**Infrasonic hearing in birds: a review of audiometry and hypothesized structure–function relationships**

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ABSTRACT

The perception of airborne infrasound (sounds below 20 Hz, inaudible to humans except at very high levels) has been documented in a handful of mammals and birds. While animals that produce vocalizations with infrasonic components (e.g. elephants) present conspicuous examples of potential use of infrasound in the context of communication, the extent to which airborne infrasound perception exists among terrestrial animals is unclear. Given that most infrasound in the environment arises from geophysical sources, many of which could be ecologically relevant, communication might not be the only use of infrasound by animals. Therefore, infrasound perception could be more common than currently realized. At least three bird species, each of which do not communicate using infrasound, are capable of detecting infrasound, but the associated auditory mechanisms are not well understood. Here we combine an evaluation of hearing measurements with anatomical observations to propose and evaluate hypotheses supporting avian infrasound detection. Environmental infrasound is mixed with non-acoustic pressure fluctuations that also occur at infrasonic frequencies. The ear can detect such non-acoustic pressure perturbations and therefore, distinguishing responses to infrasound from responses to non-acoustic perturbations presents a great challenge. Our review shows that infrasound could stimulate the ear through the middle ear (tympanic) route and by extratympanic routes bypassing the middle ear. While vibration velocities of the middle ear decline towards infrasonic frequencies, whole-body vibrations – which are normally much lower amplitude than that those of the middle ear in the ‘audible’ range (i.e. > 20 Hz) – do not exhibit a similar decline and therefore may reach vibration magnitudes comparable to the middle ear at infrasonic frequencies. Low stiffness in the middle and inner ear is expected to aid infrasound transmission. In the middle ear, this could be achieved by large air cavities in the skull connected to the middle ear and low stiffness of middle ear structures; in the inner ear, the stiffness of round windows and cochlear partitions are key factors. Within the inner ear, the sizes of the helicotrema and cochlear aqueduct are expected to play important roles in shunting low-frequency vibrations away from low-frequency hair-cell sensors in the cochlea. The basilar papilla, the auditory organ in birds, responds to infrasound in some species, and in pigeons, infrasonic-sensitive neurons were traced back to the apical, abneural end of the basilar papilla. Vestibular organs and the paratympanic organ, a hair cell organ outside of the inner ear, are additional untested candidates for infrasound detection in birds. In summary, this review brings together evidence to create a hypothetical framework for infrasonic hearing mechanisms in birds and other animals.

*Key words*: avian hearing, infrasound, low frequency hearing, bone conduction, basilar papilla, paratympanic organ, atmospheric pressure, vestibular organs.

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# **I. INTRODUCTION**

Infrasound, conventionally defined as frequencies below 20 Hz, refers to sounds that are usually thought to be inaudible to humans. By definition, therefore, infrasound is an anthropocentric concept. In actuality, humans can hear sounds below 20 Hz, but only at very high sound levels (Moller & Pedersen, 2004). In the animal kingdom, large mammals such as elephants and whales produce infrasonic communication signals, which are perhaps the most obvious examples of potential use of infrasound by animals (Berchok, Bradley & Gabrielson, 2006; Narins, Stoeger & O’Connell-Rodwell, 2016). The detection of underwater sound below 20 Hz has also been described in fishes and aquatic invertebrates (Packard, Karlsen & Sand, 1990; Sand & Karlsen, 2000). Tests of hearing sensitivities to airborne infrasound, however, are restricted to a few species of mammals and birds (Merzenich, Kitzes & Aitkin, 1973; Heffner & Heffner, 1982; Narins *et al.*, 2016). Infrasound is a pervasive feature of the global soundscape, and therefore could potentially provide ecologically relevant information to animals that are able to detect it. Our understanding of the potential uses of infrasound by animals, however, is limited by the fact that auditory tests typically do not include these low frequencies.

The ability to detect airborne infrasound has been documented in a few bird species. The early studies were conducted on the pigeon (*Columba livia*) (Yodlowski, Kreithen, & Keeton, 1977; Kreithen & Quine, 1979). Since that initial discovery, subsequent studies replicated the initial findings in pigeons and expanded tests of infrasonic hearing to other bird species (Theurich, Langner & Scheich, 1984; Warchol & Dallos, 1989; Schermuly & Klinke, 1990*a*; Heffner *et al.*, 2013; Heffner, Koay & Heffner, 2016; Hill *et al.*, 2014; Hill, 2017). Aside from direct tests of infrasonic hearing ability, there has also been interest in the possible roles of avian infrasound detection as a navigational cue (Quine & Kreithen, 1981; Hagstrum, 2013, 2019) or as a communication channel (Lieser, Berthold & Manley, 2006; Freeman & Hare, 2015). However, at present there is no comprehensive synthesis of the known infrasonic hearing abilities of birds, and infrasonic hearing mechanisms in birds remain poorly understood (Narins *et al*., 2016). Infrasonic communication of vertebrates (Narins *et al.*, 2016) and infrasonic auditory mechanisms in humans (Salt & Hullar, 2010), however, have been reviewed elsewhere.

Here we review infrasonic hearing abilities in birds and evaluate several candidate auditory mechanisms that could underlie this ability. We first describe acoustic properties of geophysical sources of infrasound in the environment and its measurement. We then evaluate the methodologies used to test bird hearing of infrasonic frequencies, discuss various hypothesized mechanisms for infrasonic hearing in birds, and finally emphasize new avenues for research in this topic.

# **II. INFRASOUND IN THE ENVIRONMENT AND ITS MEASUREMENT**

Infrasound, or low-frequency acoustic waves, refers to small pressure perturbations with amplitudes on the order of (milli)pascals. These waves propagate at the speed of sound and exist on top of atmospheric pressure fluctuations due to the weather that have amplitudes on the order of (hecto)pascals. In the infrasonic frequency band, non-acoustic perturbations are due to atmospheric turbulence, i.e. wind noise (Raspet *et al.*, 2019). Infrasound is measured worldwide by infrasound stations that are part of the International Monitoring System (IMS), a global network devised for the verification of the Comprehensive Nuclear-Test-Ban Treaty (CTBT). Filters are in place for the reduction of wind noise and operate by averaging the pressure field around an infrasound sensor. Infrasonic sources are typically large and powerful, and displace large volumes of air. Propagation over large distances is facilitated by atmospheric waveguides and low absorption rates. As atmospheric absorption is proportional to the acoustic frequency squared, higher frequencies attenuate more rapidly (Waxler & Assink, 2019).

Infrasound stations typically consist of multiple microbarometers in a spatial configuration, i.e. an array. Microbarometers are highly sensitive differential barometers that can measure small pressure perturbations in the range of ~0.01–100 Pa. By using array processing techniques (e.g. den Ouden *et al.*, 2020) that search for a coherent signal propagating at the speed of sound, the acoustic component can be identified (Matoza *et al.*, 2013). While low noise levels are beneficial for detection, the use of arrays allows for the detection of signals in adverse noise conditions, with signal-to-noise ratios down to 0.3.

Most natural sources of atmospheric infrasound arise from geophysical cues (e.g. earthquakes, meteors, colliding ocean surface waves, surf) (Le Pichon, Blanc & Hauchecorne, 2010) in various frequency bands ranging from 3.3 mHz up to 20 Hz. Some sources of infrasound are transient, while others are nearly continuous. Meteors and earthquakes are examples of transient sources, while microbaroms, created by colliding of non-linear ocean waves (Waxler & Gilbert, 2006), are continuous sources with peak energy around 0.2 Hz. Human industrial and military activities also generate infrasound, which can have regular diurnal, weekly and seasonal patterns (Pilger *et al.*, 2018). These are produced by mining explosions, aircraft activity (both subsonic and supersonic), and explosions from nuclear and chemical weapons testing (Campus & Christie, 2010).

Brown *et al.* (2014) presented the inferred global low and high noise models based on IMS data (Fig. 1). The models are derived from Power Spectral Density (PSD) estimates from raw microbarometer data. The noise models vary strongly between the IMS sites. Hence, they include all measured pressure perturbations that fall within the 5 and 95 percentiles. Exceptionally large amplitude signals (e.g. from large volcanic or large meteor explosions) are excluded. These curves of ‘raw infrasound data’ include both infrasound as well as non-acoustic atmospheric fluctuations that arise due to the interaction of wind and turbulence around the infrasound sensors (Raspet *et al.*, 2019). At the low end, the microbarom peak is visible between 0.1 and 0.4 Hz (Fig. 1). Towards the high end of the global noise distribution, the curves are dominated by non-acoustic pressure perturbations. In general, the power increases towards low frequencies, so the infrasound range is an inherently noisy channel.

In the context of bird infrasound perception, the bird ear is capable of being stimulated by both non-acoustic and acoustic pressure perturbations at infrasonic frequencies, just as a single microphone will measure both wind and sound pressure fluctuations. The thresholds for detection of static shifts in atmospheric pressure in birds are on the order of 94 Pa (pigeons) to 2.8 kPa (ducks) (Lehner & Dennis, 1971; Kreithen & Keeton, 1974) and static pressure changes applied to the middle ear air cavity can produce displacements of middle ear structures in birds (Claes *et al.*, 2018), indicating that non-acoustic pressure fluctuations could stimulate the ear. Therefore, since both fluctuations co-occur in the environment, care needs to be taken when making interpretations of behavioural responses to acoustic infrasound as distinct from responses to non-acoustic pressure perturbations. The careful measurement and presentation of infrasound stimuli is also essential for evaluating infrasonic hearing abilities and auditory mechanisms, which are discussed in the following section.

# **III. TESTS OF HEARING SENSITIVITY**

## **(1) Audiograms**

Infrasonic hearing sensitivities have been tested in a small number of bird species (reviewed in Table 1). Various techniques have been used in terms of both acoustic stimulus presentation and response measurement. The methods used to create the audiogram sensitivity curves are important to evaluate because conclusions drawn about auditory mechanisms depend on how stimuli are presented and responses are recorded. Furthermore, thresholds determined using physiological metrics, while often informative about relative sensitivity across frequencies, can deviate significantly from behavioural metrics in terms of absolute sensitivity (e.g. Brittan-Powell, Dooling & Gleich, 2010). In infrasonic hearing experiments, the production of infrasound involved both closed-field (finite volume of air being compressed) and open-field (testing in an open space) stimuli. Responses involved electrophysiological measurements, as well as measurements (both behavioural and physiological) from training experiments to associate sounds with a shock stimulus.

The electrophysiological techniques all involved recording from auditory neurons, with stimulation within a closed volume that sealed over the ear canal (Theurich *et al.*, 1984; Warchol & Dallos, 1989; Schermuly & Klinke, 1990*a*). In training experiments, positive responses to infrasound were indicated by a change in heart rate (Kreithen & Quine, 1979) or by the cessation of pecking to receive food rewards (Heffner *et al*. 2013). The infrasound stimuli in these training experiments were delivered either as an open-field stimulus, using subwoofer speakers testing to frequencies as low as 2–16 Hz, depending on the study (Heffner *et al.*, 2013, 2016; Hill *et al.*, 2014; Hill, 2017) or a loudspeaker connected by a tube to a small sealed chamber, acting on a closed volume of air (Yodlowski *et al.*, 1977; Kreithen & Quine, 1979).

These different methods all generated similar overall audiogram shapes, with frequencies of best sensitivity at 2–3 kHz, following the typical bird audiogram pattern (Dooling, Lohr & Dent, 2000). All species displayed similar patterns of increasing thresholds (indicating a decreasing auditory sensitivity) towards lower frequencies (Fig. 1), although the rate of this decrease in sensitivity varied among species. From 250 Hz to 2 Hz, the average increase in threshold in pigeon and chicken (*Gallus gallus*) was 8–9 dB/octave (halving of frequency), whereas it was 12–13 dB/octave in the mallard duck (*Anas platyrhynchos*) and budgerigar (*Melopsittacus undulatus*).

Across the studies, only a subset of the tested species of birds showed sensitivity to infrasound. Among the five species measured, the chicken, guinea fowl (Numididae), and pigeon exhibited greater sensitivity to infrasound (threshold ~60 dB at 20 Hz), and the budgerigar and mallard duck were less sensitive (threshold ~90 dB at 20 Hz) (Fig. 1). The absence of infrasound responses was also reported in the black-headed gull (*Chroicocephalus ridibundus*), tested using the same experimental technique as for guinea fowl (unpublished remark in Theurich *et al.*, 1984).

The ability to hear infrasound therefore varies among birds. At low frequencies above 20 Hz, birds show a wide range of hearing abilities, further suggesting a range of infrasonic hearing ability. For example, small passerines such as canary (*Serinus canaria*) and zebra finch (*Taeniopygia guttata*), with their relatively high thresholds at low frequencies (near 60 dB re 20 µPa at ~250 Hz: Okanoya & Dooling, 1987), could be expected to have poor infrasound sensitivity. By contrast, some species of owls, with thresholds near 10–20 dB re 20 µPa at 250 Hz (Dyson, Klump & Gauger, 1998), could be expected to have relatively greater infrasound sensitivity.

In a broader comparison with mammals, it is also the case that some mammalian species are clearly sensitive to low frequencies, including infrasound (e.g. mountain beaver *Aplodontia rufa*, black-tailed prairie dog *Cynomys ludovicianus*, elephant *Elephas maximus*) (Merzenich *et al.*, 1973; Heffner & Heffner, 1982; Heffner *et al*., 1994), while other species (e.g. mice, bats) are quite insensitive to low frequencies. The latter group has audiograms that are tuned to best frequencies above 10 kHz (e.g. see Fig. 3 of Grothe & Pecka, 2014). As a group, birds have a narrower hearing range relative to mammals, with lower best hearing frequencies in the range of several kHz (Dooling *et al*., 2000). Therefore, there could be, arguably, greater potential for infrasonic hearing in birds. If strictly behavioural audiograms are compared, infrasonic hearing thresholds determined for birds that are sensitive to infrasound (chicken and pigeon) are in a similar range as those of terrestrial mammals with exceptional low frequency hearing abilities: for the black-tailed prairie dog 90 dB at 4 Hz (behavioural audiogram: Heffner *et al*., 1994), and for the elephant 65 dB at 16 Hz (behavioural audiogram: Heffner & Heffner, 1982) (Fig. 1).

## **(2) Behavioural responses to infrasound playbacks**

Infrasound has been reported from wing beating display behaviours of two galliform birds: capercallie (*Tetrao urogallus*) and peafowl ([*Pavo cristatus*](https://en.wikipedia.org/wiki/Pavo_cristatus)). In both cases, however, since only a single microphone was used, the recordings cannot distinguish the acoustic component from non-acoustic pressure perturbations. The behavioural responses to conspecific playback experiments for such infrasonic signals are mixed. The ‘flutter jump’ displays of capercallie produce energy with peaks near 8 and 17 Hz at sound levels up to 70 dB (Lieser, Berthold & Manley, 2005), but playback to reproductive females did not cause any changes in behaviour, indicating the sound may simply be a by-product and not a communication signal (Lieser *et al.*, 2006). By contrast, in response to the peafowl’s shaking of train feathers (producing energy around 4–12 Hz up to 90–108 dB), individuals responded by adjusting their movement, alertness, and calling behaviour (Freeman & Hare, 2015), suggesting that the infrasound produced could be involved in conspecific signalling.

The production of infrasound through the vocal tract in small birds is likely to be limited given that a large air volume displacement is required to produce infrasound. However, some large birds such as cassowaries produce fundamental frequencies as low as 23 Hz (Mack, Jones & Nelson, 2003). It is also interesting to note that the species found to detect infrasound (pigeon, chicken, and guinea fowl), are found in taxonomic groups that include members known to produce low frequency closed-mouth vocalizations (Columbiformes and Galliformes) (Riede *et al*., 2016). This association indicates a possible link between low frequency acoustic communication and infrasonic hearing ability.

## **(3) Methodological considerations**

One challenge associated with testing infrasonic hearing abilities in birds is the replication of an airborne infrasound wave impinging on the body in a laboratory setting. Infrasound sources can simultaneously produce non-acoustic pressure perturbations, which are high-amplitude stimuli, but not infrasound. For example, for the wing-beating displays described for peafowl, it is not clear whether a bird responding to another bird beating its wings is responding to the acoustic component (either the pressure or particle velocity component – see online Supporting information, Appendix S1), or a mechanical, non-acoustic ‘flow’ of the moving air.

Another stimulus delivery concern is the use of closed delivery systems, which in electrophysiological studies have been the only method of stimulus delivery. In this setup, the acoustic source is sealed over the auditory canal rather than at some distance from the animal. Although sound levels can be reached more easily with a closed delivery system, the drawback of this approach is that it exaggerates the role of the middle ear rather than extra-tympanic pathways. Since they are sealed over the ear, closed delivery systems over the eardrums are unlikely to stimulate possible extratympanic pathways (see Section IV.3*b*).

The stimulation of extratympanic pathways with an open-field stimulus, however, is still not an easy task. The production of infrasound requires large equipment and insulation of the experiment from background noise. Conventional speakers are often not capable of producing infrasound, however, subwoofer speakers coupled with added resonating chambers can achieve the necessary volume displacements, and have been used effectively to produce sounds down to a few Hz (e.g. Hill *et al.*, 2014). It is also necessary to check whether the infrasonic stimulus produces any incidental energy at higher frequencies (i.e. harmonics). The presence of such harmonics in the stimulus could produce misleading results if the animal’s response is related to the harmonics rather than the test frequency of interest.

Another challenge in testing infrasonic hearing abilities is dealing with masking. Infrasound is a noisy channel (Fig. 1) and is not easily shielded, making it difficult to create quiet testing conditions. In most cases, the infrasound audiometry studies on birds to date have not completely characterized the background infrasound noise during experiments (Table 1), so it is not clear to what extent these thresholds to infrasound stimuli were masked by ambient noise. Data on the threshold shifts induced by masking noise (i.e. critical ratios; Erbe *et al.*, 2016) are available for a number of bird species, including pigeons and budgerigars (Hienz & Sachs, 1987; Dooling *et al*., 2000). However, no frequencies below 250 Hz were tested and extrapolation to the much lower infrasound frequencies involves unsupported assumptions about frequency-tuning mechanisms. Thus, the extent to which the known infrasonic thresholds might be elevated relative to quiet conditions remains speculative.

# **IV. AUDITORY STRUCTURES AND TRANSMISSION**

## **(1) Overview of the avian peripheral auditory system**

The bird auditory system can be partitioned into the middle ear and inner ear. Birds typically have a minimal outer ear, consisting of a short external auditory meatus. The basic mechanical function of the tympanic middle ear is to transmit airborne sounds into fluid vibrations in the inner ear. The vibrations of the tympanic membrane are transmitted through a cartilaginous, trifurcated extracolumella onto the bony columella and its footplate in the oval window (Fig. 2). The vibrations of the columella produce pressure waves in the fluid-filled inner ear, which stimulate the main auditory organ, the basilar papilla, running along the length of the cochlea. Pressure release occurs into the air-filled middle ear cavity *via* the round window.

The basilar papilla is supported in the middle of the cochlear duct by soft cartilaginous limbic tissue on either side towards the edges of the cochlear tube (Fig. 2C). The avian basilar papilla is ‘tonotopically’ organized, such that cells at the apical end respond best to low frequencies and cells at the basal end respond best to high frequencies. At the apex of the cochlea there is a communication between perilymph fluid in the scala tympani and scala vestibuli – the helicotrema. In birds, the anatomy of the helicotrema is complex. The scala tympani splits near the apical end of the cochlear duct, into a cavum scalae tympani, a blind recess in the limbus (the cartilagenous tissue supporting the basilar papilla on either side), and a ductus scalae tympani which continues into the helicotrema (Schwartzkopff & Winter, 1960; Kohllöffel, 1984). In addition to the duct at the apical end, a duct at the basal end, the ductus brevis, has also been observed (Kohllöffel, 1984). The cochlear aqueduct, a fluid-filled canal communication between the perilymph of the ear and the brain cavity, is present in all birds, but can be quite large in some species (Kohllöffel, 1984), and provides another opening to the fluid spaces of the inner ear.

Birds have other hair cell end organs besides the basilar papilla: the vestibular organs and the paratympanic organ. Hair cells in the vestibular system include the cristae of the semicircular canals, which detect rotational accelerations, and three otolithic vestibular organs, which detect linear accelerations: the saccule and utricle are located in the vestibule and the lagena is located in the apical end of the cochlea duct. The hair cells in these organs are embedded in a gelatinous matrix and are attached to otoconial masses. The paratympanic organ is a collection of hair cells peripheral to the inner ear, with ligamentous attachment to the columella and tympanic membrane (von Bartheld, 1994).

## **(2) Quantifying vibration transmission in the auditory system: impedance and transfer functions**

Hearing involves the conversion of airborne sounds into vibrations in tissues and fluids. The bandwidth of hearing is determined by the magnitude of vibration transmission across frequencies at multiple structural levels of the auditory system, including both middle and inner ear (Ruggero & Temchin, 2002). Vibration transmission through each of these levels can be understood in terms of impedance. Acoustic impedance describes the opposition of a structure to vibrational motion for an applied pressure, or simply the ratio between pressure and velocity. Impedance can be decomposed into resistance and reactance impedance components. Resistance impedance describes the loss of acoustic energy due to friction, while reactance impedance describes the effects of a material’s mass and stiffness. The attribution of impedance in the ear to different impedance components can be determined by the relationship between the vibration amplitude and frequency, as well as the phase relationship between the pressure and measured vibration velocity (see Appendix S2).

The performance of the ear is often measured as a transfer function of vibration transmission through the middle ear. This transfer function (in units of m/s/Pa) is inversely related to the impedance. The transfer function is measured on the tympanic membrane or columella with either a laser vibrometer or capacitive probe (Saunders, 1985; Arechvo *et al.*, 2013). The vibration of the columella represents the combined impedances of the inner ear and middle ear, since the inner ear adds a load to the vibrating middle ear (draining the inner ear fluid and measuring the resulting difference in the transfer function is a way to estimate the inner ear impedance).

The bird middle ear transfer functions have a peak or frequency band that varies to some degree among species (Fig. 3A). At low frequencies, the vibrations measured from pigeon and chicken exceed those measured from the mallard duck, which aligns with the poorer low frequency hearing of the mallard duck measured in the audiograms. The middle ear transfer function of the ostrich (*Struthio camelus*) peaks at 250 Hz, suggesting excellent low frequency hearing (Arechvo *et al.*, 2013). For all species, the middle ear transmits less sound energy as frequency decreases below the frequencies of peak vibration velocities. A 6 dB/octave decline in the middle ear velocity transfer function (i.e. velocity amplitude declines in direct proportion with frequency) is one indication of an impedance dominated by a stiffness impedance component (see Appendix S2). Such a decline is the typical pattern observed below the resonance frequency in other tetrapods with tympanic middle ears (anurans, reptiles, and mammals) (Saunders & Johnstone, 1972).

## **(3) Transmission from air to inner ear**

### (*a*) *Middle ear (tympanic pathway): stiffness as a limiting factor for infrasound transmission*

The audiograms of animals with tympanic middle ears reflect both the middle ear transfer functions and the sensitivity of the inner ear organs. Due to the middle ear’s significant role in augmenting the pressure reaching the inner ear, usually the most sensitive frequencies in the audiogram correspond to the frequencies of peak vibration of the middle ear (Saunders *et al.*, 2000). This can be seen by comparing the frequencies corresponding to the minima of audiograms with the maxima of the middle ear transfer functions in Fig. 3A.

The middle ear transforms airborne sound into fluid vibrations in the inner ear. This ‘impedance transformation’ function occurs by the augmentation of the pressure from the tympanic membrane to the columellar footplate, which occurs as a consequence of relative differences in area between these two structures (i.e. area ratios), as well as through lever mechanisms (Saunders *et al.*, 2000). However, area and lever ratios do not account for reactance impedance components (incorporating mass and stiffness), and therefore are likely not strong anatomical predictors of auditory transmission in the infrasonic hearing range. Furthermore, these metrics have limited predictive power in the peak regions of the middle ear transfer function (e.g. due to energy losses in the middle ear, and due to complex modes of middle ear vibration where the columella does not transmit all vibrational input as a rigid piston motion). For further details on criticisms of impedance transformer measurements, see Rosowski (1994) and Mason (2016).

Middle ear stiffness plays a role in limiting infrasound reaching the inner ear in human audiometry, and a similar effect likely also occurs in birds. In the human ear, middle ear impedance at low frequencies shows a stiffness-dominated impedance, increasing at 6 dB/octave as frequencies are lowered (Merchant, Ravicz & Rosowski, 1996; Aibara *et al.*, 2001; Salt & Hullar, 2010; Jurado *et al.*, 2017; Raufer, Masud & Nakajima, 2018). From the declines of approximately 6 dB/octave at the low frequency flanks of the bird middle ear transfer functions (Fig. 3A), we can also infer that the low frequency hearing limits are stiffness dominated. Phase shifts, where they have been measured in the pigeon, also support a stiffness-dominated impedance of the middle ear (Gummer, Smolders & Klinke, 1989).

A low total middle ear stiffness could occur by lowering the stiffness of the structures in the ossicular chain (i.e. tympanic membrane, extracolumella, columella, and associated ligaments) and enlarging the air cavity behind the tympanic membrane (Mason, 2016). The cartilaginous extracolumella is more easily displaced than the bony columella (Claes *et al.*, 2018), so a relatively larger extracolumella might translate into a lower total middle ear stiffness. The stiffness of the ligament holding the columella in the oval window (the ‘columella annular ligament’) also appears to play a role in middle ear stiffness at low frequencies (Lynch, Nedzelnitsky & Peake, 1982).

### (*b*) *Extratympanic pathways*

Whole-body vibrations could be a significant infrasound pathway in birds. Whole body vibration, where the body and head vibrate as one unit, represents a simple form of bone conduction [see Stenfelt (2013) for more complex bone conduction pathways]. At conventional audio frequencies, the absence of pressure amplification mechanisms in most body tissues means that the airborne vibration transmission through extratympanic tissues will be much lower than through the middle ear. Therefore, the detection of airborne sound through the vibration of the whole head is generally a much less effective hearing route than through the middle ear pathway – in fact, this likely led to the evolution of the tympanic middle ear (Christensen-Dalsgaard & Carr, 2008; Manley, 2017*a*).

Based on the assumption that the middle ear is limited by stiffness impedance at very low frequency, we can extrapolate a 6 dB/octave decline to predict bird middle ear transfer functions at infrasonic frequencies and compare them with vibrations measured in extratympanic tissues (Fig. 3B). In contrast to the middle ear measurements, the vibrations of extratympanic tissues in several organisms (salamander, human forehead, etc.) do not show a similar decline with decreasing frequency. Therefore, from a certain frequency downwards, the middle ear may not vibrate with a significantly greater magnitude than other unspecialized body tissues, and the likelihood of a dominant transmission path for infrasound through non-tympanic tissues increases.

Experimental studies on the hearing abilities of non-tympanic tetrapods (e.g. snakes, salamanders, anurans lacking tympanic middle ears) support the hypothesis that low-frequency airborne sounds can stimulate the ear through extratympanic mechanisms (Wilczynski, Resler & Capranica, 1987; Christensen *et al.*, 2012, 2015). Indeed, for small animals, such as anurans, extratympanic mechanisms dominate the auditory responses below 300 Hz (Wilczyinski *et al*., 1987), and smaller, ‘earless’ frogs (with a non-functional middle ear) even have comparable sensitivity to similar-sized eared frogs up to 1000 Hz (Womack *et al.*, 2018).

In humans, bone conduction measurements indicate the skull undergoes translational motion (i.e. moving as a rigid body back and forth) at low frequencies (von Békésy, 1948; Stenfelt & Goode, 2005; Stenfelt, 2013). At frequencies where *ka*, the product of wavenumber and radius, is smaller than 1, acoustic models predicts the absence of wave propagation into the bird body, but rather a translational motion, and at these frequencies the translation only depends on sound pressure and the density of the object. A physical model for an object vibrating in a free sound field (based on von Békésy, 1984) conforms with experimental vibration data measured from extratympanic tissues and supports this idea (Fig. 3B; see Appendix S3).

### (*c*) *Tests of the relative importance of tympanic and extratympanic pathways*

The relative contributions of extratympanic and tympanic pathways will be a species-specific and frequency-specific function that depends on the relative differences between the head and middle ear transfer functions. The middle ear transfer function at low frequencies depends primarily on stiffness, while the von Békésy model (see Appendix S3) suggests that the vibration amplitude of the extratympanic transfer function depends on density. Therefore, according to a whole-body vibration model, birds with a relatively low body density (0.6–0.9 g/cm3 range as measured by Hamershock, Seamans & Bernhardt, 1993), could be vibrated directly by airborne infrasound.

Despite the expectation for declining vibrations and increasing possibility of extratympanic stimulation at low frequencies, experiments involving damaging the tympanic membrane or columella lend some support to the hypothesis that the middle ear is the pathway for the detection of infrasound. In an experiment on pigeons, clipping the columella effectively removed infrasound responses (Yodlowski *et al.*, 1977). In chickens, perforating the tympanic membrane resulted in threshold elevations greater than 47 dB at 32 Hz, along with an inability to measure any infrasound responses due to thresholds exceeding the sound level capacities of the subwoofer (Hill *et al.*, 2014). However, a threshold shift following clipping the columella does not definitively demonstrate a tympanic pathway because bone conduction thresholds also depend on the stiffness of the openings to the inner ear. Clipping the columella could also elevate bone-conducted thresholds to some extent (e.g. Zhao, Fridberger & Stenfelt, 2019), possibly by reducing the impedance of the oval window and shunting vibrational energy away from the cochlea.

One way to examine contributions from tympanic *versus* extratympanic stimulation pathways would be to compare auditory sensitivities when infrasound is presented as an airborne stimulus as opposed to strictly a vibrational stimulus. If the magnitude of the head vibration at auditory threshold is similar in both conditions, it is an indication that head vibration (i.e. an extratympanic pathway) is sufficient to drive the auditory response to the airborne sound. This type of experimental approach has been used to test low frequency hearing in a snake (below 300 Hz), and demonstrated that the induced vibration of the head was sufficient to explain sensitivity to airborne sound (Christensen *et al*., 2012).

## **(4) Inner ear: low frequency impedance and shunting**

The input impedance of the cochlea is a major determinant of the frequency limits, both high and low, of the stimuli reaching the hair cells in the inner ear. Functional measurements of inner ear impedance in birds are almost non-existent, so it is difficult to draw general conclusions for this group. Data at low frequencies (down to 1 Hz) have only been obtained directly for one bird species, the ostrich (Muyshondt, Aerts & Dirckx, 2016*a*). This study found a regular increase in impedance of the inner ear at 6 dB/octave between 20 Hz and 1 Hz, ranging from 109 to 1010 Pa s/m3, and above 200 Hz (no measurements taken between 20 and 200 Hz)(Muyshondt *et al.*, 2016*a*). Furthermore, the ostrich inner ear impedance values were far below those measured for mammals (by one to two orders of magnitude). By comparison, the inner ear impedances of mammals typically have a relatively uniform magnitude across a large frequency range (see Table 1 of de La Rochefoucauld *et al.*, 2008), but tend to increase at very low frequencies, below 100 Hz. For example, at 20 Hz, the impedance is 3 × 1011 Pa s/m3 in humans (Merchant *et al.*, 1996), and 1 × 1011 Pa s/m3 in the guinea pig (*Cavia porcellus*) (Dancer & Franke, 1980). As already concluded above for the middle ear, the increasing impedance of the ostrich inner ear at low frequencies indicates that inner ear stiffness limits low-frequency vibration transmission. Whether a similar stiffness dominance to the inner ear occurs in smaller birds (i.e. most other birds), will have to be tested experimentally.

The round window and helicotrema are often invoked as important contributors to the low frequency stiffness impedance of the ear (Lynch *et al.*, 1982; Ruggero & Temchin, 2002). The round window of birds is typically large (larger than the oval window; Schwartzkopff & Winter, 1960) and could be a significant parameter lowering the inner ear resistance impedance. In addition, the stiffness of the cochlear partition itself will contribute to the total stiffness of the inner ear. The cochlear partition in birds and other amniotes includes softer, fibrocartilage-like limbic supports on either side of the basilar papilla (Fig 2C) (Manley, 2017*b*). This contrasts with the mammalian condition, where these supportive shelves (laminae) are bony (Manley, 2017*b*). The lower stiffness of the cochlear partition in birds could confer an advantage to low frequency hearing in birds by reducing the inner ear impedance at low frequencies.

Comparative anatomy of the inner ear of birds has revealed considerable species-specific variation in inner ear structures and prompted speculations about shunting acoustic energy through different pathways, in particular in relation to the helicotrema and the cochlear aqueduct (Schwartzkopff & Winter, 1960; Kohllöffel, 1984).

### (*a*) *Helicotrema*

In mammals, the size of the helicotrema varies among species and has been identified as a major factor determining the low frequency impedance of the cochlea (Dallos, 1970). The rationale is that a larger, low-resistance helicotrema would decrease the fluid pressure impinging on the basilar papilla, allowing low frequencies to bypass the basilar papilla. By contrast, a small, higher resistance helicotrema would diminish this shunting, forcing fluid pressure onto the basilar papilla, thereby enhancing low-frequency sensitivity. In humans, the shunting of low frequencies through the helicotrema is estimated to add an additional 6 dB/octave attenuation beginning at 40–100 Hz, beyond the 6 dB/octave attenuation attributed to the middle ear (Salt & Hullar, 2010). Findings by Kohllöffel (1984) fit the predicted effects of the helicotrema on low frequency hearing. The latter author noted a wide helicotrema in ducks and geese, and a narrower helicotrema in galliform birds, which matches the predicted association between a smaller helicotrema and greater sensitivity to infrasound (Fig. 1).

### (*b*) *Cochlear aqueduct*

Kohllöffel (1984) noted that the cochlear aqueduct can be very large in some birds (particularly aquatic birds), sometimes as large as the round window, the main vibration outlet of the inner ear (Fig. 2C, D). A cochlear aqueduct would have low-pass characteristics as it is modelled as a tube with resistance and mass impedance components (Gopen, Rosowski & Merchant, 1997). While increasing the length of the tube increases its acoustic mass impedance component, increasing the tube radius would lower both its resistance and mass impedance components (see equations 1 and 2 and Fig. 7 in Gopen *et al*., 1997). Consequently, as the diameter of the cochlear aqueduct increases, the total resistance impedance component is reduced at all frequencies, and due to a reduction in the mass impedance component, higher frequencies also pass through more easily.

The cochlear aqueduct potentially has several different effects on auditory function, which could depend further on whether tympanic or extratympanic pathways are involved. First, by providing an extra opening for vibration release, the cochlear aqueduct could add to the effect of the round window to lower the total inner ear impedance at low frequencies. Alternatively, the cochlear aqueduct could shunt energy away from the apical end of the basilar papilla and into the cranial cavity. This possibility could be most likely if there is a large ductus brevis, so that vibrational energy would bypass the cochlear partition and cochlea and pass into the cochlear aqueduct. For example, vibration transmission measured at the round window in human ears is significantly reduced at infrasonic frequencies when an opening is introduced in the superior canal (superior canal dehiscence), and this reduction increases as frequency is lowered (Raufer *et al.*, 2018).

A third hypothetical consequence of a large cochlear aqueduct could be enhanced sensitivity to sound through a bone-conducted route. Experimental studies have demonstrated that bone conduction involves the transmission of fluid vibrations within the brain cavity to the inner ear (Freeman, Sichel & Sohmer, 2000; Sohmer *et al.*, 2000), and enhances sensitivity to bone-conducted sound when there are abnormally large ‘third windows’, i.e. additional openings to the inner ear (Merchant & Rosowski, 2008; Stenfelt, 2013). These studies focused on third windows caused by semicircular canal dehiscence and large vestibular aqueduct syndrome, but according to the same principle, a larger cochlear aqueduct would allow greater vibrational input to reach the ear.

In summary, the cochlear aqueduct would act as a low-pass filter in and out of the ear, and is therefore expected to be relevant for infrasonic hearing. However, due to multiple interactive variables affecting transmission in the inner ear and the lack of experimental data, it is difficult to make a simple prediction for the consequences of cochlear aqueduct size on infrasonic hearing ability.

## **(5) Scaling low frequency hearing with ear dimensions**

In mammals, associations between body size and low frequency hearing exist; species with larger cochleae and middle ears tend to show shifts in hearing ranges to lower frequencies (West, 1985; Rosowski, 1992; Kirk & Gosselin-Ildari, 2009; Wannaprasert & Jeffrey, 2015). Whether similar relationships exist in birds is not clear. A comparative analysis of audiograms from 15 bird orders suggested that small body size could be a constraint on their low frequency hearing abilities (Dooling *et al.*, 2000). Ostriches, with their comparatively low-frequency middle ear transfer function and low-impedance inner ear, support this scaling effect (Arechvo *et al.*, 2013; Muyshondt *et al.*, 2016*a*). Altogether, the data indicate that while there is a reasonable expectation that larger birds could have an advantage in hearing lower frequencies, a comprehensive, phylogenetically controlled comparative study on this topic is still missing.

# **V. AUDITORY SENSORS**

Neurophysiological data in pigeons, chickens, and guinea fowl have indicated that the hair cells within the basilar papilla respond to infrasound. However, there is also a rationale for expecting infrasonic responses from hair cells distributed in other end organs, the vestibular organs and paratympanic organ. Otolithic vestibular organs are known to respond to airborne infrasound and are tuned to low frequencies. The paratympanic organ resides outside the inner ear, and is presumed to function as a barometer and altimeter. The responsiveness of these latter organs to atmospheric infrasound remains to be tested.

## **(1) Basilar papilla**

### (*a*) *Evidence for infrasound detection*

Electrophysiological recordings from auditory brain regions in the pigeon and in galliform birds provide evidence linking infrasound detection to cells in the basilar papilla. Recordings from the auditory midbrain in the guinea fowl (Theurich *et al*., 1984) and from the cochlear nucleus in the chicken (Warchol & Dallos, 1989) – which are exclusively auditory regions with no vestibular inputs – point to the detection of infrasound by sensory cells of the basilar papilla. Further support for infrasound detection through the basilar papilla is the demonstration that behavioural responses to infrasound in pigeons cease after removing the cochlea (Yodlowski *et al*., 1977). However, the vestibular lagenar macula was also removed by the surgery in that study, so this manipulation was confounded by the simultaneous removal of two candidate infrasound receptors.

The most direct evidence comes from single-unit recordings in the cochlear ganglion of pigeons, responding at 1–20 Hz, combined with staining of a subset of fibres which were traced back to the apical end of the basilar papilla (Schermuly & Klinke, 1990*a*,*b*). Two observations indicate that these recordings can be attributed to the basilar papilla, and not the lagena. First, none of the recordings were traced back to the lagena in the labelling experiments (Schermuly & Klinke, 1990*b*). Each neuron received input from multiple hair cells (2–10), which were distributed along the abneural side of the basilar papilla (opposite the side where the auditory nerve fibres enter). Second, the neural responses were closely time-locked to the phase of the acoustic stimuli, but only encoded one particular phase of the periodic stimuli (Schermuly & Klinke, 1990*a*), which is expected from recordings from the basilar papilla, but not vestibular epithelia. In vestibular recordings, by contrast, single-unit responses would be expected to be seen regularly at two phases of a sinusoidal cycle, 180° apart, as a result of the opposing orientations of hair cells connecting to one afferent fibre in vestibular epithelia.

### (*b*) *Atypical hair cells in the chicken and pigeon*

In the pigeon and chicken, atypical hair cell patches – the ‘papilla chaotica’ and the ‘lenticular region’, respectively – have been observed at the apical end of the basilar papilla (Fig. 2C) and hypothesized to be specialized for the detection of infrasound (Lavigne-Rebillard, Cousillas & Pujol, 1985; Schermuly, Topp & Klinke, 1991). Both structures, however, lack any experimental verification linking them to infrasound detection. The papilla chaotica is an outcrop of hair cells which ascends the medial wall of the cochlea, and consists of approximately 200 hair cells (Schermuly *et al.*, 1991). Its atypical features include hair-cell bundles oriented in a number of different, irregular directions and hair-cell bundles that have retained a kinocilium. The lenticular region described in chickens is on the very apical edge of the basilar papilla. In this region, the hair cells show some resemblance to vestibular hair cells, with bundles having a long kinocilium and a rotation in the angle of stereocilia relative to the rest of the basilar papilla (Lavigne-Rebillard *et al.*, 1985). Here the apical surfaces of the hair cells are small, and larger spaces on the papilla are occupied by supporting cell microvilli.

The existence of morphologically unusual hair cell populations in the low frequency region of the basilar papilla in two species that are sensitive to infrasound naturally leads to hypotheses about possible specialized infrasound functions. However, at present, there is no clear model for how these hair cell patches might be mechanically tuned differently than other regions of the basilar papilla. An alternative hypothesis for the unique characteristics of the hair cells in these patches is that they are immature hair cells. Birds are capable of regenerating hair cells, and newly regenerated hair cells have unstructured orientations and small cell surface areas before completing development (Cotanche *et al.*, 1994).

### (*c*) *Hair cell tuning*

It is well established that the tonotopic gradient of characteristic response frequencies in the avian basilar papilla correlates tightly with hair-bundle morphology (Köppl, 2015). This principle has been used to predict the range of frequencies of the kiwi (*Apteryx mantelli*) basilar papilla using the bundle morphology of several bird species, thus yielding information for a species that is not readily available for physiological study (Corfield *et al.*, 2011). However, using the same equations as Corfield *et al.* (2011), infrasonic frequencies result in extreme and unlikely predictions of cell bundle morphologies. The well-known associations between bundle morphology and characteristic response frequency in the conventional audio range are not likely to extend into the infrasonic range. This is also consistent with what is known about neural tuning to different frequencies and the mechanisms underlying it (Gleich & Manley, 2000).

Hair cells that respond at infrasonic frequencies might instead achieve their selectivity largely through electrical tuning. Electrical tuning is the inherent oscillation of the hair-cell membrane potential in response to mechanical or electrical stimulation. This phenomenon plays a major role in shaping the frequency selectivity of auditory hair cells in non-mammalian species. The resonant frequency of hair-cell oscillation depends on the number and kinetics of two types of interplaying ion channels: voltage-activated Ca2+ channels (Cav1.3 type) that contribute to the depolarizing phase, and K+ channels, controlling the rate of K+ outflow from the hair cell, i.e. the re-polarizing phase (Fettiplace & Fuchs, 1999). The K+ channels in this tandem are primarily of the calcium-sensitive BK type, but – particularly in the hair cells tuned to the lowest auditory frequencies – may also be of a voltage-sensitive type (Art & Fettiplace, 2006).

Work in the chicken has revealed that in hair cells sensitive to very low frequencies (< 100 Hz), K+ channels of the delayed-rectifier and inward-rectifier types predominate (Fuchs & Evans, 1990; Navaratnam *et al.*, 1995; Fettiplace & Fuchs, 1999; Art & Fettiplace, 2006). Interestingly, Fuchs (1992) speculated that the kinetics of a third type of voltage-activated K+ channel, the inactivating type, would be well suited to enhance sensitivity to infrasonic frequencies. In the chicken, the distribution of hair cells expressing this inactivating type did not include the most apical, low frequency regions of the basilar papilla, however, it extended into abneural regions (Fuchs, 1992; Murrow, 1994), that, in the pigeon, were shown to be the site of infrasound representation (Schermuly & Klinke, 1990*b*).

Furthermore, a splice isoform of the Cav1.3 voltage-activated Ca2+ channel that contributes with its specific kinetics to low-frequency membrane oscillations (around 10 Hz) was recently shown to be expressed in electroreceptors of skates and sharks (Bellono, Leitch & Julius, 2017, 2018). Elasmobranch electroreceptors and hair cells are closely related, sharing a common origin (Baker & Modrell, 2018) and, indeed, very similar splice isoforms of Cav1.3 were observed in hair cells of the basilar papilla in chickens (Kollmar *et al.*, 1997) and pigeons (Nimpf *et al.*, 2019).

In summary, the hypothesis that electrical tuning of hair cells, by adapting the specific kinetics of complementary Ca2+ and K+ channels (and perhaps others), underlies infrasound sensitivity clearly has merit and is a promising avenue for future research. Since electrical tuning is a plesiomorphic trait of hair cells, the same mechanism and adaptations could, in principle, also be at work in vestibular endorgans and the paratympanic organ (see Section V.2).

### (*d*) *Neural tuning in the ascending auditory pathway*

The neurons that respond to infrasound exhibit broad frequency tuning and distinct coding properties when compared to neurons that respond to higher frequencies. In the chicken, rather than having a well-defined centre frequency with a typical ‘V’ shape (which is characteristic of higher-frequency auditory neurons), the infrasound neurons exhibit low-pass or very broad band-pass tuning (Warchol & Dallos, 1989). The ‘low-pass’ units showed no increase in thresholds as frequencies were reduced from 100 Hz to 10 Hz, but thresholds rose with frequency above 100 Hz. For the band-pass units, the *Q*10dB values (a metric of tuning sharpness) were very low, at 0.3–0.9, with best sensitivities close to 100 Hz (Warchol & Dallos, 1989). In the pigeon, other unique coding features were observed when sound level was increased. The neurons did not increase firing rate with increasing sound level, as auditory neurons generally do, but instead showed an improvement in phase locking (timing of neuron firing relative to the position in the sound cycle; Shermuly & Klinke, 1990*a*).

The broad frequency tuning of infrasound units matches with the position of their associated hair cells on the abneural side of the papilla. At this location on the basilar papilla, hair cells tuned to conventional audio frequencies tend to be less sharply tuned as well. In both the pigeon and starling, afferent fibres that receive input from hair cells located towards the abneural edge were more broadly frequency tuned than those synapsing on neurally located hair cells (Smolders, Ding-Pfennigdorff & Klinke, 1995, Gleich, 1989).

## **(2) Alternative candidate infrasound receptors**

### (*a*) *Vestibular organs*

In humans, vestibular organs respond to low vibrations and can be stimulated by low-frequency airborne sound (Todd, Rosengren & Colebatch, 2008; Rosengren, Welgampola & Colebatch, 2010). Stimulation of vestibular organs has been hypothesized to account for individuals complaining of motion sickness symptoms in response to infrasound emanating from wind farms in some sensitive individuals (Schomer *et al.*, 2015). However, a recent study failed to measure responses of vestibular organs to airborne infrasound delivered through earphones (Jurado & Marquardt, 2019).

In other animals – fishes, aquatic invertebrates, and frogs – otolith or statolith organs are sensitive to infrasonic particle motions and substrate vibrations (Narins & Lewis, 1984; Christensen-Dalsgaard & Buhl Jørgensen, 1988; Packard *et al.*, 1990; Karlsen, 1992), and the frog sacculus also responds to intense, low-frequency airborne sound (Moffat & Capranica, 1976). Birds have three otolith vestibular organs, (saccule, utricle, and lagena), which detect internal body accelerations at low frequencies. For example, the pigeon utricle responds to accelerations at 0.5–10 Hz (Si, Angelaki & Dickman, 1997). In addition to the otolith organs, the three ampullary cristae also respond to motion at infrasonic frequencies (Landolt & Correira, 1980), and therefore might be equipped to respond to infrasound. While there is some evidence suggesting a lack of involvement of the lagena in infrasound detection (Schermuly & Klinke, 1990*a*,*b*; see Section V.1*a*), involvement of the other otolith organs, the ampullary cristae, or the papilla neglecta (a vestibular organ sharing anatomical characteristics with both otolith and ampullary cristae) (Correira, Landolt & Young, 1974) has not yet been tested.

One way that the vestibular organs can be made more sensitive to airborne sounds is through third windows (Salt & Hullar, 2010). For example, in the pigeon, making a hole in the lateral semicircular canal allowed deafened pigeons to hear sound after the cochlea was removed (Wit, Bleeker & Mulder, 1984), indicating greater stimulation of the vestibular organs. However, from the view of performance of the whole organism, a very high sensitivity of vestibular receptors to infrasound might not be desirable if it produces side effects disturbing balance (e.g. the Tullio phenomenon, or sound-induced vertigo). Therefore, such modifications might be unlikely in birds sensitive to infrasound.

### (*b*) *Paratympanic organ*

The paratympanic organ has been hypothesized to be involved in both the detection of barometric pressure and infrasound (Kreithen & Quine, 1979; von Bartheld, 1994; von Bartheld & Giannessi, 2011), although definitive tests of these proposed functions in birds are still lacking. The paratympanic organ consists of hair cells embedded in a cupula, with a thin membrane separating the organ from the middle ear cavity (Jørgensen, 1984), positioned close to the pharyngotympanic (Eustachian) tube, and dorsolateral to the columella (von Bartheld, 1994). It has ligamentous attachments to the columella (*via* Platner’s ligament) and to the tympanic membrane (*via* the superior drum tubal ligament) (von Bartheld, 1994). In the brain, the paratympanic organ nerves project to vestibular nuclei (von Bartheld, 1990), entering with the facial nerve. This organ is homologous to the spiracular organ of non-teleost fishes, an organ involved in the hyomandibular jaw joint (von Bartheld, 1990; O'Neill, 2013).

Functional measurements on the paratympanic organ suggest stimulation of this organ in response to static pressure fluctuations, but its sensitivity to lower-magnitude pressure fluctuations at infrasonic frequencies remains untested. Pressure applied to the middle ear cavity (392–588 Pa), displaces fluid in the paratympanic organ, which should be an adequate stimulus for hair cells (von Bartheld, 1994). The paratympanic organ was found to be absent in palaeognathous birds (Starck, 1995) and two owl species (Neeser & von Bartheld, 2002). Several species in these groups have excellent low frequency hearing (Dooling *et al.*, 2000; Corfield, Kubke & Köppl, 2014), suggesting this organ might not be critical for low frequency hearing. Other roles for the paratympanic organ have been proposed, such as modifying the tension of the tympanic membrane, thereby serving a potential accessory role to hearing by modifying the stiffness impedance component of the middle ear (von Bartheld, 1994).

### (*c*) *Somatic sensation*

Another possible mechanism of infrasound reception is vibrotactile reception (Landström, Lundström & Byström, 1983). Birds have Herbst corpuscles, somatosensory vibration receptors, on their wings and legs (Shen & Xu, 1994). However, the peak sensitivity of these mechanoreceptors occurs at a few hundred Hz. The displacement sensitivity of these receptors (measured on the tarsus) at the lower frequency end is 30 µm at 100 Hz, with best displacement sensitivities found at 500 Hz (Shen & Xu, 1994). Crest feathers in peafowls are another speculated low-frequency somatosensory pathway; vibrations of crest feathers will oscillate at as low as 25 Hz in response to sound (Kane, Beveren & Dakin, 2018). A stronger role for the ear, rather than somatosensory vibration, is suggested by the removal of infrasonic responses following impairments of the tympanic middle ear (Yodlowski *et al*., 1977; Hill *et al*., 2014),

# **VI. FUTURE DIRECTIONS**

Studies on the responses of freely behaving birds to infrasound in field settings could provide insights into the biological relevance of infrasonic hearing to birds. For example, infrasound data sets from networks such as IMS (<https://www.ctbto.org/specials/vdec/>), in combination with data on bird behaviour (e.g. movement-tracking data), could be used to assess whether ambient infrasound correlates with bird movement over broad scales. The responses of birds to anthropogenic sources of infrasound (e.g. mining explosions or sonic booms), which can be relatively high-amplitude stimuli (on the order of several pascals), can also be informative natural experiments (e.g. Hagstrum, 2000).

Field studies, however, are faced with the challenge of verifying that the responses of the birds are indeed related to infrasound and not to non-acoustic pressure perturbations. Since birds in nature receive infrasonic stimulation amid a mixture of interfering signals (e.g. turbulence, wind), this is not a trivial task. Another related challenge is accurately estimating the infrasound stimulus as it would be perceived by a flying bird. While small infrasound sensors could be developed for deployment as biologgers on sufficiently large birds, such sensors would still record ‘mixed’ (i.e. both acoustic and non-acoustic) pressure signals in a complex noise field with large spatio-temporal variability.

Further infrasonic hearing tests in other birds, but also in reptiles and amphibians, would add significantly to a comparative understanding of infrasonic hearing in animals. At present, we do not know how taxonomically widespread infrasonic hearing abilities are in birds and other terrestrial tetrapod groups. Given that most infrasound sources are geophysical in nature, infrasonic hearing in a variety of species should be investigated and not be limited to those known to have infrasonic vocalization.

Laboratory studies will continue to be essential for testing the various mechanistic hypotheses. Comparisons between the physiological sensitivities to whole-body infrasonic vibrations and infrasound presented as an open-field, airborne stimulus will provide a test of the extratympanic hearing hypothesis. At the end-organ level, recordings from the vestibular system in response to airborne infrasound would be a natural next step to assess the extent to which auditory and vestibular systems may have overlapping roles in infrasonic hearing in birds. Further anatomical and experimental work on the helicotrema and large cochlear aqueduct, as well as experimental measures of inner impedance, would help to determine constraints on infrasound transmission in the inner bird ear. Finally, at a molecular level, advances towards identifying ion channels involved in tuning the hair cells to infrasonic frequencies could be made with genomic sequencing data and mapping of patterns of gene expression in the basilar papilla and vestibular endorgans, combined with electrophysiological characterization.

# **VII. CONCLUSIONS**

(1) Infrasonic hearing abilities have been described in a few bird species – the chicken, pigeon, and guinea fowl – with behavioural responses to infrasound seen in peafowl. Given the small number of experimental studies and the variation in low frequency sensitivity observed in birds (Fig. 1; Gleich & Langemann, 2011), it seems likely that bird infrasonic hearing abilities could be more phylogenetically widespread than just the species discussed here, and also that these abilities vary among birds.

(2) Different features associated with infrasound sources (acoustic pressure perturbations, non-acoustic pressure perturbations, and acoustic kinetic energy) could be detected. In addition, incompressible flow associated with infrasound (e.g. a wing beat) could also be detected. In infrasound hearing tests, stimulation *via* free-field subwoofers and a behavioural assay would provide the most natural stimulation scenario, to ensure both a natural sound field and the stimulation of all possible sensors through multiple pathways.

(3) Both tympanic and extratympanic pathways may be involved in avian infrasound perception. Middle ear manipulations suggest a role for the middle ear in pigeons and chickens, but do not completely rule out extratympanic mechanisms. The frequencies at which extratympanic hearing may become a dominant auditory pathway are expected to depend on the middle ear transfer function at low frequencies (controlled by stiffness) and a bird’s density. For birds with transfer functions shifted towards higher frequencies, any infrasound detection through an extratympanic route would become more likely, as compared to a bird with a very good low-frequency middle ear transfer function (e.g. ostrich).

(4) The stiffnesses of the middle ear and inner ear have significant roles in controlling the low-frequency hearing limit. A lower middle ear stiffness can be achieved by changes in the structural properties of the middle ear structures (tympanic membrane, extracolumella, columella, and columellar annular ligament) and increases in the volume of the cranial air cavities. In the inner ear, a large round window, large cochlear aqueduct, large helicotrema, and a soft-tissue cochlear partition could all contribute to reducing inner-ear impedance at low frequencies. However, a large helicotrema and cochlear aqueduct could also reduce infrasound stimulation by shunting vibrations away from low frequency hair cells in the apical cochlea.

(5) Some aspects of the physiology of infrasound detection by the basilar papilla have been resolved. Neurons responding to infrasound have low-pass or broad tuning and a lack of increase in firing rate with increasing frequency. In pigeons, neurons responding to infrasound receive input from hair cells in the apical, abneural region of the basilar papilla. Predictions for hair-cell bundle morphology in infrasound-sensitive hair cells from known correlations in the conventional audio range yield very unrealistic dimensions, suggesting that micromechanical frequency tuning does not play a prominent role. Instead, membrane ion channels may be specially adapted to tune the hair cells electrically to infrasound frequencies. The atypical hair cell patches hypothesized to be specialized for infrasonic hearing in the chicken and pigeon (lenticular region and ‘papilla chaotica’) still need experimental verification.

(6) Multiple sensory endorgans may be involved in infrasound perception. Although the detection of infrasound by the basilar papilla has been established, alternative receptors –various vestibular organs and the paratympanic organ – are also plausible but untested. Among these, the otolithic vestibular organs could be most promising, based on previous demonstrations of responses to low-frequency airborne sound in animals from frogs to humans. Somatosensory receptors do not appear to be primary infrasound detectors in birds.

 (7) This review brings together the various experimental and anatomical observations pertaining to infrasonic hearing in birds. Our evaluation presents a framework to advance the study of infrasound detection in birds and other animals.

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# **IX. REFERENCES**

Aibara, R., Welsh, J.T., Puria, S. & Goode, R.L. (2001). Human middle-ear sound transfer function and cochlear input impedance. *Hearing Research* **152**, 100–109.

Arechvo, I., Zahnert, T., Bornitz, M., Neudert, M., Lasurashvili, N., Simkunaite-Rizgeliene, R. & Beleites, T. (2013). The ostrich middle ear for developing an ideal ossicular replacement prosthesis. *European Archives of Oto-Rhino-Laryngology* **270**, 37–44.

Art, J.J. & Fettiplace, R. (2006). Contribution of ionic currents to tuning in auditory hair cells. In *Vertebrate Hair Cells* (eds R.A. Eatock, R.R. Fay & A.N. Popper), pp. 204–248. Springer, New York, NY.

Baker, C.V.H. & Modrell, M.S. (2018). Insights into electroreceptor development and evolution from molecular comparisons with hair cells. *Integrative and Comparative Biology* **58**, 329–340.

Berchok, C.L., Bradley, D.L. & Gabrielson, T.B. (2006). St. Lawrence blue whale vocalizations revisited: Characterization of calls detected from 1998 to 2001. *The Journal of the Acoustical Society of America* **120**, 2340–2354.

Bellono, N.W., Leitch, D.B. & Julius, D. (2017). Molecular basis of ancestral vertebrate electroreception. *Nature* **543**, 391–396.

Bellono, N.W., Leitch, D.B. & Julius, D. (2018). Molecular tuning of electroreception in sharks and skates. *Nature* **558**, 122–126.

Brittan-Powell, E.F., Dooling, R.J. & Gleich, O. (2002) Auditory brainstem responses in adult budgerigars (*Melopsittacus undulatus*). *The Journal of the Acoustical Society of America* **112**, 999–1008.

Brown, D., Ceranna, L., Prior, M., Mialle, P. & Bras, R.J.L. (2014). The IDC seismic, hydroacoustic and infrasound global low and high noise models. *Pure and Applied Geophysics* **171**, 361–375.

Campus, P. & Christie, D.R. (2010). Worldwide observations of infrasonic waves. In *Infrasound Monitoring for Atmospheric Studies* (eds A. Le Pichon, E. Blanc & A. Hauchecorne), pp. 185–234. Springer Netherlands, Dordrecht.

Christensen, C.B., Christensen-Dalsgaard, J., Brandt, C. & Madsen, P.T. (2012). Hearing with an atympanic ear: good vibration and poor sound-pressure detection in the royal python, Python regius. *The Journal of Experimental Biology* **215**, 331–342.

Christensen, C.B., Lauridsen, H., Christensen-Dalsgaard, J., Pedersen, M. & Madsen, P.T. (2015). Better than fish on land? Hearing across metamorphosis in salamanders. *Proceedings of the Royal Society of London B: Biological Sciences* **282**, 20141943.

Christensen-Dalsgaard, J. & Buhl Jørgensen, M. (1988). The response characteristics of vibration-sensitive saccular fibers in the grassfrog, *Rana temporaria*. *Journal of Comparative Physiology A* **162**, 633–638.

Christensen-Dalsgaard, J. & Carr, C.E. (2008). Evolution of a sensory novelty: Tympanic ears and the associated neural processing. *Brain Research Bulletin* **75**, 365–370.

Claes, R., Muyshondt, P.G.G., Dirckx, J.J.J. & Aerts, P. (2018). Deformation of avian middle ear structures under static pressure loads, and potential regulation mechanisms. *Zoology* **126**, 128–136.

Corfield, J., Kubke, M.F., Parsons, S., Wild, J.M. & Köppl, C. (2011). Evidence for an auditory fovea in the New Zealand kiwi (*Apteryx mantelli*). *PLOS ONE* **6**, e23771.

Corfield, J.R., Kubke, M.F. & Köppl, C. (2014). Emu and kiwi: the ear and hearing in paleognathous birds. In *Insights from Comparative Hearing Research* pp. 263–287. Springer, New York, NY.

Correia, M.J., Landolt, J.P. & Young, E.R. (1974). The sensura neglecta in the pigeon: A scanning electron and light microscope study. *Journal of Comparative Neurology* **154**, 303–315.

Cotanche, D.A., Lee, K.H., Stone, J.S. & Picard, D.A. (1994). Hair cell regeneration in the bird cochlea following noise damage or ototoxic drug damage. *Anatomy and Embryology* **189**, 1–18.

Dallos, P. (1970). Low‐frequency auditory characteristics: Species dependence. *The Journal of the Acoustical Society of America* **48**, 489–499.

Dancer, A. & Franke, R. (1980). Intracochlear sound pressure measurements in guinea pigs. *Hearing Research* **2**, 191–205.

de La Rochefoucauld, O., Decraemer, W.F., Khanna, S.M. & Olson, E.S. (2008). Simultaneous measurements of ossicular velocity and intracochlear pressure leading to the cochlear input impedance in gerbil. *Journal of the Association for Research in Otolaryngology* **9**, 161–177.

den Ouden, O.F.C., Assink, J.D., Smets, P.S.M., Shani-Kadmiel, S., Averbuch, G. & Evers, L.G. (2020) CLEAN beamforming for the enhanced detection of multiple infrasonic sources. *Geophysical Journal International* **221**, 305–317. Oxford Academic.

Dooling, R.J., Lohr, B. & Dent, M.L. (2000). Hearing in birds and reptiles. In *Comparative Hearing: Birds and Reptiles* pp. 308–359. Springer, New York, NY.

du Plessis, A., le Roux, S.G. & Guelpa, A. (2016) The CT Scanner Facility at Stellenbosch University: An open access X-ray computed tomography laboratory. *Nuclear Instruments and Methods in Physics Research Section B: Beam Interactions with Materials and Atoms* **384**, 42–49.

Dyson, M.L., Klump, G.M. & Gauger, B. (1998). Absolute hearing thresholds and critical masking ratios in the European barn owl: a comparison with other owls. *Journal of Comparative Physiology A* **182**, 695–702.

Erbe, C., Reichmuth, C., Cunningham, K., Lucke, K. & Dooling, R. (2016). Communication masking in marine mammals: A review and research strategy. *Marine Pollution Bulletin* **103**, 15–38.

Fettiplace, R. & Fuchs, P.A. (1999). Mechanisms of hair cell tuning. *Annual Review of Physiology* **61**, 809–834.

Freeman, A.R. & Hare, J.F. (2015). Infrasound in mating displays: a peacock’s tale. *Animal Behaviour* **102**, 241–250.

Freeman, S., Sichel, J.-Y. & Sohmer, H. (2000). Bone conduction experiments in animals – evidence for a non-osseous mechanism. *Hearing Research* **146**, 72–80.

Fuchs, P.A. (1992). Ionic currents in cochlear hair cells. *Progress in Neurobiology* **39**, 493–505.

Fuchs, P.A. & Evans, M.G. (1990). Potassium currents in hair cells isolated from the cochlea of the chick. *The Journal of Physiology* **429**, 529–551.

Gleich, O. (1989). Auditory primary afferents in the starling: Correlation of function and morphology. *Hearing Research* **37**, 255–267.

Gleich, O. & Langemann, U. (2011). Auditory capabilities of birds in relation to the structural diversity of the basilar papilla. *Hearing Research* **273**, 80–88.

Gleich, O. & Manley, G.A. (2000). The hearing organ of birds and crocodilia. In *Comparative Hearing: Birds and Reptiles* pp. 70–138. Springer, New York, NY.

Gopen, Q., Rosowski, J.J. & Merchant, S.N. (1997). Anatomy of the normal human cochlear aqueduct with functional implications. *Hearing Research* **107**, 9–22.

Grothe, B. & Pecka, M. (2014). The natural history of sound localization in mammals – a story of neuronal inhibition. *Frontiers in Neural Circuits* **8,** 116.

Gummer, A.W., Smolders, J.W.Th. & Klinke, R. (1989). Mechanics of a single-ossicle ear: I. The extra-stapedius of the pigeon. *Hearing Research* **39**, 1–13.

Hagstrum, J.T. (2000). Infrasound and the avian navigational map. *Journal of Experimental Biology* **203**, 1103–1111.

Hagstrum, J.T. (2013). Atmospheric propagation modeling indicates homing pigeons use loft-specific infrasonic ‘map’ cues. *Journal of Experimental Biology* **216**, 687–699.

Hagstrum, J.T. (2019). A reinterpretation of “Homing pigeons’ flight over and under low stratus” based on atmospheric propagation modeling of infrasonic navigational cues. *Journal of Comparative Physiology A* **205**, 67–78.

Hamershock, D.M., Seamans, T.W. & Bernhardt, G.E. (1993). Determination of body density for twelve bird species. In: [*Flight dynamics directorate, Wright laboratory*](https://scholar.google.com/scholar_lookup?title=Flight%20dynamics%20directorate,%20Wright%20laboratory&author=&publication_year=1993). Wright-Patterson AFB: Wright Laboratory.

Heffner, H.E., Koay, G. & Heffner, R.S. (2016). Budgerigars (*Melopsittacus undulatus*) do not hear infrasound: the audiogram from 8 Hz to 10 kHz. *Journal of Comparative Physiology A* **202**, 853–857.

Heffner, H.E., Koay, G., Hill, E.M. & Heffner, R.S. (2013). Conditioned suppression/avoidance as a procedure for testing hearing in birds: The domestic pigeon (*Columba livia*). *Behavior Research Methods* **45**, 383–392.

Heffner, R.S. & Heffner, H.E. (1982). Hearing in the elephant (*Elephas maximus*): Absolute sensitivity, frequency discrimination, and sound localization. *Journal of Comparative and Physiological Psychology* **96**, 926.

Heffner, R.S., Heffner, H.E., Contos, C. & Kearns, D. (1994). Hearing in prairie dogs: Transition between surface and subterranean rodents. *Hearing Research* **73**, 185–189.

Hetherington, T. (2001). Laser vibrometric studies of sound-induced motion of the body walls and lungs of salamanders and lizards: implications for lung-based hearing. *Journal of Comparative Physiology A* **187**, 499–507.

Hienz, R.D. & Sachs, M.B. (1987). Effects of noise on pure-tone thresholds in blackbirds (*Agelaius phoeniceus* and *Molothrus ater*) and pigeons (*Columba livia*). *Journal of Comparative Psychology* **101**, 16–24.

Hill, E.M. (2017). Audiogram of the mallard duck (*Anas platyrhynchos*) from 16 Hz to 9 kHz. *Journal of Comparative Physiology A* **203**, 929–934.

Hill, E.M., Koay, G., Heffner, R.S. & Heffner, H.E. (2014). Audiogram of the chicken (*Gallus gallus domesticus*) from 2 Hz to 9 kHz. *Journal of Comparative Physiology A* **200**, 863–870.

Jackson, L.L., Heffner, R.S. & Heffner, H.E. (1999). Free-field audiogram of the Japanese macaque (*Macaca fuscata*). *The Journal of the Acoustical Society of America* **106**, 3017–3023.

Jørgensen, J.M. (1984). Fine structure of the paratympanic organ in the avian middle ear. *Acta Zoologica* **65**, 89–94.

Jurado, C., Gallegos, P., Gordillo, D. & Moore, B.C.J. (2017). The detailed shapes of equal-loudness-level contours at low frequencies. *The Journal of the Acoustical Society of America* **142**, 3821–3832.

Jurado, C. & Marquardt, T. (2019). On the effectiveness of airborne infrasound in eliciting vestibular-evoked myogenic responses. *Journal of Low Frequency Noise, Vibration and Active Control*, 1461348419833868.

Kane, S.A., Beveren, D.V. & Dakin, R. (2018). Biomechanics of the peafowl’s crest reveals frequencies tuned to social displays. *PLOS ONE* **13**, e0207247.

Karlsen, H. (1992). The inner ear is responsible for detection of infrasound in the perch (*Perca fluviatilis*). *Journal of Experimental Biology* **171**, 163–172.

Kirk, E.C. & Gosselin-Ildari, A.D. (2009). Cochlear labyrinth volume and hearing abilities in primates. *Anatomical Record (Hoboken, N.J.: 2007)* **292**, 765–776.

Kohllöffel, L.U.E. (1984). Notes on the comparative mechanics of hearing. II. On cochlear shunts in birds. *Hearing Research* **13**, 77–81.

Kollmar, R., Montgomery, L.G., Fak, J., Henry, L.J. & Hudspeth, A.J. (1997). Predominance of the α1D subunit in L-type voltage-gated Ca2+ channels of hair cells in the chicken’s cochlea. *Proceedings of the National Academy of Sciences* **94**, 14883–14888.

Köppl, C. (2015). Chapter 6 - Avian hearing. In *Sturkie’s Avian Physiology (Sixth Edition)* (ed C.G. Scanes), pp. 71–87. Academic Press, San Diego.

Kreithen, M.L. & Keeton, W.T. (1974). Detection of changes in atmospheric pressure by the homing pigeon, *Columba livia*. *Journal of Comparative Physiology* **89**, 73–82.

Kreithen, M.L. & Quine, D.B. (1979). Infrasound detection by the homing pigeon: A behavioral audiogram. *Journal of Comparative Physiology* **129**, 1–4.

Landolt, J.P. & Correia, M.J. (1980). Neurodynamic response analysis of anterior semicircular canal afferents in the pigeon. *Journal of Neurophysiology* **43**, 1746–1770.

Landström, U., Lundström, R. & Byström, M. (1983). Exposure to infrasound — perception and changes in wakefulness. *Journal of Low Frequency Noise, Vibration and Active Control* **2**, 1–11.

Lavigne-Rebillard, M., Cousillas, H. & Pujol, R. (1985). The very distal part of the basilar papilla in the chicken: A morphological approach. *The Journal of Comparative Neurology* **238**, 340–347.

Le Pichon, A., Blanc, E. & Hauchecorne, A. (2010). *Infrasound monitoring for atmospheric studies*. Springer Science & Business Media.

Lehner, P.N. & Dennis, D.S. (1971). Preliminary research on the ability of ducks to discriminate atmospheric pressure changes. *Annals of the New York Academy of Sciences* **188**, 98–109.

Lieser, M., Berthold, P. & Manley, G.A. (2005). Infrasound in the capercaillie (*Tetrao urogallus*). *Journal of Ornithology* **146**, 395–398.

Lieser, M., Berthold, P. & Manley, G.A. (2006). Infrasound in the flutter jumps of the capercaillie (*Tetrao urogallus*): apparently a physical by-product. *Journal of Ornithology* **147**, 507–509.

Lynch, T.J., Nedzelnitsky, V. & Peake, W.T. (1982). Input impedance of the cochlea in cat. *The Journal of the Acoustical Society of America* **72**, 108–130.

Mack, A.L., Jones, J. & Nelson, D.A. (2003). Low-frequency vocalizations by cassowaries (*Casuarius* spp.). *The Auk* **120**, 1062–1068.

Manley, G.A. (2017*a*). Comparative auditory neuroscience: understanding the evolution and function of ears. *Journal of the Association for Research in Otolaryngology* **18**, 1–24.

Manley, G.A. (2017*b*). The cochlea: What it is, where it came from, and what is special about it. In *Understanding the Cochlea* (eds G.A. Manley, A.W. Gummer, A.N. Popper & R.R. Fay), pp. 17–32. Springer International Publishing, Cham.

Mason, M.J. (2016). Structure and function of the mammalian middle ear. II: Inferring function from structure. *Journal of Anatomy* **228**, 300–312.

Matoza, R.S., Landès, M., Pichon, A.L., Ceranna, L. & Brown, D. (2013). Coherent ambient infrasound recorded by the International Monitoring System. *Geophysical Research Letters* **40**, 429–433.

Merchant, S.N., Ravicz, M.E. & Rosowski, J.J. (1996). Acoustic input impedance of the stapes and cochlea in human temporal bones. *Hearing Research* **97**, 30–45.

Merchant, S.N. & Rosowski, J.J. (2008). Conductive hearing loss caused by third-window lesions of the inner ear. *Otology & neurotology : official publication of the American Otological Society, American Neurotology Society [and] European Academy of Otology and Neurotology* **29**, 282–289.

Merzenich, M.M., Kitzes, L. & Aitkin, L. (1973). Anatomical and physiological evidence for auditory specialization in the mountain beaver (*Aplodontia rufa*). *Brain Research* **58**, 331–344.

Moffat, A.J.M. & Capranica, R.R. (1976). Auditory sensitivity of the saccule in the American toad (*Bufo americanus*). *Journal of Comparative Physiology* **105**, 1–8.

Moller, H. & Pedersen, C.S. (2004). Hearing at low and infrasonic frequencies. *Noise and Health* **6**, 37.

Murrow, B.W. (1994). Position-dependent expression of potassium currents by chick cochlear hair cells. *The Journal of Physiology* **480**, 247–259.

Muyshondt, P.G.G., Aerts, P. & Dirckx, J.J.J. (2016*a*). Acoustic input impedance of the avian inner ear measured in ostrich (*Struthio camelus*). *Hearing Research* **339**, 175–183.

Muyshondt, P.G.G., Soons, J.A.M., De Greef, D., Pires, F., Aerts, P. & Dirckx, J.J.J. (2016*b*). A single-ossicle ear: Acoustic response and mechanical properties measured in duck. *Hearing Research* **340**, 35–42.

Narins, P.M. & Lewis, E.R. (1984). The vertebrate ear as an exquisite seismic sensor. *The Journal of the Acoustical Society of America* **76**, 1384–1387.

Narins, P.M., Stoeger, A.S. & O’Connell-Rodwell, C. (2016). Infrasonic and seismic communication in the vertebrates with special emphasis on the afrotheria: an update and future directions. In *Vertebrate Sound Production and Acoustic Communication* pp. 191–227. Springer, Cham.

Navaratnam, D.S., Escobar, L., Covarrubias, M. & Oberholtzer, J.C. (1995). Permeation properties and differential expression across the auditory receptor epithelium of an inward rectifier K+ channel cloned from the chick inner ear. *Journal of Biological Chemistry* **270**, 19238–19245.

Neeser, J.A. & von Bartheld, C.S. (2002). Comparative anatomy of the paratympanic organ (vitali organ) in the middle ear of birds and non-avian vertebrates: focus on alligators, Parakeets and Armadillos. *Brain, Behavior and Evolution* **60**, 65–79.

Nimpf, S., Nordmann, G.C., Kagerbauer, D., Malkemper, E.P., Landler, L., Papadaki-Anastasopoulou, A., Ushakova, L., Wenninger-Weinzierl, A., Novatchkova, M., Vincent, P., Lendl, T., Colombini, M., Mason, M.J. & Keays, D.A. (2019). A putative mechanism for magnetoreception by electromagnetic induction in the pigeon inner ear. *Current Biology* **29**, 4052-4059.e4.

Okanoya, K. & Dooling, R.J. (1987). Hearing in passerine and psittacine birds: A comparative study of absolute and masked auditory thresholds. *Journal of Comparative Psychology* **101**, 7–15.

O’Neill, P. (2013). Magnetoreception and baroreception in birds. *Development, Growth & Differentiation* **55**, 188–197.

Packard, A., Karlsen, H.E. & Sand, O. (1990). Low frequency hearing in cephalopods. *Journal of Comparative Physiology A* **166**, 501–505.

Pilger, C., Ceranna, L., Ross, J.O., Vergoz, J., Pichon, A.L., Brachet, N., Blanc, E., Kero, J., Liszka, L., Gibbons, S., Kvaerna, T., Näsholm, S.P., Marchetti, E., Ripepe, M., Smets, P., *et al*. (2018). The European Infrasound Bulletin. *Pure and Applied Geophysics* **175**, 3619–3638.

Quine, D.B. & Kreithen, M.L. (1981). Frequency shift discrimination: Can homing pigeons locate infrasounds by Doppler shifts? *Journal of Comparative Physiology* **141**, 153–155.

Raspet, R., Abbott, J.-P., Webster, J., Yu, J., Talmadge, C., Alberts II, K., Collier, S. & Noble, J. (2019). New systems for wind noise reduction for infrasonic measurements. In *Infrasound Monitoring for Atmospheric Studies: Challenges in Middle Atmosphere Dynamics and Societal Benefits* (eds A. Le Pichon, E. Blanc & A. Hauchecorne), pp. 91–124. Springer International Publishing, Cham.

Raufer, S., Masud, S.F. & Nakajima, H.H. (2018). Infrasound transmission in the human ear: Implications for acoustic and vestibular responses of the normal and dehiscent inner ear. *The Journal of the Acoustical Society of America* **144**, 332–342.

Riede, T., Eliason, C.M., Miller, E.H., Goller, F. & Clarke, J.A. (2016). Coos, booms, and hoots: The evolution of closed-mouth vocal behavior in birds. *Evolution* **70**, 1734–1746.

Rosengren, S.M., Welgampola, M.S. & Colebatch, J.G. (2010). Vestibular evoked myogenic potentials: Past, present and future. *Clinical Neurophysiology* **121**, 636–651.

Rosowski, J.J. (1992). Hearing in transitional mammals: predictions from the middle-ear anatomy and hearing capabilities of extant mammals. In *The Evolutionary Biology of Hearing* (eds D.B. Webster, A.N. Popper & R.R. Fay), pp. 615–631. Springer New York, New York, NY.

Rosowski, J.J. (1994). Outer and middle ears. In *Comparative Hearing: Mammals* (eds R.R. Fay & A.N. Popper), pp. 172–247. Springer New York, New York, NY.

Ruggero, M.A. & Temchin, A.N. (2002). The roles of the external, middle, and inner ears in determining the bandwidth of hearing. *Proceedings of the National Academy of Sciences* **99**, 13206–13210.

Salt, A.N. & Hullar, T.E. (2010). Responses of the ear to low frequency sounds, infrasound and wind turbines. *Hearing Research* **268**, 12–21.

Sand, O. & Karlsen, H.E. (2000). Detection of infrasound and linear acceleration in fishes. *Philosophical Transactions of the Royal Society B: Biological Sciences* **355**, 1295–1298.

Saunders, J.C. (1985). Auditory structure and function in the bird middle ear: an evaluation by SEM and capacitive probe. *Hearing Research* **18**, 253–268.

Saunders, J.C., Duncan, R.K., Doan, D.E. & Werner, Y.L. (2000). The middle ear of reptiles and birds. In *Comparative Hearing: Birds and Reptiles* (eds R.J. Dooling, R.R. Fay & A.N. Popper), pp. 13–69. Springer New York.

Saunders, J.C. & Johnstone, B.M. (1972). A comparative analysis of middle-ear function in non-mammalian vertebrates. *Acta Oto-Laryngologica* **73**, 353–361.

Schermuly, L. & Klinke, R. (1990*a*). Infrasound sensitive neurones in the pigeon cochlear ganglion. *Journal of Comparative Physiology. A, Sensory, Neural, and Behavioral Physiology* **166**, 355–363.

Schermuly, L. & Klinke, R. (1990*b*). Origin of infrasound sensitive neurones in the papilla basilaris of the pigeon: an HRP study. *Hearing Research* **48**, 69–77.

Schermuly, L., Topp, G. & Klinke, R. (1991). A previously unknown hair cell epithelium in the pigeon cochlea: the papilla chaotica. *Hearing Research* **53**, 49–56.

Schomer, P.D., Erdreich, J., Pamidighantam, P.K. & Boyle, J.H. (2015). A theory to explain some physiological effects of the infrasonic emissions at some wind farm sites. *The Journal of the Acoustical Society of America* **137**, 1356–1365.

Schwartzkopff, J. & Winter, P. (1960). Zur anatomie der vogel-cochlea unter natürlichen bedingungen. *Biologisches Zentralblatt* **79**, 607–625.

Shen, J.X. & Xu, Z.M. (1994). Response characteristics of Herbst corpuscles in the interosseous region of the pigeon’s hind limb. *Journal of Comparative Physiology A* **175**, 667–674.

Si, X., Angelaki, D.E. & Dickman, J.D. (1997). Response properties of pigeon otolith afferents to linear acceleration. *Experimental Brain Research* **117**, 242–250.

Smolders, J.W.T., Ding-Pfennigdorff, D. & Klinke, R. (1995). A functional map of the pigeon basilar papilla: correlation of the properties of single auditory nerve fibres and their peripheral origin. *Hearing Research* **92**, 151–169.

Sohmer, H., Freeman, S., Geal-Dor, M., Adelman, C. & Savion, I. (2000). Bone conduction experiments in humans – a fluid pathway from bone to ear. *Hearing Research* **146**, 81–88.

Starck, J.M. (1995). Comparative anatomy of the external and middle ear of palaeognathous birds. In *Comparative Anatomy of the External and Middle Ear of Palaeognathous Birds* pp. 1–16. Springer, Berlin, Heidelberg.

Stenfelt, S. (2013). Bone conduction and the middle ear. In *The Middle Ear* pp. 135–169. Springer, New York, NY.

Stenfelt, S. & Goode, R.L. (2005). Transmission properties of bone conducted sound: Measurements in cadaver heads. *The Journal of the Acoustical Society of America* **118**, 2373–2391.

Theurich, M., Langner, G. & Scheich, H. (1984). Infrasound responses in the midbrain of the guinea fowl. *Neuroscience Letters* **49**, 81–86.

Todd, N.P.M., Rosengren, S.M. & Colebatch, J.G. (2008). Tuning and sensitivity of the human vestibular system to low-frequency vibration. *Neuroscience Letters* **444**, 36–41.

von Bartheld, C.S. (1990). Development and innervation of the paratympanic organ (Vitali organ) in chick embryos. *Brain, Behavior and Evolution* **35**, 1–15.

von Bartheld, C.S. (1994). Functional morphology of the paratympanic organ in the middle ear of birds. *Brain, Behavior and Evolution* **44**, 61–73.

von Bartheld, C.S. & Giannessi, F. (2011). The paratympanic organ: a barometer and altimeter in the middle ear of birds? *Journal of Experimental Zoology. Part B, Molecular and Developmental Evolution* **316**, 402–408.

von Békésy, G. (1948). Vibration of the head in a sound field and its role in hearing by bone conduction. *The Journal of the Acoustical Society of America* **20**, 749–760.

Wannaprasert, T. & Jeffrey, N. (2015). Variations of mammalian cochlear shape in relation to hearing frequency and skull size. *Tropical Natural History* **15**, 41–54.

Warchol, M.E. & Dallos, P. (1989). Neural response to very low-frequency sound in the avian cochlear nucleus. *Journal of Comparative Physiology A* **166**, 83–95.

Waxler, R. & Assink, J. (2019). Propagation Modeling Through Realistic Atmosphere and Benchmarking. In *Infrasound Monitoring for Atmospheric Studies: Challenges in Middle Atmosphere Dynamics and Societal Benefits* (eds A. Le Pichon, E. Blanc & A. Hauchecorne), pp. 509–549. Springer International Publishing, Cham.

Waxler, R. & Gilbert, K.E. (2006). The radiation of atmospheric microbaroms by ocean waves. *The Journal of the Acoustical Society of America* **119**, 2651–2664.

West, C.D. (1985). The relationship of the spiral turns of the cochlea and the length of the basilar membrane to the range of audible frequencies in ground dwelling mammals. *The Journal of the Acoustical Society of America* **77**, 1091–1101.

Wilczynski, W., Resler, C. & Capranica, R.R. (1987). Tympanic and extratympanic sound transmission in the leopard frog. *Journal of Comparative Physiology A* **161**, 659–669.

Wit, H.P., Bleeker, J.D. & Mulder, H.H. (1984). Responses of pigeon vestibular nerve fibers to sound and vibration with audiofrequencies. *The Journal of the Acoustical Society of America* **75**, 202–208.

Womack, M.C., Christensen-Dalsgaard, J., Coloma, L.A. & Hoke, K.L. (2018). Sensitive high-frequency hearing in earless and partially eared harlequin frogs (*Atelopus*). *Journal of Experimental Biology* **221**, jeb169664.

Yodlowski, M.L., Kreithen, M.L. & Keeton, W.T. (1977). Detection of atmospheric infrasound by homing pigeons. *Nature* **265**, 725–726.

Yost, W.A. (2001). Fundamentals of Hearing: An Introduction (4th edition). *The Journal of the Acoustical Society of America* **110**, 1713–1714.

Zhao, M., Fridberger, A. & Stenfelt, S. (2019). Bone conduction hearing in the Guinea pig and the effect of artificially induced middle ear lesions. *Hearing Research* **379**, 21–30.

**X. SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1.** Near-field particle velocity.

**Fig. S1.** Decline in particle velocity with increasing distance from the source.

**Appendix S2.** Resistance and reactance components of acoustic impedance.

**Appendix S3.** Model for a sphere vibrating in a free field.

**Fig. S2.** Computation of vibrations for two spheres of different volumes but constant density range.

**Figure legends**

**Fig. 1.** Audiograms depicting bird hearing at infrasonic frequencies, overlaid on conservative estimates of the range of global atmospheric infrasound background noise levels. Note that both behavioural and electrophysiological methods are included here, therefore absolute thresholds may not be directly comparable across all studies. Line types indicate the different methods used for scoring positive hearing responses (solid lines = behavioural response, short dashed line = electrophysiological response, long dashed line = conditioned heart rate response). Data sources and additional experimental details are provided in Table 1. The 20 Hz upper boundary of infrasound is indicated with a vertical dotted line. The frequency axis is on a logarithmic scale. Decibel (dB) units, where dB = 20 × log10(*x* µPa/20 µPa), where *x* is the measured sound pressure, are also logarithmic. Auditory thresholds at the lowest tested frequencies determined from black-tailed prairie dog (*Cynomys ludovicianus*) (Heffner *et al.*, 1994), mountain beaver (*Aplodontia rufa*) (Merzenich *et al*., 1973), and elephant (*Elephas maximus*) (Heffner & Heffner, 1982) audiograms, and a human audiogram (Jackson *et al*., 1999) are plotted for comparison. Point symbols indicate the method used for scoring positive hearing response (circles = conditioned behavioural response, square = electrophysiological response). The noise models (shaded area) represent minimum and maximum levels of power spectral densities (5th and 95th percentiles) sampled across all atmospheric infrasound International Monitoring System (IMS) stations over the course of one year (Brown *et al.*, 2014). These curves include both infrasound and non-acoustic pressure perturbations.

**Fig. 2.** Anatomical structures of the bird ear. Middle (A) and inner ear (B) structures represented by three-dimensional (3D) renderings of a sooty shearwater (*Ardenna grisea*) ear imaged from micro-focussed X-ray computed tomography (microCT) scans. (A) The tympanic membrane connects to the single ossicle (columella) *via* the cartilaginous extracolumella, and vibrations of the columella footplate are transmitted to the inner ear at the oval window of the inner ear. (B) The oval window and round window, highlighted by a cubic area of bone in the inset, and corresponding to the dashed box region, are the major openings to the bone surrounding the inner ear, allowing vibration input and output. The basilar papilla, the auditory end organ in birds, runs along the length of the cochlear duct. Two of the three otolithic vestibular endorgans, the sacculus and utriculus, are located in the vestibule, and the third, the lagena, is located at the apical end of the cochlear duct. (C) Schematics depicting auditory structures. The basilar papilla lies largely on the basilar membrane, and partly on the fibrocartilage-like limbic tissue that surrounds and supports the basilar membrane along the cochlear duct. Together these structures make up the cochlear partition. Two ducts have been identified across the cochlear partition: the helicotrema at the apical end, and the ductus brevis at the basal end. The cochlear aqueduct is a ‘third window’ to the inner ear. This is a fluid-filled communication connecting the perilymph fluid between the ear and the brain, and varies in size across birds. (D, E) The perimeters of the cochlear aqueduct (blue) and round window (yellow) are highlighted in a bird with a large cochlear aqueduct (D, sooty shearwater), and a bird with a small cochlear aqueduct (E, pigeon *Columba livia*). MicroCT slices that transect through the round window and cochlear aqueduct provide further anatomical details (position of plane indicated by dashed lines on the 3D rendering). All 3D renderings are of left ears, and anatomical coordinates are abbreviated as follows: L = lateral, M = medial, R = rostral, C = caudal, S = superior, I = inferior.

**Fig. 3.** (A) A comparison of bird middle ear velocity transfer functions and audiograms. Curves are redrawn from the following studies: chicken (*Gallus gallus*; blue) (Saunders, 1985), ostrich (*Struthio camelus*; purple) (Arechvo *et al.*, 2013), pigeon (*Columba livia*; green) (Saunders *et al.*, 2000), mallard duck (*Anas platyrhynchos*; orange) (Muyshondt *et al.*, 2016*b*). Audiograms of chicken, pigeon, and mallard duck from Fig. 1 are re-plotted on the second *y* axis (dashed lines). (B) Middle ear transfer functions from A (black) plotted together with vibration velocities measured from unspecialized body tissues (purple) at ‘audible’ (> 20 Hz) frequencies [unspecialized tissues: snake (1) (Christensen *et al.*, 2012); human forehead (2) (von Békésy, 1948); salamander (3) (Hetherington, 2001)]. Dotted lines extending from the middle ear transfer functions in both panels represent 6 dB/octave declines with decreasing frequency. The black stippled lines over the unspecialized tissue vibrations express the magnitude of vibrational motion calculated for a sphere (2 cm radius) vibrating in a free field (see text and Appendix S3 for more details) for the range of whole-body densities expected for birds (0.6–0.9 g/cm3). (C) Depictions of translational and differential motion. In translational motion, the whole head moves as a rigid body, back and forth in the direction of the stimulating sound. In differential motion, a vibration wave transmits into the head and vibrations compress and expand the head in multiple directions.