

SHORT COMMUNICATION

Chickens have excellent sound localization ability

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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 deg for frequencies of 500, 1000, 2000 and 4000 Hz, respectively. Broadband-noise MAA was 12.2 deg, 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 interaural time difference cues alone at low frequencies of 500 and 1000 Hz, whereas at 2000 and 4000 Hz, interaural level differences may be the dominant cue.

KEY WORDS: Behavioural acuity, Interaural time difference, Interaural level difference, Bird, Perceived physical cues

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 (SPL) between the ears for localizing 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 behaviour in mammals and birds may be comparable (Peña et al., 2019).

Because of 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 pressure 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 250–4000 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, *Gallus gallus* (Linnaeus 1758), were successfully trained for the MAA task, a Wyandotte Bantam breed (Coco, female, age 30 months at the end of the experiment) and a Welsumer Bantam breed (Flocke, female, age 32 months at end the of the experiment). 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 (2.1×2.1×2.5 m³, L×W×H; Fig. 1). For echo reduction, the chamber was lined with sound-absorbing foam (PLANO 50/0

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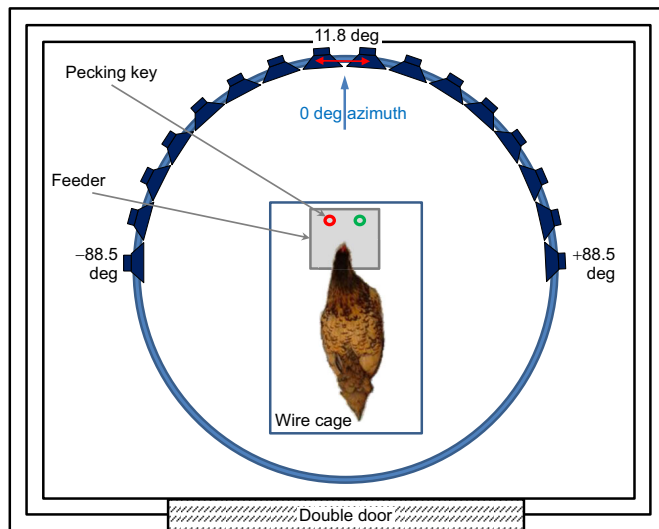


Fig. 1. Behavioural setup with the experimental wire mesh cage situated in a double-walled sound-attenuating chamber. The reference location of 0 deg azimuth is indicated by the blue arrow. A metal ring (140 cm diameter) surrounding the cage supported 16 loudspeakers with a distance of 11.8 deg between 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. Setup viewed from above, not to scale.

covered with WAFFLE 65/125 Seyboth & Co, reverberation time $T_{30} < 20$ ms for frequencies $f \geq 700$ Hz, $T_{30} < 30$ ms for $f < 700$ Hz). The experimental cage ($0.72 \times 0.39 \times 0.58$ m³, L×W×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) 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 deg, 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 interface output was distributed to three amplifiers (RMB-1506, Rotel), driving the 16 loudspeakers. Based on measured loudspeaker impulse responses, the SPL 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 and 8000 Hz. All stimuli had an effective duration of 100 ms (including 25 ms raised cosine onset 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 deg 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 to 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 of 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 deg. Negative signs indicate locations to the left of the animal; positive signs indicate 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 deg) and a set of 14 test trials (7 left, 7 right) that were presented in pseudo-random order.

Estimating the MMA

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 killed with an overdose of Narcoren[®] 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). 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. As head movement of the chickens during behavioural sessions was not restricted, their actual interaural cues would have varied somewhat over time.

Interaural transfer model

Because 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 Köppl's (2019) 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 as a result of 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 figs 2 and 3 in Köppl (2019) very well. Comprehensive details about the model and fitting procedure are provided in the Supplementary Materials and Methods. 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 (see below) 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).

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 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. Fig. 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 deg (median difference). Mean MAA values were 12.3, 9.3, 8.9 and 14.5 deg for frequencies of 500, 1000, 2000 and 4000 Hz, respectively. The MAA for BB noise was 12.2 deg. Thus, the chickens' MAA was frequency dependent, and followed a U-shaped function ($F_{4,5}=12.6$, $P=0.008$; Fig. 2, bottom right). Localization acuity in our chickens was best (MAA smallest) at 2000 Hz, a frequency where chickens hear most sensitively (Hill et al., 2014). There were significant differences for 2000 Hz versus 500 Hz ($P=0.015$), 2000 Hz versus 4000 Hz ($P=0.002$) and 2000 Hz versus BB noise ($P=0.016$).

Between 500 and 2000 Hz, the chickens' MAA function is comparable to that of barn owls (Krumm et al., 2019), but chicken MAA values worsened at higher test frequencies and also for BB noise (Fig. 2, bottom right). In contrast, MAA of the European starling (*Sturnus vulgaris*: Feinkohl and Klump, 2013) was considerably larger than that of both chickens and barn owls, with MAA values of between 20 and 30 deg. The starlings' 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, the two 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 25–30 deg 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 20–26 deg. 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 deg) and budgerigars (*Melopsittacus undulatus*) performed best at 6000 Hz (45 deg). Zebra finch (*Taeniopygia guttata*) performance was poorer, with the best threshold at 4000 Hz (71 deg).

Localization 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 Fig. 3 (left). 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) and consistent with previous measurements (Schnyder et al., 2014). The slopes of the chicken ITD functions estimated about ± 40 deg around the midline decreased from $2.7 \mu\text{s deg}^{-1}$ at 500 Hz to $1.8 \mu\text{s deg}^{-1}$ at 4000 Hz. The corresponding slopes of the ILD functions

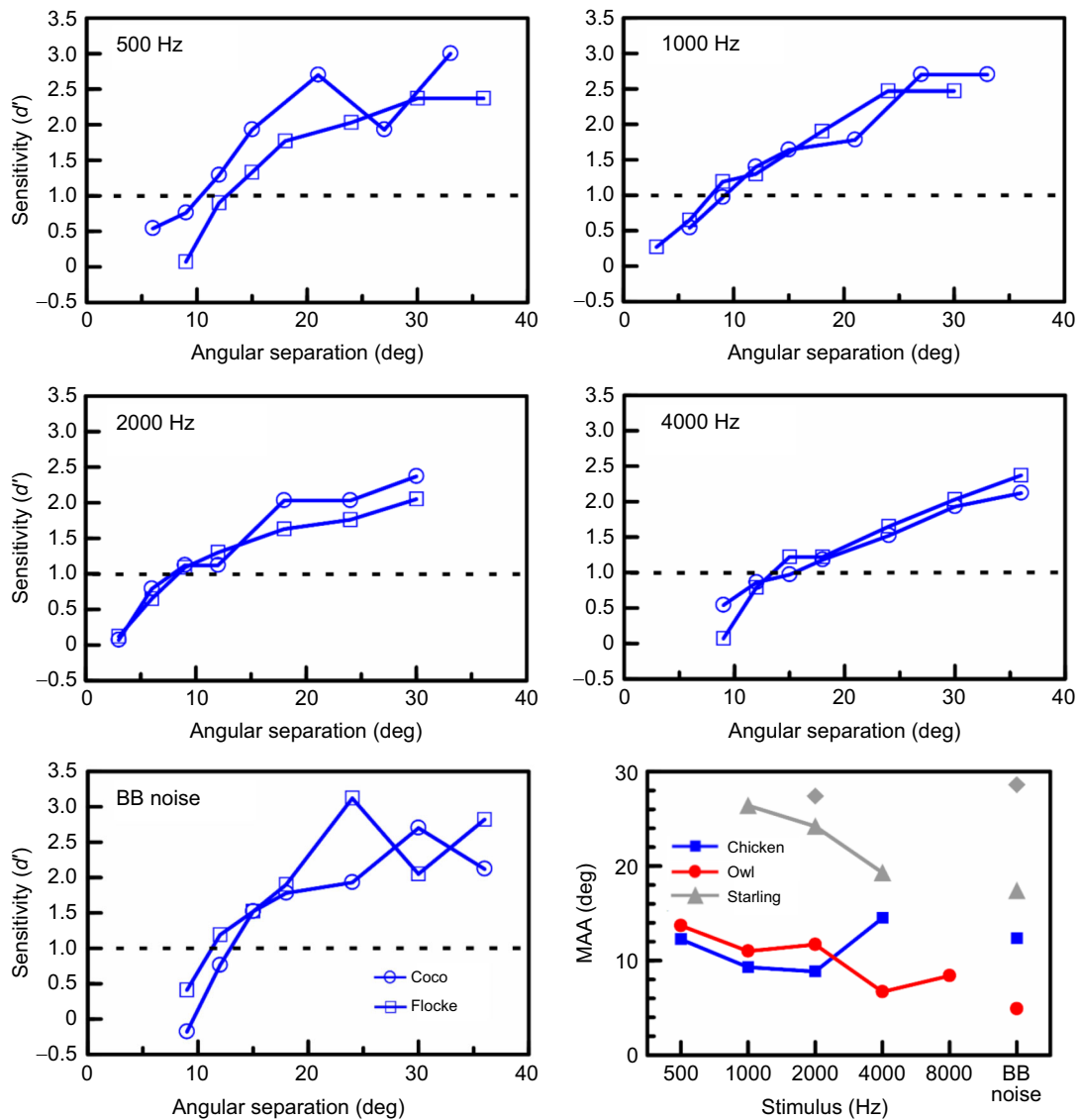


Fig. 2. Psychometric functions for the different stimulus types, obtained from two chickens with a reference location at 0 deg azimuth. Sensitivity (d') is plotted as a function of angular separation between reference and test stimuli. Signal type is indicated at the top of each panel. Dashed lines indicate the threshold criterion. The bottom right panel displays the two chickens' average minimum audible angle (MAA) as a function of stimulus type, in comparison with that of two other bird species (barn owls: Krumm et al., 2019; European starlings – triangles show data obtained with 1 s stimulus duration, diamonds show data obtained with 0.1 s stimulus duration: Feinkohl and Klump, 2013).

increased from 0.03 dB deg^{-1} at 500 Hz to 0.09 dB deg^{-1} 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 (Köppel, 2019). Thus, internal cues reflect what the animal actually experiences. Again, estimated about ± 40 deg 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 $3.0 \mu\text{s deg}^{-1}$ at 1000 Hz and from 2.0 to $2.4 \mu\text{s deg}^{-1}$ 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 deg^{-1} . In summary, the most informative internal ITD cues for 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 (Fig. 2, bottom right).

Fig. 3 (right) shows the internal ITD and ILD that chickens 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 chickens, surprisingly low ITD values were predicted to be sufficient to reach MAA threshold (Fig. 3, right). At frequencies of 500, 1000 and 2000 Hz, ITDs corresponding to the MAA of the specialist barn owl were considerably larger than the ITDs corresponding to chicken MAA. The ITD cues underlying starling MAA at 1000 and 2000 Hz were similar to those for barn owls, but larger than in chickens. The ILD cues corresponding to the MAA at 2000 and 4000 Hz were similar in starlings and chickens. Because of their asymmetrical ears, barn owl ILDs represent elevation rather than azimuth (Moiseff, 1989), and thus cannot meaningfully be compared regarding the azimuthal MAA.

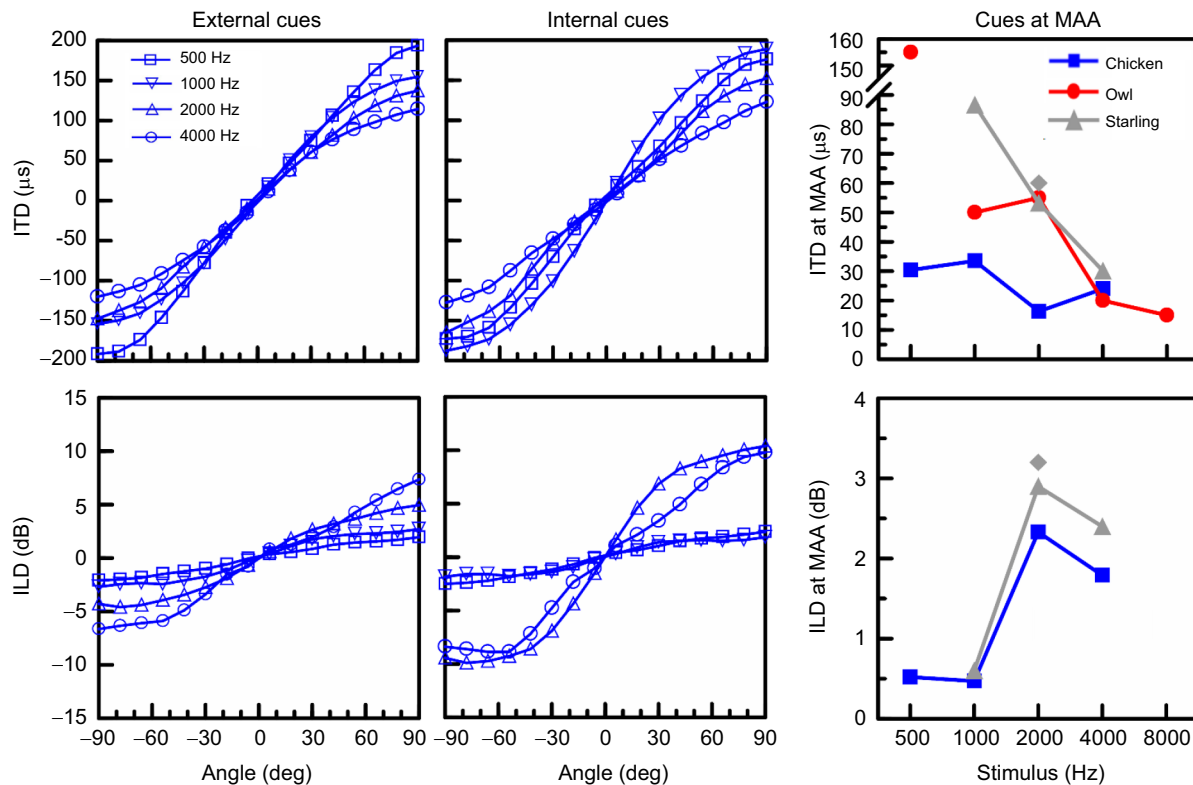


Fig. 3. Comparison of azimuthal sound cues as a function of stimulus frequency. Left: external interaural time differences (ITDs) and interaural level differences (ILDs) calculated from chicken head-related transfer function (HRTF) measurements as a function of angular separation. Middle: internal ITDs 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: internal ITD and ILD values corresponding to the MAA threshold for chickens (0.1 s stimulus), barn owls (0.1 s stimulus: Krumm et al., 2019) and European starlings (triangles: 1 s stimulus, diamonds: 0.1 s stimulus: Feinkohl and Klump, 2013).

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, Schwartzkopf (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 3–4 dB for sound source lateralization, the study by Schwartzkopf (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 probably relied on ITD cues alone, whereas at 2000 and 4000 Hz, ILD cues may be dominant.

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 in the barn owl, there is no evidence for combining the two 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, this selectivity 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. Because of 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 the IC, ITD selectivity is present up to BFs of 3.5–4 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 and 3 spikes s^{-1} dB $^{-1}$ (Aralla et al., 2020). With a dynamic rate range of 100–200 spikes s^{-1} , 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 that of the barn owl, which 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 or financial interests.

Author contributions

Conceptualization: G.M.K.; Software: G.M.K., R.B.; Formal analysis: B.K., G.M.K., C.K., R.B., U.L.; Investigation: B.K., U.L.; Resources: G.M.K., C.K.; Data curation: B.K., G.M.K., R.B., U.L.; Writing - original draft: B.K., G.M.K., C.K., R.B., U.L.; Writing - review & editing: G.M.K., C.K., U.L.; Visualization: B.K., G.M.K., R.B., U.L.; Supervision: G.M.K., C.K.; Project administration: B.K., G.M.K., U.L.; Funding acquisition: G.M.K., C.K.

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References

- Aralla, R., Ashida, G. and Köppl, C. (2020). Binaural responses in the auditory midbrain of chicken (*Gallus gallus*). *Eur. J. Neurosci.* **51**, 1290–1304. doi:10.1111/ejn.13891
- Ashida, G. (2015). Barn owl and sound localization. *Acoust. Sci. Technol.* **36**, 275–285. doi:10.1250/ast.36.275
- Blauert, J. (1997). *Spatial Hearing: The Psychophysics of Human Sound Localization*. Cambridge, MA: The MIT Press.
- De Groof, G., George, I., Touj, S., Stacho, M., Jonckers, E., Cousillas, H., Hausberger, M., Güntürkün, O. and Van der Linden, A. (2016). A three-dimensional digital atlas of the starling brain. *Brain Struct. Funct.* **221**, 1899–1909. doi:10.1007/s00429-015-1011-1
- Dooling, R. J. and Okanoya, K. (1995). The method of constant stimuli in testing auditory sensitivity in small birds. In *Methods in Comparative Psychoacoustics* (ed. G. M. Klump, R. J. Dooling, R. R. Fay and W. C. Stebbins), pp. 161–169. Basel: Birkhäuser.
- Dooling, R. J., Lohr, B. and Dent, M. L. (2000). Hearing in birds and reptiles. In *Comparative Hearing: Birds and Reptiles* (ed. R. J. Dooling, R. R. Fay and A. N. Popper), pp. 308–359. New York: Springer.
- Feinkohl, A. and Klump, G. M. (2013). Azimuthal sound localization in the European starling (*Stumus vulgaris*): II. Psychophysical results. *J. Comp. Physiol. A* **199**, 127–138. doi:10.1007/s00359-012-0774-6
- Feinkohl, A., Borzeszkowski, K. M. and Klump, G. M. (2016). Azimuthal sound localization in the European starling (*Stumus vulgaris*): III. Comparison of sound localization measures. *Hear. Res.* **332**, 238–248. doi:10.1016/j.heares.2015.04.001
- Green, D. M. and Swets, J. A. (1966). *Signal Detection Theory and Psychophysics*. New York: Wiley.
- Grothe, B. and Pecka, M. (2014). The natural history of sound localization in mammals—a story of neuronal inhibition. *Front Neural Circuits* **8**, 116. doi:10.3389/fncir.2014.00116
- Hill, E. M., Koay, G., Heffner, R. S. and Heffner, H. E. (2014). Audiogram of the chicken (*Gallus gallus domesticus*) from 2 Hz to 9 kHz. *J. Comp. Physiol. A* **200**, 863–870. doi:10.1007/s00359-014-0929-8
- Keller, C. H. and Takahashi, T. T. (1996). Binaural cross-correlation predicts the responses of neurons in the owl's auditory space map under conditions simulation summing localization. *J. Neurosci.* **16**, 4300–4309. doi:10.1523/JNEUROSCI.16-13-04300.1996
- Kettler, L. and Carr, C. E. (2019). Neuroethology of sound localization in birds. In *Reference Module in Life Sciences: Encyclopedia of Animal Behavior*, 2nd edn, pp 156–164. Amsterdam: Elsevier.
- Klump, G. M. and Larsen, O. N. (1992). Azimuthal sound localization in the European starling (*Stumus vulgaris*): I. Physical binaural cues. *J. Comp. Physiol. A* **170**, 243–251. doi:10.1007/BF00196906
- Klump, G. M., Windt, W. and Curio, E. (1986). The great tit's (*Parus major*) auditory resolution in azimuth. *J. Comp. Physiol. A* **158**, 383–390. doi:10.1007/BF00603622
- Köppl, C. (2009). Evolution of sound localisation in land vertebrates. *Curr. Biol.* **19**, R635–R639. doi:10.1016/j.cub.2009.05.035
- Köppl, C. (2019). Internally coupled middle ears enhance the range of interaural time differences heard by the chicken. *J. Exp. Biol.* **222**, jeb199232. doi:10.1242/jeb.199232
- Köppl, C. and Carr, C. E. (2008). Maps of interaural time difference in the chicken's brainstem nucleus laminaris. *Biol. Cybern.* **98**, 541–559. doi:10.1007/s00422-008-0220-6
- Konishi, M. (1973). How the owl tracks its prey. *Am. Sci.* **61**, 414–424.
- Konishi, M. (2003). Coding of auditory space. *Annu. Rev. Neurosci.* **26**, 31–55. doi:10.1146/annurev.neuro.26.041002.131123
- Krumm, B., Klump, G. M., Köppl, C. and Langemann, U. (2019). The barn owls' minimum audible angle. *PLoS One* **14**, e0220652. doi:10.1371/journal.pone.0220652
- Kubke, M. F. and Carr, C. E. (2000). Development of the auditory brainstem of birds: comparison between barn owls and chickens. *Hear. Res.* **147**, 1–20. doi:10.1016/S0378-5955(00)00116-7
- Kuhn, G. F. (1977). Model for the interaural time differences in the azimuthal plane. *J. Acoust. Soc. Am.* **62**, 157–167. doi:10.1121/1.381498
- Lewald, J. (1987). Interaural time and intensity difference thresholds of the pigeon (*Columba livia*). *Naturwissenschaften* **74**, 449–451. doi:10.1007/BF00446106
- Macmillan, N. A. and Creelman, C. D. (2005). *Detection Theory: A User's Guide*. Mahwah, NJ, USA: Lawrence Erlbaum.
- Moiseff, A. (1989). Bi-coordinate sound localization by the barn owl. *J. Comp. Physiol. A* **164**, 637–644. doi:10.1007/BF00614506
- Moiseff, A. and Konishi, M. (1981). Neuronal and behavioral sensitivity to binaural time differences in the owl. *J. Neurosci.* **1**, 40–48. doi:10.1523/JNEUROSCI.01-01-00040.1981
- Overholt, E. M., Rubel, E. W. and Hyson, R. L. (1992). A circuit for coding interaural time differences in the chick brainstem. *J. Neurosci.* **12**, 1698–1708. doi:10.1523/JNEUROSCI.12-05-01698.1992
- Palanca-Castan, N. and Köppl, C. (2015). Change in the coding of interaural time difference along the tonotopic axis of the chicken nucleus laminaris. *Front. Neural Circuits* **9**, 43. doi:10.3389/fncir.2015.00043
- Park, T. J. and Dooling, R. J. (1991). Sound localization in small birds: absolute localization in azimuth. *J. Comp. Psychol.* **105**, 125–133. doi:10.1037/0735-7036.105.2.125
- Peña, J. L., Cazes, F., Beckert, M. V. and Fischer, B. J. (2019). Synthesis of Hemispheric ITD Tuning from the Readout of a Neural Map: Commonalities of Proposed Coding Schemes in Birds and Mammals. *J. Neurosci.* **39**, 9053–9061. doi:10.1523/JNEUROSCI.0873-19.2019
- Sato, T., Fukui, I. and Ohmori, H. (2010). Interaural phase difference modulates the neural activity in the nucleus angularis and improves the processing of level difference cue in the lateral lemniscal nucleus in the chicken. *Neurosci. Res.* **66**, 198–212. doi:10.1016/j.neures.2009.11.001
- Schnyder, H. A., Vanderelst, D., Bartenstein, S., Firzlaff, U. and Luksch, H. (2014). The avian head induces cues for sound localization in elevation. *PLoS ONE* **9**, e112178. doi:10.1371/journal.pone.0112178
- Schwartzkopf, J. (1950). Beitrag zum Problem des Richtungshörens bei Vögeln. *Z. Vgl. Physiol.* **32**, 319–327. doi:10.1007/BF00340693
- Schwartzkopf, J. (1952). Untersuchungen über die Arbeitsweise des Mittelohres und das Richtungshören der Singvögel unter Verwendung von Cochlea-Potentialen. *Z. Vgl. Physiol.* **34**, 46–68. doi:10.1007/BF00298942
- Vedurmudi, A. P., Young, B. A. and van Hemmen, J. L. (2016). Internally coupled ears: mathematical structures and mechanisms underlying ICE. *Biol. Cybern.* **110**, 359–382. doi:10.1007/s00422-016-0696-4
- Wang, Y. and Karten, H. J. (2010). Three subdivisions of the auditory midbrain in chicks (*Gallus gallus*) identified by their afferent and commissural projections. *J. Comp. Neurol.* **518**, 1199–1219. doi:10.1002/cne.22315
- Welch, T. E. and Dent, M. L. (2011). Lateralization of acoustic signals by dichotically listening budgerigars (*Melopsittacus undulatus*). *J. Acoust. Soc. Am.* **130**, 2293–2301. doi:10.1121/1.3628335
- Zwicker, E. and Fastl, H. (1990). *Psychoacoustics*. Berlin: Springer.