of sound localization cues when exposed to cue alterations (see Carlile, 2014, for a review). Such adaptation can either be mediated by remapping (i.e., learning a new relationship between sound localization cues and corresponding locations in space; e.g., Shinn-Cunningham et al., 1998) or reweighting (i.e., a stronger relative weighting of unaltered or reliable cues compared to altered or unreliable cues). Such reweighting has been shown for monaural (spectral-shape) cues (resulting from the directional filtering of the outer ears) relative to binaural cues for horizontal sound localization (Keating et al., 2013; Kumpik et al., 2010; Van Wanrooij & van Opstal, 2007). Usually, monaural cues do not contribute to horizontal sound localization if binaural cues are available (Macpherson & Middlebrooks, 2002; Slattery & Middlebrooks, 1994).

Additionally, three recent studies have demonstrated reweighting of binaural cues. Kumpik et al. (2019) observed an increase in ILD weighting after the ITDs of broadband noise stimuli were randomized during the completion of a visual task, but no corresponding increase in ITD weighting after ILDs were randomized. Klingel et al. (2020) also observed an increase in ILD weighting after participants received response feedback consistent with the ILDs of a mid-frequency (2–4 kHz) narrow-band noise stimulus in an auditory discrimination task, but did not test a group receiving feedback consistent with the ITDs. Finally, Klingel et al. (2021) observed a comparably strong increase in either the ITD or the ILD weighting of the same 2–4-kHz noise stimulus, depending on which cue was visually reinforced during a lateralization task in a virtual audio-visual environment.

In summary, there is evidence that listeners can adjust their weighting of sound localization cues, and particularly their binaural-cue weighting. It is, however, still unclear whether such binaural-cue reweighting can be achieved for low- or high-frequency stimuli, for which either ITDs or ILDs are known to dominate. If the baseline weight of the reinforced cue is already strong, there might not be room for a further increase (i.e., ceiling effects). On the other hand, if the baseline weight of the reinforced cue is low, the dominance of the other cue might limit the access to the reinforced cue, thus preventing binaural-cue reweighting. Finally, we were interested in whether such reweighting is specific to the trained frequency band or whether it generalizes to untrained stimuli. Wright and Fitzgerald (2001), for example, observed different generalization patterns for ITD and ILD sensitivity training.

By conducting two experiments, the present study investigates the pattern of baseline binaural-cue weights across

different frequency regions (i.e., whether weights gradually or abruptly change from ITD- to ILD-dominant with increasing frequency), whether the weighting can be changed via visual reinforcement for different frequencies, and whether such binaural-cue reweighting generalizes to untrained stimuli. Experiment 1 addressed all of these questions but some questions about the potential roles of the stimulus' azimuthal range, the presentation mode of frequency bands (randomized vs. blocked), and the frequency range required for reweighting remained. These questions were addressed in experiment 2.

Experiment 1

The aim of this experiment was to test whether binaural-cue weights, measured similarly to Macpherson and Middlebrooks (2002), will show gradual weight changes across different frequency regions or whether they will show divergence for the lowest and highest frequency bands but constant weights in between, similar to the results reported by Ahrens et al. (2020). We further investigated whether binaural-cue reweighting can be induced for different frequency regions using the paradigm of Klingel et al. (2021; see description of methods below). Finally, we were interested in whether binaural-cue reweighting is specific to the trained frequency band or whether it generalizes to untrained frequency bands or to a broad-band stimulus.

Methods

Participants. Nineteen normal-hearing participants took part in experiment 1. All participants gave written informed consent before starting the experiment and received monetary compensation for their participation. The research protocol was approved by the Acoustics Research Institute's ethics committee. Participants were randomly assigned to two experimental groups: For the ITD group, ITDs were reinforced during training and for the ILD group, ILDs were reinforced during training. Ten participants (four female, mean age: 27.10 years, $SD = 4.33$, range 21–33) were assigned to the ITD group. The remaining nine participants (five female, mean age: 29.67 years, $SD = 7.25$, range 22–48 years) were assigned to the ILD group.

Apparatus and Stimuli. Participants stood on a platform surrounded by a circular railing inside a sound booth. Visual stimuli were presented binocularly via a head-mounted display (Oculus Rift, CV1). Participants' head position and orientation were tracked using the Oculus device and software, and the visual environment was rendered accordingly in real-time. The virtual visual environment was programmed in Unity (Unity Technologies, San Francisco, CA), connected to the Oculus device via the Oculus Integration tool¹, and communicated with our experimental software via custom scripts programmed in C². It consisted of a gray sphere with a reference position (red dot) straight

ahead and vertical stings of blue dots every 45° in azimuth for guidance. Additionally, a crosshair was displayed showing the azimuth of the head orientation, which was locked at 0° elevation to force participants to respond in the horizontal plane (while the rest of the visual environment followed vertical head rotations to encourage immersion).

Binaural auditory stimuli were generated using a computer and output via a digital audio interface (ADI-8, RME) at a 48-kHz sampling rate and presented via headphones (HD 580, Sennheiser). They were band-pass filtered white noise bursts (1/3 octave wide), randomly generated on each trial. Four frequency bands were used: A low-frequency band centered at 1000 Hz (low, 793.7–1259.9 Hz), a mid-low-frequency band centered at 1587.4 Hz (mid-low, 1414.2–1781.8 Hz), a mid-high-frequency band centered at 2519.8 Hz (mid-high, 2244.9–2828.4 Hz), and a high-frequency band centered at 4000 Hz (high, 3563.6–4489.8 Hz). These stimuli were chosen to have equally spaced frequency bands while minimizing physical and perceptual overlap between bands in a similar frequency range to Ahrens et al.'s (2020) "removed" condition. We did not test the full range presented in Ahrens et al. (2020) to keep the experimental time reasonable, since we presented the frequency bands sequentially. Additionally, a stimulus comprising all four bands (multiband) was used. The stimulus duration was 500 ms, including 50-ms raised-cosine on/off ramps. The mean overall sound pressure level (SPL) was 63 dB for an ILD of zero. For the multiband condition, the individual bands were equalized in level. To discourage participants from using differences in the absolute level rather than ILDs for lateralization, the overall level was roved randomly from trial to trial within a ± 2.5 dB range. The stimuli were not filtered with head related transfer functions (HRTFs). This was to ensure that they did not convey monaural spectral localization cues that are potentially informative about the stimulus azimuth (e.g., Hebrank & Wright, 1974), which might confound the binaural-cue weight estimation (although the narrow bandwidth and frequency range of the stimuli would have made this unlikely). Instead, ITDs ranging from -396 to $+396$ μ s and ILDs ranging from -14.95 to $+14.95$ dB were imposed on these source stimuli. ITDs that matched azimuths ranging from -45° to $+45^\circ$ with a 6° spacing were determined based on Xie's (2013) estimation using the HRTFs of the KEMAR head with DB-61 small pinna at a source distance of 1.4 m. In Xie (2013), ITD values were obtained via broadband cross-correlation of the left and right ear head-related impulse responses (HRIRs). ILDs matching the same azimuths were determined individually for each frequency band based on the mean HRTF magnitudes at the respective center frequencies of four participants that did not take part in this study (taken from the HRTF database³ of the Acoustics Research Institute). For the multiband stimulus, the ILDs determined for each frequency band were used for the respective part of the stimulus. The azimuth range of $\pm 45^\circ$ was chosen to ensure monotonically increasing ILDs with increasing azimuths

for all frequency bands. Figure 1 shows the dependence of ITDs (panel a) and ILDs (panel b) on azimuth as determined according to the described methods, with the used binaural cues marked by symbols up to the dashed black line (symbols beyond that line refer to experiment 2).

ITDs and ILDs were combined into “consistent-cue” and “inconsistent-cue” conditions. In consistent-cue conditions, the ITD and ILD cue of the auditory stimulus corresponded to the same azimuth, while they corresponded to disparate azimuths in inconsistent-cue conditions. Cue disparities (i.e., the difference between the azimuths corresponding to the binaural cues within each stimulus) were restricted to a maximum value of 24° to avoid the perception of split images which can occur in case of large cue disparities (Gaik, 1993). During training, either the ITD or the ILD cue was visually reinforced as described below. Reinforced-cue azimuths ranged from -21° to $+21^\circ$ (with 6° spacing) and azimuths corresponding to the unreinforced cue were uniformly distributed $\pm 24^\circ$ (also with 6° spacing) around each reinforced-cue azimuth (Figure 1d in yellow). By symmetrically varying the unreinforced-cue azimuth around each reinforced-cue azimuth [resulting in a larger range of unreinforced-cue azimuths ($\pm 45^\circ$) than reinforced-cue azimuths ($\pm 21^\circ$)], the reinforced cue was more stable, which might encourage reweighting in addition to the visual reinforcement (Dahmen et al., 2010). In the pre- and posttest in which neither of the two cues was reinforced, azimuths in *both* the ITD and ILD dimension were uniformly distributed $\pm 24^\circ$ around each azimuth from -21° to $+21^\circ$ (Figure 1c in yellow).

Procedure. The same task as in Klingel *et al.* (2021) was used. It involved lateralizing auditory stimuli in a virtual environment via head-turn. By asking participants to lateralize stimuli containing spatially inconsistent binaural cues and comparing the response azimuth to the azimuths of each binaural cue, it can be inferred how much each cue contributes to the azimuthal percept, thus, providing the binaural-cue weights (Macpherson & Middlebrooks, 2002; Stecker, 2010). The time course of tasks is shown in Table 1. The experiment started with a practice session in which participants familiarized themselves with the task, a pretest to measure the initial ITD and ILD weights, a training in which one of the binaural cues was visually reinforced as described below, and a posttest to remeasure the weights after the training. The experimental protocol was split into two sessions (either completed on consecutive days or with a one-day break in between). This was done to avoid fatigue and to potentially make use of consolidation overnight. In the first session, participants completed the practice session, the pretest, and the first training session. In the second session, participants completed the second training session and the posttest. The approximate duration was 2h for the first and 1.5h for the second session.

Practice. The practice session was performed at the beginning of the experiment and involved the same task as the

training (see below). It consisted of 60 trials with spatially consistent ITD/ILD-combinations in which each azimuth from -33° to $+33^\circ$ (with 6° spacing) was presented once for each frequency-band condition (low, mid-low, mid-high, high, and multiband). The trials were presented in random order and, as in the training, visual reinforcement was provided.

Testing. The pretest and the posttest procedures were identical for the two groups and did not include visual reinforcement. On each trial, participants initiated the sound presentation by facing the reference position (straight ahead) and pressing a button. If they moved their head away from the reference position before the sound presentation finished, a warning tone was played and participants had to repeat the sound presentation. They then indicated the perceived azimuth via head turn and button press. The head orientation at the button press was recorded as the response azimuth. Participants then returned to the reference position to initiate the next trial. A total of 460 trials were presented, consisting of each ITD/ILD-combination shown in Figure 1c in yellow presented once for each frequency-band condition (low, mid-low, mid-high, high, and multiband). The trials were presented in random order and after each 115 trials, participants took a short break.

Training. The training procedure consisted of 6 steps (shown in Figure 2): 1) Initiating the sound presentation and listening to the auditory stimulus while facing the reference position, 2) indicating the perceived azimuth via head turn and button press, 3) receiving visual reinforcement (a rotating cube) at the reinforced-cue azimuth, 4) finding and confirming the reinforced-cue azimuth via head turn and button press, 5) returning to the reference position and initiating the presentation of the same auditory stimulus again while the visual reinforcement is still visible, and 6) confirming the reinforced-cue azimuth again via head turn and button press after which the visual reinforcement disappeared. In steps 1), 4), 5), and 6), the button-press was accepted only if the head-orientation was within $\pm 5^\circ$ of the reference position or the reinforced-cue azimuth, respectively. If participants moved their head away from the reference position before the sound presentation finished, a warning tone was played, and participants had to repeat the sound presentation.

Auditory stimuli included both inconsistent and consistent ITD/ILD-combinations, as shown in Figure 1d in yellow. The training procedure was the same for the two groups except for which cue was visually reinforced and presented in a limited azimuth range. Thus, for the ITD group, ITD azimuths did not exceed $\pm 21^\circ$ and for the ILD group, ILD azimuths did not exceed $\pm 21^\circ$. Each training session consisted of 432 trials presented in two blocks of 216 trials each. Within each block, trials were presented in a random order and each ITD/ILD combination shown in Figure 1d in yellow was presented once for the low, mid-high, and high bands. We chose the low and high bands for training to test for reweighting potential in frequency regions where one of

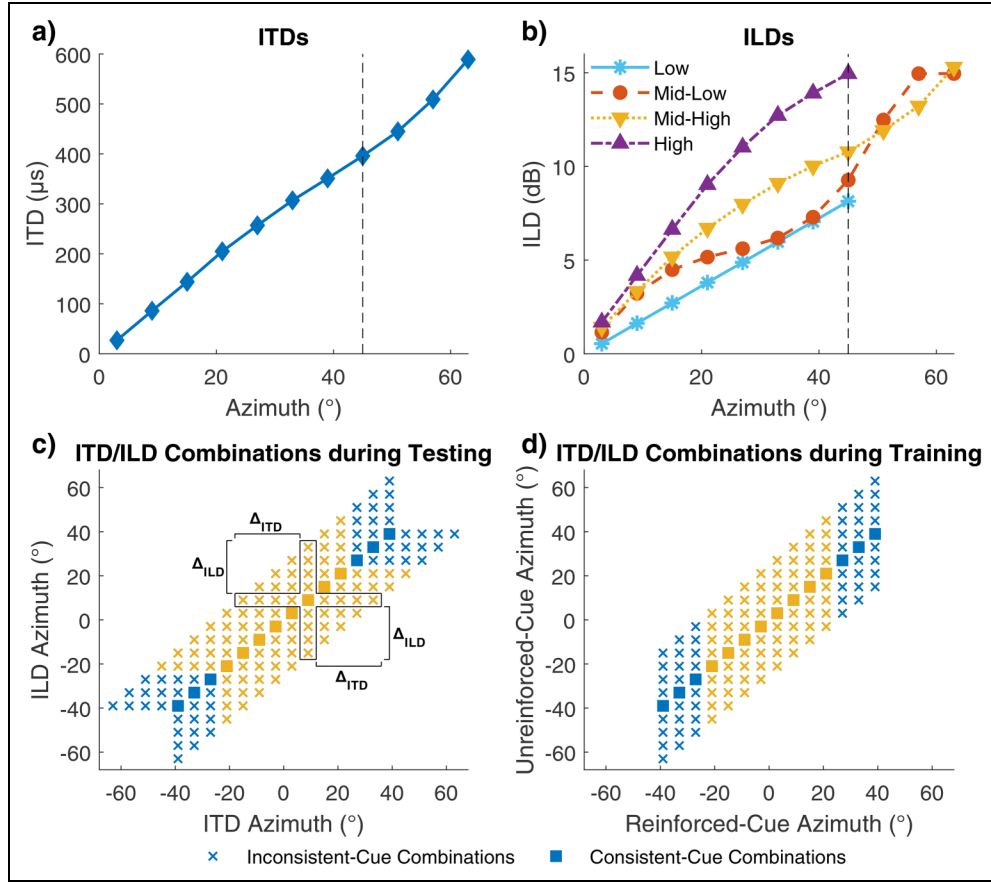


Figure 1. Experimental setup and stimuli. Panels a) and b) show the functional relation between the azimuth and the binaural cues. ITDs are derived by Xie (2013) based on broadband cross-correlation of the left and right ear head-related impulse responses (HRIRs) of the KEMAR head. ILDs are based on the mean HRTF magnitudes at the respective center frequency of four new participants. In experiment 1, binaural-cues only up to the black dashed line were used. Panel c) shows all the ITD/ILD-azimuth combinations used in the pre- and posttest. In experiment 1, only yellow combinations were used. In experiment 2, both yellow and blue combinations were included. The frame indicates the azimuthal offsets Δ_{ITD} and Δ_{ILD} that were used to estimate the model parameters for the pre-/posttest data at one example azimuth (9°). Panel d) shows all cue combinations used in the training. For the ITD group, reinforced and unreinforced cues were ITD and ILD, respectively, and for the ILD group, reinforced and unreinforced cues were ILD and ITD, respectively.

Table 1. Time Course (top to Bottom) for Each Experiment. The Tested Frequency Bands are Shown in Parentheses. Tasks Involving Visual Reinforcement are shown in italic.

	Experiment 1	Experiment 2
Session 1	Practice (<i>all bands</i>)	Practice (<i>mid-low</i>)
	Pretest (<i>all bands</i>)	Pretest (<i>mid-low</i>)
	Training (<i>low, mid-high, high</i>)	Training (<i>mid-low</i>)
Session 2	Training (<i>low, mid-high, high</i>)	Training (<i>mid-low</i>)
	Posttest (<i>all bands</i>)	Posttest (<i>mid-low</i>)
		Posttest (<i>mid-high</i>)

the cues clearly dominates. The mid-high band was chosen because it was close in center frequency to the stimuli used in Klingel *et al.* (2021), for which both ITD and ILD

reweighting was shown. Thus, the mid-low and the multi-band conditions were not presented during training to test whether the training effects generalize to them. After every 72 trials, participants took a short break.

Analysis. Analogous to Klingel *et al.* (2021), we estimated binaural-cue weights for each participant based on a regression analysis, which measured the effect of varying the ILD on the responses at each ITD azimuth and vice versa. The resulting regression coefficients were then combined to yield the normalized ILD weight (see below). A resulting ILD weight of 1 means that participants always responded at the ILD azimuth, an ILD weight of 0 means participants always responded at the ITD azimuth, and an ILD weight of 0.5 represents equal weighting of the two cues. Note that due to this normalization, the ITD weight can be directly inferred from the ILD weight (ITD weight = $1 - \text{ILD weight}$), which is why we report only ILD weight values. The regression analysis was

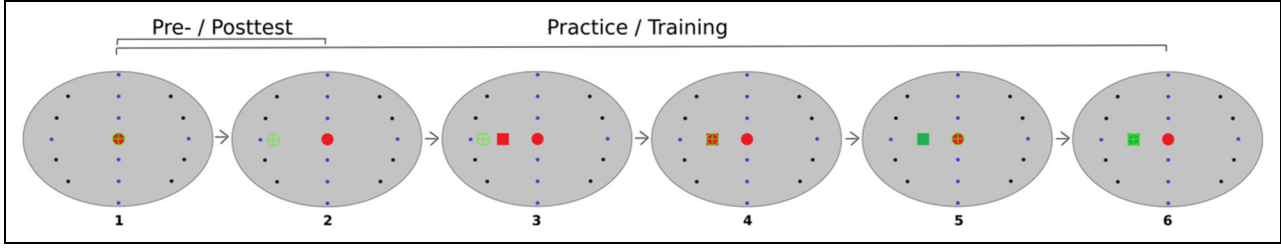


Figure 2. Time course of a trial during the pre- and posttest (panels 1-2) and the practice session as well as the training (panels 3-6). 1) Participants oriented towards the reference position (indicated by a red sphere) and pressed a button to elicit the sound presentation. 2) Participants turned their head (guiding a green crosshair) to the perceived azimuth and pressed the button (in this example, they turned their head to the left). 3) Visual reinforcement (a rotating red cube) appeared at the reinforced-cue azimuth. 4) The reinforced-cue azimuth was confirmed via a head-turn to the visual reinforcement and a button-press. 5) The visual reinforcement turned green, participants returned to the reference position, and elicited the second sound presentation (while the visual reinforcement was still visible) with another button-press. 6) Participants confirmed the reinforced-cue azimuth again via another head-turn and button-press.

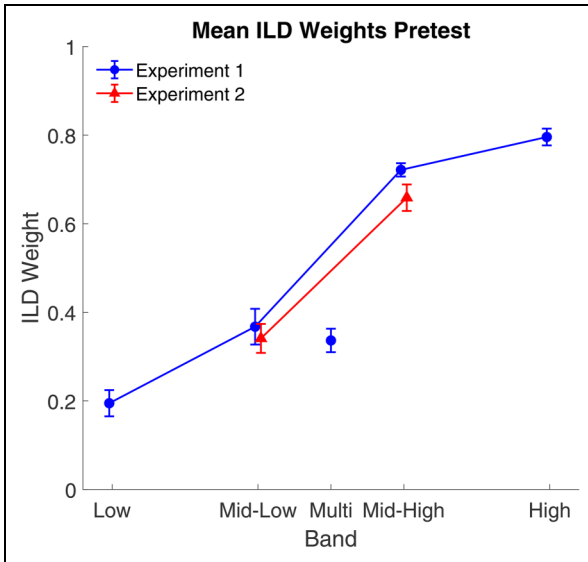


Figure 3. Pretest ILD weights (normalized, i.e., ILD weight = 1 – ITD weight) for each frequency band, averaged across azimuths. Blue circles show the results of experiment 1 and red triangles show the results of experiment 2. The averaged azimuths were restricted to the range that was tested in both experiments (3°–21°). Error bars show the standard error of the mean. ILD weights gradually and significantly increase for single-band conditions from low (794–1260 Hz), to mid-low (1414–1782 Hz), to mid-high (2245–2828 Hz), to high (3564–4490 Hz). These conditions are connected by a line. The multiband condition (multi, plotted as a separate data point) shows ILD weights similar to the mid-low condition.

fitted separately for each azimuth α (between 3° and 21° with a 6° spacing between azimuths) after mirroring the data across the midline. The regression model equations are as follows:

$$R_{ITD}(\alpha, \Delta_{ITD}) = k_{ITD}(\alpha) * \Delta_{ITD} + Q_{ITD}(\alpha)$$

$$R_{ILD}(\alpha, \Delta_{ILD}) = k_{ILD}(\alpha) * \Delta_{ILD} + Q_{ILD}(\alpha)$$

$$w_{ILD}(\alpha) = \frac{\text{atan}\left(\frac{k_{ILD}(\alpha)}{k_{ITD}(\alpha)}\right)}{\frac{\pi}{2}}$$

$$Q(\alpha) = \frac{Q_{ILD}(\alpha) + Q_{ITD}(\alpha)}{2} \quad (\text{Eq.1})$$

where R_{ITD} (R_{ILD}) is the participant's mean response azimuth in a trial for which the ILD (ITD) corresponded to azimuth α and the ITD (ILD) corresponded to azimuth $\alpha + \Delta_{ITD}$ ($\alpha + \Delta_{ILD}$). That is, Δ_{ITD} and Δ_{ILD} are not values in μs or dB but refer to the azimuth difference between α and the azimuth corresponding to the other cue. The parameters k_{ITD} and k_{ILD} are the estimated linear regression slopes at azimuth α (determining the individual binaural-cue contributions), and Q is the estimated response azimuth for consistent-cue stimuli corresponding to azimuth α . Parameter k_{ITD} (k_{ILD}) was estimated at each α by considering various azimuthal offsets (from -24° to $+24^\circ$ with 6° spacing) of the cue Δ_{ITD} (Δ_{ILD}) while setting the offset of the other cue, Δ_{ILD} (Δ_{ITD}), to zero. Thus, the model was fitted for each azimuth α , indicated by a yellow square in Figure 1c, by considering only items of the row (for k_{ITD}) and of the column (for k_{ILD}) that include that yellow square (indicated by the frame for an example azimuth of 9°). These estimates of k_{ITD} and k_{ILD} were then combined to derive the ILD weight, w_{ILD} (recall that $w_{ILD} + w_{ITD} = 1$). This differs from the weights reported by Macpherson and Middlebrooks (2002), who used the individual regression slopes (i.e., k_{ITD} and k_{ILD}) as weights. Instead, it is similar to the “binaural weighting index” reported by Kumpik et al. (2019), even though they forced the values to fall between -0.5 and $+0.5$ instead of 0 and 1. Finally, parameter Q was estimated as the average of the constants obtained in the regressions for ITD and ILD.

The data were analyzed using MATLAB R2018b (The MathWorks, Natick, MA). Statistical analyses were performed using SPSS Statistics 20 (IBM, Armonk, NY).

Results

Overall Binaural-Cue Weights. The blue circles in Figure 3 show the pretest ILD weights averaged across azimuths as a function of frequency band. The data were pooled across all participants, because up until the pretest, the procedure was identical between the two groups.

To test, whether ILD weights change gradually from low- to high-frequency bands, we ran a 5 (*frequency band*) $\times$ 4 (*azimuth*) ANOVA across the pretest data (to exclude any possible effects of training) of all participants. The ANOVA yielded a significant main effect of *frequency band* ($F(4,72) = 143.91$, $p < .001$, $\eta_p^2 = .889$). Follow-up pairwise comparisons showed significant differences in the ILD weight between all bands (all $p < .008$, Bonferroni-corrected) except between the mid-low and the multiband conditions ($p > .999$, Bonferroni-corrected). ILD weights gradually increased from the low ($M = .195$, $SEM = .030$) to mid-low ($M = .368$, $SEM = .040$) to mid-high ($M = .722$, $SEM = .015$) to the high band ($M = .796$, $SEM = .019$). The multiband condition ($M = .336$, $SEM = .026$) showed ILD weights similar to the mid-low band.

While the pretest ILD weight averaged across the four narrow bands was close to 0.5 ($M = .486$, $SEM = .019$), it was significantly smaller than 0.5 for the multiband ($M = .337$, $SEM = .026$; $t(18) = -6.17$, $p < .001$, two-tailed, $d_z = -1.42$). This suggests that the low (i.e., ITD dominant) frequencies received more weight in the multiband stimulus.

The ANOVA additionally yielded a significant main effect of *azimuth* ($F(3,54) = 3.71$, $p = .017$, $\eta_p^2 = .171$). Follow-up pairwise comparisons showed significant differences in the ILD weight between 3° and 21° azimuth ($p = .015$, Bonferroni-corrected) with larger ILD weights at 3° ($M = .504$, $SEM = .019$) compared to 21° azimuth ($M = .458$, $SEM = .024$). This suggests that ILD weights were larger at central compared to lateral azimuths. Figure 4 depicts the detailed patterns of ILD weights across azimuths, separately for each band and group (blue circles denote data from experiment 1). Note how in most panels, the blue lines with filled circles (pretest results) trend downwards (indicating lower ILD weights) from central (left on the x-axis) to lateral (right on the x-axis) azimuths.

There was no significant *frequency band* $\times$ *azimuth* interaction ($F(5.38,96.87) = 1.56$, $p = .175$, $\eta_p^2 = .080$, Greenhouse-Geisser-corrected).

Binaural-Cue Reweighting. The results are visualized in Figure 4 (recall that blue circles denote data from experiment 1). The separate panels show the results in each frequency band (columns) and group (rows). The expected reweighting effect would be indicated by open symbols (posttest results) falling below (indicating lower ILD weight, therefore higher ITD weight) filled symbols (pretest results) in the ITD group (top row) and by open symbols falling above (indicating higher ILD weight) filled symbols in the ILD group (bottom row). We analyzed the data separately for each frequency band and group.

In the ITD group, a 2 (*pre- vs. posttest*) $\times$ 4 (*azimuth*) repeated measures (RM) ANOVA yielded no significant effects for the low band (all $p > .199$).

For the mid-low band, the 2 $\times$ 4 RM ANOVA yielded a significant main effect of *azimuth* ($F(3,27) = 6.70$, $p = .002$, $\eta_p^2 = .427$) as well as a significant *time* $\times$ *azimuth* interaction ($F(3,27) = 4.92$, $p = .007$, $\eta_p^2 = .353$), but no significant main effect of *time*. Follow-up pairwise comparisons showed that the *time* $\times$ *azimuth* interaction was driven by a significant decrease of ILD weights at 9° azimuth ($p = .022$, Bonferroni-corrected), but no difference between time points at other azimuths (all $p > .532$, Bonferroni-corrected). This suggests that participants reweighted the binaural cues in the expected direction, but only at 9° azimuth. The follow-up pairwise comparisons further showed significant differences in the ILD weights between 3° and 21° azimuth ($p = .005$, Bonferroni-corrected), as well as between 9° and 21° azimuth ($p = .049$, Bonferroni-corrected). ILD weights at 21° azimuth ($M = .286$, $SEM = .058$) were lower compared to 3° ($M = .422$, $SEM = .049$) and 9° azimuth ($M = .435$, $SEM = .051$). This suggests that ILD weights were larger at central compared to lateral azimuths.

For the mid-high band, the 2 $\times$ 4 RM ANOVA yielded no significant effects (all $p > .219$).

For the high band, the 2 $\times$ 4 RM ANOVA yielded a significant main effect of *azimuth* ($F(3,27) = 6.33$, $p = .002$, $\eta_p^2 = .413$) as well as a significant *time* $\times$ *azimuth* interaction ($F(3,27) = 3.08$, $p = .044$, $\eta_p^2 = .255$), but no significant main effect of *time*. Follow-up pairwise comparisons showed significant differences in the ILD weight between 3° and 21° azimuth ($p = .017$, Bonferroni-corrected) with lower ILD weights at 3° azimuth ($M = .796$, $SEM = .021$) compared to 21° azimuth ($M = .878$, $SEM = .024$), again suggesting larger ILD weights at central azimuths, but there were no significant weight changes from pre- to posttest at any azimuth (all $p > .107$, Bonferroni-corrected).

For the multiband condition, the 2 $\times$ 4 RM ANOVA yielded no significant effects (all $p > .086$).

In the ILD group, the 2 $\times$ 4 RM ANOVA for the low band yielded a significant main effect of *azimuth* ($F(3,24) = 4.25$, $p = .015$, $\eta_p^2 = .347$), but neither a significant main effect of *time* nor a *time* $\times$ *azimuth* interaction. Follow-up pairwise comparisons showed significant differences in the ILD weight between 3° and 21° azimuth ($p = .034$, Bonferroni-corrected) with higher ILD weights at 3° azimuth ($M = .239$, $SEM = .048$) compared to 21° azimuth ($M = .149$, $SEM = .033$). This again suggests that ILD weights were larger at central compared to lateral azimuths.

The 2 $\times$ 4 RM ANOVA yielded no significant effects for either the mid-low band (all $p > .200$) or the mid-high band (all $p > .289$).

For the high band, the 2 $\times$ 4 RM ANOVA yielded a significant main effect of *time* ($F(1,8) = 21.67$, $p = .002$, $\eta_p^2 = .730$) with smaller ILD weights in the pretest ($M = .756$, $SEM = .020$) compared to the posttest ($M =$

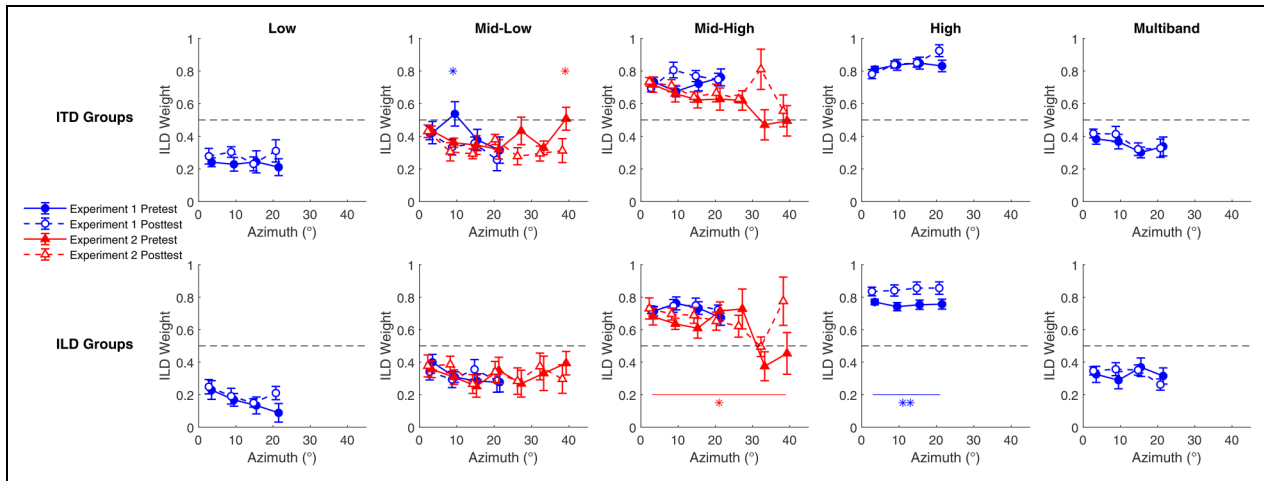


Figure 4. ILD weights (normalized, i.e., $\text{ILD weight} = 1 - \text{ITD weight}$) as a function of azimuth for each frequency band (columns) and group (rows). The top row shows results of the ITD groups (i.e., participants for whom ITDs were reinforced during training) and the bottom row shows results of the ILD groups (i.e., participants for whom ILDs were reinforced during training). Solid lines and filled symbols show pretest results, dashed lines and open symbols show posttest results. Blue circles show the results of experiment 1 and red triangles show the results of experiment 2. Error bars show the standard error of the mean. ILD weights gradually increase from low-, to mid-low-, to mid-high-, to high-frequency stimuli and on average are lower for lateral azimuths. Significant weight changes, indicated by the asterisks in the respective colors (* denotes $p < .05$, ** denotes $p < .01$), from pre- to posttest were observed for the ILD group in experiment 1 for the high-frequency band as well as in experiment 2 for the mid-high-frequency band. Additionally, a significant weight change from pre- to posttest was observed for the ITD group in experiment 1 for the mid-low-frequency band at 9° azimuth as well as in experiment 2 at 39° azimuth.

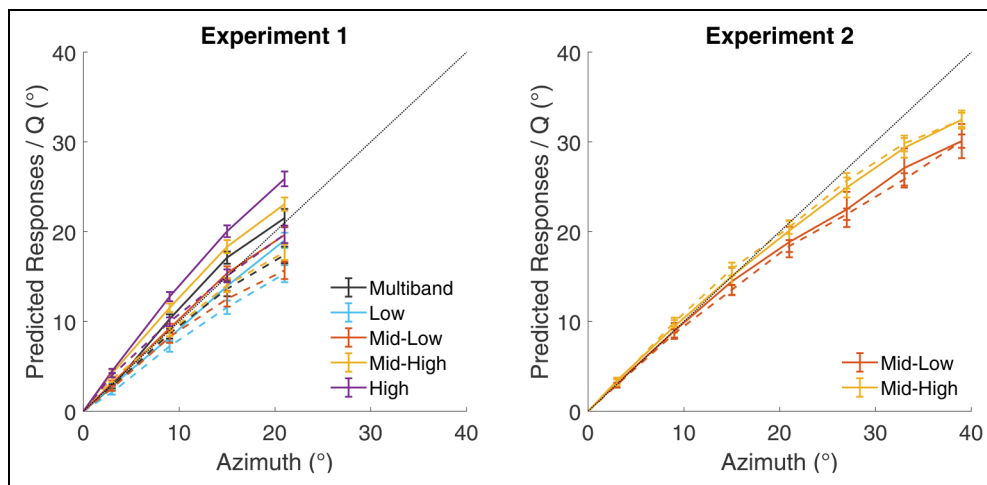


Figure 5. Predicted responses for consistent-cue combinations by the regression analysis (i.e., factor Q) as a function of azimuth. Solid lines show pretest results and dashed lines show posttest results. Error bars show the standard error of the mean. Lateralization slopes are steeper for higher frequencies. Experiment 1 shows response compression from pre- to posttest (i.e., lateralization slopes are shallower in the post- compared to the pretest) while in experiment 2, responses are already compressed in the pretest and therefore no difference between time points is observed.

.847, $SEM = .029$), but neither a significant main effect of *azimuth* nor *time x azimuth* interaction. This suggests that participants reweighted the binaural cues in the expected direction.

For the multiband condition, the 2×4 RM ANOVA yielded no significant effects (all $p > .090$).

Lateralization Functions. We additionally analyzed the lateralization pattern independent of binaural-cue weights for the different frequency bands and tests, because Klingel et al. (2021) observed a compression of responses from pre- to posttest. To that end, we fitted linear regressions to the responses for consistent-cue conditions predicted by the

regression analysis (i.e., the factor Q). Figure 5 shows the factor Q as a function of azimuth. Shallower functions in the post- compared to the pretest would indicate such a response compression. Using the factor Q is a more reliable estimate than fitting linear regressions to the responses in consistent-cue conditions alone, as the regression analysis includes all responses (i.e., also inconsistent-cue conditions).

We then submitted the resulting lateralization slopes of each participant to a 5 (*frequency band*) $\times$ 2 (*pre- vs. posttest*) RM ANOVA. The ANOVA yielded significant main effects of *frequency band* ($F(2.77, 49.81) = 39.24$, $p < .001$, $\eta_p^2 = .686$, Greenhouse-Geisser-corrected) and *time* ($F(1, 18) = 39.76$, $p < .001$, $\eta_p^2 = .688$), with steeper lateralization slopes in the pretest ($M = 1.08$, $SEM = 0.04$) compared to the posttest ($M = 0.86$, $SEM = 0.05$). Additionally, there was a significant *frequency band* $\times$ *time* interaction ($F(4, 72) = 8.93$, $p < .001$, $\eta_p^2 = .332$). Follow-up pairwise comparisons showed significant differences between the pre- and posttest for all frequency bands (all $p < .002$, Bonferroni-corrected). This suggests a compression of responses from pre- to posttest. They further showed significant differences between all frequency bands (all $p < .003$, Bonferroni-corrected) except between the multiband and the mid-low ($p = .286$, Bonferroni-corrected) as well as the mid-high bands ($p = .904$, Bonferroni-corrected), and between the low and mid-low bands ($p = .230$, Bonferroni-corrected). Lateralization slopes gradually increased from the low band ($M = 0.832$, $SEM = 0.04$) to the mid-high band ($M = 1.03$, $SEM = 0.04$) to the high band ($M = 1.13$, $SEM = 0.04$). The multiband ($M = 0.97$, $SEM = 0.04$) showed lateralization slopes similar to the mid-low band ($M = 0.88$, $SEM = 0.04$) and the mid-high band.

We further tested if lateralization slopes differed significantly from 1. A lateralization slope of 1 would indicate the expected lateralization behavior, smaller slopes would indicate compressed responses, and larger slopes would indicate expanded responses. In the pretest, lateralization slopes did not differ significantly from 1 for the low and mid-low band as well as the multiband (all $p > .053$, two-tailed). However, they were significantly larger than 1 for the mid-high ($t(18) = 4.09$, $p = .001$, two-tailed, $d_z = 0.94$) and the high band ($t(18) = 6.97$, $p < .001$, two-tailed, $d_z = 1.60$). In the posttest, slopes were significantly smaller than 1 for the low ($t(18) = -5.18$, $p < .001$, two-tailed, $d_z = -1.19$), mid-low ($t(18) = -4.01$, $p = .001$, two-tailed, $d_z = -0.92$), and mid-high band ($t(18) = -2.37$, $p = .029$, two-tailed, $d_z = -0.54$) as well as the multiband ($t(18) = -2.71$, $p = .014$, two-tailed, $d_z = -0.62$), but not for the high band.

Summary of Results

In this section we summarize the results of Experiment 1, which will then be discussed together with those of experiment 2 in the General Discussion. The baseline (i.e. pretest) results showed that binaural-cue weights gradually

changed from being ITD dominant to ILD dominant from low-, to mid-low-, to mid-high-, to high-frequency-band conditions. The multiband stimulus was weighted similarly to the mid-low band, meaning that ITDs dominated the percept when both ITD and ILD dominant bands were combined into one stimulus. On average across frequency bands, we further observed higher ILD weights at central compared to lateral azimuths, although deviations from this effect are observed for some conditions in band-specific analyses that included the posttest data. Additionally, we found steeper lateralization functions for higher frequencies and shallower lateralization functions in the post- compared to the pretest.

The results regarding training-induced changes in binaural-cue weights from pre- to posttest were unexpected. We expected to see an increase in the reinforced-cue weight and a respective decrease in the unreinforced-cue weight from pre- to posttest (i.e., reweighting) at least for the trained mid-high band, since it is similar in center frequency to the stimulus used in Klingel *et al.* (2021), where reweighting was shown in both the ITD and ILD groups. However, for the mid-high band, no reweighting was found in either group. There were, however, reweighting effects for some other conditions. The ILD group showed reweighting for the trained high band, which did not generalize to untrained conditions (i.e., mid-low and multiband). The ITD group, on the other hand, showed reweighting for the mid-low band, but only at 9° azimuth. This is surprising, as the mid-low condition was *not* trained. For all other bands, the ITD group showed no reweighting effects.

A closer look at the mid-high band showed that while it was similar in center frequency to the frequency band tested in Klingel *et al.* (2021), the baseline (pretest) binaural-cue weighting differed between the two studies. The ILD weight reported in Klingel *et al.* (2021) was lower than the ILD weight for the mid-high band in the present study. Instead, it closely matched the ILD weight for the mid-low band. This is likely due to the different bandwidths of the stimuli: In Klingel *et al.* (2021), stimuli were 1-octave wide while they were only 1/3-octave wide in the present study to minimize spectral overlap between frequency bands. As ITDs are known to dominate for broadband stimuli (Macpherson & Middlebrooks, 2002), it is likely that the lower-frequency part of the 1-octave wide band in Klingel *et al.* (2021) dominated the overall binaural-cue weighting of that stimulus.

Considering the design of the present study and of Klingel *et al.* (2021), we identified three potential reasons for the lack of reweighting in most conditions. 1) We had to restrict the azimuth range to ensure monotonic ILDs for all frequency bands. In Klingel *et al.* (2021), however, the largest effect was observed for more lateral azimuths (although the *time* $\times$ *azimuth* interaction did not reach significance). 2) We presented the different frequency bands randomly in one block. As they all had very different baseline weights, this may have been confusing, especially during training where visual

reinforcement was provided. And 3), we did not train participants with the mid-low band, which was closest in baseline ILD weight to the stimuli in Klingel et al. (2021). If the baseline ILD weight predicts the reweighting potential, training with this stimulus might increase chances for reweighting. To address these issues, we conducted a follow-up experiment. In experiment 2, we only included the mid-low- and mid-high bands, for which ILDs were monotonic up to 63° azimuth. This allowed us to use a wider range of azimuths than in experiment 1 (reinforced-cue azimuths up to 39° and unreinforced-cue azimuths up to 63° while experiment 1 included reinforced-cue azimuths only up to 21° and unreinforced-cue azimuths up to 45°). To avoid confusion, the two frequency bands were presented in blocks during practice as well as the pre- and posttest and only one frequency band (mid-low) was used during training.

Experiment 2

Based on the considerations discussed above, a follow-up experiment was performed. Experiment 2 was conducted identically to experiment 1 except for the changes described in the following.

Methods

Participants. Twenty new participants were recruited to participate in experiment 2. All participants gave written informed consent before starting the experiment and received monetary compensation for their participation. Ten participants (four female, mean age: 27.70 years, $SD = 5.29$, range 22–37) were randomly assigned to the ITD group. The remaining ten participants (four female, mean age: 25.60 years, $SD = 2.76$, range 20–30 years) were assigned to the ILD group.

Apparatus and Stimuli. Only the mid-low and the mid-high bands were presented. The reinforced-cue azimuth range was increased to $\pm 39^\circ$ (and therefore the unreinforced-cue azimuth range to $\pm 63^\circ$). As a consequence, ITDs ranged from -589 to $+589 \mu s$ and ILDs ranged from -15.30 to $+15.30$ dB. The binaural cues used are shown in Figure 1a and b (all azimuths). For training, only the mid-low band was used, as its binaural-cue weighting closely matched the weighting reported in Klingel et al. (2021).

Procedure. To avoid confusion by presenting all frequency bands randomized in one block, the mid-low and the mid-high bands were now presented in separate blocks. The time course of tasks is shown in Table 1. The experiment started with a practice session with the mid-low band followed by the pretest with the mid-low band. Then, a practice session with the mid-high band was performed, followed by the pretest with the mid-high band. Afterwards, the training (with the mid-low band) was performed, followed by the posttests, first with the mid-low band and then with the mid-high band. The experimental protocol was again split into two sessions (either completed on consecutive days or

with a one-day break in between). In the first session, participants completed both practice sessions, both pretests, and the first training session. In the second session, participants completed the second training session and both posttests. The approximate duration was 1.5h for the first and 1h for the second session.

Practice. Each practice session (one for each frequency band) consisted of 32 trials with spatially consistent ITD/ILD-combinations in which each azimuth from -45° to $+45^\circ$ (with 6° spacing) was presented twice. The trials were presented in random order and, as in the training, visual reinforcement was provided.

Testing. Each pre- and posttest (one for each frequency band) consisted of 146 trials, each ITD/ILD-combination shown in Figure 1c (both yellow and blue) presented once. The trials were presented in random order and visual reinforcement was not provided.

Training. Each training session consisted of 252 trials presented in two blocks of 126 trials each. Within each block, trials were presented in a random order and each ITD/ILD combination shown in Figure 1d (both yellow and blue) was presented once. After every 63 trials, participants took a short break.

Analysis. The analysis was performed identically to experiment 1, except that binaural-cue weights were estimated for each azimuth α between 3° and 39° (i.e., additionally for azimuths of 27° , 33° , and 39°).

Results

Overall Binaural-Cue Weights. Figures 3 and 4 show a similar pattern in overall binaural-cue weights in the two experiments (blue circles for experiment 1 and red triangles for experiment 2).

Binaural-Cue Reweighting. The red triangles in Figure 4 show the ILD weights as a function of azimuth in separate panels for each frequency band and group. As in experiment 1, the expected reweighting effect would be indicated by open symbols (posttest results) falling below (indicating lower ILD weight, therefore higher ITD weight) filled symbols (pretest results) in the ITD group (top row) and by open symbols falling above (indicating higher ILD weight) filled symbols in the ILD group (bottom row). We analyzed the data separately for each frequency band and group.

In the ITD group, a 2 (*pre- vs. posttest*) $\times$ 7 (*azimuth*) RM ANOVA yielded a significant *time* $\times$ *azimuth* interaction for the mid-low band ($F(6,54) = 2.36$, $p = .042$, $\eta_p^2 = .208$), but neither a significant main effect of *time* nor *azimuth*. Follow-up pairwise comparisons showed that the interaction was driven by a significant decrease in ILD weight from pre- ($M = .508$, $SEM = .070$) to posttest ($M = .312$, $SEM = .073$) at 39° azimuth ($p = .021$, Bonferroni-corrected), but no significant differences at other azimuths (all $p > .127$, Bonferroni-corrected). This suggests that participants reweighted the binaural cues in the expected direction, but only at 39° azimuth.

For the mid-high band, the 2×7 RM ANOVA yielded a significant main effect of *azimuth* ($F(6,54) = 4.09$, $p = .002$, $\eta_p^2 = .312$), but neither a significant main effect of *time* nor *time x azimuth* interaction. Follow-up pairwise comparisons showed a significant difference between 3° and 15° azimuth ($p = .024$, Bonferroni-corrected) with larger ILD weights at 3° ($M = .725$, $SEM = .030$) compared to 15° azimuth ($M = .632$, $SEM = .032$). This suggests that ILD weights were larger at central compared to lateral azimuths.

In the ILD group, the 2×7 RM ANOVA yielded no significant effects for the mid-low band (all $p > .407$).

For the mid-high band, the 2×7 RM ANOVA yielded a significant main effect of *time* ($F(1,9) = 5.17$, $p = .049$, $\eta_p^2 = .365$), with smaller ILD weights in the pre- ($M = .600$, $SEM = .046$) compared to the posttest ($M = .666$, $SEM = .040$). This suggests that participants reweighted the binaural cues in the expected direction. There further was a significant main effect of *azimuth* ($F(2.45,22.08) = 5.97$, $p = .006$, $\eta_p^2 = .399$, Greenhouse-Geisser-corrected). Follow-up pairwise comparisons showed significant differences between 33° and 3° ($p = .039$, Bonferroni-corrected), 15° ($p = .030$, Bonferroni-corrected), as well as 21° azimuth ($p = .018$, Bonferroni-corrected). ILD weights were smaller at 33° azimuth ($M = .435$, $SEM = .058$) compared to 3° ($M = .706$, $SEM = .046$), 15° ($M = .649$, $SEM = .050$), and 21° azimuth ($M = .684$, $SEM = .051$). This suggests that ILD weights were again larger at central compared to lateral azimuths. There was no significant *time x azimuth* interaction.

Lateralization Functions. We again determined lateralization slopes based on the factor Q from the regression analysis and submitted them to a 2 (*frequency band*) $\times$ 2 (*pre- vs. posttest*) RM ANOVA. The ANOVA yielded a significant main effect of *frequency band* ($F(1,19) = 7.83$, $p = .011$, $\eta_p^2 = .292$) with steeper lateralization slopes for the mid-high band ($M = 0.90$, $SEM = 0.03$) compared to the mid-low band ($M = 0.82$, $SEM = 0.04$), but no significant main effect of *time* nor *time x frequency band* interaction. This suggests that there was no response compression from pre- to posttest.

All lateralization slopes were significantly smaller than 1. In the pretest, both the mid-low band ($M = .825$, $SEM = .064$; $t(19) = -2.73$, $p = .013$, two-tailed, $d_Z = -0.61$) and the mid-high band ($M = .892$, $SEM = .034$; $t(19) = -3.17$, $p = .005$, two-tailed, $d_Z = -0.71$) had lateralization slopes smaller than 1. This suggests that responses were already compressed in the pretest. In the posttest, again both the mid-low band ($M = .804$, $SEM = .021$; $t(19) = -9.37$, $p < .001$, two-tailed, $d_Z = -2.09$) and the mid-high band ($M = .906$, $SEM = .026$; $t(19) = -3.58$, $p = .002$, two-tailed, $d_Z = -0.80$) had lateralization slopes smaller than 1.

Summary of Results

In experiment 2, we observed binaural-cue reweighting in the ILD group at the mid-high band, which was not trained, but not for the trained mid-low band. This is surprising, given

that we did not observe reweighting at the mid-high band in experiment 1, even though it was trained. In the ITD group, we observed binaural-cue reweighting for the trained mid-low band only at 39° azimuth, which is in line with the expectation based on Klingel et al. (2021) that a stronger reweighting effect occurs for more lateral azimuths. However, we did not observe reweighting at 9° azimuth as we did in experiment 1. This reweighting did not generalize to the mid-high band.

We suspected that the trial-by-trial switching between frequency bands might have contributed to the overall small reweighting effect in experiment 1 and, therefore, used blocked presentation during testing and included just one band during training in experiment 2. However, as only the *untrained* mid-high band in the ILD group showed more reweighting in experiment 2 compared to experiment 1, there is no evidence that trial-by-trial switching between frequency bands had an impact on reweighting.

Consistent with the results of experiment 1, we observed stronger ILD weights and steeper lateralization functions for the mid-high compared to the mid-low band. However, there was no response compression from pre- to posttest. Instead, especially at the larger azimuths tested in experiment 2, responses were already compressed in the pretest (i.e., pretest lateralization slopes were significantly smaller than 1 and shallower than in experiment 1). This might be attributable to the larger azimuth range presented in experiment 2. Namely, participants may have tended to respond inside of the visual markers of $\pm 45^\circ$, even though the unreinforced cue extended that range. Note that while a larger azimuth range was also used in Klingel et al. (2020), who observed compression only in the posttest, they used visual markers every 15° and participants were therefore accustomed to respond beyond the markers.

General Discussion

The present study investigated whether binaural-cue weights gradually change from low- to high-frequency bands, whether binaural-cue reweighting can be induced in different frequency regions, and whether binaural-cue reweighting is specific to the trained frequency band or whether it generalizes to untrained frequency bands.

Binaural-Cue Weights Across Spectral Regions

We observed gradually increasing ILD weights with increasing spectral region of narrow-band noise stimuli. These baseline weights appear to be robust, as similar pretest weights were obtained in both experiments involving different participants and presentation modes (randomized vs. blocked). The finding of gradually increasing ILD weights with increasing frequency extends Macpherson and Middlebrooks (2002) results involving a low- and a high-pass stimulus but differs from Ahrens et al.'s (2020) observation, who

measured the contributions of different frequency bands in a multiband stimulus to binaural-cue weighting. Ahrens et al. (2020) found significant differences mainly for the lowest and the highest frequency band and similar weights for in-between frequency bands, irrespective of the absolute frequency range of presented bands. These different results likely resulted from differences in the methodology: While the frequency bands were presented in isolation in the present study, they were presented as part of a multiband stimulus in Ahrens et al. (2020), leading to an “edge effect” (i.e., stronger weighting of information at the edges). Instead, the present results are more in line with the sensitivity pattern to ITD and ILD as a function of center frequency for narrow-band noise stimuli. Compared to ITD thresholds, ILD thresholds are fairly constant across frequencies, but tend to decrease with increasing center frequency (Gabriel et al., 1992), although there are some local peaks in the threshold function (Goupell & Stakhovskaya, 2018). Additionally, ILDs are physically smaller for low- compared to high-frequency stimuli (leading to a shallower slope of the cue-versus-azimuth function) and therefore more informative at high frequencies. In contrast, ITDs are physically almost frequency-independent and ITD thresholds increase with increasing center frequency from approx. 800 Hz towards higher (at least up to 4000 Hz) frequencies (Buchholz et al., 2018; Gabriel et al., 1992; Klumpp & Eady, 1956; Smoski & Trahiotis, 1986; Trahiotis & Bernstein, 1990), because of decreasing access to fine-structure ITD.

For the multiband stimulus, comprising all tested bands, ITDs dominated the percept, similar to Macpherson and Middlebrooks (2002) broadband stimuli. While the pretest ILD weight averaged across the four frequency bands of experiment 1 was close to 0.5, it was significantly lower than 0.5 for the multiband stimulus. This suggests that for broadband sounds, the auditory system performs a weighted integration of binaural cues across frequencies, where ITDs receive more weight than ILDs.

Training-Induced Binaural-Cue Reweighting Across Spectral Regions

In the ILD group, a training-induced change in binaural-cue weights was observed for the trained high-frequency band (experiment 1) and for the untrained mid-high-frequency band (experiment 2), but not for the other conditions. In the ITD group, binaural-cue reweighting was observed for the untrained mid-low-frequency band (experiment 1, only at 9° azimuth) and for the same band when it was trained (experiment 2, only at 39° azimuth). While it may seem like these results are driven by noise in the pretest (given that participants get more accustomed with the setup and task over time), it should be noted that the chosen correction method for the post-hoc comparisons (Bonferroni) is very conservative and similar noise in other conditions did not

yield significant results, suggesting that the reported results are meaningful. There was no significant reweighting effect for the other frequency bands.

Given that both trained and untrained stimuli showed some effects in both groups, band-specific training does not seem to be crucial. This may suggest some across-frequency generalization of binaural-cue reweighting. Instead, the occurrence of reweighting seems to depend on an appropriate match between the stimulus’ spectral region and the binaural cue that is reinforced. In the ILD group, effects were only observed for the mid-high and high bands, while in the ITD group, effects were only observed for the mid-low band (at specific azimuths). This suggests that inducing an increase in ILD weighting only works for sufficiently high frequencies: The strongest effect was observed for the high band (centered at 4000 Hz) and a less robust effect (only present in experiment 2, close to the significance threshold) occurred for the mid-high band (centered at 2520 Hz). Similarly, sufficiently low frequencies seem to be needed to induce an increase in ITD weighting, as only the mid-low band (centered at 1587 Hz) showed some effects in the ITD group. However, if the stimuli included the low-frequency temporal fine structure region that provides exquisite ITD sensitivity (i.e., for the low band centered at 1000 Hz and the multiband), no change in binaural-cue weights was observed. This suggests that ITD reweighting was based on envelope-ITD information. Compared to Klingel et al. (2021), the reweighting effects observed in the present study are relatively weak. In the ITD group, the effect for the mid-low band was so small that it only reached significance for specific azimuths. In the ILD group, the effect for the mid-high band reached significance in only one of the two experiments. Solely the effect for the high band in the ILD group showed comparable strength to the effects reported in Klingel et al. (2021). Nevertheless, the present results agree with the results reported by Klingel et al. (2021), who used bandpass-filtered (2–4 kHz) noise and found a reweighting effect in both directions (i.e., for both their ILD and ITD group). The 2–4 kHz stimulus both included “sufficiently high” and “sufficiently low” frequencies but did not touch the frequency region providing highest ITD sensitivity (i.e., the fine-structure region), and thus seems to be optimally suited to induce binaural-cue reweighting.

Additional Effects Independent of Binaural-Cue Reweighting

On average across frequency bands, we observed higher ILD weights at central compared to lateral azimuths. This is surprising, as the opposite pattern was observed in Klingel et al. (2020), who used a discrimination task to measure binaural-cue weights. In Klingel et al. (2021), who used the same auditory stimuli as Klingel et al. (2020) and the same

lateralization task as the present study, no significant effect of azimuth was observed. Therefore, the effect of azimuth does not appear to be robust and may depend on the task and auditory stimuli used. The pattern of higher ILD weights at central azimuths observed in the present study may be due to different sensitivity patterns for ITDs and ILDs across azimuths. Variations of ITD sensitivity across azimuths appear to be fully accounted for by the azimuth dependence of the ITD cue itself rather than by decreasing ITD sensitivity with increasing reference ITD (Smith & Price, 2014). Given that for the azimuth range included here ITDs increased relatively linearly with increasing azimuth (see Figure 1a), ITD sensitivity is expected to be constant across azimuths. ILD sensitivity, on the other hand, decreases with increasing reference ILD in addition to the physical dependence of ILD magnitude on azimuth (Brown et al., 2018). For the mid-low, mid-high, and high bands, the ILD magnitude increases less strongly (i.e., the slope of the cue-versus-azimuth function is shallower) for azimuths between approximately 21° – 39° compared to azimuths between 3° – 15° (see Figure 1b). The combined effect of decreasing ILD sensitivity with increasing reference ILD as well as the reduced increase in ILD magnitude for more lateral azimuths (leading to a reduced acoustic “goodness” of the cue) may, therefore, have contributed to the stronger ILD weighting at central compared to lateral azimuths.

Additionally, we found steeper lateralization functions for higher frequencies. This could be explained by two factors regarding ILDs, which dominate the percept at higher frequencies. First, for natural sounds arriving at the outer ears (at least for the frequency range used in this study), ITDs are almost frequency-independent, whereas ILDs are larger at higher frequencies (e.g., Middlebrooks & Green, 1991). Second, Bernstein and Trahiotis (2011) showed that even for a constant ILD magnitude, higher frequencies produce a larger extent of laterality than lower frequencies. The steeper lateralization functions at higher frequencies in our study could be due to both of these factors. We also observed shallower lateralization functions in the post- compared to the pretest in experiment 1. The same pattern was observed in Klingel et al. (2021) and attributed to a training-induced response compression, due to a response mapping to the visually reinforced range. This compression was not observed in experiment 2, possibly because responses were already compressed in the pretest. Importantly, any differences in the slope of the lateralization functions do not influence the estimated binaural-cue weights, as they affect k_{ITD} and k_{ILD} equally and therefore cancel out in the final weight estimation.

Limitations and Future Directions

A general limitation of the impact of training-induced changes in binaural-cue weights is their strong dependence on the auditory stimulus. In addition to requiring either sufficiently high or sufficiently low frequencies, reweighting

seems to be restricted to conditions where low-frequency temporal-fine-structure ITDs do not contribute, which limits the ecological importance of the phenomenon in the normal auditory system where such cues are often available.

However, the results may be relevant for hearing-impaired or cochlear-implant (CI) listeners. Lacher-Fougère and Demany’s (2005) results suggest that listeners with sensorineural hearing loss may not have access to fine-structure ITD cues, while retaining some sensitivity to envelope ITD cues. Also, CI listeners seem to have access to envelope ITD cues only. Many CI stimulation strategies encode ITDs only via the envelope of the stimulus waveform and, even when encoding ITDs via the pulse timing, CI listeners’ sensitivity pattern resembles that for envelope ITDs in acoustic hearing (Bernstein & Trahiotis, 2002; Laback et al., 2007). In fact, binaural-cue reweighting has recently been observed in CI listeners when ITDs were encoded via the pulse timing of low-rate pulse trains (Klingel & Laback, 2021).

We presented auditory stimuli via headphones without HRTF filtering. This ensured that participants did not have access to monaural spectral localization cues, which might provide information about the stimulus azimuth and, thus, might prevent purely binaural-cue reweighting. Kumpik et al. (2010), for example, observed an increased weighting of monaural cues for azimuthal sound localization but no adaptation to changed binaural cues after training, when binaural cues were modified but monaural spectral cues were preserved at one ear. But open questions remain. For example, it is unclear whether the resulting lack of externalization in our study affected the weighting. Kumpik et al. (2019) used (non-individualized) HRTFs as well as reverberation to promote externalization and observed slightly (but significantly) ILD-dominant weights for their broadband stimuli. However, given that Macpherson and Middlebrooks (2002) also included HRTFs, the higher ILD weights in Kumpik et al. (2019) compared to Macpherson & Middlebrooks’ wideband and our multiband stimuli more likely resulted from the added reverberation, which makes ITDs less reliable (Rakerd & Hartmann, 2010), than from the HRTFs or from externalization. Comparing our low- and high-frequency band as well as the multiband stimuli to Macpherson and Middlebrooks’ low-pass, high-pass, and wideband stimuli results in very similar weight estimates. Additionally, it would be an interesting topic for future studies to clarify under which conditions binaural-cue reweighting and binaural-to-monaural-cue reweighting occurs for azimuthal sound localization. Particularly interesting are situations where listeners have access to spectral localization cues but access to low-frequency fine-structure ITD cues is prevented, e.g., due to traffic noise.

Summary and Conclusions

The present study is, to our knowledge, the first to show gradually increasing ILD weights (or decreasing ITD weights)

with increasing frequency (i.e., spectral region) of narrow-band stimuli. It therefore extends our knowledge on the duplex theory of sound localization, particularly on the transition from ITD- to ILD-dominant frequency regions. The across-frequency pattern of weights appears to be consistent with the corresponding patterns of ITD and ILD sensitivity from the literature as well as with the acoustic “goodness” of the cue. We further showed that binaural-cue reweighting is frequency dependent: To induce an increase in ILD weighting, the stimulus frequency needs to be sufficiently high and to induce an increase in ITD weighting, the stimulus frequency needs to be sufficiently low without including the low-frequency region providing fine-structure ITD cues. However, the observed increase in ITD weighting was so small that it reached significance only at specific azimuths. Which frequency band is used for training does not appear to influence the results systematically, suggesting some across-frequency generalization of binaural-cue reweighting. Such reweighting likely plays a role when listeners adapt to acoustic environments with altered robustness of binaural cues (e.g., when low-frequency ITD cues are masked by traffic noise) and has potential applications, such as supervised training after introducing a previously impeded cue to hearing devices such as cochlear implants.

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Research Data Availability Statement

The data is directly available for download from <http://amttoolbox.org/amt-1.1.1-dev/auxdata/klingel2022/> and part of the Auditory Modeling Toolbox (AMT) development repository (i.e., they will be part of the next release). In the meantime, they can be accessed via the AMT functions “data_klingel2022” (raw data), and “exp_klingel2022” (ILD weights) as a download from sourceforge: https://sourceforge.net/p/amttoolbox/code/ci/master/tree/data/data_klingel2022.m and https://sourceforge.net/p/amttoolbox/code/ci/master/tree/experiments/exp_klingel2022.m, respectively.

Declaration of Conflicting Interests

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Notes

1. <https://assetstore.unity.com/packages/tools/integration/oculus-integration-82022>
2. The package is available for download at <https://sourceforge.net/p/expsuite/code/HEAD/tree/FrameWork/Unity/ViWoMI/>.
3. <https://www.oeaw.ac.at/isf/das-institut/software/hrtf-data-base>

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2.4 Reweighting of binaural localization cues in bilateral cochlear-implant listeners

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Research Article

Reweightings of Binaural Localization Cues in Bilateral Cochlear-Implant Listeners

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ABSTRACT

Normal-hearing (NH) listeners rely on two binaural cues, the interaural time (ITD) and level difference (ILD), for azimuthal sound localization. Cochlear-implant (CI) listeners, however, rely almost entirely on ILDs. One reason is that present-day clinical CI stimulation strategies do not convey salient ITD cues. But even when presenting ITDs under optimal conditions using a research interface, ITD sensitivity is lower in CI compared to NH listeners. Since it has recently been shown that NH listeners change their ITD/ILD weighting when only one of the cues is consistent with visual information, such reweighting might add to CI listeners' low perceptual contribution of ITDs, given their daily exposure to reliable ILDs but unreliable ITDs. Six bilateral CI listeners completed a multi-day lateralization training visually reinforcing ITDs, flanked by a pre- and post-measurement of ITD/ILD weights without visual reinforcement. Using direct electric stimulation, we presented 100- and 300-pps pulse trains at a single interaurally place-matched electrode pair, conveying ITDs and ILDs in various spatially consistent and inconsistent combinations. The listeners' task was to lateralize the stimuli in a virtual environment. Additionally, ITD and ILD thresholds were measured before and after training. For 100-pps stimuli, the lateralization training increased the contribution of ITDs slightly, but significantly. Thresholds were neither affected by the training nor correlated with weights. For 300-pps stimuli, ITD weights were lower and ITD thresholds larger, but there was no effect of training. On average across test sessions,

adding azimuth-dependent ITDs to stimuli containing ILDs increased the extent of lateralization for both 100- and 300-pps stimuli. The results suggest that low-rate ITD cues, robustly encoded with future CI systems, may be better exploitable for sound localization after increasing their perceptual weight via training.

Keywords: Interaural time difference, Interaural level difference, Plasticity, Training, Thresholds

INTRODUCTION

Binaural hearing allows listeners to localize sound sources and facilitates understanding speech in noise. Consequently, bilateral cochlear implantation is becoming the standard treatment for bilateral severe to profound deafness and has proven to be advantageous over unilateral cochlear-implant (CI) use. However, even when using both implants, CI listeners generally perform worse than normal-hearing (NH) listeners in the above-mentioned tasks (Kan and Litovsky 2015).

NH listeners rely on two binaural cues for azimuthal sound localization (i.e., in the horizontal dimension, referred to as lateralization), the interaural time difference (ITD) and the interaural level difference (ILD). ITD cues are conveyed via the carrier signal (i.e., the temporal fine structure) at low frequencies and via the temporal envelope at high carrier frequencies. ILDs, on the other hand, are physically negligible at low frequencies but provide strong lateralization cues at high frequencies (e.g., Macpherson and Middlebrooks 2002). Consequently, NH listeners weight ITD and ILD cues mainly based on the

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frequency content of the sound (i.e., the cues contribute to different amounts to the azimuthal percept) with ILDs dominating for high-frequency stimuli and ITDs dominating for low-frequency and wideband stimuli (Macpherson and Middlebrooks 2002). In contrast, bilateral CI recipients rely almost entirely on ILDs with little to no contribution of ITDs (Grantham et al. 2007; Seeber and Fastl 2008).

The reasons for the low contribution of ITD cues to lateralization of CI listeners are manifold. Technical factors include that present-day envelope-based stimulation strategies do not convey pulse-ITDs (i.e., ITD cues encoded via the pulse timing), and that envelope-ITD cues, which are conveyed by such strategies, are not sufficiently salient for important everyday-life stimuli such as speech because their envelope shape is typically too shallow (Laback et al. 2004, 2011). Furthermore, these envelope-based stimulation strategies typically use high-rate pulse carriers whereas CI listeners' sensitivity (both in terms of thresholds and extent of lateralization) to ITD cues, conveyed via the pulse timing using a research interface that bypasses the clinical CI system, deteriorates for pulse rates above 100–200 pps (Laback et al. 2015). Therefore, even if ITD information was conveyed via the pulse timing, it would not be perceivable and CI listeners who use envelope-based stimulation strategies thus do not have access to reliable and salient ITD cues in their everyday lives.

Consequently, strategies aiming to better transmit ITD cues are being developed. One approach is to encode acoustic fine-structure cues via the pulse timing using low pulse rates [e.g., FSP (Hochmair et al. 2006), PDT (van Hoesel et al. 2008), PP (Williges et al. 2018)]. However, even though such a “fine-structure” processing strategy (FS4) improved ITD detection thresholds for pure-tone stimuli of a subset of CI listeners (Zirn et al. 2016), these benefits do not or only slightly translate to real-life situations such as sound localization (van Hoesel et al. 2008; Dillon et al. 2016) or speech understanding in noise (Dillon et al. 2016; Magnusson 2011; de Bodt and van de Heyning 2014; Riss et al. 2011; van Hoesel et al. 2008; Zirn et al. 2016).

In addition, perceptual factors play a role in the low contribution of ITDs in electric hearing. Even when ITDs are presented under the most favorable conditions (i.e., via the pulse timing and at a single interaurally place-matched electrode pair, directly stimulated via a research interface using the most sensitive pulse rate), CI listeners' ITD sensitivity is lower and much more variable across listeners compared to that of NH listeners (Laback et al. 2007; Majdak et al. 2006; van Hoesel 2007; Thakkar et al. 2020). Several explanations have been proposed for this perceptual deficit in electric hearing (see Laback et al. 2015, for a review). For instance, deprivation of binaural experience due to long periods before or between implantation on both ears results in cortical anomalies

(Gordon et al. 2010) as well as degraded neural ITD coding (Chung et al. 2019; Hancock et al. 2010). Accordingly, Thakkar et al. (2020) reported that ITD sensitivity is related to the duration of bilateral hearing impairment and to CI experience. Another factor may be a mismatch between stimulation rate and membrane and synaptic parameters of binaural cells, which may explain the decline in sensitivity with increasing rate (Chung et al. 2015). This rate limitation is not only observed in discrimination thresholds, but also affects lateralization ranges (i.e., how far stimuli are lateralized to the sides; Anderson et al. 2019). Interestingly, the decline in pulse-ITD sensitivity with increasing rate (for unmodulated pulse trains) matches the decline in envelope-ITD sensitivity with increasing modulation rate observed in acoustic hearing (e.g., Bernstein and Trahiotis 2002; van Hoesel 2007; Laback et al. 2007; Stecker and Brown 2010). Although the auditory nerve can follow temporal information at high electric stimulation rates (e.g., Dynes and Delgutte 1992), this suggests that the neural pathway that encodes high-rate carrier ITDs in normal hearing is not accessed in electric stimulation. Instead, pulse-ITDs appear to activate the envelope-ITD pathway.

Here, we investigate another mechanism potentially contributing to the low perceptual impact of optimally conveyed pulse-ITD cues in electric hearing. It is conceivable that the lack of reliable and salient pulse-ITD cues CI listeners experience in their everyday lives leads to reweighting of the binaural cues, i.e., a change in the relative contribution of the cues to sound lateralization: CI listeners might learn over time to increase the perceptual weighting of ILDs which correctly indicate the location of many sound sources in daily life, and decrease the perceptual weighting of pulse-ITDs which arise at random or are not perceived at all. This seems plausible given that NH listeners reweight binaural localization cues based on the reliability of each cue: They showed increased weighting for ILDs and correspondingly reduced weighting for ITDs after task-irrelevant auditory stimuli containing stable ILD and random ITD cues were presented during a visual oddball task (Kumpik et al. 2019). Furthermore, a recent study in our lab showed that the relative weight of either ITDs or ILDs can be increased in NH listeners, depending on which cue is reinforced during a lateralization training in a virtual audio-visual environment by presenting visual cues spatially consistent with one binaural cue while varying the other cue (Klingel et al. 2021). We are now interested in whether an increased weighting for ILDs in CI listeners can be reversed by presenting reliable pulse-ITDs (referred to as ITDs in the following) and varying ILDs.

Therefore, this study investigates whether the paradigm used by Klingel et al. (2021) can induce an increase in ITD weighting in CI listeners. We were further interested in how the perceptual weight given to each binaural cue relates to binaural-cue thresholds and whether

TABLE 1

Listener data. The italicized listeners were excluded from the analyses

Listener	Implant L	Implant R	Age at testing	Etiology	Age at onset of deafness	Age at implantation (L/R)	Electrode tested (L/R)	ITDs doubled (100/300 pps)	Pulse rate trained first
CI3	C40+	C40+	35	Meningitis	20	20/20	11/10	No/No	300
<i>CI17</i>	<i>Synchrony</i>	<i>Synchrony</i>	72	<i>Idiopathic</i>	41	69/58	8/8	<i>Yes/Not tested</i>	100
CI62	C40+	C40+	19	Connexin 26	0	2/0	11/11	No/No	300
CI66	Synchrony	Concerto	55	Progressive	Childhood	37/46	8/6	No/Yes	300
CI74	Concerto	Sonata	49	Progressive	Adulthood	43/42	8/9	No/No	300
<i>CI77</i>	<i>Sonata</i>	<i>Sonata</i>	66	<i>Sudden hearing loss</i>	33 (L)/57 (R)	58/57	8/6	<i>No/Yes</i>	100
CI100	Implant L	C40+	22	Unknown	Childhood	8/2	9/9	Yes/Yes	100
CI117	C40+	C40+	38	Etiology	Early adulthood	37/22	8/9	Yes/Yes	100

binaural-cue reweighting will also be reflected in a change in binaural-cue thresholds (i.e., whether binaural-cue weighting is simply a reflection of the sensitivity to each binaural cue or whether it is a supra-threshold mechanism). We tested two pulse rates. The 100-pps condition explored reweighting for stimuli that provide the highest ITD sensitivity. The 300-pps condition (representing any carrier rate that is too high to permit pulse-ITD sensitivity) investigated whether the rate limitation is connected to reweighting. Specifically, if reweighting contributes to the rate limitation, given that CI listeners are mostly exposed to high-rate carriers with their clinical devices, we may see reweighting at 300 pps. However, if the rate limitation results from a processing deficit independent of reweighting, no effect of training is expected at that rate. Finally, unrelated to binaural-cue reweighting, we addressed the practically relevant question if the combined presentation of salient ITDs and ILDs is beneficial for lateralization. Specifically, we tested whether the

additional presentation of nonzero ITDs significantly contributes to the extent of lateralization beyond lateralization based on ILDs alone.

METHODS

Participants

Six CI listeners, bilaterally implanted with MED-EL Corp. devices (Innsbruck, Austria), completed the experiment. Two additional listeners participated in the study but were excluded: One listener experienced dizziness induced by the head-mounted display and dropped out of the study. The other listener had difficulties lateralizing the stimuli without visual reinforcement leading to most stimuli being perceived at either -90° or $+90^\circ$ azimuth. The listener and device information are summarized in Table 1. All listeners gave informed consent and

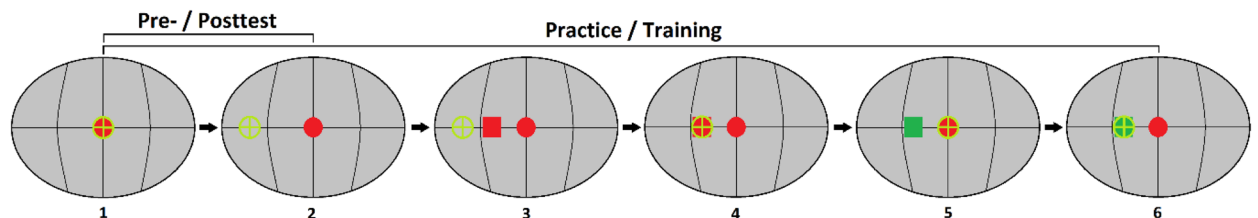


FIG. 1 Time course of a trial during the binaural-cue weight measurement (panels 1–2) and the practice session as well as the lateralization training (panels 1–6). (1) Listeners oriented towards the reference position (indicated by a red sphere) and pressed a button to elicit the sound presentation. (2) Listeners turned their head (guiding a green crosshair) to the perceived azimuth and pressed the button (in this example, they turned their head to the left). (3) Visual reinforcement (a rotating red cube) appeared at the ITD azimuth.

(4) The ITD azimuth was confirmed via a head-turn to the visual reinforcement and a button-press. (5) The visual reinforcement turned green, listeners returned to the reference position, and elicited the second sound presentation (while the visual reinforcement was still visible) with another button-press. (6) Listeners confirmed the ITD azimuth again via another head-turn and button-press. In steps (4) and (6), the button-press was accepted only if the head orientation (green crosshair) was within $\pm 5^\circ$ of the ITD azimuth

received monetary compensation for their participation. The research protocol was submitted to the Acoustics Research Institute's ethics committee for consideration, comments, guidance, and approval. After taking ethical issues, local laws, and regulations into account, the ethical committee approved the protocol.

Apparatus and Stimuli

For the binaural-cue weight measurements as well as the training, a lateralization task in a virtual audio-visual environment was used. The virtual environment served to mediate the lateralization process and to present visual reinforcement during the lateralization training. Visual stimuli were presented binocularly via a head-mounted display (Oculus Rift DK1). The visual environment (Fig. 1) consisted of a reference position straight ahead, a crosshair in the direction the head is oriented, a single horizontal line at eye level, and vertical lines every 15° in azimuth for guidance. A rotating cube was used as visual reinforcement. Listeners were seated on a desk chair that was allowed to rotate. Their head position and orientation were tracked with a head-mounted tracking sensor (Flock of Birds, Ascension) and the visual environment was rendered accordingly in real time (with a latency between head movements and the updated visual information of less than 37.3 ms). The rendering of the visual environment using Pure Data (with GEM, IEM, Graz) was based on the left/right rotation information from the tracking sensor while the up/down information was ignored to force listeners to respond only in the horizontal plane.

Auditory stimuli were generated on a personal computer and were directly presented to the two CIs via a research interface (RIB2) developed at the Institute of Ion Physics and Applied Physics, Leopold-Franzens University of Innsbruck, Austria, allowing precisely controlled interaurally coordinated stimulation. Listeners were thus isolated from any audio-visual signals besides the experimental stimuli during the experiment, while they used their clinical devices during breaks and between sessions. Prior to the main experiment, the threshold (THR), comfortable level (CL), and maximum comfort-

All stimulation pulses were symmetric-, biphasic-, and cathodic-phase leading. The duration of a phase was 26.7 μ s and there was no inter-phase gap. If sufficient loudness could not be reached, the phase duration was increased to 40 μ s.

Auditory stimuli in the main experiment were unmodulated electric pulse trains with a pulse rate of either 100 or 300 pps and a duration of 500 ms, presented at a single interaurally place-matched electrode pair (see “5” for details and Table 1 for chosen electrodes). Various combinations of ITDs and ILDs were imposed on these stimuli. A range of ILDs was determined individually for each listener during the parameter determination (see “5” for details), with the goal to elicit a set of perceived azimuths (referred to as ILD azimuths) equally spaced between -69° (left) and $+69^\circ$ (right). This range is analogous to Klingel et al. (2021). For ITDs, we did not determine listener-specific ITDs matching that azimuth range, because it was foreseeable from pilot tests and other studies (e.g., Anderson et al. 2019) that listeners would never lateralize across such a wide range of azimuths. Thus, we accepted that ILDs would dominate the lateralization percept in the pretest, while leaving room for increasing the contribution of ITDs. Instead, naturally occurring ITDs were used that ranged from -654 to $+654$ μ s, corresponding to an azimuth range from -69° to $+69^\circ$ (referred to as ITD azimuths), as estimated by Xie (2013) using broadband cross-correlation of the head-related impulse responses of the KEMAR head with DB-61 small pinna at a source distance of 1.4 m. If the listener's left/right discrimination threshold for ITDs was larger than two times the largest ITD used (i.e., 1308 μ s), all ITDs were doubled¹ to increase the likelihood that ITDs provided useful lateralization cues (see Table 1). For CI74, ITDs were not doubled at 300 pps, even though that listener's threshold exceeded 1308 μ s. However, we believe this does not change the overall interpretation of the results, since CI74's 300-pps threshold exceeded 3200 μ s and doubling the ITDs would therefore have been unlikely to affect the results. ILDs are reported in percent of the dynamic range (%DR) between the threshold (THR), comfortable level (CL), and maximum comfortable level (MCL) of each listener (Eq. 1).

$$\text{If ILD(\%DR)} < 0 : \text{Amp}_L = \text{CL}_L + \frac{-\text{ILD} * (\text{MCL}_L - \text{CL}_L)}{200}; \text{Amp}_R = \text{CL}_R - \frac{-\text{ILD} * (\text{CL}_R - \text{THR}_R)}{100}$$

$$\text{If ILD(\%DR)} > 0 : \text{Amp}_L = \text{CL}_L - \frac{\text{ILD} * (\text{CL}_L - \text{THR}_L)}{100}; \text{Amp}_R = \text{CL}_R + \frac{\text{ILD} * (\text{MCL}_R - \text{CL}_R)}{200} \quad (1)$$

able level (MCL) were determined manually using a continuous scale from “not audible” to “uncomfortably loud”. For stimuli with zero ILD, the CL measured at each ear was used (for stimuli including ILDs, see below).

¹ Because ITDs exceeding about one-third of the inter-pulse interval can potentially introduce a left/right ambiguity in the ongoing signal, we checked the potential influence of such an effect. Removing possibly “critical” conditions (i.e., an alpha of 45° for the 300-pps condition) from the weight analysis did not impact the outcome.

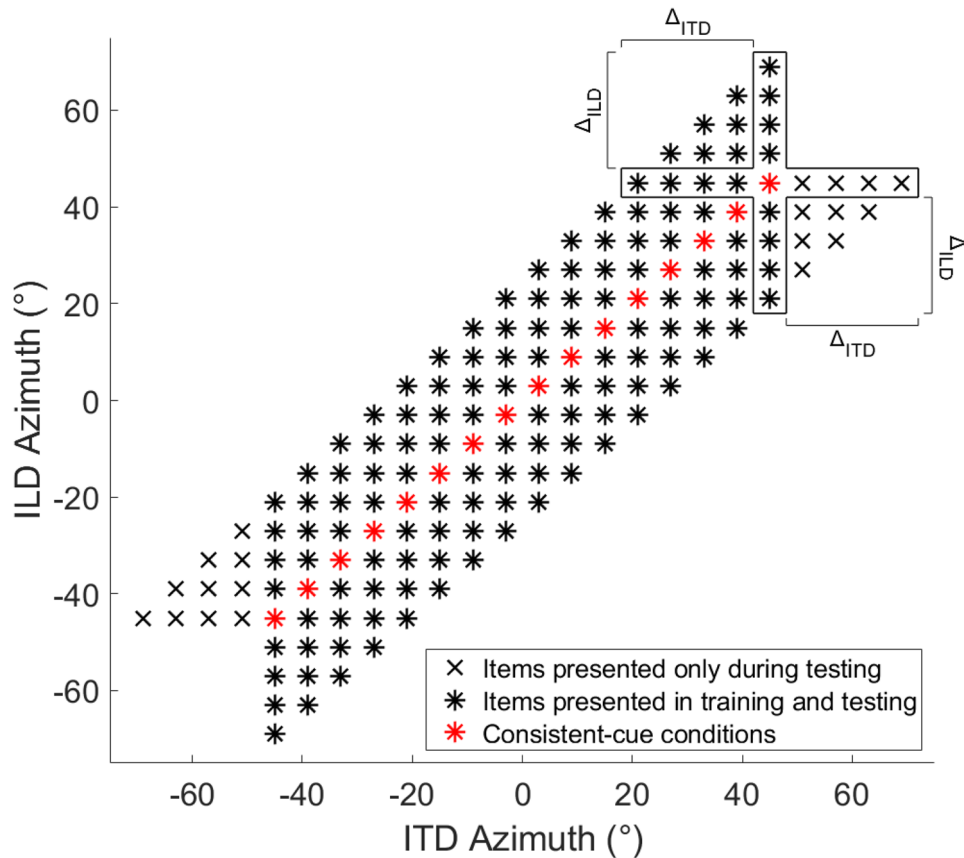


FIG. 2 ITD/ILD combinations presented in this study. During lateralization training, ILD azimuths were uniformly distributed around each ITD azimuth (columns of asterisks). During the lateralization tests used for estimating binaural-cue weights, ITD/ILD combinations marked with an “x” were additionally presented to also

ensure a uniform distribution of ITD azimuths around each ILD azimuth, which was needed for the binaural-cue weight estimation (the frame indicates items that were used to estimate the ITD weight at an example azimuth of 45°)

This ILD specification aimed at providing roughly constant loudness across a wide range of ILDs, following earlier research (Best et al. 2011).

ITDs and ILDs were then combined into “consistent-cue” and “inconsistent-cue” conditions. In consistent-cue conditions, the ITD and ILD cue of the auditory stimulus corresponded to the same azimuth (red asterisks along the diagonal in Fig. 2), while they corresponded to disparate azimuths in inconsistent-cue conditions. Recall that ILD azimuths are psychophysical estimates based on each listener’s perception while ITD azimuths are based on acoustical measurements in a dummy head. Therefore, consistent-cue stimuli are only nominally consistent and might not reflect a perceptually consistent binaural-cue combination. To address this, listeners could familiarize themselves with the consistent-cue stimuli during a practice session with each pulse rate (see below). Furthermore, since the parameters were held constant throughout the experiment, potential mismatches should not influence the comparisons across test phases. Cue disparities (i.e., the difference between the

ITD and ILD azimuth of a stimulus) were restricted to a maximal value of 24°, to avoid the perception of split images that can occur in case of large cue disparities (Gaik 1993). In the lateralization tests, ITD and ILD cues were uniformly distributed $\pm 24^\circ$ around each azimuth on the diagonal of Fig. 2, in both the ITD and ILD dimensions (all symbols in Fig. 2 in rows and columns, respectively). In the lateralization training, ITD azimuths were visually reinforced, and their range was restricted to $\pm 45^\circ$ (all asterisks in Fig. 2). The restricted ITD azimuth range was chosen to ensure that the visual reinforcement was always visible when facing the reference position (i.e., $\pm 45^\circ$ was the field of view of the head-mounted display), encouraging multisensory bottom-up processes during simultaneous presentation of the auditory stimulus and visual reinforcement. Moreover, by symmetrically varying the ILD azimuth around each ITD azimuth [resulting in a larger range of ILD azimuths ($\pm 69^\circ$) than ITD azimuths ($\pm 45^\circ$)], the ITD was the more stable cue which might further encourage reweighting (Dahmen et al. 2010).

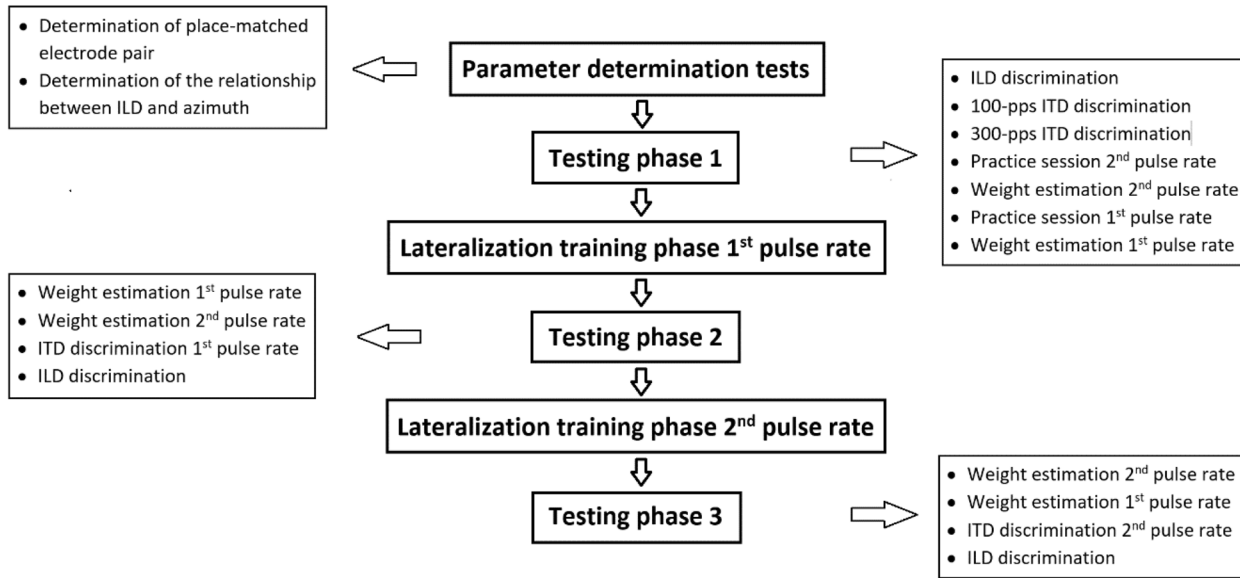


FIG. 3 Experimental structure. The experimental phases, completed from top to bottom, are shown in the center. The boxes on the sides show the tests completed during parameter determination and during each testing phase, also sorted top to bottom

For the threshold measurements, listeners were seated in front of the screen of a personal computer and gave left/right responses with a gamepad. The auditory stimuli, unmodulated 100- or 300-pps pulse trains, were again directly presented to the two CIs via the RIB2.

Procedure

The general structure of the experiment is shown in Fig. 3. At the beginning, several tests were performed to determine the parameters for the main experiment. In the testing phases [before (1), in-between (2), or after (3) the two lateralization training phases reinforcing ITD cues], binaural-cue weights (via a lateralization task) as well as binaural-cue sensitivity (via a discrimination task) were measured. Which of the two pulse rates was trained first was counter-balanced across listeners. However, the drop-out of two listeners resulted in 4 of the included listeners starting with 300-pps training while 2 listeners started with 100-pps training. The data collection per listener took 4–5 days to complete.

Parameter Determination We determined a place-matched binaural electrode pair using a well-established procedure (e.g., Majdak et al. 2006, or Laback et al. 2007) using unmodulated 1515-pps pulse trains to reduce the potentially confounding effect of rate pitch at lower rates. That procedure involved pitch magnitude estimation of loudness-matched stimulation electrodes at both ears followed by pitch discrimination of pitch-matched pair candidates. An electrode pair at the basal region that elicited pitch discrimination at chance level was then selected for the rest of the study. We chose a basal

electrode pair to provide the best conditions for ITD sensitivity (see Laback et al. 2015). Furthermore, assuming that the pulse rate in electric stimulation is perceptually analogous to the envelope rate in acoustic hearing (Stecker and Brown 2010), basal electrodes correspond to the cochlear place where envelope cues are represented in normal hearing. If a place-matched electrode pair had already been determined for a listener in a previous study at the authors' lab using the same methodology (as for CI3, CI62, CI100, and CI74), that pair was also used in the present study. We then determined THR, CL, and MCL separately for 100 and 300 pps at the place-matched electrode pair members.

To determine the relationship between ILD and perceived azimuth, we presented 6 left- and 6 right-leading ILDs (10 repetitions each) and asked the listeners to lateralize the stimuli in the virtual environment (see steps 1 and 2 in Fig. 1). On each trial, participants listened to the auditory stimulus while facing the reference position and then indicated the perceived azimuth via head turn and button press. After they returned to the reference position, the next auditory stimulus was presented. We then averaged the response azimuths for each ILD and fitted either a linear function or an inverse tangent function, depending on which fitted the data better as indicated by a higher R^2 (see Fig. 4). Finally, ILDs were read out from the fitted function to obtain ILDs corresponding to the azimuths used in the main experiment (thus, defining the ILD azimuths). Due to limited testing time and because we did not expect the functions to differ between pulse rates, only 100-pps stimuli were used for fitting ILD values to azimuths. The assumption of comparable

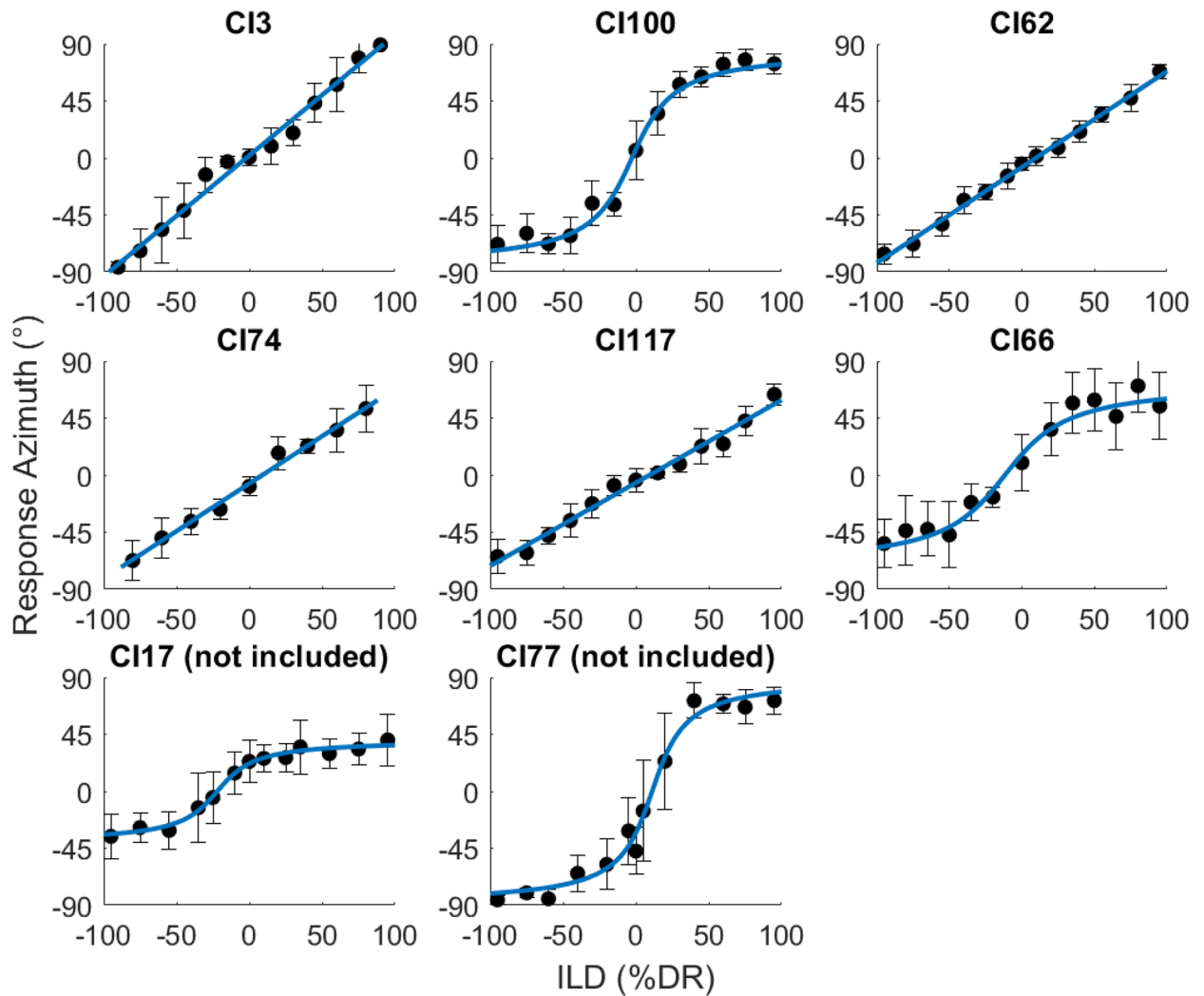


FIG. 4 Lateralization data used to determine the relationship between ILDs and perceived azimuths. Error bars show standard errors of the mean. The blue lines show the fitted functions. Linear fits were used for CI3, CI62, CI74, and CI117, inverse tangent fits were used for CI100, CI66, CI17, and CI77. CI17 and CI77 were excluded from the study

lateralization functions for 100- and 300-pps pulse trains was confirmed post hoc (see yellow downward pointing triangles in Fig. 5).²

Testing Phase The sequence of measurements performed during each testing phase is shown in Fig. 3. In all testing phases, we measured binaural-cue weights for both pulse rates with a lateralization task as well as binaural cue thresholds with a discrimination task. In testing phase 1 only, listeners additionally performed a practice session including visual reinforcement (see description of the training task below) to get accustomed to the

lateralization training task. In the practice session, only consistent-cue combinations (red asterisks in Fig. 2) were presented, 4 repetitions per azimuth (i.e., 64 trials total). This was done separately with 100- and 300-pps stimuli right before the respective lateralization test.

Binaural-cue weights were measured with a lateralization task in the virtual audio-visual environment without visual reinforcement. Namely, by obtaining lateralization responses for stimuli containing spatially inconsistent ITD and ILD, it can be inferred how much each cue contributes to the azimuthal percept by comparing the response azimuth to the respective binaural-cue azimuths (Macpherson and Middlebrooks 2002; see “10” below). On each trial, the auditory stimulus was presented while listeners faced the reference position and then indicated the perceived azimuth via head turn and button press.

² A 2 (100 vs. 300 pps) $\times$ 10 (azimuth) ANOVA yields neither a significant effect of rate ($F(1,5)=0.32$; $p=.595$; $\eta_p^2=.060$) nor a significant rate $\times$ azimuth interaction ($F(9,45)=0.80$; $p=.616$; $\eta_p^2=.138$).

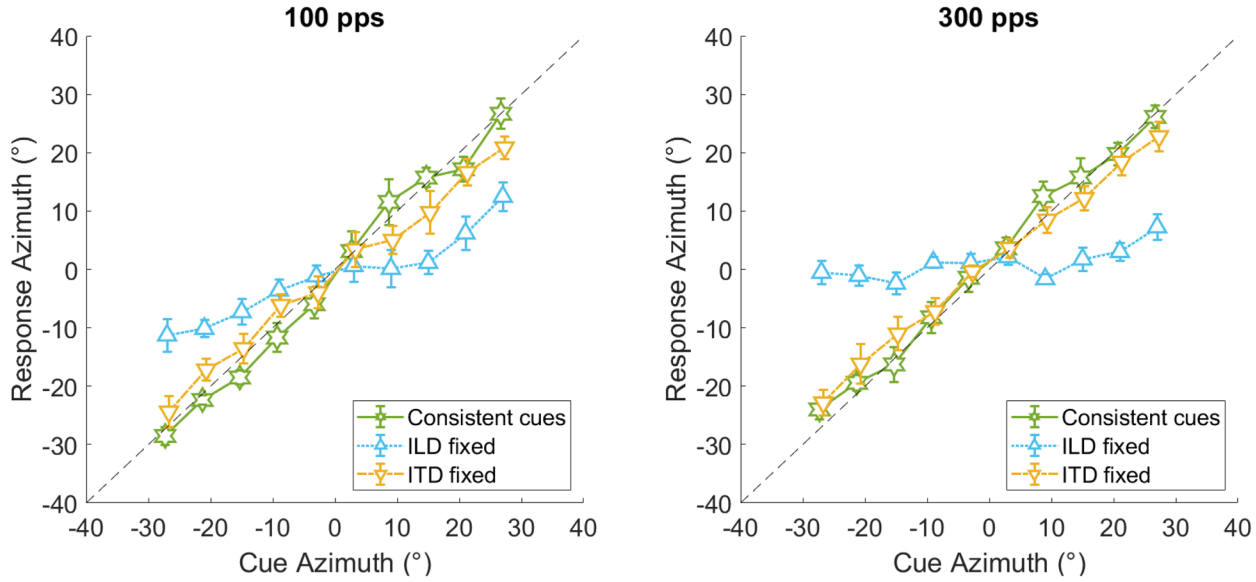


FIG. 5 Mean response azimuths for varying ITDs (ILDs fixed at $\pm 3^\circ$), varying ILDs (ITDs fixed at $\pm 3^\circ$) and for consistent cues after averaging across all 3 test phases. Results for the 100-pps condition are shown on the left and results for the 300-pps condition

are shown on the right. Error bars show the standard error of the mean. Note that varying ITDs and ILDs correspond to the parameters Δ_{ITD} and Δ_{ILD} , respectively, in the regression analysis (Eq. 2)

When they returned to the reference position, the next item was presented (steps 1 and 2 in Fig. 1). After each 124 trials, listeners took a short break. Each ITD/ILD combination (i.e., all data points shown in Fig. 2) was presented 3 times, resulting in 492 trials in total. In addition, a centered item was presented at the beginning as well as after each break to help listeners build up their audio-visual reference frame. This measurement was done in separate blocks for the 100- and 300-pps stimuli.

For measuring ITD and ILD thresholds, we used a constant-stimuli, cued left/right discrimination paradigm. The first interval of each trial consisted of a centered stimulus (zero ITD and zero ILD; note that zero ILD refers to an ILD causing a centered image). The second interval consisted of the same stimulus with, depending on which cue was tested, either a nonzero ITD or a nonzero ILD while the other was left at zero. The listeners had to indicate on which side (left or right) the second stimulus was perceived compared to the first stimulus by pressing the corresponding button on a gamepad. They received feedback (correct/incorrect) after each response. During ITD threshold estimation, we tested ITDs of $\pm 100, \pm 200, \pm 400, \pm 800$, and $\pm 1600 \mu s$. If it was known from previous tests that the 100-pps threshold of a listener was outside of this range, the range of ITDs tested was adjusted accordingly (smallest ITD tested: $25 \mu s$). ITD thresholds were measured separately for 100 and 300 pps in testing phase 1 and after the training phase with the respective pulse rate. During ILD threshold estimation, ILDs were chosen based on the listener's ILD lateralization results during parameter determination. ILD

thresholds were measured using 100-pps stimuli during all three testing phases. For both ITD and ILD threshold estimations, 100 repetitions were tested per cue value.

Lateralization Training Phase Listeners were trained with a lateralization task in the virtual audio-visual environment using visual reinforcement consistent with the ITD azimuth (Fig. 1). A training trial started with the presentation of the auditory stimulus while listeners faced the reference position. They indicated the perceived azimuth via head turn and button press, so far identical to the lateralization testing trials described above. It proceeded with visual reinforcement appearing at the ITD azimuth. Listeners were instructed to perform a corrective head turn from the response azimuth to the displayed azimuth and confirm it with a button press. When they returned to the reference position and pressed the button, the same auditory stimulus was presented again, now simultaneously with the visual reinforcement. Then, the displayed azimuth had to be confirmed again via another head turn and button press. Finally, listeners returned to the reference position to start a new trial. Thus, the training utilized two forms of visually guided auditory spatial calibration: (1) visual stimuli presented after the auditory stimuli, serving as top-down (i.e., involving cognition) feedback comparable to the “feedback” experiments of Shinn-Cunningham et al. (1998), and (2) simultaneously presented auditory and visual stimuli, encouraging multisensory bottom-up (i.e., stimulus-driven) processes equivalent to those evoked in the ventriloquism aftereffect paradigm (Recanzone 1998). After each 73 trials, listeners

took a short break. One training block consisted of 146 trials, namely each ITD azimuth combined with each ILD azimuth $\pm 24^\circ$ around that ITD azimuth (columns of asterisks in Fig. 2) plus a centered item at the beginning and after each break to help listeners to orient themselves. Listeners completed five training blocks per pulse rate.

Analysis

Analogous to Klingel et al. (2021), we estimated binaural-cue weights individually for each listener based on a regression analysis motivated by the experimental design, which measured the effect of varying the ILD on the responses at each ITD azimuth and vice versa. A resulting ITD weight of 1 means that listeners always responded at the ITD azimuth, an ITD weight of 0 means listeners always responded at the ILD azimuth, and an ITD weight of 0.5 represents equal weighting of the two cues. The regression analysis was fitted separately for each azimuth α (between 3° and 45° with a 6° spacing between azimuths) after averaging repetitions and mirroring the data across the midline.³ The regression model equations are as follows:

$$R_{ITD}(\alpha, \Delta_{ITD}) = k_{ITD}(\alpha) * \Delta_{ITD} + Q_{ITD}(\alpha)$$

$$R_{ILD}(\alpha, \Delta_{ILD}) = k_{ILD}(\alpha) * \Delta_{ILD} + Q_{ILD}(\alpha)$$

$$w_{ITD}(\alpha) = \frac{\text{atan}\left(\frac{k_{ITD}(\alpha)}{k_{ILD}(\alpha)}\right)}{\frac{\pi}{2}}$$

$$Q(\alpha) = \frac{Q_{ILD}(\alpha) + Q_{ITD}(\alpha)}{2} \quad (2)$$

where R_{ITD} (R_{ILD})⁴ is the listener's mean response azimuth in a trial for which the ILD (ITD) corresponded to azimuth α and the ITD (ILD) corresponded to azimuth $\alpha + \Delta_{ITD}$ ($\alpha + \Delta_{ILD}$). The parameters k_{ITD} and k_{ILD} are the estimated linear regression slopes at azimuth α (determining the individual binaural-cue contributions), and Q is the estimated response azimuth for consistent-cue stimuli corresponding to azimuth α . Parameter k_{ITD} (k_{ILD}) was estimated at each α by considering various azimuthal offsets (from -24° to $+24^\circ$ with 6° spacing) of the cue Δ_{ITD} (Δ_{ILD}) while setting the offset of the other cue, Δ_{ILD} (Δ_{ITD}), to zero. Thus, the model was fitted for each azimuth α , indicated by a red asterisk in Fig. 2, by considering only items of the row (for k_{ITD}) and column

(for k_{ILD}) that include that red asterisk (indicated by the frame for an example azimuth of 45°). These estimates of k_{ITD} and k_{ILD} , representing orthogonal vectors, were then combined to derive the ITD weight, w_{ITD} (note that $w_{ILD} = 1 - w_{ITD}$). Finally, parameter Q was estimated as the average of the constants obtained in the regressions for ITD and ILD. To compare pre- and post-training weights across listeners, we averaged the estimated weights obtained before or after the lateralization training, depending on which pulse rate was trained first (i.e., for determining 100-pps weights, if the listener started with 100-pps training, lateralization test 1 constitutes the pretest and the estimated weights from lateralization tests 2 and 3 were averaged to constitute the posttest. If the listener started with 300-pps training, 100-pps weights from lateralization tests 1 and 2 were averaged to constitute the pretest and lateralization test 3 constitutes the posttest).

Binaural-cue thresholds at a performance level of 75% (i.e., halfway between chance and perfect performance) were determined with the MATLAB toolbox psignifit 4 (Schütt et al. 2015). ITD values were logarithmized using the natural logarithm before fitting the psychometric function. To determine ILD thresholds, the difference between the reference and target stimulus in current units (cu) was evaluated. As a conservative means to reflect that the listeners may not make judgments based on the difference between the reference and the target stimulus, but rather compare the target stimulus to previously presented targets, the obtained threshold values were doubled for both ITD and ILD thresholds (Hartmann and Rakerd 1989).

The data were analyzed using MATLAB R2018b (The MathWorks, Natick, MA). Statistical analyses were performed using SPSS Statistics 20 (IBM, Armonk, NY).

RESULTS

Binaural-Cue Weights

Figure 6 shows the ITD weights averaged across listeners as a function of azimuth for the pretest (open symbols) and the posttest (filled symbols). Data for 100-pps stimuli are shown in the left panel and data for 300-pps stimuli are shown in the right panel. ITD weights were subjected to a 2 (100 vs. 300 pps) $\times 2$ (pre- vs. post-test) $\times 8$ (azimuth) repeated-measures (RM) ANOVA. The ANOVA yielded a significant main effect of pulse rate ($F(1,5) = 10.26$, $p = 0.024$, $\eta_p^2 = 0.672$) with larger ITD weights at 100 pps ($M = 0.19$, $SD = 0.17$) than 300 pps ($M = 0.03$, $SD = 0.06$), a significant main effect of azimuth ($F(7,35) = 7.28$, $p < 0.000$, $\eta_p^2 = 0.593$) with smaller ITD weights at more lateral azimuths, and a significant pulse rate $\times$ testing time interaction ($F(1,5) = 8.76$, $p = 0.032$, $\eta_p^2 = 0.637$). Post hoc pairwise comparisons showed that the pulse rate $\times$ testing time interaction was driven by a

³ Before mirroring the data, we tested whether the ITD weights at the two hemispheres differed significantly. This was not the case ($F(1,5) = 0.06$; $p = .818$; $\eta_p^2 = .012$).

⁴ Here and in the remainder of the paragraph, the “other” (counterpart) cue is referred to in parentheses.

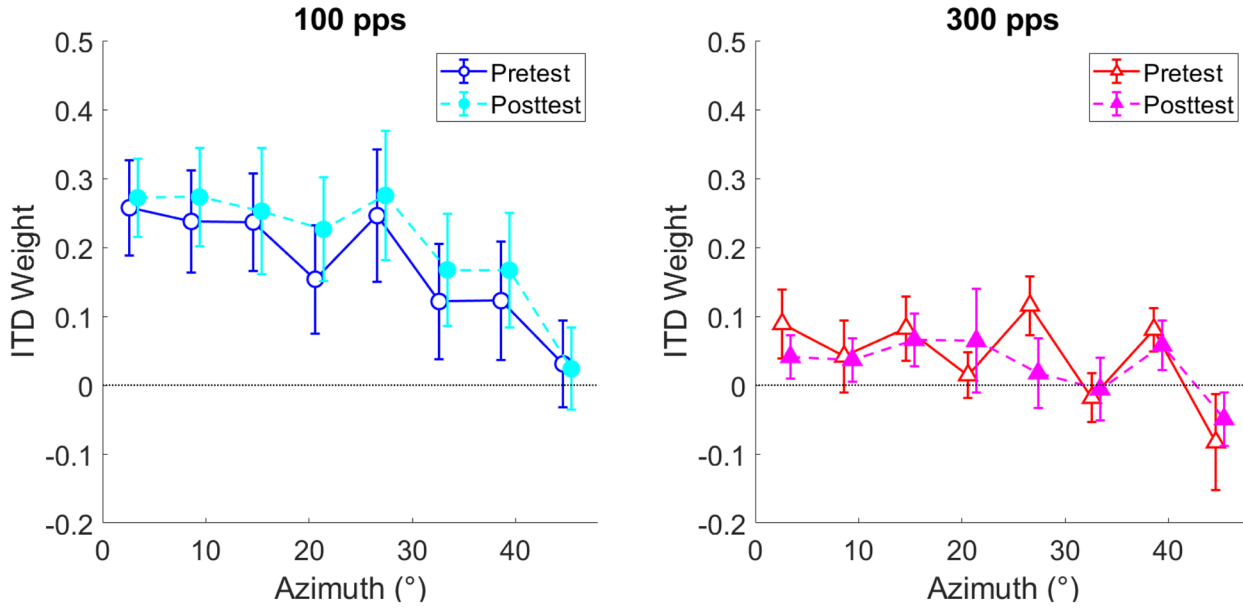


FIG. 6 Mean ITD weights averaged across listeners as a function of azimuth for the 100-pps condition (left panel) and the 300-pps condition (right panel). Error bars show the standard error of the mean

significant increase of ITD weights from pre- to posttest in the 100-pps condition ($p=0.046$, Bonferroni-corrected), but no effect of testing time in the 300-pps condition ($p=0.443$, Bonferroni-corrected). Taken together, these results suggest that listeners increased their ITD weighting for 100-pps but not for 300-pps stimuli as a function of testing time and that ITD weights were consistently lower for 300 pps and at lateral azimuths.

Figure 7 shows the ITD weights of the individual listeners for further illustration. Overall ITD weights differed widely among listeners, ranging from essentially zero at both pulse rates in CI117 to about 0.5 for 100-pps stimuli in CI62. For five out of six listeners, the 100-pps posttest data point lies above the 100-pps pretest data point. The difference in ITD weights between 100 and 300 pps was most pronounced for CI3 and CI62 and barely observable for CI117 and CI66 (the latter likely due to floor effects). For cross-study comparison, the NH ITD weights from Klingel et al. (2021) are shown on the far right. Subjecting the 100-pps CI results and the NH results (both averaged across azimuths) to a 2 (CI vs. NH) $\times$ 2 (pre- vs. posttest) mixed-design ANOVA yielded a significant effect of group ($F(1,14)=48.86$, $p<0.001$, $\eta_p^2=0.777$) and testing time ($F(1,14)=7.66$, $p=0.015$, $\eta_p^2=0.354$), but no significant testing time $\times$ group interaction ($F(1,14)=1.73$, $p=0.210$, $\eta_p^2=0.110$). This suggests overall stronger ITD weighting in NH listeners, but it provides no evidence for different amounts of reweighting in the two listener groups.

To test which listeners significantly changed the binaural-cue weighting for 100-pps stimuli, we used a metric that provides sufficient power for within-listener statistics,

namely the ITD bias (in degrees) for each item. The ITD bias is defined as the difference between response and ITD azimuth in the direction of the ILD azimuth (i.e., a small bias indicates a large ITD weight, as the response is close to the ITD azimuth). Consistent-cue items were excluded. As in the weight analyses, either test phases 1 and 2 or test phases 2 and 3 were averaged to yield the pre- and posttest. We then ran a 2 (pre- vs. posttest) $\times$ 4 (cue disparity) RM ANOVA for each listener, since the bias is expected to be larger the further ITD and ILD azimuths are apart. This was confirmed by a significant main effect of cue disparity for each of the six listeners (all $p<0.001$). There further was a significant main effect of time for CI66 ($F(1,101)=6.29$, $p=0.014$, Benjamini-Hochberg-corrected $p=0.036$, $\eta_p^2=0.059$) with smaller ITD biases in the post- compared to the pretest, providing conservative within-listener statistical evidence that one of the six listeners significantly increased their ITD weighting for 100-pps stimuli. For CI3 ($F(1,101)=5.25$, $p=0.024$, Benjamini-Hochberg-corrected $p=0.052$, $\eta_p^2=0.049$) and CI74 ($F(1,101)=5.10$, $p=0.026$, Benjamini-Hochberg-corrected $p=0.052$, $\eta_p^2=0.048$), the main effect of time just missed the significance level after correcting for multiple comparisons.

Discrimination Thresholds

Figure 8 summarizes the results of the ITD and ILD sensitivity measurements. The individual panels show the psychometric functions for left/right discrimination performance of each listener, based on ITDs for 100-pps (top row) and 300-pps (middle row), and on ILDs for 100-pps

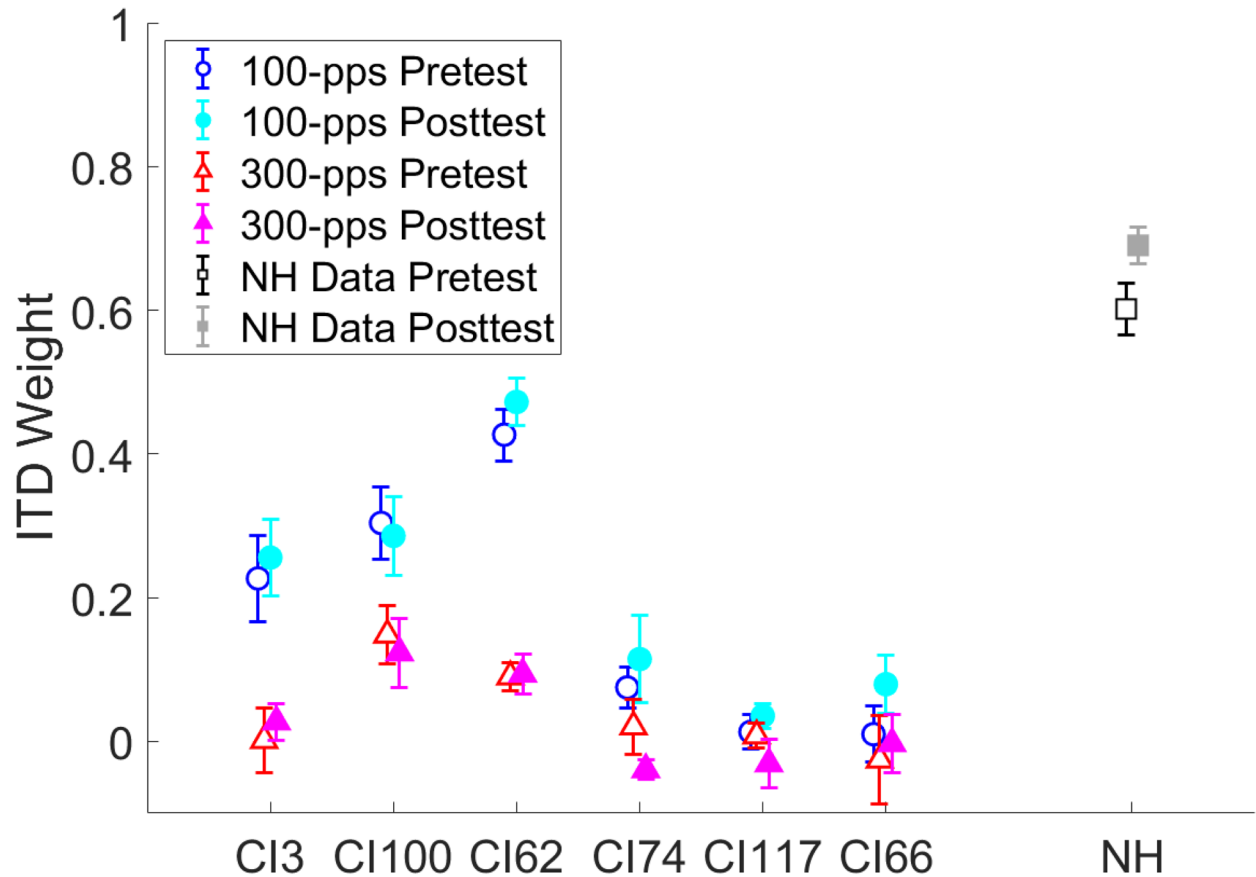


FIG. 7 ITD weights averaged across azimuths of each listener compared to the NH data at a group level of Klingel et al. (2021). Circles show 100-pps and triangles show 300-pps CI results. Squares show NH results. Pretest results are marked by open and posttest

results are marked by filled symbols. Error bars indicate the variation across azimuths (standard error of the mean), individually for CI listeners and pooled across listeners for the NH data

(bottom row) pulse trains. The results for different test phases are indicated with different colors.

100-pps ITD thresholds were determinable for all listeners. For 300 pps, four out of the six listeners did not reach the targeted 75% performance level even for the largest ITD tested. For the other two listeners, thresholds were determinable, but much higher than at 100 pps. These results are consistent with the typically observed rate limitation in ITD sensitivity. Because of the undeterminable thresholds for most listeners, the 300-pps data were excluded from the statistical analyses. For ILDs (100 pps), thresholds were determinable although one listener (CI13) was so sensitive that even for the smallest possible ILD of one current unit, the performance exceeded the threshold criterion. Table 2 summarizes the thresholds estimated from the psychometric functions for the different conditions and test phases. Overall, performance varied widely among listeners for both ITD and ILD thresholds.

The median estimated pre- and posttest ITD thresholds at 100 pps were 591 μ s (IQR = 1762) and 426 μ s

(IQR = 2804), respectively. The thresholds were subjected to a Wilcoxon signed-rank test, which did not yield a significant effect ($Z = -0.31$, $p = 0.753$, $r = -0.128$), suggesting that the lateralization training had no effect on 100-pps ITD thresholds. ILD thresholds were subjected to a RM ANOVA with the factor testing time (test 1 vs. test 2 vs. test 3), as they were measured during all three test phases. Median thresholds were 4.89 cu (IQR = 1.13) for test 1, 3.09 cu (IQR = 2.87) for test 2 and 3.53 cu (IQR = 2.06) for test 3. The ANOVA did not yield a significant effect of testing time ($F(2,10) = 0.42$, $p = 0.666$, $\eta_p^2 = 0.078$), suggesting that the lateralization training had no effect on ILD thresholds.

Relationship Between Cue Weights and Discrimination Thresholds

To determine if there is a relationship between the cue weights estimated from the lateralization task and the cue discrimination thresholds, we performed correlation analyses based on ITD weights and thresholds. Since ITD

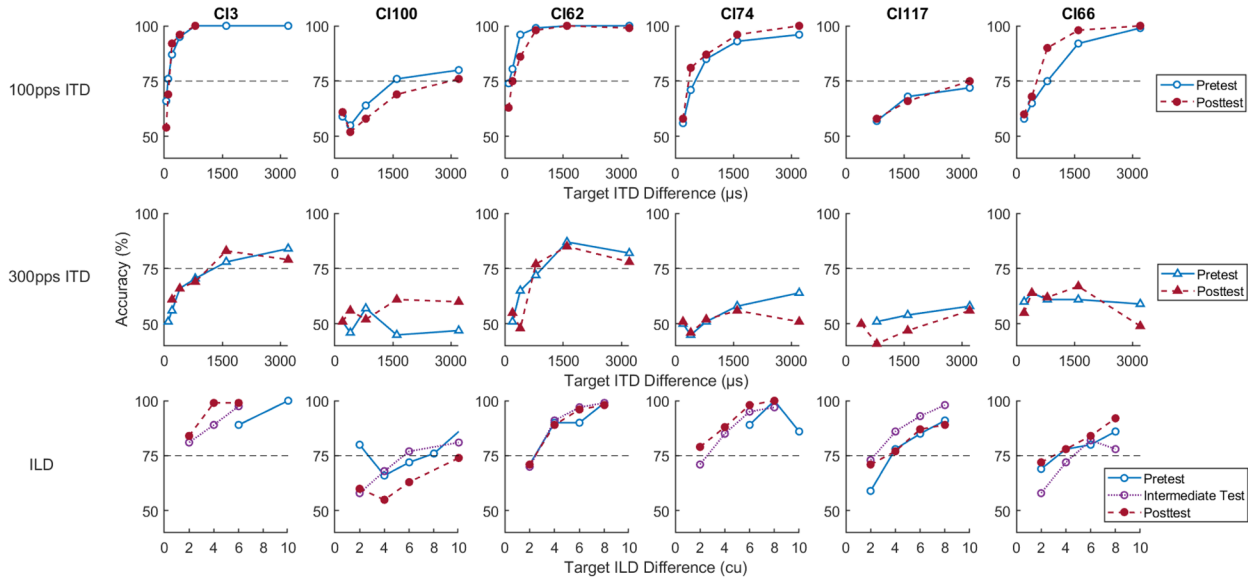


Fig. 8 Psychometric functions of each listener (columns) for 100-pps ITDs (top row), 300-pps ITDs (middle row), and ILDs (bottom row). Since ILD psychometric functions were measured during all three test phases, “pretest” refers to test phase 1, “intermediate test” refers to test phase 2, and “posttest” refers to test phase 3. The x-axis shows the target ITD or ILD difference, i.e., two times the presented binaural cue

thresholds were unmeasurable for 300-pps pulse trains, we restricted these analyses to the 100-pps rate. For the ITD weights, the most central azimuths (at $\pm 3^\circ$) were selected because the ITD thresholds were also estimated at the perceived center (i.e., the reference stimulus had a zero ITD). Pretest ITD thresholds were not correlated with the pretest ITD weights ($r(4) = -0.354$, $p = 0.491$), suggesting that baseline ITD thresholds do not predict baseline ITD weighting.

Response Compression

In the previous NH study (Klingel et al. 2021), posttest responses were shifted towards the midline compared to pretest responses, which was attributed to the limited

azimuth range of the reinforced cue compared to the perceived azimuth in the lateralization training. To evaluate this effect in the present study, Fig. 9 shows, separately for the three test phases, the response azimuth as a function of cue azimuth. The response azimuth was estimated by the parameter Q of the regression analysis, which considers all lateralization responses and is, therefore, a more reliable measure than only analyzing responses in consistent-cue conditions. For 100 pps, the slope of lateralization responses falls on the diagonal in test phase 1 and is shallower for test phases 2 and 3, which is consistent with Klingel et al. (2021). At 300 pps, the lateralization slope is already shallower in test phase 1 and differs only marginally thereafter. The shallower slope in test phase 1 for 300 compared to 100 pps is likely due to the

TABLE 2

ITD and ILD thresholds of the individual listeners. Denoted values correspond to two times the estimated thresholds. Since ILD thresholds were measured during all three test phases, “pretest” refers to test phase 1, “intermediate test” refers to test phase 2, and “posttest” refers to test phase 3

Listener	Pretest 100-pps target ITD difference (μ s)	Posttest 100-pps target ITD difference (μ s)	Pretest 300-pps target ITD difference (μ s)	Posttest 300-pps target ITD difference (μ s)	Pretest target ILD difference (cu)	Intermediate test target ILD difference (cu)	Posttest target ILD difference (cu)
CI3	96	118	1246	1260	5.08	2.32	1.72
CI62	134	202	782	784	2.96	2.78	2.86
CI66	682	460	N/A	N/A	4.70	5.64	4.52
CI74	500	390	N/A	N/A	5.76	3.12	2.44
CI100	1896	3006	N/A	N/A	5.98	7.40	10.42
CI117	3696	3174	N/A	N/A	4.62	3.06	4.18

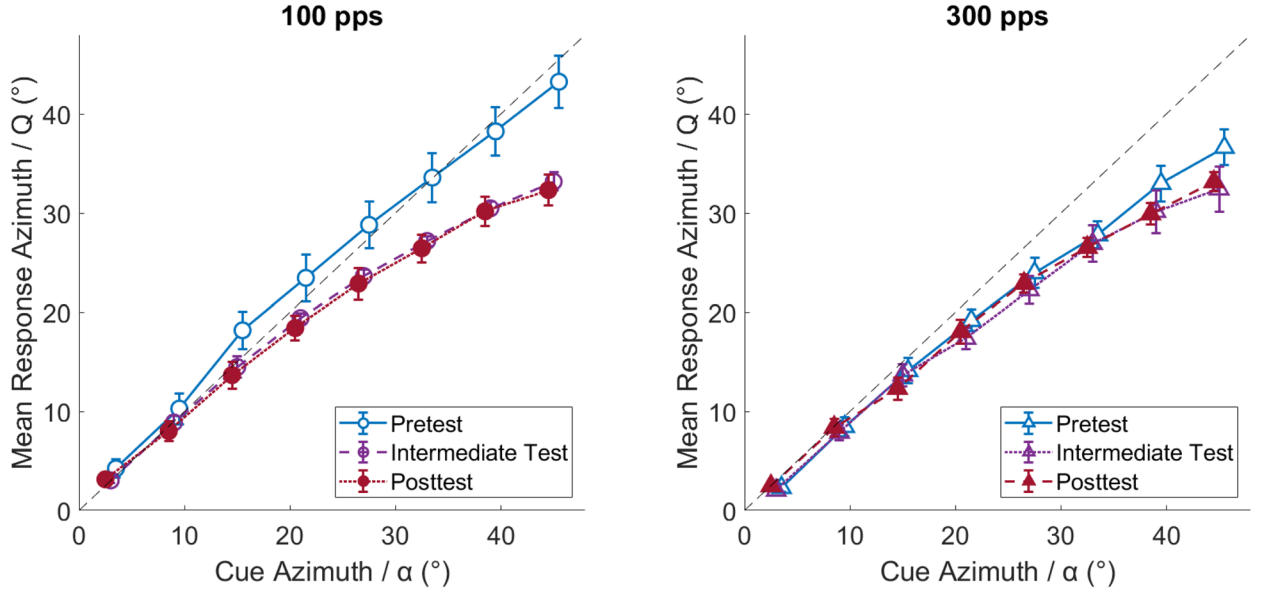


Fig. 9 Mean response azimuths estimated by the factor Q of the regression analysis at each azimuth α . The left panel shows results for the 100-pps stimuli and the right panel shows the results for the 300-pps stimuli. “Pretest” refers to test phase 1, “intermediate test” refers to test phase 2, and “posttest” refers to test phase 3. Error bars show standard errors of the mean

unbalanced test order of the two rates: Since two listeners, who started with 100-pps training, were excluded from the study, most included listeners did the 300-pps test 1 after the 100-pps test 1; thus, after responses were already compressed. This conclusion is further supported by the observation that test phases 2 and 3 differed neither from each other nor across pulse rates (i.e., it cannot be explained by an effect of rate). Importantly, different lateralization slopes do not affect the binaural-cue weight estimates, because the overall lateralization slope affects parameters k_{ITD} and k_{ILD} equally and therefore cancels out in the final weight estimation (see Klingel et al. 2021).

Response Variability

The final examination of the impact of training concerned the lateralization precision, which refers to the consistency or variability in lateralization responses (see Heffner and Heffner 2005). To obtain a variability measure that is independent of binaural-cue weighting, the standard deviation of the residuals of the regression analysis (Eq. 2) was computed. The residual for a response is defined as the deviation of the actual response azimuth from the response azimuth predicted by the regression analysis. Figure 10 shows the response variability as a function of binaural cue disparity for the three testing phases (with the two pulse rates shown in separate panels). Averaged across pulse rates and cue disparities, lateralization precision improved from the first testing phase

(12.20°) to the last testing phase (8.64°). For comparison, the NH study by Klingel et al. (2021) reported a similar relative improvement from their pretest (10.62°) to posttest (6.54°). The slightly higher absolute values are not surprising given that sound localization of CI listeners is overall worse than for NH listeners. This improvement in lateralization precision can be interpreted in terms of procedural training (i.e., by focusing attention or more precisely using the equipment) or overall perceptual training (Hawkey et al. 2004). Variability appears to be independent of cue disparity (i.e., the difference between the ITD and ILD azimuth of a stimulus), suggesting that listeners perceived a single, compact image for all cue disparities used. Finally, there is an apparent effect of pulse rate in test phase 1, showing higher variability for 100 pps than 300 pps, which can likely be attributed to the unbalanced test order, as already observed in the analysis of response compression: It is not surprising that response variability is higher in the very first lateralization test performed, which was the 100-pps condition in testing phase 1 for most listeners. This interpretation is consistent with the finding that such order effects did not influence testing phases 2 and 3. The above findings were supported by a 2 (100 vs. 300 pps) $\times$ 3 (test 1 vs. test 2 vs. test 3) $\times$ 5 (cue disparity) RM ANOVA, yielding a significant main effect of testing time ($F(2,10) = 4.65$, $p = 0.037$, $\eta_p^2 = 0.482$), no significant effect of cue disparity ($F(4,20) = 0.14$, $p = 0.964$, $\eta_p^2 = 0.028$), and a significant rate $\times$ testing time interaction ($F(2,10) = 10.29$, $p = 0.004$, $\eta_p^2 = 0.673$).

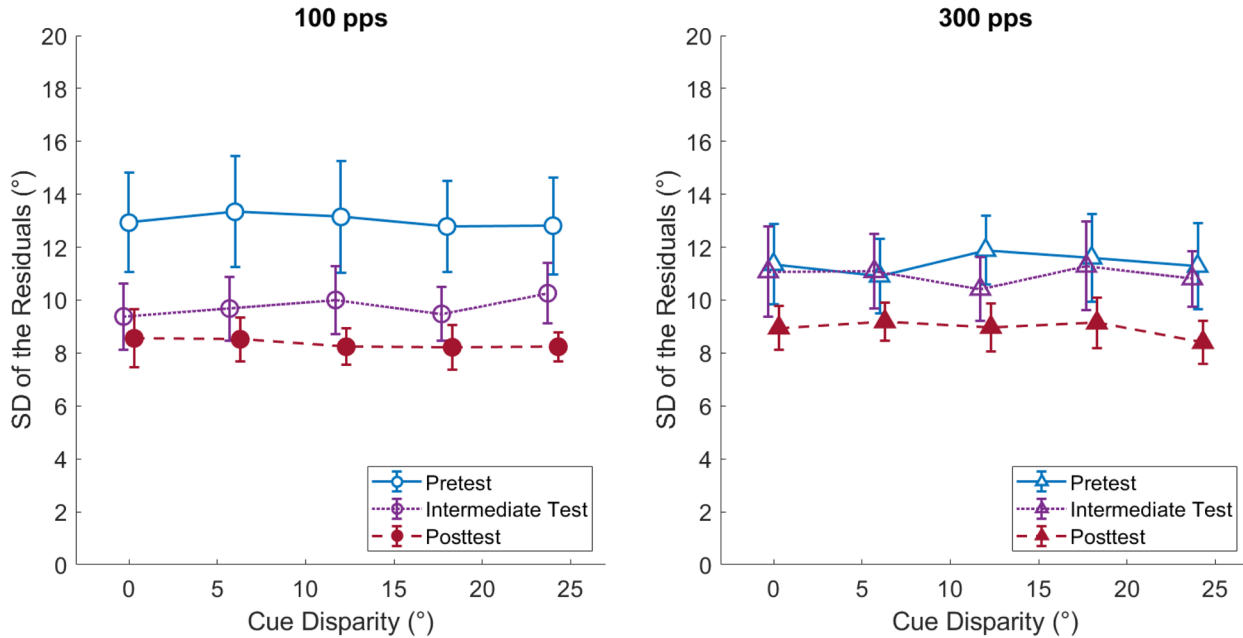


FIG. 10 Mean response variability (defined here as the standard deviation of the residuals of the regression analysis) as a function of cue disparity in the three testing phases. The left panel shows results for the 100-pps stimuli, and the right panel shows the results

for the 300-pps stimuli. “Pretest” refers to test phase 1, “intermediate test” refers to test phase 2, and “posttest” refers to test phase 3. Error bars show standard errors of the mean

Complementary Effects of the Two Binaural Cues

Apart from the effect of lateralization training, we were also interested in the practically relevant question if the addition of nonzero ITDs to nonzero ILDs significantly contributes to the extent of lateralization. For this purpose, we compared lateralization responses across an azimuth range of $\pm 27^\circ$, varying either ITDs (fixing ILDs roughly at zero), ILDs (fixing ITDs roughly at zero), or both ITDs and ILDs (i.e., presenting consistent-cue combinations). Since we did not test items with one of the cues set exactly to zero during the lateralization task, we approximated the zero position by averaging response azimuths for cue azimuths of -3° and $+3^\circ$. Lateralization responses were averaged across all three test phases. Figure 5 shows the results for the pulse rates of 100 pps (left panel) and 300 pps (right panel). Linear-regression slopes fitted to the lateralization responses from Fig. 5 were significantly steeper for consistent cues than for fixed ITDs in both the 100-pps condition ($T(5)=2.24$, $p=0.038$, $d_z=0.92$) and the 300-pps condition ($T(5)=3.64$, $p=0.008$, $d_z=1.49$), suggesting that the addition of nonzero ITDs to nonzero ILDs significantly increases the extent of lateralization at both pulse rates. Finally, the slopes for fixed ILDs differed significantly from zero not only at 100 pps ($M=0.39$, $SD=0.17$, $T(5)=5.48$, $p=0.001$, $d_z=2.24$) but also at 300 pps, even though the latter slope was close to zero ($M=0.11$, $SD=0.12$, $T(5)=2.25$, $p=0.037$, $d_z=0.92$).

This suggests that in conditions with fixed ILDs, location judgments were influenced by varying ITDs, but only marginally at 300 pps.

DISCUSSION

We investigated a mechanism potentially contributing to the previous finding that sound localization with clinical CI systems is largely based on ILDs (Grantham et al. 2007; Seeber and Fastl 2008) and the extent of laterality evoked by ITDs is largely reduced in CI users compared to NH listeners, even when presented as well-controlled pulse-ITDs to the implanted electrodes via a research interface (e.g., Anderson et al. 2019; Laback et al. 2015). Specifically, we assumed that CI listeners reduce their ITD weighting based on their everyday experience with clinical CI systems, which lacks reliable and salient ITD cues while ILD cues are largely preserved. Therefore, we addressed the question if lateralization training can induce an increase in ITD weighting (i.e., reverse the maladaptive weighting) in CI listeners when pulse-ITDs are presented reliably and saliently via a research interface and are visually reinforced while ILDs are varied to render them unreliable.

A small but significant effect on a group level at 100 pps showed that the ITD weight can indeed be increased in CI listeners. On an individual level, one of the six tested listeners showed significantly increased ITD

weights and two further listeners showed a strong trend for increased ITD weights. This suggests that, at least for some listeners, the low contribution of ITDs to lateralization in electric hearing is partially reversible with training once ITDs are presented saliently. Compared to NH data from Klingel et al. (2021), CI listeners' ITD weighting was lower, consistent with the reduced ITD sensitivity in CI listeners and the assumption that CI listeners increase their ILD weighting based on the experience with their clinical devices. However, there was no evidence for different amounts of reweighting in the two listener groups.

In contrast, the 300-pps results showed no reweighting and ITD weights were consistently lower compared to 100 pps. Together with the observation that ITD thresholds for 300-pps stimuli exceeded the range of tested ITDs (100–1600 μ s) for four of our six listeners, this suggests that the mechanism causing the rate limitation for ITDs is independent of the mechanism responsible for binaural-cue reweighting. Rather, this pattern is consistent with data from NH listeners presented with envelope-ITD cues: Stecker (2010) observed that ITD/ILD trading ratios increasingly favored ILDs over ITDs as the envelope rate of Gabor click trains (centered at 4 kHz) increased, as predicted based on the established rate limitation for envelope-ITDs. Thus, the results support the interpretation that (a) pulse-ITDs in electric pulse trains and envelope-ITDs in acoustic hearing provide comparable information to the binaural processing stages, and (b) the upper rate limit of that binaural pathway prevents reweighting for 300-pps electric pulse trains.

As binaural-cue weights do not change without intervention in NH listeners (Klingel et al. 2020), it was considered unlikely that simple re-testing would lead to reweighting in CI listeners. Such an explanation for the 100-pps results is also ruled out by the null effect at 300 pps, which thus serves as a control condition. The null effect at 300 pps further suggests that onset ITD cues did not play a major role in the present results, as they were equally present in the 100- and the 300-pps conditions.

In addition to binaural-cue weights, binaural-cue thresholds were measured to test whether the lateralization training influences cue sensitivity. Neither ITD nor ILD thresholds systematically differed between the test phases, suggesting that the training had no influence on binaural-cue sensitivity. The range of ITD thresholds we measured is consistent with previous studies (see Laback et al. 2015). ILD sensitivity was very good overall, consistent with previous studies using either direct stimulation (e.g., Lawson et al. 1998) or clinical processors (e.g., Laback et al. 2004). For four out of six listeners, the estimated ILD thresholds approached or even fell below the smallest current level difference realizable with the implants.

We were further interested in whether binaural-cue weights and binaural-cue thresholds are related. Interestingly, ITD weights did not correlate significantly with

ITD thresholds. This suggests that the weight and threshold estimates are independent from each other. The lack of a significant correlation between these measures could be due to the small number of listeners and, thus, insufficient statistical power. However, it might also be due to differences between the two tasks: While binaural-cue thresholds were measured with a relative task as listeners had to detect shifts relative to a reference stimulus, binaural-cue weights were measured with an absolute task as listeners had to indicate the perceived azimuth of the stimulus. Furthermore, thresholds were estimated at the center, while weights were estimated at different azimuths between $\pm 45^\circ$. We tried to address this by only considering the estimated weight at $\pm 3^\circ$ azimuth (i.e., the most central azimuth tested during the lateralization task) for the correlation analysis, but since reweighting appears to be stronger at lateral azimuths, measuring thresholds at lateral azimuths might have been more informative. Finally, either ITDs or ILDs were set to zero during threshold estimation, while both ITDs and ILDs varied during the binaural-cue weight estimation, which thus may involve interactions between ITD and ILD cues. Therefore, it might be interesting for future studies to use not only threshold measurements but also tasks involving supra-threshold cue combinations (as in the present binaural-cue weight measurement) to predict performance in real-life situations where the two binaural cues interact.

In the present study, the estimated ITD weights were overall smaller at more lateral azimuths compared to central azimuths. A similar pattern was observed in NH listeners (Klingel et al. 2020, but also see Klingel et al. 2021). The current results might, however, also be attributable to an insufficient perceptual match in linking ITDs and ILDs to azimuths. While we selected the ILD values on an individual basis during the parameter determination to encompass the targeted azimuthal range, we used a fixed range of ITD cues, which was only crudely adapted to the individual listener's sensitivity. While this limits the interpretability of the effect of azimuth, it should be noted that our primary interest was the overall effect of lateralization training on cue weighting and different azimuths were tested primarily for explorative purposes and to avoid that listeners respond strategically (i.e., memorizing specific cue-combinations and locations).

The neural mechanisms underlying binaural-cue reweighting are still unknown. A recent study demonstrated improved neural ITD sensitivity in the inferior colliculus of early-deafened rabbits that were chronically exposed to ITD cues consistent with the visual environment during their developmental period as compared to early-deafened rabbits that were not exposed to ITD cues (Sunwoo et al. 2021). This effect was found even at high rates (around 300 pps) for which we did not observe reweighting. However, besides the difference in species, a potentially important difference between their and our study is that our human listeners experienced deprivation

from binaural cues and completed our lateralization training during adulthood, where plastic changes may occur at different neural sites (but see Tirko and Ryugo 2012). Future physiological studies may address the reweighting mechanism in adulthood.

Finally, unrelated to binaural-cue reweighting, we took the opportunity to address the practically relevant question if the addition of nonzero ITDs to nonzero ILDs significantly contributes to the extent of lateralization. Presenting spatially consistent ILD and ITD cues indeed produced steeper functions of lateralization responses than presenting stimuli with ITDs fixed at roughly zero not only for 100-pps but also for 300-pps stimuli. This complementary effect of providing spatially consistent ILD and ITD cues is remarkable particularly for the 300-pps rate, for which presenting ITDs alone (i.e., fixing ILDs at roughly zero) caused rather shallow functions (though differing significantly from zero) and ITD thresholds were extremely high or undeterminable. This suggests that providing reliable pulse-ITD cues with future stimulation strategies might aid lateralization even for stimulation rates for which ITD-based measures reveal little to no evidence for sensitivity.

A general limitation of the present study is the small number of six bilateral implantees that could be recruited to complete this time-consuming study. Also, because only one of the six listeners showed significant reweighting at 100 pps based on conservative within-participant analyses, the current results do not allow generalization to the population of bilateral implantees, which is known to be heterogeneous. Future studies should, thus, extend the pool of participants and identify factors responsible for the variability in outcomes.

Another potential limitation is the unbalanced number of listeners who started training with either pulse rate in our experiment, which resulted from the need to exclude two listeners included in the original design. If reweighting would generalize across pulse rates, this might have favored reweighting for 100-pps stimuli as the total training time was longer after completing both lateralization training phases. However, we believe that this would be accounted for by averaging across test phases: Since testing phases 1 and 2 were averaged to constitute the 100-pps pretest for these listeners, a potential reweighting effect induced by the 300-pps training already influences the 100-pps pretest, thus reducing the pre vs. post difference. Another potential source of asymmetry is that the averaging of test phases leads to more accurate estimates for 100-pps pretests and 300-pps posttests than for 100-pps posttests and 300-pps pretests for most of the listeners. However, there is no reason to assume that this would systematically affect the pre vs. post difference. In summary, we believe that the unbalanced test order did not systematically affect the reweighting results reported here.

The present results are directly applicable for stimulation strategies that aim to encode ITD cues via the pulse timing using low stimulation rates. To extend the findings towards envelope-coding strategies, future studies may investigate, whether ITD weighting can also be increased for high-rate pulse trains conveying enhanced envelope-ITD cues either via envelope-shape modification (Monaghan and Seeber 2016; Francart et al. 2014) or via short interpulse-interval pulses inserted at a low rate (Srinivasan et al. 2018). Because both low-rate pulse trains and high-rate pulse trains with low-rate modulation likely activate the same binaural pathway (Srinivasan et al. 2020; van Hoesel et al. 2009), the current findings will likely extrapolate to the latter stimulus types. Since ITDs may be particularly important for azimuth ranges where ILDs change non-monotonically with azimuth, in acoustic situations where ILDs are not robust (Macauley et al. 2010), and for understanding speech in multi-talker environments (e.g., Kidd et al. 2010), increased ITD weighting could be particularly helpful in these situations.

In conclusion, by reinforcing ITD cues during a lateralization training, listeners significantly increased the perceptual weight given to pulse-ITDs conveyed by low-rate pulse trains (100 pps). For higher-rate pulse trains (300 pps), however, no reweighting was found, suggesting that separate mechanisms underlie the well-known increase of ITD thresholds with increasing pulse rate and binaural-cue reweighting. Apart from this rate dependency, binaural-cue weights and binaural-cue thresholds were not significantly correlated. The present results are promising in terms of making low-rate ITD cues better usable for sound localization with future CI systems that convey reliable and salient ITD information.

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3. General Discussion

This thesis investigated the flexibility with which ITDs and ILDs are combined to form a spatial percept in normal-hearing and in CI listeners. In normal-hearing listeners, we measured binaural-cue weights for various noise bands and employed two different training paradigms (a lateralization and a discrimination task) to induce a change in these binaural-cue weights. In CI listeners, we measured binaural-cue thresholds as well as binaural-cue weights for 100-pps and 300-pps pulse trains and used a lateralization task to induce an increase in ITD weights.

3.1 Baseline binaural-cue weighting

Previous literature has shown that the binaural-cue weighting mainly depends on the sound's frequency content with ITDs dominating for low- or wideband and ILDs dominating for high-frequency stimuli (Macpherson & Middlebrooks, 2002; Wightman & Kistler, 1992). It remained unclear, however, whether the weighting gradually changes as the sound's frequency is increased or whether it abruptly switches from being ITD to being ILD dominant.

To compare the present results with the previous literature, we calculated pretest binaural-cue weights. They are a good estimate of the baseline weight of the respective stimulus since they were measured before training. For mid-frequency noise (2-4 kHz), the binaural-cue weights measured with the lateralization task were dominated by ITDs (i.e., ILD weights were significantly lower than 0.5) (Klingel et al., 2021). The same pattern was observed for the multiband stimulus (encompassing frequencies from approximately 0.8-4.5 kHz) (Klingel & Laback, 2022) and these two stimuli did not differ significantly in their ILD weights ($t(37) = 0.47$, $p = .641$, two-tailed, $d = 0.15$), even though the two stimuli were tested in different listener groups. This is consistent with Macpherson and Middlebrooks' (2002) wideband (0.5-16 kHz) results and suggests that if a stimulus includes the ITD-dominant frequency region, ITDs dominate the percept even if the center frequency of the stimulus lies in an ILD-dominant frequency region. ILD weights for the 2-4 kHz stimulus measured with the discrimination task, on the other hand, were closer to 0.5 (Klingel et al., 2020) and significantly higher than the ILD

weights measured with the lateralization task for the same stimulus ($t(39) = -2.67, p = .011$, two-tailed, $d = -0.84$). It should be noted, however, that the range of measured ILD weights was comparable between the two tasks (0.159-0.674 for the lateralization task and 0.186-0.686 for the discrimination task). The difference in mean weights rather resulted from differences in the distribution: More participants that completed the discrimination task had an ILD weight close to 0.5. Since chance performance with such a two-alternative-forced-choice discrimination task would also result in an ILD weight of 0.5, it cannot be ruled out that random responses influenced the weights measured with the discrimination task. This may be responsible for the differences in ILD weights between the two different tasks. Additionally, weights measured with the discrimination task were not estimated using the regression analysis but represented the ratio of ILD favored trials. This may further contribute to the observed differences.

For 1/3-octave-wide bands measured with the lateralization task, we observed gradually increasing baseline ILD weights with increasing spectral region (Klingel & Laback, 2022). This finding extends Macpherson and Middlebrooks' (2002) results involving a low- (0.5-2 kHz) and a high-pass stimulus (4-16 kHz) but differs from Ahrens et al.'s (2020) observation, who measured the binaural-cue contributions of different frequency bands in a multiband stimulus. They found significant differences for the lowest and the highest frequency band, but constant weights for in-between frequency bands, irrespective of the absolute frequency range of presented bands. This suggests that the simultaneous presentation of frequency bands led to an "edge effect" (i.e., stronger weighting of information at the edges). Therefore, the present results show a clearer picture of the binaural-cue weighting of each frequency band individually. Furthermore, the measured baseline weights for 1/3-octave-wide bands appear to be robust, since two experiments involving different participants and presentation modes (randomized vs. blocked) resulted in comparable estimates. Finally, the observed gradual increase in ILD weights with increasing frequency is in line with the sensitivity pattern to ITD and ILD as a function of center frequency for narrow-band noise stimuli. Between center frequencies of 1 and 4 kHz (i.e., the center frequency range of stimuli included in this thesis), ILD thresholds tend to decrease with

increasing frequency (Gabriel et al., 1992; Goupell & Stakhovskaya, 2018), while ITD thresholds gradually increase with increasing frequency (Buchholz et al., 2018; Gabriel et al., 1992; Klumpp & Eady, 1956; Smoski & Trahiotis, 1986; Trahiotis & Bernstein, 1990). Additionally, while ITDs are physically almost frequency-independent, ILDs are physically smaller for low- compared to high-frequency stimuli and therefore more informative at high frequencies, which may also contribute to the binaural-cue weighting.

3.2 Binaural-cue weighting across azimuths

When comparing binaural-cue weights between different azimuths, the observed pattern varies across experiments. Using 2-4 kHz noise, weights obtained with the lateralization task did not differ significantly between azimuths (Klingel et al., 2021), but weights obtained with the discrimination task showed stronger ILD weighting for lateral compared to central azimuths (Klingel et al., 2020). Stronger ILD weights at lateral azimuths (using the lateralization task) were also observed for the CI data (Klingel & Laback, 2021), but the opposite pattern (i.e., stronger ITD weighting at lateral azimuths) was observed for 1/3-octave noise bands in acoustic hearing (Klingel & Laback, 2022). This suggests that the pattern of binaural-cue weights across azimuths depends on the specific stimuli and tasks used.

The dependence of binaural-cue weights on azimuth may result from different sensitivity patterns for ITDs and ILDs across azimuths as well as the amount of physical change in the underlying cue. ILD sensitivity decreases with increasing reference ILD in addition to the physical dependence of ILD magnitude on azimuth (Brown et al., 2018), while variations of ITD sensitivity with increasing reference ITD appear to be fully accounted for by the physical azimuth dependence of the ITD cue rather than by decreasing ITD sensitivity (Smith & Price, 2014). Since ITDs increased relatively linearly with increasing azimuth for the azimuth range included here, ITD sensitivity was likely constant across azimuths and the observed changes likely resulted from differences in the ILD.

Regarding the 1/3-octave noise stimulus, the ILD magnitude increases less strongly for azimuths between approximately 21°-39° compared to azimuths between 3°-15° for the mid-low, mid-

high, and high bands (Klingel & Laback, 2022). Therefore, the combined effect of decreasing ILD sensitivity with increasing reference ILD as well as the reduced increase in ILD magnitude for more lateral azimuths may have contributed to the stronger ILD weighting at central compared to lateral azimuths for these stimuli. For the 2-4 kHz noise, however, the employed ILD magnitude increases less strongly for azimuths between approximately, 1.8° - 16.2° compared to azimuths between 19.8° - 37.8° (Klingel et al, 2021). Therefore, the effect of decreasing ILD sensitivity with increasing reference ILD and the stronger increase in ILD magnitude for more lateral azimuths may have counteracted each other for this stimulus, resulting in no significant differences between azimuths in the experiment using the lateralization task.

The discrimination task using the same stimulus, however, showed stronger ILD weights at lateral azimuths (Klingel et al., 2020). This might be explained by differences in the perceived distance of the stimuli. For lateral sound sources near the head, the ILD is a cue indicating the distance of a sound source with larger ILDs indicating sound sources closer to the head (Shinn-Cunningham, Santarelli, & Kopčo, 2000). While the lateralization task involved a visual environment suggesting equal distance of all stimuli, the discrimination task did not and simply asked participants to judge whether the second sound was perceived left or right from the first. For lateral azimuths, listening to the ILD during the discrimination task may, therefore, have been confounded by distance cues: Increasing the ILD for a stimulus on the right may either be perceived as movement to the right (assuming equal distance of the two stimuli) or movement towards the ear, which would be to the left along the interaural axis. It is, however, unclear how such a potential ambiguity might have resulted in stronger ILD weights at lateral azimuths.

Finally, the stronger ILD weighting at lateral compared to central azimuths observed in CI listeners (Klingel & Laback, 2021) might be due to an insufficient perceptual match in linking ITDs and ILDs to azimuths. While ILD values were perceptually selected on an individual basis in a pretest, a fixed range of ITD cues based on acoustical measurements with a dummy head was used, which was only crudely adapted to the individual listener's sensitivity. This may have made the ITDs less salient at lateral azimuths.

It should be noted, however, that different azimuths were primarily tested for explorative purposes and to avoid strategic responses (i.e., memorizing specific cue-combinations and locations). Our primary interest was the overall effect of reinforcing one cue during training on the cue weighting, which will be discussed in the following.

3.3 Reweighting with 2-4 kHz noise

We induced a change in binaural-cue weights for 2-4 kHz noise with two different training methods, a lateralization task in a virtual environment (Klingel et al., 2021) and a desktop-based left/right discrimination task (Klingel et al., 2020). Using the lateralization task, we trained two experimental groups by visually reinforcing either ITD or ILD information. Depending on the group, participants significantly increased either their ITD or their ILD weighting from pre- to posttest, suggesting that binaural-cue reweighting can be induced for both cues. This extends Kumpik et al.'s (2019) findings, who observed an increase in ILD weighting in conditions where either ITDs were randomized or consistent binaural cues were presented, but no increase in ITD weighting when ILDs were randomized. Considering the present results with 2-4 kHz noise using the lateralization task, the lack of an increase in ITD weighting in Kumpik et al. (2019) may have resulted from applying reverberation (presumably making the ITDs less reliable) or the task used (i.e., a visual oddball task for which the auditory stimuli were irrelevant and therefore may not have received enough attention).

Using the discrimination task (Klingel et al., 2020), we tested an experimental group receiving feedback (correct/incorrect) consistent with the ILDs and a no-training control group. While the experimental group showed significantly increased ILD weights in the posttest, the no-training control group showed no difference in binaural-cue weights between the pre- and posttest. This suggests that binaural-cue reweighting can be induced with different methods (i.e., via a discrimination as well as a lateralization task) and that the change in binaural-cue weights is indeed induced by the training (i.e., there was no effect for the no-training control group). The null result of Jeffress and McFadden (1971), who also attempted to induce a change in the binaural-cue weighting using a left/right discrimination

task, can therefore not be attributed to the training task. It may instead have resulted from the stimuli used (noise centered at 500 Hz), the binaural cues which were close to the binaural-cue threshold and may therefore not have been salient enough, or the lack of simultaneous presentation of auditory and visual stimuli if bottom-up multisensory integration were important for binaural-cue reweighting. Considering our results with 1/3-octave-wide noise (Klingel & Laback, 2022; see below), the most likely reason for the lack of reweighting in Jeffress and McFadden (1971) is the stimulus' center frequency of 500 Hz: We did not observe reweighting for stimuli providing access to fine-structure ITD cues and their 500-Hz stimulus provided such fine-structure ITDs.

3.4 Reweighting in different frequency regions and its generalization

Using the lateralization task, we attempted to induce binaural-cue reweighting for four 1/3-octave-wide noise bands centered at 1000, 1587, 2520, and 4000 Hz as well as a multiband stimulus comprising all four bands and assessed generalization of binaural-cue reweighting to untrained frequency bands (Klingel & Laback, 2022). We conducted two experiments involving different participants, azimuth ranges, presentation modes (randomized vs. blocked), and trained/tested frequency bands (in experiment 1, all bands were tested and the bands centered at 1000, 2520, and 4000 Hz were trained; in experiment 2, bands centered at 1587 and 2520 Hz were tested and the 1587-Hz-band was trained). In both experiments, we tested two experimental groups, visually reinforcing ITDs or ILDs, respectively.

We observed a robust increase in ILD weights for the trained 4000-Hz-band after ILDs were visually reinforced. Additionally, a less robust increase in ILD weights was observed for the 2520-Hz-band, which was present in experiment 2 (untrained) but not in experiment 1 (trained). No effects occurred for the other stimuli. When ITDs were visually reinforced, binaural-cue reweighting was observed for the 1587-Hz-band, but only at specific azimuths independent of whether the 1587-Hz-band was presented during training (experiment 2, reweighting observed at 39° azimuth) or not (experiment 1, reweighting observed at 9° azimuth). No effects occurred for the other frequency bands. Given that

both trained and untrained stimuli showed some effects, band-specific training does not seem to be crucial, possibly indicating across-frequency generalization of binaural-cue reweighting. Instead, the occurrence of reweighting seems to depend on an appropriate match between the stimulus' spectral region and the binaural cue that is reinforced: When ILDs were reinforced, effects were only observed at 2520 and 4000 Hz, while in the ITD groups, effects were only observed at 1587 Hz (but only at specific azimuths). This suggests that inducing an increase in ILD weighting requires sufficiently high frequencies, while sufficiently low frequencies seem to be needed to induce an increase in ITD weighting. However, no reweighting occurred for stimuli including the low-frequency temporal fine structure region (i.e., for the 1000-Hz-band and the multiband). This suggests that ITD reweighting was based on envelope-ITD information. These results are consistent with the robust reweighting effect in both the ITD and ILD direction for the 2-4 kHz stimulus discussed above (Klingel et al., 2021), which included both “sufficiently high” and “sufficiently low” frequencies without touching the frequency region providing highest ITD sensitivity (i.e., the fine-structure region).

3.5 Reweighting in electric hearing

Since CI listeners do not experience reliable and salient ITD cues with their clinical devices while ILDs consistently indicate the sound source location, we hypothesized that they increase their ILD weighting similar to the NH listeners in the experiments discussed above. We were therefore interested in whether the weighting for ITDs can be increased in CI listeners (i.e., whether this maladaptive weighting can be reversed) when ITDs are reliably presented via a research system to a single place-matched electrode pair and visually reinforced using the lateralization task. We studied two pulse rates, namely a rate providing best ITD sensitivity (100 pps) and a rate representing carrier rates too high to permit pulse-ITD sensitivity (300 pps), and additionally measured binaural-cue thresholds before and after the training to disentangle the roles of binaural-cue weighting and binaural-cue sensitivity to the low contribution of ITDs to sound lateralization of CI listeners (Klingel & Laback, 2021).

On a group level, CI listeners increased their ITD weighting at 100 pps slightly but significantly. On an individual level, three of the six tested listeners showed a strong trend or significantly increased ITD weights in the posttest. This suggests that, at least for some listeners, the low contribution of ITDs to lateralization in electric hearing is partially reversible with training. CI listeners' ITD weighting was lower compared to the NH data with 2-4 kHz noise (Klingel et al., 2021), consistent with the reduced ITD sensitivity in CI listeners and the assumption that CI listeners increase their ILD weighting based on the experience with their clinical devices.

In contrast, no reweighting was observed at 300-pps and ITD weights were consistently lower than at 100 pps. The lower ITD weight at 300 compared to 100 pps is in line with data from NH listeners showing decreasing ITD weighting with increasing envelope rate of click trains (Stecker, 2010), which is consistent with the established rate limitation for envelope-ITDs in NH listeners (i.e., lower ITD sensitivity for higher envelope rates). Thus, the present results are consistent with the interpretation that pulse-ITDs in electric pulse trains and envelope-ITDs in acoustic hearing provide comparable information to the binaural system. Given that we did observe a reweighting effect in the 100-pps CI data, this interpretation is also supported by the observation discussed above that binaural-cue reweighting in acoustic hearing is based on envelope cues (and does not occur when fine-structure ITD cues are available). Additionally, the present results suggest that the upper rate limit of the binaural envelope pathway prevents reweighting for 300-pps electric pulse trains and, therefore, lower pulse or envelope rates are needed.

Neither ITD nor ILD thresholds differed significantly between test phases, suggesting that the lateralization training had no influence on binaural-cue sensitivity. Furthermore, ITD weights did not correlate significantly with ITD thresholds. Together with the observed reweighting effect at 100-pps (i.e., there was a change in weights but not in thresholds between test phases), this suggests that, in electric hearing, binaural-cue weighting does not simply reflect binaural-cue sensitivity and that reweighting occurred on a supra-threshold level.

3.6 Additional effects independent of binaural-cue (re-)weighting

In most experiments using the lateralization task, we observed response compression from pre- to posttest (i.e., shallower lateralization slopes in the posttest). This was attributed to the visual reinforcement being presented in a restricted range during training, which likely triggered a mapping to this restricted range, and to fatigue or decreased willingness to exploit the whole azimuthal response range in the posttest. This response compression occurred similarly for all stimuli used and in both NH and CI listeners. Interestingly, there seems to be a limit to how much responses will be compressed: In the CI study, responses did not compress further from testing phase 2 to 3 (Klingel & Laback, 2021) and in experiment 2 of the study involving 1/3-octave noise (Klingel & Laback, 2022), in which responses were already compressed in the pretest, no response compression was observed. An advantage of the discrimination task is that such response compression cannot occur since no lateralization responses are given. For the discrimination task, the pre- and posttest are, therefore, directly comparable. However, it should be noted that response compression affects both cues equally, so its effect on the slopes k_{ITD} and k_{ILD} cancels out in the final weight estimation reported here (i.e., binaural-cue weights measured with the lateralization task can also be compared across tests).

Additionally, as a measure of lateralization precision independent of the binaural-cue weighting, we examined the response variability in NH listeners for 2-4 kHz noise (Klingel et al., 2021) and for the CI data (Klingel & Laback, 2021). In both listener groups, response variability decreased (i.e., lateralization precision increased) from pre- to posttest by a comparable amount. The absolute values of response variability were slightly higher for CI compared to NH listeners, consistent with the overall worse sound localization ability of CI listeners. For both listener groups, response variability was independent of cue disparity (i.e., the difference between the ITD and ILD azimuth of a stimulus), suggesting that listeners perceived a single image for all cue disparities used.

Finally, the CI data showed that adding nonzero ITDs to nonzero ILDs significantly contributes to the extent of lateralization for both 100-pps and 300-pps stimuli (Klingel & Laback, 2021). This complementary effect of presenting spatially consistent ILDs and ITDs is remarkable particularly for 300-

pps stimuli, for which presenting ITDs alone (i.e., fixing ILDs at roughly zero) resulted in rather shallow lateralization functions and ITD thresholds were extremely high or undeterminable. This suggests that providing reliable pulse-ITD cues aids lateralization even for stimulation rates for which ITD-based measures reveal little to no evidence for sensitivity, which is promising for future clinical stimulation strategies.

3.7 Future directions

We presented auditory stimuli without HRTF filtering via headphones. This prevented access to monaural spectral localization cues, which might provide information about the stimulus azimuth. Such access might prevent purely binaural-cue reweighting as concluded by Kumpik et al. (2010), who found stronger weighting of unaltered monaural compared to binaural cues instead. However, as monaural and binaural localization cues interact in everyday life, the effect of binaural-cue reweighting on more realistic stimuli is an interesting topic for future studies. For example, it would be interesting to clarify under which conditions binaural-cue reweighting and binaural-to-monaural-cue reweighting occurs for azimuthal sound localization. Particularly interesting are situations in which listeners have access to monaural spectral localization cues but access to low-frequency fine-structure ITD cues is prevented, e.g., due to traffic noise. Additionally, it is unclear whether the lack of externalization resulting from the exclusion of spectral cues affected the binaural-cue weighting. Kumpik et al. (2019) used HRTFs as well as reverberation to promote externalization and found stronger ILD weighting for their broadband stimuli compared to our results. However, Macpherson and Middlebrooks (2002) also included HRTFs and obtained similar estimates for their wideband compared to our multiband stimuli. Therefore, the higher ILD weights in Kumpik et al. (2019) more likely resulted from the added reverberation, which makes ITDs less reliable (Rakerd & Hartmann, 2010), than from HRTFs or externalization. Nevertheless, it would be interesting to systematically disentangle the effects of these sound properties on binaural-cue weighting.

Binaural-cue reweighting might be useful for situations in which one of the cues is particularly informative while the other cue is less reliable or even misleading. For example, since listeners benefit from the presence of both ILD and ITD cues in spatial release from speech masking (e.g., Ellinger et al. 2017; Kidd et al. 2010), binaural-cue reweighting may be a means to cope with the changing reliability of binaural cues in speech in multi-talker or acoustically challenging environments. It would, therefore, be interesting to test whether binaural-cue reweighting improves speech understanding in environments for which the reinforced cue is more reliable.

The neural mechanisms of binaural-cue reweighting are still unknown. The binaural cues are processed in different parts of the superior olivary complex in the brainstem. While the lateral superior olive (LSO) selectively responds to ILDs as well as envelope ITDs, the medial superior olive (MSO) selectively responds to fine-structure ITDs (Joris, 1996). Therefore, a straightforward explanation would be an inhibition of either the MSO or the LSO pathway to decrease the weighting of ITDs or ILDs, respectively. However, the present results suggest that binaural-cue reweighting is based on envelope ITD cues, making this interpretation unlikely. Physiological studies are needed to clarify, at what point in the binaural pathway reweighting occurs.

The present results for CI listeners are directly applicable for stimulation strategies aiming to encode ITDs via the pulse timing using low stimulation rates. To extend the findings towards envelope-coding strategies, which are more prevalent clinically, future studies may investigate, whether ITD weighting can also be increased for high-rate pulse trains conveying enhanced envelope-ITD cues either via envelope-shape modification (Monaghan and Seeber 2016; Francart et al. 2014) or via short interpulse-interval pulses inserted at a low rate (Srinivasan et al. 2018). Because both low-rate pulse trains and high-rate pulse trains with low-rate modulation likely activate the same binaural pathway (Srinivasan et al. 2020; van Hoesel et al. 2009), the current findings will likely extrapolate to the latter stimulus types.

3.8 Summary and conclusions

We observed that binaural-cue weights gradually change from being ITD dominant to being ILD dominant as the stimulus frequency is increased. For broadband sounds or if the frequency band is wide enough to include ITD-dominant frequency regions, ITDs dominated the percept. This binaural-cue weighting could be changed in NH listeners via both lateralization and discrimination training under certain stimulus conditions. Namely, to induce an increase in ILD weighting, the stimulus frequency needed to be sufficiently high and to induce an increase in ITD weighting, the stimulus frequency needed to be sufficiently low without including frequency regions that reveal fine-structure ITD sensitivity. This suggests that ITD reweighting is likely based on envelope-ITD cues. Finally, ITD weights could also be increased in CI listeners for 100-pps but not for 300-pps electric pulse trains, suggesting that basic sensitivity is needed for binaural-cue reweighting. This change in binaural-cue weights was not associated with a corresponding change in binaural-cue sensitivity. Therefore, binaural-cue reweighting likely is a supra-threshold mechanism. These results are promising in terms of making ITD information better usable by users of future CI systems that reliably and saliently convey ITD cues.

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Zusammenfassung (German Abstract)

Normalhörende verwenden sowohl die interaurale Laufzeit- (ITD) als auch Pegeldifferenz (ILD) zur Schalllokalisation in der Horizontalebene. Diese beiden binauralen Merkmale werden, hauptsächlich auf Basis der Frequenz des Schallsignals, unterschiedlich stark gewichtet, wobei ITDs für tief- und ILDs für hochfrequente Signale dominieren. Die Schalllokalisation mit Cochleaimplantaten (CIs) basiert jedoch hauptsächlich auf ILDs. Da aktuelle Hüllkurven-basierte Stimulierungsstrategien keine salienten ITDs übertragen, ist es denkbar, dass CI-Träger:innen aufgrund ihrer Hörerfahrung im Alltag lernen, sich nur auf ILDs zu verlassen.

Es wurde eine Experimentalreihe durchgeführt, um eine solche ITD/ILD Umgewichtung näher zu untersuchen. Bei Normalhörenden maßen wir die ITD/ILD Gewichtung für verschiedene, über Kopfhörer präsentierte Rauschbänder und versuchten, mithilfe von zwei verschiedenen Trainingsparadigmen (einer Lateralisations- und einer Diskriminationsaufgabe) eine Umgewichtung zu erzielen. Bei CI-Träger:innen maßen wir die ITD/ILD Gewichtung sowie die ITD und ILD Sensitivität für 100-pps und 300-pps Pulsketten (präsentiert mittels direkter Stimulation eines interauralen Elektrodenpaars), welche mit hoher beziehungsweise niedriger ITD-Sensitivität assoziiert sind, und nutzten die Lateralisationsaufgabe, um eine Erhöhung des ITD Gewichts zu erreichen.

Bei Normalhörenden änderte sich die ITD/ILD Gewichtung graduell von ITD-dominant zu ILD-dominant mit Erhöhung der Frequenz. Für Breitband-Signale oder wenn das Frequenzband breit genug war, um ITD-dominante Regionen einzuschließen, dominierten ITDs die Wahrnehmung. Diese ITD/ILD Gewichtung konnte bei Normalhörenden unter bestimmten Signalbedingungen sowohl mittels der Lateralisations- als auch der Diskriminationsaufgabe verändert werden: Um die ILD Gewichtung zu erhöhen, musste die Frequenz ausreichend hoch sein, während sie ausreichend tief sein musste, allerdings ohne Feinstruktur-ITDs zu übertragen, um die ITD Gewichtung zu erhöhen. Bei CI-Träger:innen konnte die ITD Gewichtung für 100-pps, aber nicht für 300-pps Pulsketten erhöht werden. Dies weist darauf hin, dass eine ITD-Basissensitivität für eine ITD/ILD Umgewichtung gegeben sein muss. Die Umgewichtung ging nicht mit einer entsprechenden Veränderung der Sensitivität einher, was darauf hindeutet,

dass ITD/ILD Umgewichtung auf einer Ebene über der Wahrnehmungsschwelle stattfindet. Die Ergebnisse sind vielversprechend, um ITD Information besser auswertbar zu machen, sobald ITDs mit zukünftigen CI-Systemen zuverlässig und salient übertragen werden.