

Chickens have excellent sound localization ability

Bianca Krumm^{1,2}, Georg M. Klump¹, Christine Köppl²,
Rainer Beutelmann¹, Ulrike Langemann^{1*}

¹Cluster of Excellence "Hearing4all 2.0", Division for Animal Physiology and Behaviour, School of Medicine and Health Sciences, Department of Neuroscience, Carl von Ossietzky University of Oldenburg, Oldenburg, Germany

²Cluster of Excellence "Hearing4all 2.0", Division for Cochlea and auditory brainstem physiology, School of Medicine and Health Sciences, Department of Neuroscience, Carl von Ossietzky University of Oldenburg, Oldenburg, Germany

*Correspondence should be addressed to: Ulrike Langemann
Cluster of Excellence "Hearing4all 2.0"

Animal Physiology and Behaviour Group, Department of Neuroscience
School of Medicine and Health Sciences, University of Oldenburg
D-26111 Oldenburg, Germany
Phone: xx49-441-798-3401
E-mail: ulrike.langemann@uni-oldenburg.de

Abstract

The mechanisms of sound localization are actively debated, especially which cues are predominately used and why. Our study provides behavioural data in chickens (*Gallus gallus*) and relates these to estimates of the perceived physical cues. Sound localization acuity was quantified as the Minimum Audible Angle (MAA) in azimuth. Pure-tone MAA was 12.3°, 9.3°, 8.9° and 14.5° for frequencies of 500, 1000, 2000, and 4000 Hz, respectively. Broadband-noise MAA was 12.2°, which indicates excellent behavioural acuity. We determined "external cues" from head-related transfer functions of chickens. These were used to derive "internal cues", taking into account published data on the effect of the coupled middle ears. Our estimates of the internal cues indicate that chickens likely relied on ITD cues alone at low frequencies of 500 and 1000 Hz, whereas at 2000 and 4000 Hz, ILD may be the dominant cue.

Introduction

Sound localization supports communication in both humans and animals, and it is often crucial to animals for finding their mobile prey and for not falling prey themselves. The central auditory system makes use of microsecond differences in time of arrival or sound-pressure level between the ears for localising sound (interaural time differences, ITD, and interaural level differences, ILD). The usefulness of the different cues depends on a number of factors, among them the head size of the animal and the presence and shape of outer ears. As a result, the mechanisms underlying sound localization in various animal species may differ. Recently, a lively debate was triggered on the evolution of sound localization in land vertebrates and its representation by the central auditory system (Köppl, 2009; Grothe and Pecka, 2014; Kettler and Carr, 2019). More published evidence has supported the notion that the neural processing underlying localization behavior in mammals and birds may be comparable (Pena et al., 2019).

Due to its highly specialized auditory system, the barn owl (*Tyto alba*) is a classic animal model in the neuroethology of sound localization. Its exquisite auditory precision resulted from selective pressures for localizing prey using acoustic cues (Ashida, 2015; Konishi, 1973, 2003). However, to identify core mechanisms for sound localization, it is important to compare auditory generalists with specialists. Auditory localization research often uses Mongolian gerbils (*Meriones unguiculatus*) or cats (*Felis catus*) that both have very broad hearing ranges, including ultrasonic frequencies. In contrast, the hearing range of humans is more limited and the behaviourally most relevant range of speech signals is about 250 to 4000 Hz. Thus birds, with a hearing range limited to frequencies below 10 kHz, provide suitable models for human hearing (Dooling et al., 2000; Zwicker and Fastl, 1990).

By providing important behavioural data, our study informs the debate on the mechanisms underlying sound localization. The chicken (*Gallus gallus*) is commonly chosen in auditory physiology, because it is assumed to reflect a "non-specialized" bird (Hill et al., 2014; Kubke and Carr, 2000). There are, however, surprisingly few behavioural studies on the chicken's hearing that enable the linking of neural sensitivity to behavioural performance. Behavioural work with chickens is challenging. Chickens are naturally gregarious and thus require prolonged training to tolerate the common experimental test situation, in which they are alone. Furthermore, their natural feeding behaviour involves searching for and ingesting food over most of the day. A carefully designed dietary and deprivation scheme is needed for optimal motivation in experimental sessions. Our aim was to behaviourally assess the chicken's sound localization ability and link it to the binaural cues available and their neural processing. Localization acuity was determined as the minimum audible angle (MAA) in azimuth.

Materials and methods

Subjects. Two hens were successfully trained for the MAA task, a Wyandotte Bantam breed ("Coco", female, age 30 months at end of experiments) and a Welsumer Bantam breed ("Flocke", female, age 32 months at end of experiments). Initially, 9 hens were taken into training. Some of them never trained up to adequate stimulus control, and some developed an obvious side bias (preferentially responding to stimuli from only one side) that could not be counter-trained. The experimental subjects were kept in close proximity to other chickens, but in individual outdoor aviaries equipped with perches, a sand bath and water dispensers. Food was generally restricted, with the bulk given during the experiment and supplementary food provided later in the day, after the training sessions (Deuka All Mesh chicken pellets). The hens became accustomed to either being transported in a wire cage or

walking voluntarily to and from the experimental chamber when the doors were opened and a few grains offered. The care and treatment of the birds were approved by the Landesamt für Verbraucherschutz und Lebensmittelsicherheit (LAVES), Lower Saxony, Germany.

Experimental set-up. Experiments were carried out in a custom-built sound-attenuating chamber (2.1 x 2.1 x 2.5 m³, L x W x H, Figure 1). For echo reduction, the chamber was lined with sound-absorbing foam (PLANO 50/0 covered with WAFFLE 65/125 Seyboth & Co, $T_{30} < 20$ ms for $f \geq 700$ Hz, $T_{30} < 30$ ms for $f < 700$ Hz). The experimental cage (0.72 x 0.39 x 0.58 m³, L x W x H) was placed on top of a wire rack and equipped with two LED-lit pecking keys. Operated by a stepping motor, a custom-built feeder at the front of the cage provided defined amounts of food as rewards. For the sound output, 16 loudspeakers (Vifa XT25TG30-04, ASE, Germany) were mounted on a metal ring in a semi-circle at about the height of the chicken's head, with an angular speaker separation of 11.8°, relative to the centre of the semi-circle. The chicken's behaviour and the position of its head were monitored by two cameras (QuickCam Pro 9000, Logitech, Conrad 150001 CMOS b/w camera module). An LED light-strip on the chamber's ceiling lit the set-up. A Linux-operated computer controlled the experiment using custom-made software written in C++. Two synchronized external 8-channel sound interfaces (Hammerfall DSP Multiface II, RME) generated all acoustic stimuli. The sound interfaces' output was distributed to three amplifiers (RMB-1506, Rotel), driving the 16 loudspeakers. Based on measured loudspeaker impulse responses, the sound-pressure level and frequency responses of the 16 loudspeakers were equalized individually with a 128th order minimum-phase FIR filter for each loudspeaker. As a result, each loudspeaker's spectrum within the frequency range from 500 Hz to 8 kHz was within ± 2 dB of the spectrum averaged over all 16 loudspeakers.

Test signals. Test signals were pure tones with frequencies of 500, 1000, 2000, and 4000 Hz and a broadband (BB) noise between 500 Hz and 8000 Hz. All stimuli had an effective duration of 100 ms (including 25 ms raised cosine on- and offset ramps) and were presented at 80 dB SPL (± 3 dB roving level). In each experimental session, only one "stimulus type" was presented: one of the four pure-tone frequencies or the BB noise stimulus. Stimuli were presented either from a single loudspeaker in a defined physical location or from two neighbouring loudspeakers, using summing localization to create between-loudspeaker phantom sources. Previous studies have shown that the percept of summing localization is indeed a sound source located between the two loudspeakers (*Tyto furcata*, Keller and Takahashi, 1996; *Sturnus vulgaris*, Feinkohl and Klump, 2013; *Homo sapiens*, Blauert, 1997).

Procedures of operant testing. Using a Go/NoGo paradigm, the birds were trained to repeatedly peck the "observation key", while a train of reference stimuli was presented from the reference location at 0° azimuth, and to peck the "response key" when a test stimulus was played from a different location. The sequence within a single experimental trial was started with the first peck on the observation key. After a random waiting interval of between 1 and 5 s, another peck on the observation key resulted in the presentation of either a test stimulus (i.e., a stimulus presented from a different location than the reference location) or a catch stimulus (i.e., the normal reference stimulus with no change in location). Reference stimuli were presented every 1.3 s and the test (or catch) stimulus was played only once before the reference stimuli were resumed. If the chicken responded within 1.7 s after the onset of the test signal (scoring a HIT), it was rewarded with food. If no response occurred (MISS), the next trial was initiated after the response interval had elapsed. A response to a catch stimulus was a FALSE ALARM. False alarms were used to calculate the discrimination performance (see below). Responses during the waiting interval or upon a catch stimulus both resulted in a silent time-out and a blackout, typically between 5 and 20 s. Thresholds were obtained by the method of constant

stimuli (Dooling and Okanoya, 1995), using a stimulus set of pre-defined angular separations. The step size of angular separation between the reference location and test-stimulus location was 3°. Negative signs indicate locations to the left of the animal, positive sign locations to the right. A session consisted of 4 blocks of 17 trials each (68 trials in total). Each block consisted of 3 catch trials (0°) and a set of 14 test trials (7 left, 7 right) that were presented in pseudo-random order.

Estimating the minimum audible angle. The discrimination between reference and test stimuli was quantified as the sensitivity measure d' , based on signal-detection theory and calculated using HIT and FALSE ALARM rates (Green and Swets, 1966; Macmillan and Creelman, 2005). A specific stimulus type was tested in successive experimental sessions until at least 3 valid sessions were obtained. Thus, each angular separation was presented at least 24 times for the final threshold estimate. To minimize training effects, the sequence of testing of the five stimulus types was randomized for each individual. Criteria for a valid session were (1) a false alarm rate $\leq 20\%$, (2) $d' < 1.0$ at the narrowest angle of the stimulus set in question, and (3) $d' > 1.8$ at the largest angle. The threshold defining the chicken's MAA was then computed by linear interpolation of the psychometric function, as the angular separation at which $d' = 1.0$.

Estimating free-field cues. We used the bodies of two hens (similar in size to each of the two experimental chickens) that were sacrificed with an overdose of Narcoren^(R) immediately before measuring interaural time and level differences in the ear canal with in-ear microphones (Etymotic ER-7C). Each of the hens was mounted in a typical listening position within the experimental cage. Head-related transfer functions (HRTFs) were measured by playing a chirp from each of the loudspeakers in turn while recording from the in-ear microphones. The chirp signal was 30 s long and its instantaneous frequency swept logarithmically from 100 Hz to 22 kHz. The recordings were deconvolved with the original chirp signal to obtain the head-related

impulse responses (HRIRs) as well as the HRTFs after fast Fourier transform (FFT). Interaural time- and level differences (ITDs and ILDs) at the stimulus frequencies were derived from the amplitude and phase of the HRTFs by calculating the median across a third-octave band centred on the respective stimulus frequency. In both recordings, there was a slight azimuth mismatch of a few degrees between the chickens' individual median plane of the head and zero speaker azimuth. We eliminated the mismatch by fitting a spherical head model to the measured interaural differences and shifted the head-referenced interaural differences derived from the HRTFs towards the speaker-referenced centre by linear interpolation. Since head movement of the chickens during behavioural sessions was not restricted, their actual interaural cues would have varied somewhat over time.

Interaural transfer model. Due to the fact that chickens have internally coupled ears, the actual binaural differences between acoustic signals at the tympani differ from the external interaural differences measured with the procedure described above. Therefore, we used cochlear-microphonic data from Köppl (2019), recorded simultaneously from both ears in response to closed-field binaural acoustical stimulation, with varying ITD. A model of frequency-dependent amplitude and phase transfer during the internal passage of sound was fitted to each of her subjects' data using MATLAB (The Mathworks, Inc.). The model assumes that (for each single frequency) the external sound pressure at a given ear is attenuated and phase shifted due to the transfer through the tympanum and interaural connections, and is subsequently subtracted from the external sound pressure at the contralateral ear and vice versa. Although attenuation and phase shifts were estimated with a different method, they matched Figures 2 and 3 in Köppl (2019) very well. Comprehensive details about the model and fitting procedure are provided in the supplementary material. Estimated internal interaural differences were calculated from the fitted interaural transfer function (median across individual subjects) using the measured external ITDs and ILDs as the input. This approximates the binaural

stimulus that the chickens actually perceived during the experiment. The internal interaural cues for starlings shown in Figure 3 were estimated in a similar way: External interaural differences were estimated with an appropriate spherical head model (diameter according to De Groof et al., 2016), and the interaural attenuation and phase-transfer function was taken from Klump and Larsen (1992, p. 248). Barn owl ITD at their respective MAA was taken directly from Krumm et al. (2019).

Data analysis of behavioural data. Differences in sensitivity (in terms of d') between the two chickens with increasing angular separation will be only descriptive. We applied a repeated-measure analysis of variance to test for the effect of the stimulus type (pure tones of 500, 1000, 2000, and 4000 Hz and BB noise) on the MAA. Planned contrasts were evaluated using t-tests. All p-values are two-tailed.

Results and discussion

Behavioural localization acuity.

We employed an operant reward-based Go/NoGo paradigm to estimate the sound localization acuity of chickens (MAA) for pure tones and BB noise. Figure 2 shows the chickens' individual psychometric functions relating the sensitivity for discriminating reference and target sound source locations to the difference in the angle of sound incidence. The sensitivity measure d' varied between about -0.5 and 3.0 across all signal types and angular separations. Sensitivity increased with increasing angular separation between reference and test locations. The psychometric functions of both chickens were consistent, such that the difference between their individual MAA thresholds was only about 1° (median difference). Mean MAA values were 12.3° , 9.3° , 8.9° and 14.5° for frequencies of 500, 1000, 2000 and 4000 Hz, respectively. The MAA for BB noise was 12.2° . Thus the chickens' MAA was frequency dependent, and followed a U-shaped function ($F[4,5]=12.6$, $p=0.008$, Figure 2, lower right panel).

Localization acuity was best (MAA smallest) at 2000 Hz, a frequency where chickens hear most sensitively (Hill et al., 2014). There were significant differences between 2000 Hz vs 500 Hz ($p=0.015$), 2000 Hz vs 4000 Hz ($p=0.002$) and 2000 Hz vs BB noise ($p=0.016$).

Between 500 and 2000 Hz, the chicken's MAA function is comparable to the barn owl's (Krumm et al., 2019), but chicken MAA values worsen at higher test frequencies and also for BB noise (Figure 2, lower right panel). In contrast, MAA of the European starling (*Sturnus vulgaris*, Feinkohl and Klump, 2013) is considerably larger than that of both chickens and barn owls. The starling showed MAA values of between 20° and 30°. The starling's performance, however, matches behavioural data from other small birds. In these small birds a different metric was used making comparisons less straightforward (see Feinkohl et al., 2016, for details). Earlier studies commonly did not use a reference stimulus; instead, the animal had to indicate the absolute location of a sound source. This procedure estimates the "Minimum resolvable angle" (MRA). Thresholds from absolute sound-source localization (MRA) may differ from estimates of relative sound localization (MAA). In many cases, however, both measures are comparable, provided that the stimulus type and the number of stimuli are considered (Feinkohl and Klump, 2013). Schwartzkopff (1950) estimated a directional localization accuracy in bullfinches (*Pyrrhula pyrrhula*) of 25° to 30° at frequencies of 1500 and 3000 Hz. Estimates in great tits (*Parus major*, Klump et al., 1986) for frequencies between 1000 and 4000 Hz, and for BB noise, yielded MRA thresholds of about 20° to 26°. Park and Dooling (1991) estimated localization thresholds in three bird species for frequencies between 500 and 6000 Hz. Canaries (*Serinus canarius*) showed best performance for sound source separation at 4000 Hz (25°) and budgerigars (*Melopsittacus undulatus*) performed best at 6000 Hz (45°). Zebrafinch (*Taeniopygia guttata*) performance was poorer, with the best threshold at 4000 Hz (71°).

Localisation cues that underlie behaviour.

A well-known argument to explain such different behavioural localization performance is that animals with different head sizes experience correspondingly smaller or larger interaural differences. Our aim was to assess what the chickens actually heard - and potentially used - for their decisions during the experiments. The physical cues available in the external ear canal are displayed in Figure 3 (left column). These "external cues" were calculated from chicken HRTFs measured within the same experimental setup and using the same signal frequencies as for behaviour. The ranges of external ITD and ILD cues and their frequency-dependent differences were as expected (Kuhn, 1977). The slopes of the chicken ITD functions estimated about $\pm 40^\circ$ around the midline decreased from 2.7 $\mu\text{s}/\text{degree}$ at 500 Hz to 1.8 $\mu\text{s}/\text{degree}$ at 4000 Hz. The corresponding slopes of the ILD functions increased from 0.03 dB/degree at 500 Hz to 0.09 dB/degree at 4000 Hz.

"Internal cues" (Vedurmudi et al., 2016) were calculated based on the external cues and taking into account the transfer through the tympanum and interaural connection estimated from chicken cochlear microphonics (Köppl, 2019). Thus, internal cues reflect what the animal actually experiences. Again estimated about $\pm 40^\circ$ around the midline, the internal ITD cues were enhanced relative to the external cues, as expected, particularly at 1000 and 2000 Hz. ITD slopes were increased from 2.5 to 3.0 $\mu\text{s}/\text{degree}$ at 1000 Hz and from 2.0 to 2.4 $\mu\text{s}/\text{degree}$ at 2000 Hz. For ILD functions, the effect was even more pronounced throughout the frequency range. For example, at 2000 Hz, the slope of the ILD function tripled, from 0.08 to 0.26 dB/degree. In summary, the most informative internal ITD cues for the chickens are available at frequencies up to 2000 Hz, and the most informative internal ILDs cues occur at 2000 Hz and above. Consistent with that, the smallest MAA was found at 2000 Hz (Figure 2, lower right).

Figure 3 (right column) shows the internal ITD and ILD that the chicken experienced when discriminating MAA at different frequencies. Comparable data are also shown for two other bird species, the barn owl (Krumm et al., 2019) and the European starling (Feinkohl and Klump, 2013). For the chicken, surprisingly low ITD values are predicted to be sufficient to reach MAA threshold (Figure 3, right column). At frequencies of 500, 1000 and 2000 Hz, ITDs corresponding to the MAA of the specialist barn owl are considerably larger than the ITDs corresponding to the chicken's MAA. The ITD cues underlying the starling's MAA at 1000 and 2000 Hz are similar to those for the barn owl, but larger than in the chicken. The ILD cues corresponding to the MAA at 2000 and 4000 Hz are similar in the starling and chicken. Due to their asymmetrical ears, barn owl ILDs represent elevation rather than azimuth (Moiseff, 1989), and thus cannot meaningfully be compared regarding the azimuthal MAA.

Can this comparison of internal cues inform us about the basis of behavioural decisions? Although we cannot prove what is used, we can infer which cues are sufficiently accurate to explain the MAA. Behavioural experiments with budgerigars (Welch and Dent, 2011) demonstrated that at 2000 Hz, interaural phase shifts corresponding to an ITD of less than 20 μ s are sufficient to lateralize a sound. In the barn owl, this ITD limit may be as low as 10 μ s (Moiseff and Konishi, 1981). Thus, matching the results from behavioural studies to the internal ITD cues predicts that birds are able to use ITDs as small as 20 μ s for detecting a shift in the sound-source location - provided their auditory neurones show the required temporal precision. We return to the question of neural coding below and suggest that solving the MAA task by evaluating ITDs is plausible for the chicken.

In the bullfinch, Schwartzkopff (1952) demonstrated that ILDs as small as 1.4 dB enable the lateralization of a tone at 3200 Hz. Although behavioural studies in the pigeon (*Columba livia*, Lewald, 1987) and the budgerigar (Welch and Dent, 2011)

resulted in somewhat higher ILD thresholds of 3 to 4 dB for sound source lateralization, the study by Schwartzkopff (1952) suggests that the chicken and the starling can solve the MAA task based on ILDs at 2000 and 4000 Hz. This suggests that at 500 and 1000 Hz, chickens likely relied on ITD cues alone, whereas at 2000 and 4000 Hz, ILD may be the dominant cue.

The chicken's neural acuity.

Next, we turn to the question whether the chicken's behavioural localization performance reflects its neural selectivity to ITD and ILD resulting from binaural integration in the brainstem. Neurones of the brainstem nucleus laminaris derive their ITD selectivity from binaural coincidence detection between phase-locked inputs and are topographically arranged according to their best ITD (Overholt et al., 1992; Köppl and Carr, 2008; Palanca-Castan and Köppl, 2015). This ITD selectivity is relayed to the inferior colliculus (IC; Wang and Karten, 2010; Aralla et al., 2020). Selectivity for ILD is first established by the interaction of ipsilateral inhibition and contralateral excitation in a nucleus of the lateral lemniscus (Sato et al., 2010). This is then also relayed to the IC and further modified, resulting in several types of ILD-sensitive neurones in the IC (Aralla et al., 2020). A still open question is how this ITD and ILD information in the chicken central auditory system possibly interacts and relates to sound localization behaviour. Unlike the barn owl, there is no evidence for combining both cues in the IC into a neural map of auditory space. Although about half of all IC units proved selective for both ITD and ILD, these selectivities did not code for a consistent spatial coordinate (Aralla et al., 2020).

Nevertheless, specific subtypes of IC neurones should be suitable to resolve either the physical ITD or ILD available to the chicken. Due to the nature of the binaural phase comparison, ITD-selectivity of individual neurones typically follows a cosine shape and the slope of the most sensitive change in discharge rate increases with

increasing best frequency (BF) of the neuron. In the chicken brainstem, including IC, ITD selectivity is present up to BFs of 3.5 to 4 kHz (Köppl and Carr, 2008; Aralla et al., 2020). For the frequency range explored here, these data predict that the most suitable subset of neurones, with maximal slopes near the acoustical midline (zero ITD), would signal between 4% (at 500 Hz) and 30% (at 4 kHz) change in their dynamic discharge rate for the ITD change that corresponds to the chicken's MAA. Such neurones are relatively more common at high BFs (>2 kHz). A rare population of ITD-selective neurones in the IC, which are broadband in the frequency domain and always showed maximal slopes near the acoustical midline (Aralla et al., 2020), might be particularly informative to the chicken when localizing BB noise.

Neurones sensitive to ILD in the chicken's IC were more diverse. Generally, the most sensitive dynamic range of many ILD-sensitive neurones fell within ± 10 dB ILD, corresponding to the range of internal ILD cues shown here. Their actual slopes typically fell between 1 to 3 spikes/s/dB (Aralla et al., 2020). With a dynamic rate range of 100 to 200 spikes/s, neurones with maximal slopes near the acoustical midline (zero ILD) would thus change their discharge rate between 2% and 10% for the ILD changes that correspond to the chicken's MAAs.

In summary, the chicken's behaviourally determined MAA for tones indicates an excellent sound localization ability, even in comparison to the barn owl that is a sound localization specialist. The internal ITD cues resulting from the coupled middle ears would allow chickens to discriminate two sound source locations at a frequency of 2000 Hz and below. These ITD cues are even smaller than in the barn owl for the same task. Internal ILD cues of 2.5 and 1.5 dB at 2000 and 4000 Hz, respectively, appear to be sufficient for distinguishing two sound source locations. Thus, the neural processing mechanisms for ITD and ILD processing in the chicken's auditory system must be quite sensitive.

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Competing interests

The authors declare no competing interests.

Author contributions

Conceptualization of the study was by GMK, supervision, resources and funding acquisition by CK and GMK, investigation by BK and UL, software by RB and GMK, project administration by BK, UL and GMK, data curation and visualization by BK, RB, GMK and UL, formal analysis and writing of the original draft by all authors, writing, review & editing by GMK, CK and UL.

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Figures

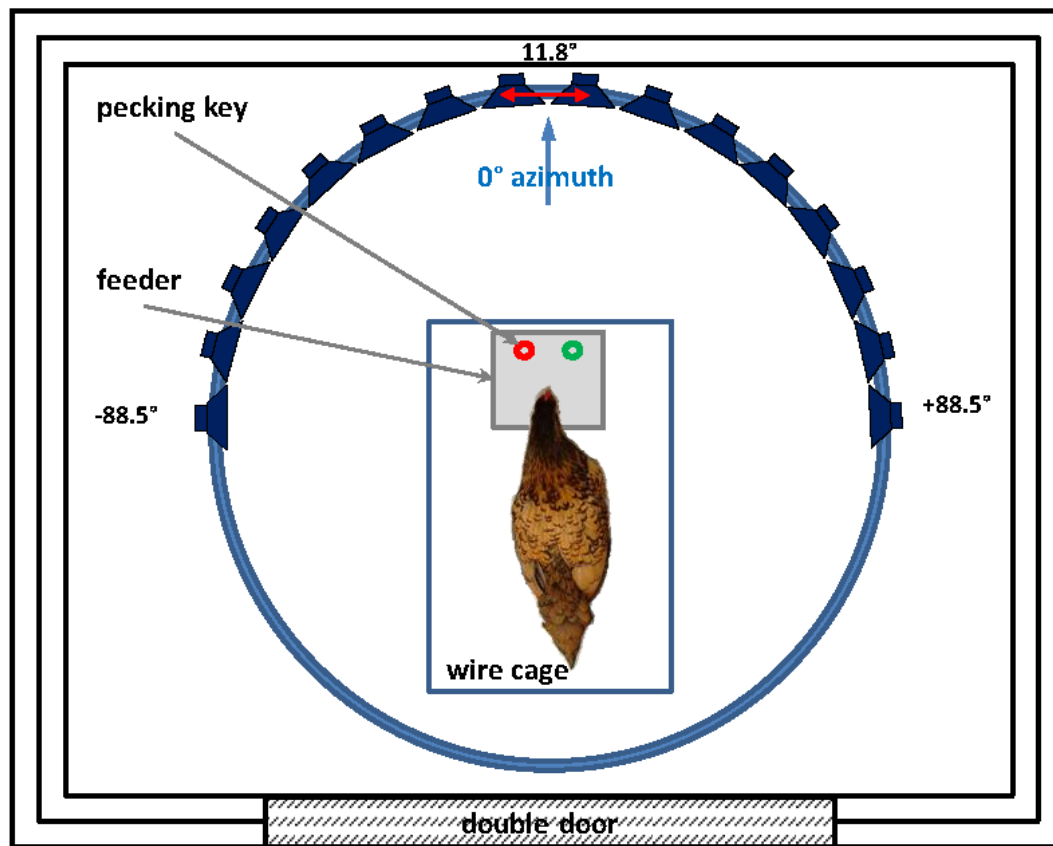


Figure 1. Behavioural setup with the experimental wire mesh cage situated in a double-walled sound-attenuating chamber (viewed from above, not to scale). The reference location of 0° azimuth is indicated by the blue arrow. A metal ring (\varnothing 140 cm) surrounding the cage supported 16 loudspeakers with a distance of 11.8° between adjacent speakers. Two pecking keys in front of the chicken registered its behavioural responses. Food rewards were delivered by a feeder placed under the front end of the cage.

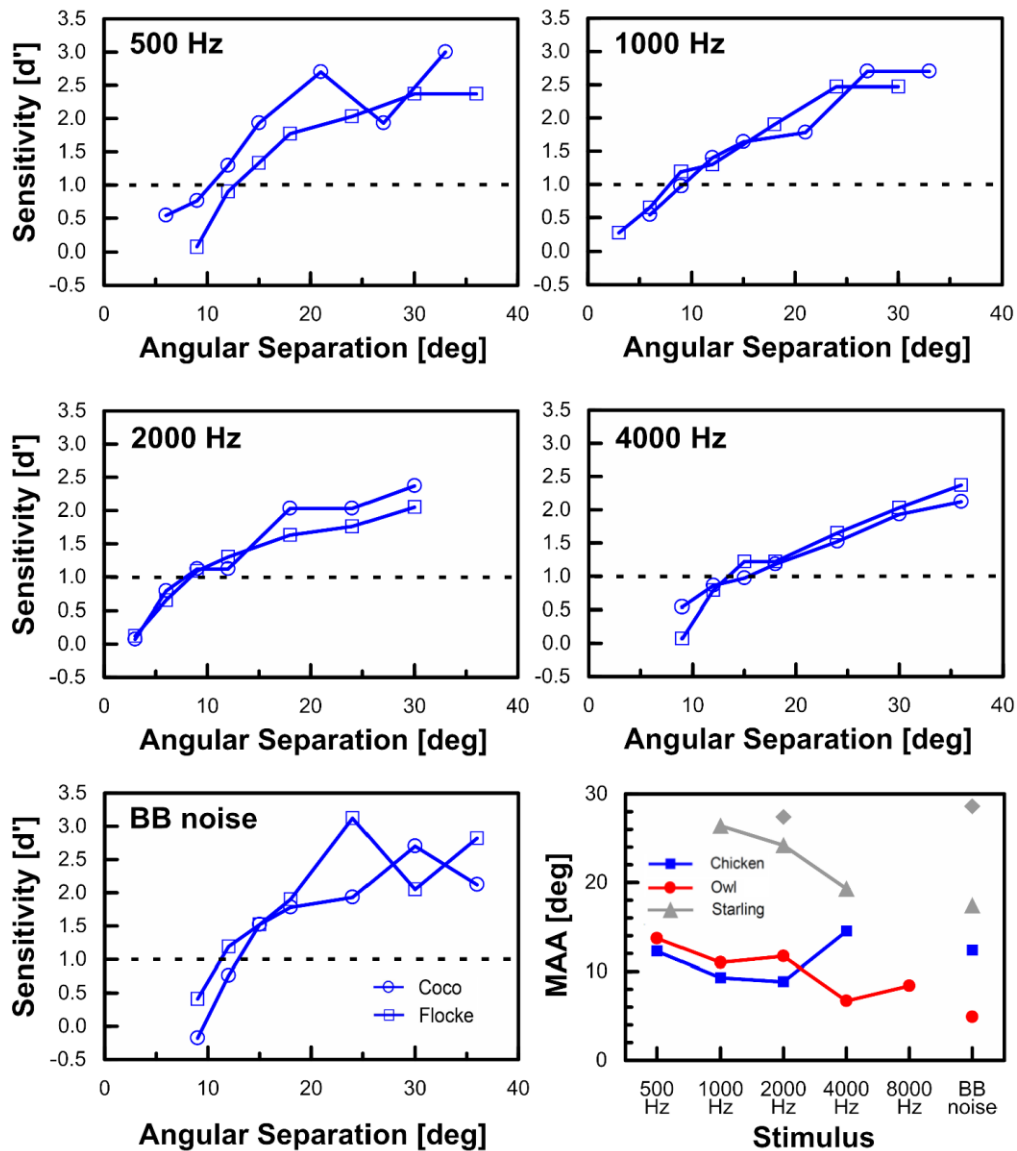


Figure 2. Psychometric functions for the different stimulus types, obtained from two chickens with a reference location at 0° azimuth. Sensitivity (d') is plotted as a function of angular separation between reference and test stimuli. Dashed lines indicate the threshold criterion. **Lower right panel** displays the two chickens' average MAA (blue squares) as a function of stimulus type, in comparison to two other bird species (red circles: barn owls from Krumm et al., 2019; grey symbols: starlings from Feinkohl and Klump, 2013, triangles show data obtained with 1s stimulus duration, diamonds show data obtained with 0.1s stimulus duration).

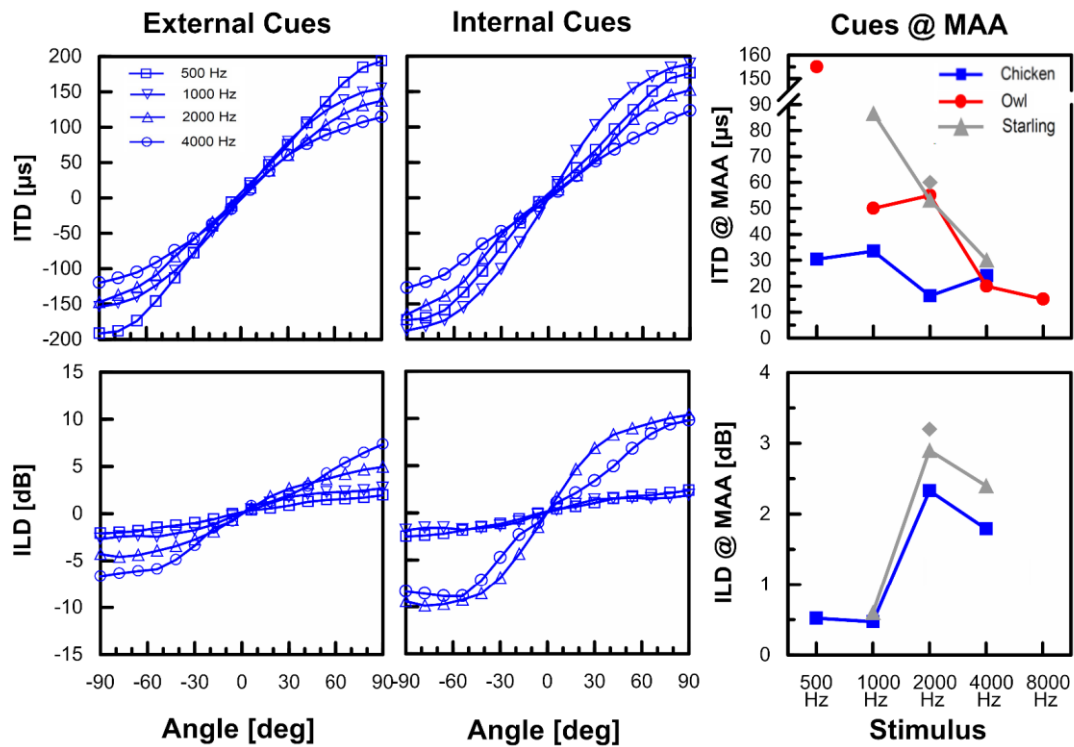


Figure 3. Comparison of azimuthal sound cues as a function of stimulus frequency. **Left column:** external ITDs and ILDs calculated from chicken HRTF measurements as a function of angular separation. **Middle column:** internal ITDs and ILDs estimated from the external cues obtained from the HRTFs and from chicken cochlear microphonics (Köppl, 2019) as a function of angular separation. **Right column:** Internal ITD and ILD values corresponding to the MAA threshold for chickens (blue squares: 0.1s stimulus), barn owls (red circles: 0.1s stimulus, Krumm et al., 2019), and European starlings (grey triangles: 1s stimulus, grey diamonds: 0.1s stimulus, Feinkohl and Klump, 2013).

Supplementary Material

This supplementary document reports the derivation and explanation of a model of internally coupled ear transmission. The model was used in the main paper to estimate how interaural time and level differences occurring externally at the ears of chickens are converted into “internal” interaural time and level differences at the eardrum. The internal coupling can enhance the “internal” interaural cues quite substantially with respect to the externally presented cues and thus facilitate spatial perception.

1. Model

1.1 Definition of external stimulus and parameters

The external sound pressure of an harmonic wave at the right ear (without loss of generality) is defined by:

$$p(t) = p_r^{ex}(t) = e^{i\omega t} . \quad (1)$$

The physically measurable pressure is the real part, $\Re \{p_r^{ex}(t)\}$.

We define the complex head related transfer function (HRTF) with respect to the right ear as a function of angular frequency $\omega = 2\pi f$:

$$h(\omega) = \alpha(\omega)e^{-i\varphi(\omega)} , \quad (2)$$

where

$$ILD(\omega) = -20 \log_{10} (\alpha(\omega)) \quad (3)$$

is the interaural level difference and

$$ITD(\omega) = d\varphi(\omega)/d\omega \quad (4)$$

is the interaural time difference, or, for sinusoidal signals, the interaural phase difference

$$IPD(\omega) = \varphi(\omega)/\omega . \quad (5)$$

The sign convention of ILD, ITD and IPD is that negative signs correspond to negative azimuths, that is, the left hemisphere as seen from the receiver's position.

The external sound pressure at the left ear is then given by

$$p_l^{ex}(t) = h(\omega)p_r^{ex}(t) . \quad (6)$$

1.2 Definition of internal interaural transfer function

The compound effect of the sound transfer from the ipsilateral tympanic membrane through the internal connection to the contralateral tympanic membrane is also summarized into a frequency-dependent internal interaural transfer function:

$$x(\omega) = A(\omega)e^{-i\Phi(\omega)} , \quad (7)$$

where $A(\omega)$ is the attenuation and $\Phi(\omega)$ is the phase delay of the interaural connection.

1.3 Definition of transfer model equations

Assuming a very simple, one-dimensional model of the sound transfer, the resulting pressure at each tympanic membrane (TM), $p_l(t)$ and $p_r(t)$, is given by a pair of equations:

$$p_l(t) = p_l^{ex}(t) - x(\omega)p_r^{ex}(t) \quad (8a)$$

$$p_r(t) = p_r^{ex}(t) - x(\omega)p_l^{ex}(t) \quad (8b)$$

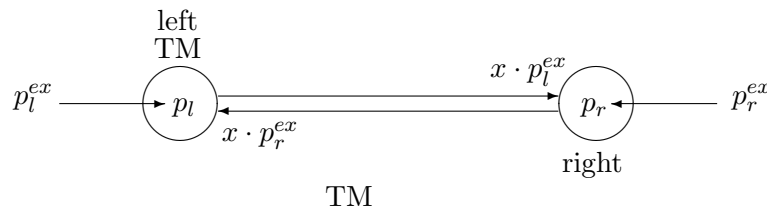


Fig. S1. Schematic of the simple interaural transfer model. External sound waves ($p_l^{ex}(t)$ and $p_r^{ex}(t)$) enter the ears from left and right, pass through the respective ipsilateral tympanic membrane (TM) and result in a difference pressure ($p_l(t)$ and $p_r(t)$) at the contralateral TM after passage through the interaural connection.

Solving these equations for $p_l(t)$ and $p_r(t)$ results in

$$p_l(t) = (h(\omega) - x(\omega))p(t) \quad (9a)$$

$$p_r(t) = (1 - x(\omega)h(\omega))p(t) \quad (9b)$$

The internal interaural differences result from dividing eq. (9a) by eq. (9b):

$$h^{in}(\omega) = \frac{h(\omega) - x(\omega)}{1 - x(\omega)h(\omega)}, \quad (10)$$

with the calculation of internal interaural differences corresponding to (3), (4), and (5).

1.4 Fit of the model to recorded data

The complex internal head-related transfer function $h^{in}(\omega)$ was fitted to amplitude ratios and phase delays derived from recorded cochlear microphonic (CM) signals taken from Köppl (2019a,b), assuming that the CM signals represent the actual amplitude ratio and phase difference at the TMs in a sufficiently linear fashion. Amplitude ratios and phase differences for starlings, also derived from CM recordings, were taken directly from the results section of Klump und Larsen (1992, p. 248).

1.4.1 Sound reproduction and measurement offsets

In order to accommodate the real, slightly imperfect reproduction of the nominal external ILD and ITD at the chickens' ears as well as imbalances in electrode impedance during cochlear microphonics recording, two additional complex fitting parameters $\delta(\omega)$ and $\varepsilon(\omega)$ were introduced:

$$h(\omega) = \delta(\omega)h^{ideal}(\omega) \quad (11)$$

$$h^{CM}(\omega) = \varepsilon(\omega)h^{in}(\omega) \quad (12)$$

which result in the final function that was fitted to the recorded CM data and the nominal ITDs (ILD = 0 dB throughout the experiments) using $x(\omega)$, $\delta(\omega)$, and $\varepsilon(\omega)$ as parameters:

$$h^{CM}(\omega) = \varepsilon(\omega) \frac{\delta(\omega)h(\omega) - x(\omega)}{1 - x(\omega)\delta(\omega)h(\omega)}. \quad (13)$$

1.4.2 Better fits utilizing complex geometry

Fitting this function is facilitated by identifying it as a Möbius transformation (Schwerdtfeger, 2020), which has the general form

$$f(z) = \frac{az + b}{cz + d}. \quad (14)$$

For this specific problem the following identities hold:

$$z = h(\omega) \quad (15)$$

$$a = \varepsilon(\omega)\delta(\omega) \quad b = -\varepsilon(\omega)x(\omega) \quad (16)$$

$$c = -\delta(\omega)x(\omega) \quad d = 1 \quad (17)$$

A Möbius transformation maps – in the complex plane – circles to rotated, scaled and translated circles and is uniquely defined by the relation between three distinct points and

their transformed image (Schwerdtfeger, 2020). The external interaural differences used in the chicken CM experiments (Köppl, 2019a,b) with varying ITDs and ILD = 0 correspond to values of $h^{ideal}(\omega)$ on the complex unit circle $h = e^{-i\varphi}$. The recorded CM data was measured for 11 or 21 ITD steps per condition (covering the range between IPDs of -2π and $+2\pi$), so that the solution of (14) is overdetermined. If the model is applicable, the values of $h^{CM}(\omega)$ should also approximately lie on a circle, so that the parameters of (14) can be fitted well.

The reverse conversion of Möbius transform parameters into the physical model parameters is given by

$$x(\omega) = \mp \sqrt{\frac{bc}{a}} \quad \delta(\omega) = \pm \sqrt{\frac{ac}{b}} \quad \varepsilon(\omega) = \pm \sqrt{\frac{ab}{c}} \quad (18)$$

The signs were chosen to center the phases of $\delta(\omega)$ and $\varepsilon(\omega)$ around zero, assuming that the absolute phase offsets were small.

For each binaural recording file in the chicken CM data set (Köppl, 2019a), that is, for each animal and stimulus frequency/level combination, a separate set of parameters was fitted, assuming that sound reproduction and CM electrode parameters could have changed between sessions. Recordings with blocked interaural connection were omitted.

1.4.3 Estimates of internal interaural differences

Estimates of internal interaural differences were calculated using (10), that is, with $\delta(\omega) = 1$ and $\varepsilon(\omega) = 1$, since there is neither sound reproduction nor CM measurement offset involved in the free-field sound perception of behaving chickens. From each measured HRTF data set (cf. main manuscript), internal interaural differences were calculated for each fitted parameter set. The results were first averaged across parameter sets, weighting with the reciprocal variance of the fit residuals, and then across both chickens used for HRTF measurement.

For starlings, no HRTF data was available. The external interaural differences were instead derived from a spherical head model (Duda und Martens, 1998), using a head diameter of 1.8 cm (measured in a starling brain atlas, De Groof et al., 2016) times a factor of 1.5 due to wavelengths much larger than the head diameter (Kuhn, 1977).

2. Results

In Fig. 2, two examples of model fits are shown. The match between fit and measured data was similarly good for most of the data sets. In almost all data sets the data points actually lay on a circular shape in the complex plane, suggesting that the model generally represents the interaural transfer very well.

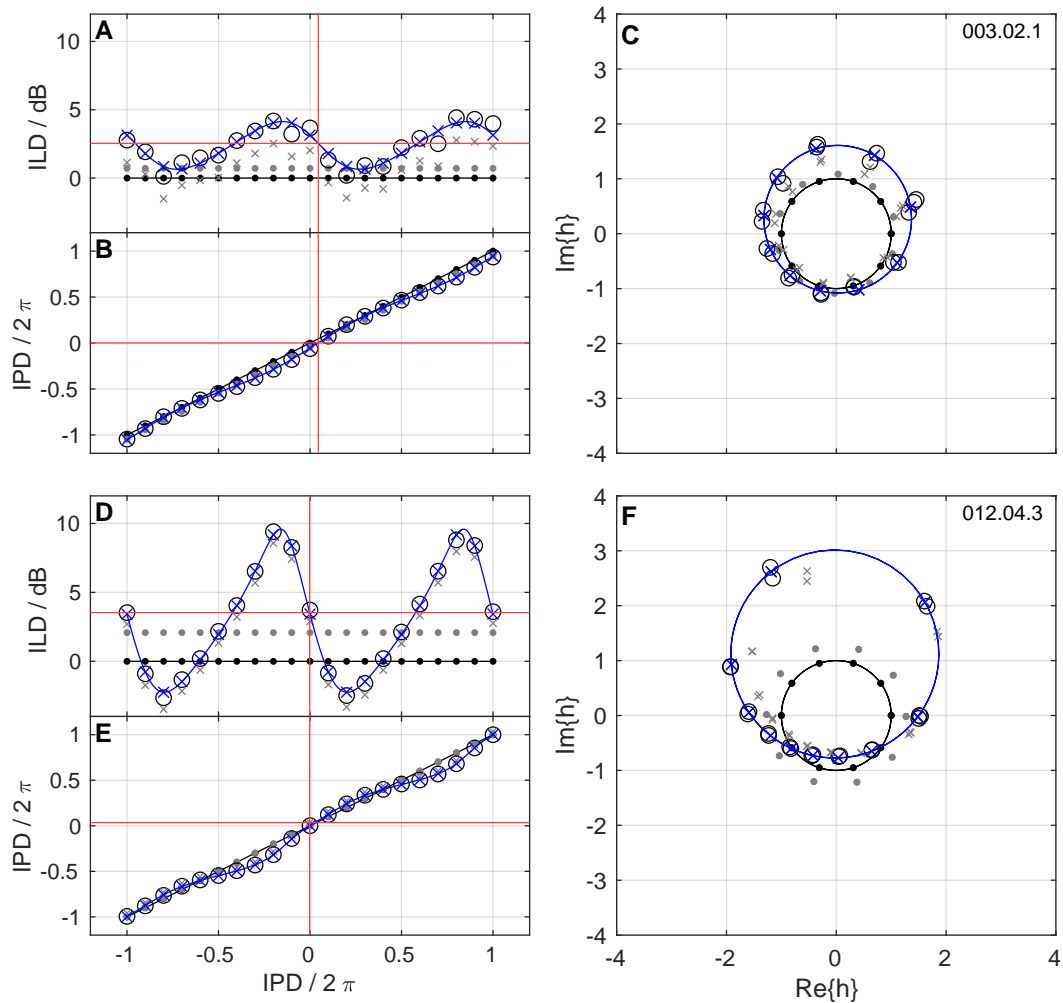


Fig. S2. Two examples of model fits. All panels show measured CM data (black circles), modelled CM data (blue crosses and line), nominal external data (black dots and line), real external data (grey dots), and CM data with removed fitted measurement offset $\varepsilon(\omega)$. Red lines show the phases of $\delta(\omega)$ (vertical lines) and $\varepsilon(\omega)$ (horizontal line in B and E) as well as the combined level offset (horizontal line in panels A and D). Panels A and D show interaural level difference (ILD), panels B and E show interaural phase difference (IPD), and panels C and F show a complex representation of the interaural parameters with 0° at positive real values, IPD in counter-clockwise direction and interaural amplitude ratio as absolute value.

However, since detailed geometrical and physical constraints of the interaural connections have not been taken into account, there is no straightforward way to precisely assess the validity of the fitted transfer parameters. Nevertheless, they appear to be reliable when compared to more directly measured parameters, which can be seen in Fig. 3. The original data set from (Köppl, 2019b, black circles and lines), measured with a monaural stimulation paradigm, but in the same setup and with the same individual subjects, shows almost the same distribution of interaural attenuation and phase shift as the model parameters (blue crosses and lines). At frequencies above 1 kHz, both measured and modeled data match quite well with the theoretical transmission delay through an average-length chicken interaural connection (≈ 3 cm). Median values across individuals ranged from -23 dB to -9 dB for $|x(\omega)|$, 1 dB to 3 dB for $|\delta(\omega)|$ and $|\varepsilon(\omega)|$ for different frequencies. The medians across frequencies of these medians were -15 dB, 2.6 dB, and 2.2 dB, respectively. For the phases, median values across individuals ranged from -98° to 50° for $\text{Arg}(x(\omega))$, -11° to 11° for $\text{Arg}(\delta(\omega))$ and -6° to 18° $\text{Arg}(\varepsilon(\omega))$. The medians across frequencies of these medians were -55° , -1° , and 2° , respectively.

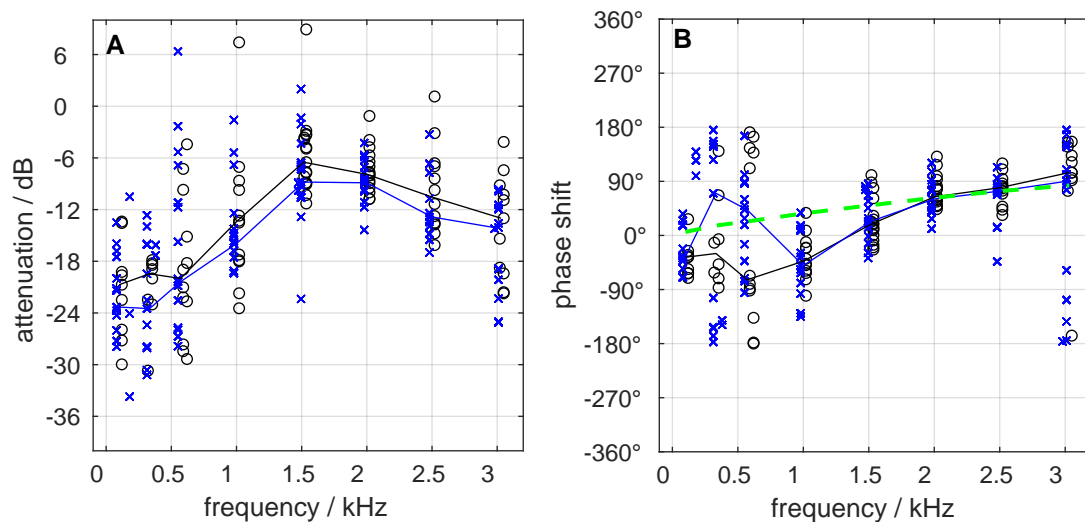


Fig. S3. (adapted from Köppl, 2019) A: Interaural amplitude transmission attenuation $A(\omega)$ with respect to stimulus frequency. Individual data from 8 chickens and median (black circles and line, original data from Köppl, 2019). Individual modeled data and median (blue crosses and line). B: Interaural phase shift $\Phi(\omega)$. The phase inversion due to sound pressure coming from the inside of the tympanic membrane has been removed from the measured data (black circles). Symbols and colors are the same as in A. Theoretical direct-path phase delay assuming a distance of approximately 3 cm (green dashed line).

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