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A Comparison of Hearing and Auditory Functioning Between Dogs and Humans

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Given the range of tasks that requires dogs and humans to work effectively together, it is important for us to appreciate the similarities and differences in hearing ability across the two species, as well as the limits of our knowledge of this comparative information. Humans often assume that dogs' hearing abilities are similar to their own and try to communicate with them verbally as they do with other humans. In the first part of this review, we compare the auditory system of the two species in relation to their ability to function generally as a sound amplification and detection system before considering the specific capacities of the system in the second part. We then examine the factors that disturb hearing function before reviewing a range of potentially problematic behavioral responses that are closely associated with the functioning of the auditory system. Finally, we consider important aspects of comparative auditory perception and related cognitive processes. A major observation of this review is how little research has been done in investigating the auditory capabilities of the dog. There may be significant mismatches between what we expect dogs (and perhaps specific types of dog, given historic functional breed selection) can hear versus what they can actually hear. This has significant implications for what should be considered if we wish to select specific dogs for work associated with particular hearing abilities and to protect and maintain their hearing throughout life. Only with a more complete understanding of the dogs' hearing ability compared with our own can we more fully appreciate perceptual and associated cognitive differences between the species alongside behavioral differences that might occur when we are exposed to a given soundscape.

Keywords: *hearing*, *auditory functioning*, *dog*, *human*

Introduction

It is widely believed that dogs have better hearing than humans and that they may be able to hear sounds that are up to 4 times farther away than humans can (e.g., 90 m in humans and 400 m in dogs; Audicus, 2015; Cole, 2010). However, hearing involves not just detection but also the resolution of sounds and, from a functional perspective, the recognition of certain compositions as meaningful in some way. For effective auditory communication between species, such as humans and dogs, each must appreciate at some level what sounds the other can detect and the informational content of different sound qualities. Some of this may be based on general physical properties of the sound, such as the relationship between body size and vocalization frequencies, whereas other levels may be more species specific. To this end, researchers have found that humans and dogs do indeed have some reciprocal appreciation of the qualities of each other's vocalizations (Pongrácz, Molnár, & Miklósi, 2006; Yong & Ruffman, 2014). This result is perhaps not surprising given the history of the two species and the range of challenges involving dogs and humans working together effectively. Nonetheless, it is clear that compared with humans, dogs have a different understanding of word meanings (Braem & Mills, 2010; Fukuzawa, Mills, & Cooper, 2005b; Markman & Abelev, 2004; Mills, 2005; Ramos & Ades, 2012; van der Zee, Zulch, & Mills, 2012). Even when this is appreciated, humans often assume that dogs' hearing abilities are similar to their own, but there is surprisingly little research to support this. Further, given the enormous morphological and functional diversity of dogs, it would perhaps be surprising if there was not considerable variability in their hearing ability. Where direct evidence of hearing ability is limited, it is possible to make working assumptions based on our understanding of the functional anatomy of sound detection and perception until more direct evidence becomes available. Therefore, in this review we not only compare what is known about the hearing ability of dogs and humans but highlight important considerations based on such fundamental principles.

Part 1: General Comparative Anatomy and Functioning of the Auditory System as a Sound Amplified in Dogs and Humans

The auditory systems of dogs and humans share the same basic plan and physical structures with sound waves collected in the outer ear and amplified via the middle ear before being transduced into electrical signals by the inner ear. The main body of this review assumes that the reader has a general working knowledge of the nature of sound and structures making up the auditory system in terrestrial mammals (though details of this are provided in the Supplementary Information), and so we focus here on comparing the specific details in humans and dogs and their functional consequences. Available data on the physical characteristics of the component structures are summarized in Table 1. Needless to say, there is greater variation among dogs given their adult size and morphological variability, so comparisons with humans need to be carefully appraised to determine to what extent they apply at the level of dog versus some more specific morphological feature within the species. As a general observation, there appears to be a widespread lack of empirical data quantifying the variability that occurs in dogs and its correlates. For example, as discussed in the next section, surprisingly little attention appears to have been given to characterizing the obvious heterogeneity of the external pinnae among dogs, which plays an obviously important role in the general ability of an individual to detect sound waves (sensitivity to sound). The auditory system is tuned to amplify some frequencies better than others; for example, as a result of anatomic constraints, some wavelengths may be caught by the pinna or collected by the external auditory meatus (EAM) with variable levels of efficiency; sensitivity is further related to the characteristics of the basilar membrane and the auditory pathway, which are tuned to enhance some frequencies more than others. Variability between humans and dogs

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will likely reflect, to a large extent, the differing but also shared ecology of the two species over the whole of their evolutionary history (phylogeny) and within dogs on breed function, where this has been maintained (Fadel et al., 2016). The extent to which domestication has caused changes to the auditory system akin to those noted for the visual system (see Burda, 1985; Burda & Branis, 1988; McGreevy, Grassi, & Harman, 2004) remains unknown. Nonetheless, the occurrence of consistent differences within subpopulations of dogs would suggest potential selection in favor of or against these traits. This has important implications for the potential future breeding of individuals to perform better in different soundscapes.

Pinna

At its simplest, the pinna acts as a sound funnel, which passively but selectively collects and amplifies certain wavelengths (Fletcher, 1992). The pinna plays a substantial role in the localization of sound which, in the horizontal plane, has been reported to be more accurate than the vertical plane (Heffner & Heffner, 1998). The pinna is especially important for the attenuation of high frequencies from behind and thus reduces front–back confusion in the sound localization (Keidel & Neff, 1975).

In humans, very little variation in pinnae size has been observed, though males have slightly bigger pinna than females (Brucker et al., 2003; Ito et al., 2001; Salvinelli et al., 1991). In contrast, pinna shape and size vary immensely in dogs; this is based on not only body and head size but also breed-specific characteristics: A Pomeranian might have an ear size of a few centimeters, whereas in the *Guinness Book of World Records* some dogs have ear sizes between 34.3 and 34.9 cm (Guinness World Records Ltd., 2015; for human data, see Table 1). Three main forms of pinna are described in the dog: (a) erect (e.g., huskies, German shepherds), (b) semi-erect (e.g., pugs, greyhounds), and (c) dropped (e.g., beagles, poodles).

Within these main types (see Figure 1), there are several subcategories (e.g., rose, button, candle flame, cocked, V-shaped, Filbert shaped, folded, hooded, bat ears, round tipped, cropped). Surprisingly, there appears to be no systematic evaluation of amplification effects of different pinna shapes in dogs. However, it can be assumed that dogs with large erect ears are especially good at localizing distant noises (Nummela, 2008; Strain, 2011). Both the flexibility of its constituent cartilage and the presence of hair on the reflective surface of the pinna affect its acoustic properties. The ability to control the orientation of their pinnae is thought to improve hearing sensitivity by as much as 28 dB, particularly at higher frequencies (Phillips, Calford, Pettigrew, Aitkin, & Semple, 1982; Strain, 2011). It has been proposed that dogs with erect upright pinnae amplify both high- and low-frequency sounds (Strain, 2011); this would appear to increase their hearing range compared with dogs with other ear shapes, which are anecdotally reported to experience greater limitation in the amplification of sounds (Denzer, 2018). How any of these compare with the human pinna shape remains unknown.

External Auditory Meatus

Sound waves collected by the pinnae are transmitted along the EAM to the tympanum (eardrum; Figure 2). Physical properties of the EAM—for example, its length, width, and surface characteristics—determine which wavelengths are attenuated and transmitted and thus the peak frequency of sound sensitivity. Given the morphological variation in the EAM of different breeds and even individual dogs (e.g., because of the presence of hair), it is likely that dogs may vary considerably in the sounds they are most able to detect at this level. In humans, consistent variation in the EAM based on sex

Figure 1. Examples of dog ear shapes: erect, semi-erect, and dropped, from left to right.

Table 1. Comparison of Physical Features of the Auditory System of Dogs and Humans.

Part of the Ear	Auditory Structure	Measure	Species	Specifications	Data (*M ± SD* Where Available)	Method	Reference
Outer ear	*Pinna*	Length	Human	*N* = 123, ages 18–65 y Male *n* = 34	63 mm Male ear 6.5% bigger	Unknown	Brucker et al., 2003
			Human	*N* = 280, ages 18–60 y Male *n* = 80 Female *n* = 60	63.5 ± 12 mm Male: 63.0 ± 12.9 mm Female: 59.0 ± 11.2 mm	Postmortem	Salvinelli et al., 1991
			Human	*N* = 1,958, ages 0–94 y		Vital samples	Ito et al., 2001
				Ages 10–14 y	Male: 62 mm Female: 59 mm		
				Ages > 60 y	Male: > 72 mm Female: > 66 mm		
			Dog		Unknown	Unknown	
	External auditory meatus	Length	Human	*N* = 280, ages 18–60 y Male *n* = 80 Female *n* = 60	23.5 ± 2.5 mm Male: 25.2 ± 2.6 mm Female: 22.5 ± 2.3 mm	Postmortem	Salvinelli et al., 1991
			Human		25–31 mm	Unknown	Pensak & Choo, 2015
			Dog	*N* = 28, diff breed, age (2–13 y), and sex	53 ± 10 mm Range = 30–70 mm	Postmortem	Huang, Little, & McNeil, 2009
			Dog		22–57 mm	Unknown	Harvey, Harari, & Delauche, 2001
		Diameter	Human	*N* = 280, ages 18–60 y	Max: 9.3 ± 1.5 mm Min: 4.8 ± 0.5 mm	Postmortem	Salvinelli et al., 1991
				Male *n* = 80	Max: 9.7 ± 1.1 mm Min: 5.1 ± 0.7 mm		
				Female *n* = 60	Max: 8.5 ± 0.7 mm Min: 4.4 ± 0.3 mm		
			Human		6–9 mm	Unknown	Pensak & Choo, 2015
			Dog	*N* = 28, diff breed, age (2–13 y), and sex	Max: 58 ± 15 mm Max range: 21–79 mm Min: 7 ± 2 mm Min range: 3–10 mm	Unknown	Huang et al., 2009
			Dog		Max: 21–79 mm	Unknown	Harvey et al., 2001
Middle ear	*Tympanic membrane*	Diameter	Human	*N* = 280, Ages 18–60 y Male *n* = 80 Female *n* = 60	9.4 ± 1.5 mm 9.7 ± 1.8 mm 9.2 ± 1.2 mm	Unknown	Salvinelli et al., 1991
		Area	Human		90 mm^2	Unknown	Pensak & Choo, 2015
			Human		68.3 mm^2	Unknown	Hemilä, Nummela, & Reuter, 1995
			Dog	Small dog: 4.3 kg Large dog: 45.5 kg	30 mm^2 63 mm^2	Unknown	Heffner, 1983
					63.3 mm^2	Unknown	Hemilä et al., 1995
	Tympanic cavity	Length	Human		Unknown	Unknown	
			Dog		Tympanic cavity proper: < 10 mm Ventral cavity: 15 mm	Unknown	Harvey et al., 2001
			Dog		14.2–22.6 mm	Unknown	Wysocki, 2006
		Volume	Human	*N* = 51, diff sex (male *n* = 19, female *n* = 25), and age (age range = 19–69 y)	*M* = 5.2 ± 3.1 ml Range = 0.6–13.4 ml	CT scan	Ahn et al., 2008

Part of the Ear	Auditory Structure	Measure	Species	Specifications	Data ($M \pm SD$ Where Available)	Method	Reference
Middle ear (*continued*)	*Tympanic cavity* (continued)	Volume (*continued*)	Human	$N = 91$, diff sex (male $n = 45$, female $n = 46$), and age ($M = 48.1$ y)	0.49 ± 0.0436 cm^3	Cavalieri principle	Kürkçüoğlu et al., 2010
			Human	$N = 55$	$M = 6.5$ cm^3 Range = 2–22 cm^3	Postmortem, acoustic method, X-ray, measure includes mastoid cells	Molvær, Vallersnes, & Kringlebotn, 1978
			Human		Male right ear: 0.52 cm^3 Male left ear: 0.55 cm^3 Female right ear: 0.45 cm^3 Female left ear: 0.49 cm^3	CT cavaliere method	Kavakli et al., 2004
			Dog		Tympanic cavity proper: 2.5 cm^3	Unknown	Harvey et al., 2001
			Dog		1.5 ml	Unknown	Cole, 2009
			Dog	$N = 8$, diff breed, age, mesocephalic	1.85 ± 0.15 ml	CT, postmortem	Defalque, Rosenstein, & Rosser, 2005
			Dog	$N = 8$, diff breed, age, mesocephalic	2 ± 0.2 ml	Water-filling method, postmortem	Defalque et al., 2005
			Dog	$N = 18$, diff breed, age ($M = 4.8$ y), and sex (male $n = 10$, female $n = 8$), M weight = 20.5 kg, mesocephalic	1.5 ± 0.8 ml	CT, vital samples	Defalque et al., 2005
	Malleus		Human	$N = 50$, male ears	7.8 mm	Postmortem	Sodhi et al., 2017
			Human	$N = 870$	7.72 mm	Summary of average length of 14 studies	Sodhi et al., 2017
			Human	$N = 92$	8.16 mm	Postmortem	Heron, 1923
			Dog		10 mm	Unknown	Harvey et al., 2001
	Incus		Human	$N = 50$, male ears	6.45 mm	Postmortem	Sodhi et al., 2017
			Human	$N = 578$	6.07 mm	Summary of average length of 10 studies	Sodhi et al., 2017
			Human	$N = 94$	5.2 mm	Unknown	Heron, 1923
			Dog		4 mm	Unknown	Harvey et al., 2001
	Stapes		Human	$N = 50$, male ears	3.4 mm	Postmortem	Sodhi et al., 2017
			Human	$N = 734$	3.21 mm	Summary of average length of 12 studies	Sodhi et al., 2017
			Human	$N = 31$	3.45 mm	Unknown	Heron, 1923
			Dog		2 mm	Unknown	Harvey et al., 2001
	Auditory tube	Diameter	Human		3 mm	Unknown	
			Dog		1.5 mm	Unknown	Cole, 2009
		Length	Human		35 mm	Unknown	Pensak & Choo, 2015
			Human	$N = 90$, adults	42.9 mm	CT scan	Takasaki et al., 2007
			Dog		15–20 mm	Unknown	Harvey et al., 2001
			Dog		10–15 mm	Unknown	Berghes et al., 2010

(*continues*)

Table 1. Comparison of Physical Features of the Auditory System of Dogs and Humans. (Continued)

Part of the Ear	Auditory Structure	Measure	Species	Specifications	Data (*M ± SD* Where Available)	Method	Reference
Middle ear (*continued*)	Oval window	Area	Human		2.98 mm²	Unknown	Hemilä et al., 1995
			Dog		1.96 mm²	Unknown	Hemilä et al., 1995
Inner ear	*Vestibule*	Diameter	Human		5 mm	Unknown	Harvey et al., 2001
			Human		4 mm	Unknown	Pensak & Choo, 2015
			Dog		3 mm	Unknown	Harvey et al., 2001
	Cochlea	Length	Human		33.5 mm	Unknown	Manoussaki et al., 2008
			Human		32 mm	Unknown	Pensak & Choo, 2015
			Human		35 mm	Unknown	Fay & Popper, 1994
			Dog		Unknown	Unknown	
		Height	Human		5 mm	Unknown	Pensak & Choo, 2015
			Dog		7 mm	Unknown	Harvey & Ter Haar, 2017
			Dog		5.85–7.4 mm	Unknown	Wysocki, 2006
		Turns	Human		2.75	Unknown	Pensak & Choo, 2015
			Human		2.5	Unknown	Wolfe et al., 2010
			Human		2.5	Unknown	Manoussaki et al., 2008
			Dog		3.25	Unknown	Harvey et al., 2001
	Helicotrema	Area	Human		0.25 mm²	Unknown	Littler, 1965
			Dog		Unknown	Unknown	
	Outer hair cells	Number	Human		11,000	Unknown	Wolfe et al., 2010
					12,000–15,000	Unknown	Pensak & Choo, 2015
			Dog		10,500	Unknown	Dukes & Reece, 2004
	Inner hair cells	Number	Human		3,500	Unknown	Wolfe et al., 2010
			Human		3,000–3,500	Unknown	Pensak & Choo, 2015
			Dog		2,500	Unknown	Dukes & Reece, 2004
	Round window	Area	Human		0.2–1.26 mm²	Unknown	Jain et al., 2019
			Dog		Unknown	Unknown	

Note: For a pictorial overview of the anatomical features of a dogs and humans ear, see Figure 2. CT = computerized tomography; diff = different; NA = not applicable; y = years.

differences have been described (Table 1), but it is not known whether this also applies to dogs. In general, the EAMs of dogs are relatively longer, wider in diameter, more mobile, and more cone-like than those of humans, which may improve the amplification of and thus sensitivity to sound and specific wavelengths depending on the actual shape in a given individual (Harvey & Ter Haar, 2017). However, there is a lack of systematic investigation of the practical consequences of these physical effects in dogs.

For those with hair within the EAM, the number of hairs tends to decrease toward the tympanum, although some dog breeds may have a large amount of hair in the EAM (hirsute ears), such as cocker spaniels and poodles (Cole, 2009), and it is likely that this results in greater attenuation of sound waves in these instances. This may make certain breeds less sensitive to sound, and it is probably not a coincidence that some of those breeds, typically with hairy EAM (e.g., cocker and springer spaniel), also have dropped ears and so may

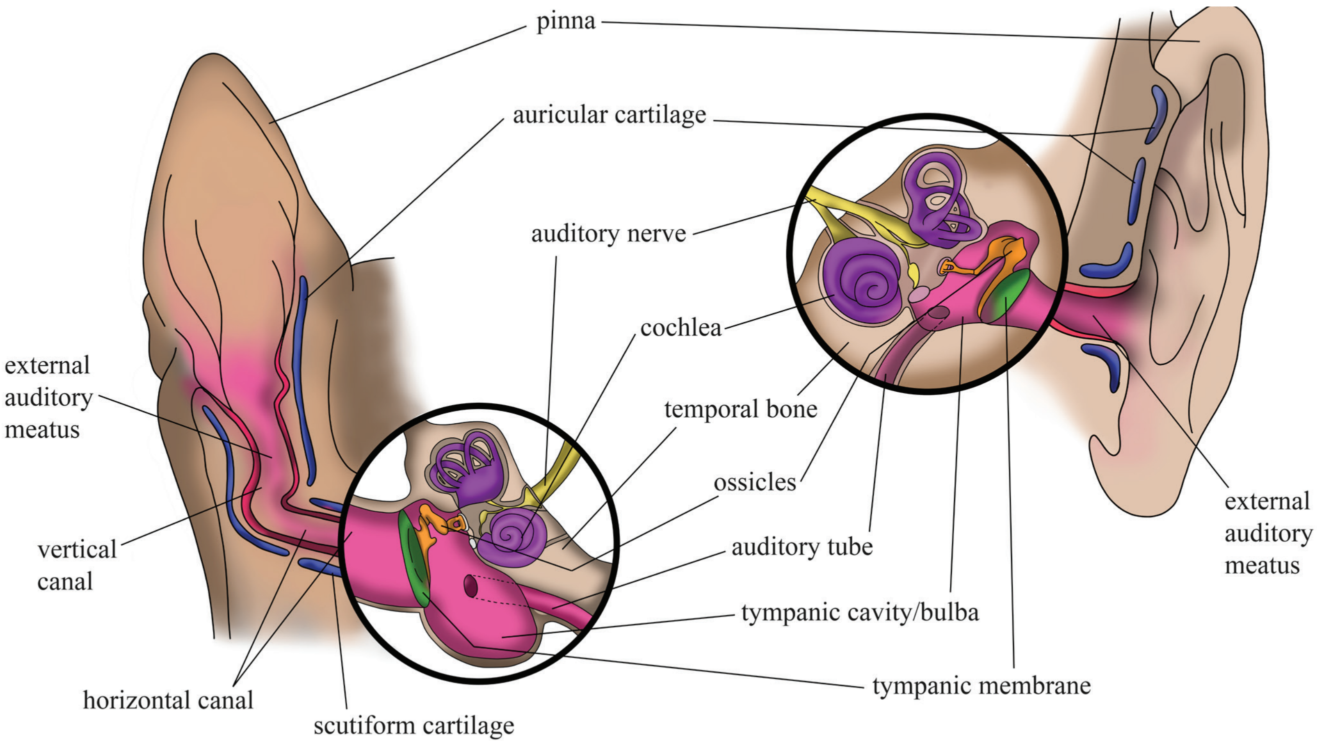


Figure 2. Scheme of a dog ear (left) and human ear (right). Not to scale.

be less disturbed by loud sounds such as gunshots. Further indirect evidence comes from the widespread observation that when dogs are exposed to loud noises, they will typically fold back their ears so they are more dropped (Blackshaw et al., 1990). It seems reasonable to suppose that this limits both incoming frequency range and volume.

A notable difference between humans and dogs is the proportion of the EAM being covered by cartilage or temporal bone (30% in humans vs. up to 98% in dogs; Huang et al., 2009), though this varies with breed (Harvey & Ter Haar, 2017). Especially the differences in cartilage coverage may reflect may reflect differences in the mobility of the ears between species but comes at a potential cost in terms of the efficiency of sound wave conveyance along the EAM.

Tympanic Membrane and Ossicular Chain

The tympanic membrane (TM) both absorbs and shunts acoustic energy to prevent the reflection of sounds within the ear, so it plays an important role in auditory sensitivity (Bergevin & Olson, 2014). In both humans and dogs, the TM is a rounded, cone-shaped structure with reports of consistent differences associated with body size (Table 1; Harvey et al., 2001; Heffner & Heffner, 1983; Hemilä et al., 1995; Salvinelli et al., 1991). Unlike humans, sex differences in the size of the TM of dogs have not been reported. Once again, variability in size is much greater among dogs than humans, but the size of the TM does not relate to the hearing frequency range or the absolute threshold of hearing in dogs (Heffner, 1983) and so may be of little practical consequence.

The three ossicles (Figure 3), which act as levers across the air-filled space of the middle ear, are much more important in this regard. Transducing sound waves from the outer ear to a liquid pressure wave in the inner ear show evidence of inter- and intraspecific variation. The broad shape of the ossicles in humans and dogs resemble each other (Berghes et al., 2010), but the malleus of the dog is relatively bigger (Table 1), and its consequentially greater leverage increases magnification toward the incus so that more energy can be transduced effectively. The malleus-to-incus ratio (lever ratio) is 3:1 in dogs but only 1:3 in humans (El-Mofty & El-Serafy, 1967; Harvey et al., 2001), and this increases dogs' potential sensitivity to sound (Strain, 2011; Wendell Todd & Creighton, 2013). However, there are also reports that although the ossicular chain amplifies pressure waves by a factor of 20 in dogs, it is increased by a factor of 22 in humans (Pensak & Choo, 2015; Strain, 2011), which

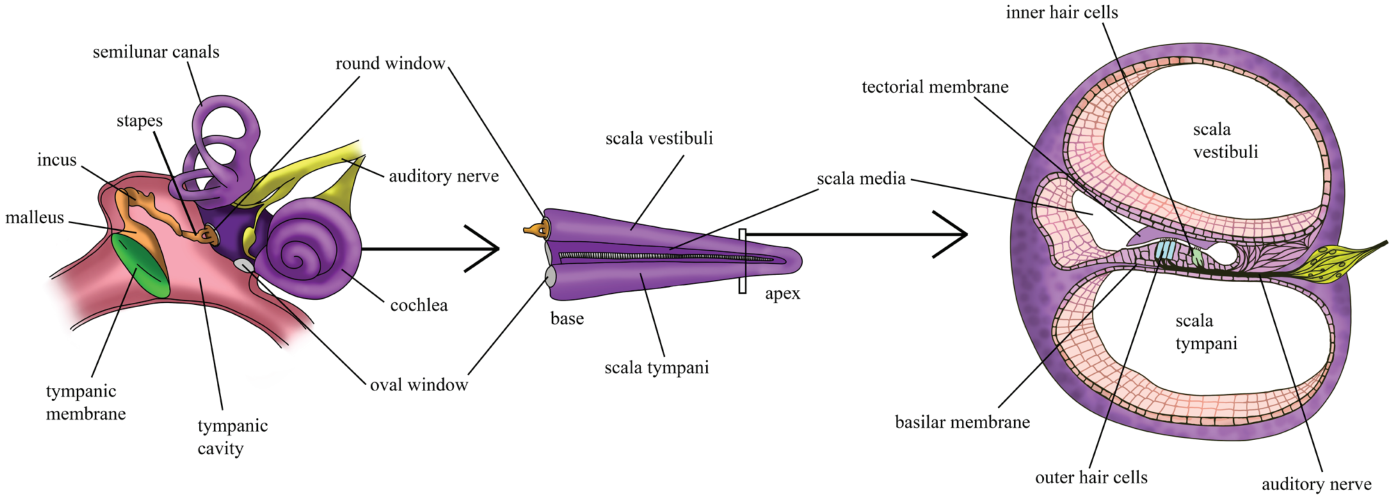


Figure 3. Structures of the middle and inner ear. Not to scale.

appears to be at odds with the anatomical conclusions. This inconsistency might relate to experimental measures being taken at noncomparable frequencies and highlights the problem of making simple generalizations about sensitivity to sound, without reference to specific frequencies—an issue that we discuss further later on.

Cochlea

Ossicular chain vibrations are transmitted to the cochlea via the oval window. In the cochlea, these vibrations travel in the form of a tsunami wave (commonly known as a traveling wave), which increases in amplitude as it propagates within the cochlear fluid and basilar membrane. The cochlear has several adaptations that affect the detection and decomposition of different frequencies (i.e., the pitch of a sound) of the traveling wave within it (Robles & Ruggero, 2001).

First, the basilar membrane is thicker, narrower, and stiffer at the base compared with the apex (Figure 4). Thus, high-frequency energy in the traveling sound wave displaces only regions close to the cochlear base, whereas lower frequency waves can travel farther along the cochlear spiral, achieving maximal amplitude near the apex (Manoussaki et al., 2008). The subsequent differences in the deflection of basal hair cells within the cochlea along different lengths determine the information available on sound pitch at this level (place coding). The basilar membrane of dogs is generally stiffer in the basal regions compared to that of humans (Fay & Popper, 1994), and this difference may be the cause for their ability to hear higher frequencies; however, the extent to which the stiffness of the basilar membrane (disregarding other anatomical differences) affects the variability in high-frequency hearing between species remains unknown.

Second, afferent nerve fibers fire when the hair cells are in an upward movement, and the frequency with which they fire may also aid hearing specific frequencies (phase locking). For example, when the nerve will fire 100 times per second, this would indicate that the original sound wave contains a 100 Hz component. However, this is consistent only for certain sound frequencies. For humans, this mechanism has been described to be consistent only for frequencies up to 1000 Hz; synchronization of action potentials is lost above this frequency (Fettiplace, 2002) because the maximum rate of action potential firing of the auditory nerve is exceeded. Of interest, some perceptual biases can be measured in humans below 1000 Hz, in spite of perfect synchronization between action potentials and sound cycles. Humans seem to show a “perceptual magnet” effect centered around the note A. This means that the perception of a tone (G#, 414 Hz) is distorted by its neighboring tone (A, 440 Hz), and this error seems to be associated with the use of A as the universal tuning frequency (Athos et al., 2007). There do not appear to be any reports of phase locking in dogs, but it seems reasonable to assume that a similar process occurs for some frequency ranges.

The value of these two processes (place coding and phase locking) is evident from our poorer perception of sound near our hearing thresholds, where one of the aforementioned mechanisms is engaged. In general, place coding is more accurate in the basal region and

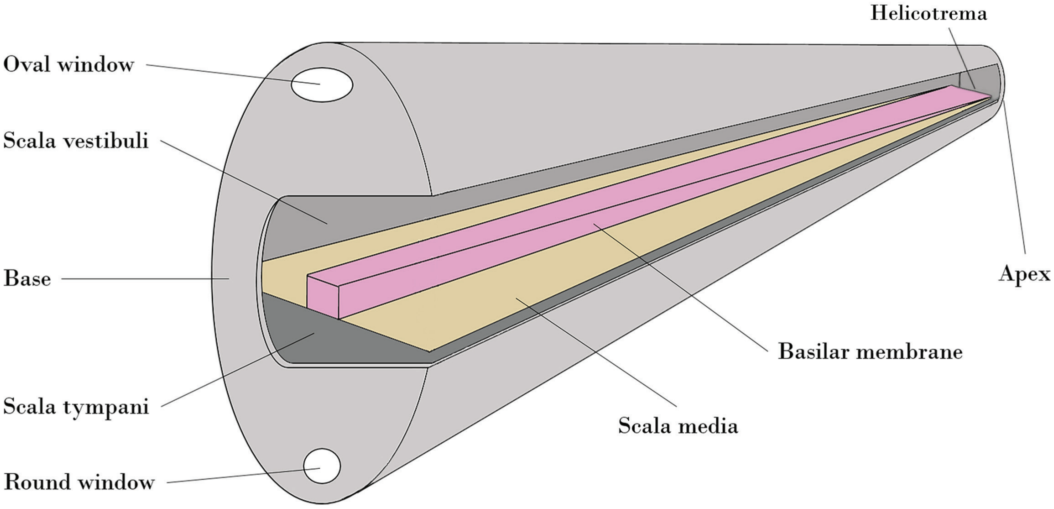


Figure 4. Schema of an uncoiled cochlea with basilar membrane.

phase locking more accurate around the more apical regions where it can occur (Fay & Popper, 1994).

The presentation of signals to the brain from the inner ear depends on the activation of hair cells, and so the number and the location of these are important. Stimulation of the inner hair cells (IHC) provides the primary information within the auditory nerve, whereas the outer hair cells (OHC) make up a feedback system that actively and selectively amplifies parts of the traveling wave (the cochlear amplifier), resulting in improved detection of sound and frequency resolution. This process results in measurable low-intensity sound coming from the ear, referred to as otoacoustic emissions (OAE); these are the product of the back projection of sound via the OHC and signal normal cochlear functioning (see Supplementary Information for further details on this phenomenon). In humans, females have been reported to produce significantly greater amplitude and more OAE (McFadden, 1998; Sax, 2010); this may, at least in part, explain a lower tolerance to background noises and higher sensitivity, especially to high frequencies. There do not seem to be comparable data for dogs, but a similar sex effect has been reported in rhesus monkeys and sheep (McFadden, Pasanen, Raper, Lange, & Wallen, 2006; McFadden, Pasanen, Valero, Roberts, & Lee, 2009); there is also growing evidence that female dogs may be at higher risk of developing noise-related fears (e.g., Storengen & Lingaas, 2015), which could provide indirect evidence of similar processes and issues in this species as occurs in humans. We suggest that it would be useful to establish whether the production of OAE can be used to predict the risk of noise sensitivities and the potential suitability of individual dogs for work in noisy environments.

Humans have been reported to have, on average, between 14,500 and 19,000 hair cells (11,000–15,000 OHC and 3,000–3,500 IHC; Wolfe et al., 2010; Pensak & Choo, 2015); in contrast, dogs appear to have fewer, with around 13,000 hair cells (10,500 OHC and 2,500 IHC; Dukes & Reece, 2004). These differences may appear surprising, given the longer cochlea in dogs, but may not be related to the hearing range; instead it may reflect a demand to be able to resolve different frequencies more accurately by humans, given our use of language in communication. At 1000 Hz, humans can detect changes of 3 Hz, whereas dogs have been reported to discriminate changes of only 8–10 Hz (Fay & Popper, 1994; Sinnott & Brown, 1993). However, it should be noted that 1000 Hz is not near the frequency best heard by dogs, which is 8000 Hz (for further reading, see below) but 4000 Hz in humans. It would be useful to evaluate sensitivity thresholds in the full range or "range of best hearing" for dogs compared with humans.

The extent to which a cell is displaced is a function of the amplitude of the wave and reflects the loudness on the sound. Human hair cells have been reported to be sensitive to deflections of only 1 nm, and the hair cells can react to differences as little as 10 µs. As a result, humans may be sensitive to volume changes of less than 1 decibel or 1 Hz (Wolfe et al., 2010). Comparable, physiological data, which might indicate the equivalent thresholds in dogs, appear to be absent.

Part 2: Specific Hearing Capacities in Dogs and Humans

Threshold of Hearing

Hearing threshold, and thus to some extent hearing range, depends on factors beyond the amplification processes of the ear discussed in the first part of this review. It is widely assumed that dogs' sensitivity to sound is greater than humans', which has been shown to be around 20 dB higher at frequencies of 4000–8000 Hz (Lipman & Grassi, 1942). However, at lower frequencies, the sensitivities of dogs and humans do not differ substantially. Thus, one must recognize that the absolute threshold of hearing varies with pitch. Pitch detection generally differs with size, with smaller individuals generally able to perceive higher frequencies (Heffner, 1983). This may relate to the interaural distance that is determined not only by the size of an individual but also the specific skull morphology, which is highly variable in dogs. To allow comparison, the threshold of hearing is reported to be normally 20 μPa or 0 dB (sound pressure level [SPL]) at 1000 Hz for humans and 0 dB (SPL) at between 1000 Hz and 16000 Hz for dogs, depending on their size (Heffner, 1983). Thus, there may be some overlap between dogs and humans regarding the thresholds, but where exactly the similarities lie will depend on the size of the dogs and sound frequency used.

It is generally believed that a sound needs to last for at least 100–200 ms to be detected reliably by either dogs or humans (Baru, 1971; Poulsen, 1981). Longer signals are more readily perceived because of differences in the temporal integration of the signal. For example, dogs may perceive a sound of a given frequency presented for only 1 ms at 28 dB but require the more typical 100 ms when presented at 0 dB (Fay & Popper, 1994). How this perception is influenced by the nature of sound (see, e.g., supplementary Figure 1) and by differences in the audible frequency range, both between dogs and human and between dog breeds of different sizes and physical appearance, still needs scientific evaluation.

Frequency Range Detection and Sensitivity Within It

The relationship between the ability to detect sound waves of different frequencies and size obviously impacts on the frequency range that animals of different sizes may be able to perceive. Nonetheless, other factors such as the form and shape of auditory structures, cochlear length, and the stiffness of the basal area of the basilar membrane (Fay & Popper 1994) are perhaps of more importance in this regard. Sensitivity within the audible range may also be driven, at least in part, by size, its relationship with the pitch of certain vocalizations, and the importance of conspecific size detection (Bowling et al., 2017). The ability to generate lower pitch sounds within a given vocalization can serve as an honest signal of size and thus possibly resource holding potential in any future contest. Indeed, in dogs it has been found that the pitch of growls may be used to infer the size of another individual (Faragó et al., 2010). Thus it is expected that humans and dogs will differ not only in the range of pitches they can detect but also in their perceptual sensitivity to specific frequencies within it. Some of this sensitivity may occur through differential amplification or reduction of sensory signals within auditory structures.

The length of the cochlear basilar membrane is widely thought to be critical in determining the extent of the hearing frequency range, although an earlier report by West (1985) claims that the cochlear length is not correlated with frequency range detection. Longer basilar membranes, such as those that occur in dogs relative to humans (Table 1), are believed to be able to detect a wider range of frequencies (Fay & Popper 1994; Heffner & Heffner, 1998, 2008), and this is consistent with the data summarized in Table 2. An audiogram of the hearing frequency range of an animal should include the absolute upper and lower thresholds for frequencies and their sensitivity throughout their hearing range. Audiograms are commonly recorded at a sound pressure level of 60 dB (SPL) but, depending on the study question, deviations from this do occur (Table 2). Typically, the human hearing range is reported to be between 20 and 20000 Hz and that of dogs between 65 and 45000 Hz, but as the amplitude (loudness) increases, so the hearing range widens. Accordingly, the detectable hearing frequency range can be increased by having larger ears, but the relationship is not absolute. Indeed, even though some dogs have substantially larger pinnae than humans, it seems that humans generally outperform dogs in their sensitivity to lower frequencies.

There is a clearly established physical relationship between the size of an animal and the frequencies it is able to generate for vocal communication (Bowling et al., 2017; Titze, Riede, & Mau, 2016), and this is often reflected in their hearing range (Heffner & Heffner, 2008). Although Heffner (1983) argued that hearing range in dogs may depend on species-typical size rather than individual differences, this appears to be based on a single behavioral study, comparing four dogs of

Table 2. Hearing Frequency Ranges of Dogs and Humans for Different Intensity Levels

Species	Amplitude	Frequency Range	Publication
Human	60 dB (SPL)	29–19000 Hz	West, 1985
Human	60 dB (SPL)	31–17600 Hz	H. E. Heffner, 1998
Human	30 dB (SPL)	110–16000 Hz	West, 1985
Human	30 dB (SPL)	130–16000 Hz	Nadol, as cited in Fay & Popper, 1994
Human	10 dB (SPL)	250–8100 Hz	H. E. Heffner & Heffner, 2007
Human	Unknown	64–23000 Hz	Strain, 2011
Human	Unknown	16–20000 Hz	Alberti, 2001
Dog	60 dB (SPL)	62–45000 Hz	H. E. Heffner, 1976
Dog	60 dB (SPL)	67–45000 Hz	H. E. Heffner, 1983
Dog	60 dB (SPL)	64–44000 Hz	West, 1985
Dog	60 dB (SPL)	67–44000 Hz	H. E. Heffner, 1998
Dog	30 dB (SPL)	200–36000 Hz	West, 1985
Dog	10 dB (SPL)	1800–22000 Hz	H. E. Heffner & Heffner, 2007
Dog	Unknown	67–45000 Hz	Strain, 2011

Note: SPL = sound pressure level.

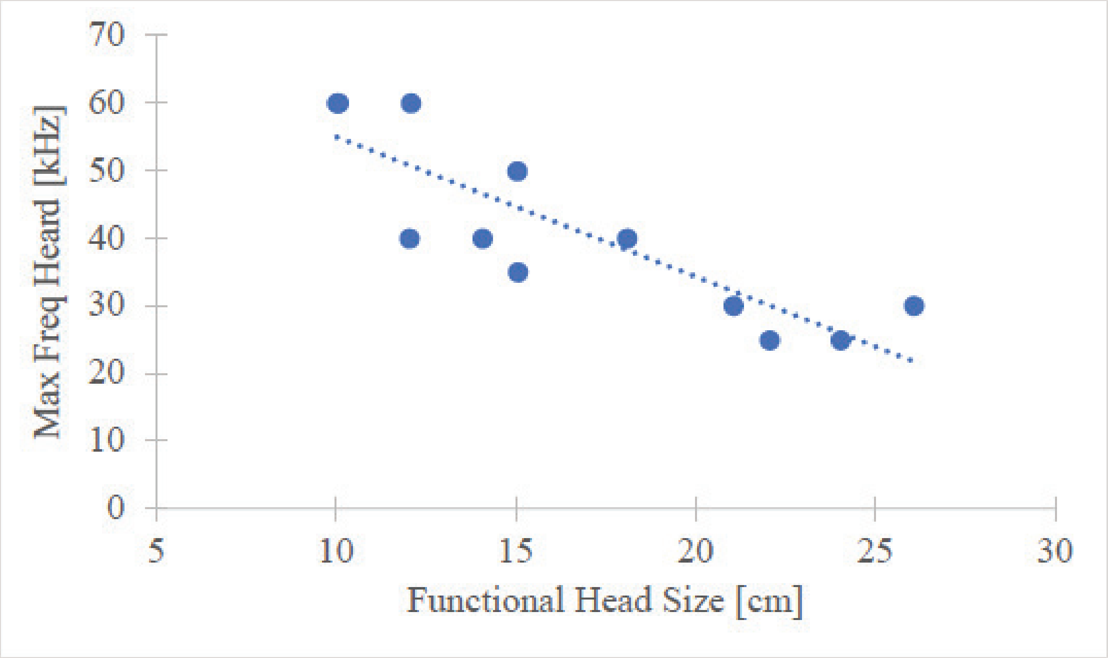


Figure 5. Relationship between functional head size (interaural distance) of dogs and highest frequency heard (from McMahon, 2015). Stimuli were presented at 70 dB (sound pressure level; measured at a distance of 50 cm from the speaker, using calibrated equipment) covering the frequency range of 0–70 kHz.

different size and different pinna characteristics. By contrast, a more recent unpublished study (McMahon, 2015), supervised by some of the authors, suggests that this biological relationship is maintained between dogs of substantially different sizes (see Figure 5).

It is likely, within the ranges of hearing relating to dogs and human, that the lower limit of detection of frequencies may actually be more dependent on properties of the TM and tympanic cavity (TC; Fay & Popper, 1994; Heffner & Heffner, 2003), which are larger in humans than dogs (Table 1). A larger TC is more capable of amplifying low-frequency components and compensating for associated pressure changes. This is important because high intra-TC pressure is assumed to increase the pressure on the TM, which in turn will be more impeded in its vibratory abilities (Packer, 1987). The size of the TM is also important, with larger TM more readily able to transduce lower frequencies.

Dogs can hear and potentially respond to frequencies that humans cannot perceive, which has the potential to cause confusion for a handler who may be unaware of this. For example, many dogs are probably able to perceive the ultrasonic vocalization produced by mice or some insects (e.g., fundamental frequency of mice is 40000 Hz, and dogs can hear up to 60000 Hz; Arriaga & Jarvis, 2013; McMahon, 2015; Peterson, Heaton, & Wruble, 1969), which is outside the hearing range of a human. Further, there are many artificial sources that transmit high-frequency sounds that are inaudible to humans but that can most likely be heard by dogs (for further reading, see **Part 4**).

Extension of hearing into higher frequency ranges can be assisted by several adaptations of the auditory system. Specific folds of the pinna cartilage might improve sensitivity to high frequencies by selectively collecting and amplifying certain high-frequency sounds (Heffner & Heffner, 2008). Such folds are more evident in the outer ear of humans compared with dogs but may be more important in sound localization than recognition (see following section). The nature of structures within the middle and inner ear may be particularly important for increasing high-frequency hearing. Within the middle ear, the TM-to-oval-window ratio and lever ratio of the ossicular chain (Puria & Steele, 2010) favors dogs over humans. Within the inner ear, a particularly narrow and thick (i.e., stiffer) basal membrane within the cochlea (Fay & Popper, 1994), as well as shorter OHC (Vater & Kössl, 2011), will enable better high-frequency hearing abilities. Adult humans do not generally perceive sounds above approximately 20000 Hz, whereas dogs are generally believed to hear up to 45000 Hz. However, some authors have found that dogs can hear up to 60000 Hz (McMahon, 2015). Dogs, in comparison to humans, also hear better by approximately 15 dB at 10000 Hz and up to 20 dB at 16000 Hz (Dworkin, Katzman, Hutchison, & McCabe, 1940). Strong systematic differences are believed to exist in the upper frequency limit between closely related species; this may relate to preferred prey and their typical vocalization frequencies (dog ~60000 Hz, coyotes ~80000 Hz, wolves ~80000 Hz, red fox ~65000 Hz, cat ~100000 Hz; Peterson et al., 1969). (It should be noted that the methods used by Peterson et al., 1969, are outdated and require validation but are included here to show that species-specific differences may be expected, at least to a certain degree.) Some dog breeds have been historically selected for finding and killing small prey (e.g., Jack Russell terriers), whereas others have been bred to do the same for larger ground dwelling species (e.g., dachshund). Therefore it might be expected that their respective hearing ranges would reflect this, but the nature and extent of variability in hearing frequency range between dog breeds based on their original function is unknown. Even in the absence of breed-specific variability data in dogs, such clear anatomical correlates with function and historical selection of breeds provide a strong argument for genetic differentiation between breeds and individuals in hearing frequency range, and the potential opportunity to select for this.

Every species (and potentially every breed of dog) can be expected to have a range of best-perceived frequencies, which are the frequencies for which the ear is most sensitive and hence detectable at very low amplitudes. In humans the best-perceived frequencies are between 128 and 4000 Hz (Fay & Popper, 1994). The human TM and ossicles have been reported to transmit sounds best for the frequency ranges between 800–1600 and 500–3000 Hz, respectively, and therefore enhance sensitivity to sounds between 500 and 3000 Hz, which are the important frequencies in human speech (Pensak & Choo, 2015). The frequency with the highest sensitivity (i.e., lowest detectable amplitude) in humans is 4000 Hz with a sensitivity of −10 dB (SPL; H. E. Heffner, 1998). For dogs, in general, it is believed that they are most sensitive in the frequency range of 200–15000 Hz (depending on size) and the best perceived frequency with a sensitivity of −1 dB (SPL) is 8000 Hz (Beaver, 1999; Heffner & Heffner, 1998), but it is not known to what extent there might be breed variation in this regard. In addition, it is not known which structures of the ear might transduce particular frequencies best in the dog.

It would also be valuable to determine if the perception and preference of frequencies in dogs has changed because of selective pressure. Certain breeds living or working in close audible contact with humans may have been selected for increased sensitivity toward human vocal communication, requiring perception of a range of frequencies that is well below a frequency range to which they have been most sensitive (Riede & Fitch 1999; Traunmüller & Eriksson 1994).

The importance of higher frequency sounds to some animals deserves special consideration. Reasons for this may exist, but the importance of crying by young dependents (Daga & Panditrao, 2011; Solomon, Luschei, & Liu, 1995) and distress vocalizations (Pongrácz et al., 2006), which typically involve higher pitch sounds, may also be selected for. Selective amplification of these sounds may be important because these higher frequencies are attenuated easily and therefore rapidly reduce with distance. It is therefore not surprising that research shows that female humans are more sensitive to higher pitch sounds after giving birth and during specific phases of the oestrous cycle (McFadden, 1998), a relationship that suggests an important role for hormonal factors in temporal differences in sensitivity. Whether similar changes occur in dogs has not been evaluated, but its potential occurrence should be noted by those working with dogs in tasks potentially dependent on their hearing acuity. The effects of neutering also remains unknown. It should also be recognized that higher frequency sounds are more generally thought to be more salient, causing more attentiveness and alertness than lower frequency sounds. Indeed, the cries of a human baby will cause distress to a dog, even though the vocalization is not of direct evolutionary importance (Huber, Barber, Faragó, Müller, & Huber, 2017; Yong & Ruffman, 2014).

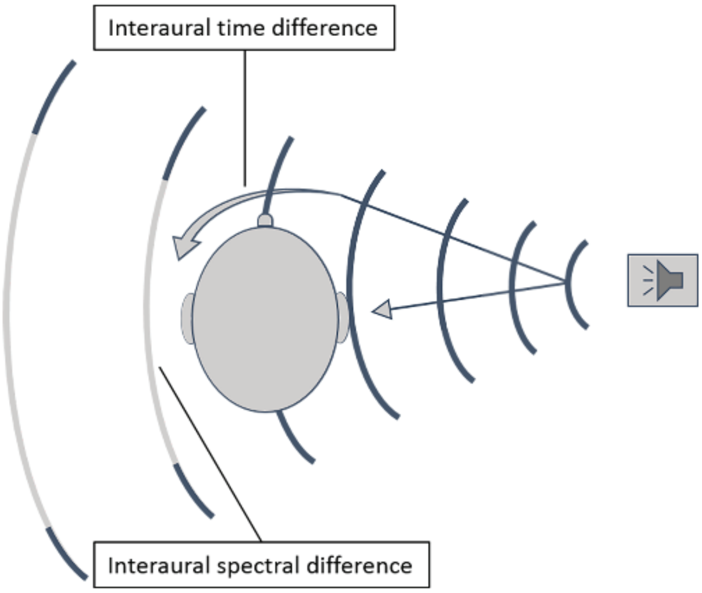
Sound Localization and Distance Detection

Research suggests that the most important role of sound localization is its role in the orientation of the eyes toward a sound source (Heffner, 1998); however, some dogs can be observed to hunt blind (e.g., diving on prey through thick snow). For sound localization, high-frequency components of the sound source are indispensable, with localization becoming inaccurate and even impossible, when the high frequencies of a sound are filtered out (Heffner & Heffner, 2008). Humans have been reported to primarily (though not exclusively) use frequencies above 4000 Hz for localizing sound sources (Heffner & Heffner, 2008), but there is no comparable work for dogs.

To localize sounds in the environment, it has been suggested that two aspects are of importance; these relate to interaural differences: binaural temporal differences and binaural spectral differences (Fay & Popper, 1994; Heffner & Heffner, 2008; Keidel & Neff, 1975; Sterbing-D'Angelo, 2010; see Figure 6). Binaural temporal differences occur because of an offset in the time of arrival of a sound at each ear depending on its source relative to each ear (Heffner, 1997). There are also slight differences in the intensity, and therefore spectral composition of the sound received by the two ears, as frequencies (and especially higher frequencies) attenuate the longer they travel and may be modified by reflection or shadowing from the head or pinna (Heffner, 1997). This explains the functional value of the folds within the pinnae, which particularly affect higher frequency sound waves. In humans the temporal interaural difference for sound is 900 µs on average, whereas in dogs the interaural difference has been reported to be 450 µs (Heffner & Heffner, 2003), and breed differences can be expected because of differences in skull size. However, interaural distance alone is not, in itself, predictive of the accuracy of sound localization in dogs (Heffner & Heffner, 2008; Heffner, 1997). Nonetheless, it would be interesting to establish whether sound localization is generally better in smaller dogs, because of their potentially increased use of higher frequencies.

The specific structure of the cartilage of the pinnae has an important function for directional hearing (Heffner &

Figure 6. Visualization of interaural time and spectral differences.



Heffner, 1992), and any distortion of the pinna (surgically, e.g., by cropping or even by piercings in humans) may require readaptation of the auditory system. In humans, temporary flattening of the pinnae has been shown to reduce the effective localization of sounds in the vertical plane (Keidel & Neff, 1975). Although empirical evidence is lacking, it seems reasonable to argue that ear cropping may not only impair hearing by reducing the effective funnel size of the ear but also reduce the ability of a dog to localize a sound. Accordingly, it is recommended that working dogs, who may depend on good quality hearing, should not have their ears cropped.

Humans have been reported to have a sound localization accuracy of 1°–2° (Heffner & Heffner, 2003; Pujol, 2010), whereas studies on dogs report a wider range of values, from 4°–8° in laboratory studies (Heffner & Heffner, 2003) to approximately 20° in the field, with the sound source being 300 m away (for review, see Fay & Popper 1994). This relatively poor performance may simply reflect the fact that the primary function of sound localization at such a distance will be to direct visual orientation toward a source. Species with a narrow field of view and high dependence on visual acuity, such as humans, may therefore benefit more from better sound localization acuity than those who may not need to locate a sound source so precisely (Heffner & Heffner, 2003). However, it is worth noting that current studies on dogs have used only breeds with a moderate visual streak rather than ones with a focal spot comparable with that seen in humans, which may be associated with greater visual dependence (dolichocephalic vs. mesocephalic vs. brachycephalic; McGreevy et al., 2004; Peichl, 1992). It might be that brachycephalic breeds, with their more pronounced area centralis, also have higher sound localization acuity compared with other breeds, such as dolichocephalic sight hounds.

Hearing can also provide an animal with important cues about the distance of a source from the subject via its frequency composition and amplitude. In general, it is easier to detect broadband sounds than pure tones, and several factors interfere with the ability to estimate the distance of an audible sound, including the presence of environmental structures (hard, soft ground, barriers), which will differentially attenuate various sound frequencies (Wiley & Richards, 1978). It is known that wolves can hear another wolf howling with a frequency range of 300–1800 Hz for 14 s, from up to 6 miles (~10 km) away in a forest and up to 10 miles (~16 km) in a flat country (Mech & Boitani, 2003), but this relates more to their auditory threshold than a specific distance estimate beyond knowing that the other wolf is within this range. In general, the amplitude of a sound source drops by 6 dB when the distance of the sound source is doubled (Holt, Schusterman, Kastak, & Southall, 2005; Klump & Shalter, 1984; Kolarik, Moore, Zahorik, Cirstea, & Pardhan, 2016; Wiley & Richards, 1978), and so it may be possible to estimate the distance of a sound source only if the sound source has an expected volume. Indeed, there is little evidence for accurate distance perception in nonecholocating mammals (Moore & King, 1999).

Part 3: Disturbances of the Auditory System

Disturbances to the auditory system can be evoked by noises of high amplitude and can be temporary or permanent, partial or complete. High-frequency hearing is most frequently affected, and noise damage is typically most extensive to frequencies above those involved in the exposure (Ryan, Kujawa, Hammill, Le Prell, & Kil, 2016). Severity and recovery depend on factors such as stimulus type (impact or continuous), exposure and resting times, and sound characteristics (temporal characteristics, intensity, range, etc.) but also on individual preconditions (sex, age, health status, preexposure, etc.; Ryan et al., 2016). Long-term desensitization is commonly caused by modulations of the auditory nervous system, whereas short-term attenuation of sounds is most often caused by reversible changes of the connective and muscular tissue of the middle ear. It is possible for an exposure that damages hearing to be neither annoying nor painful — for example, prolonged exposure to loud music or infrasound (Harding, Bohne, Lee, & Salt, 2007).

Hearing loss in humans has been studied extensively, and guidelines for noise exposure have been formulated. The Occupational Safety and Health Administration states that on a daily basis 40 million individuals in the United States are exposed to hazardous noise levels that could cause permanent hearing damage, and in the United Kingdom approximately 20% of the total population suffers from hearing loss (Lynch & Kil, 2005; NHS England, 2014; World Health Organization, 2013). Commonly, the pain threshold for humans is defined as 120–130 dB (SPL), which is a noise comparable to an amplified speaker at a heavy metal concert. However, depending on the frequency composition of the noise, thresholds can be higher or lower (including infra- and ultrasounds; Lawton, 2001; Leventhal, 2003). Every 3 dB increase of amplitude is accompanied by a doubling of sound energy, and it has been recommended that every 5 dB increase in sound exposure requires a 50% reduction in exposure time (Lynch & Kil, 2005). Further, it is recommended that no one should be exposed to noises greater than 140 dB, even for short periods. However, a shot with a rifle reaches around 150 dB and can therefore, without proper hearing protection, result in noise-induced hearing loss (NIHL; Lynch & Kil 2005). This is especially important to consider for both humans and dogs in military and police services, as well as hunters.

Surprisingly little research has investigated disturbances to hearing in dogs. In reality, dogs are often exposed to noises such as traffic, sirens, construction sites, music, children, or daily household noises, and working dogs may be exposed to exceptionally noisy environments (e.g., kennels, gunshots, transport), which may result in disturbances to the auditory system. In a comparison of several kennel environments, research has shown that kennels can have a continuous noise level above 100 dB (Scheifele, Martin, Clark, Kemper, & Wells, 2012) with peaks of around 120 dB (Coppola, Enns, & Grandin, 2006). In humans, such noise levels require hearing protection to prevent NIHL, if exposure lasts more than 1 hr (Table 3; Ryan et al., 2016). Indeed, an assessment of 14 dogs that were exposed to kennel noises for 6 months revealed that nine of the 14 dogs suffered a threshold shift of greater than 10 dB. It could not be determined whether this threshold shift was of a temporary or permanent nature, and the range of affected frequencies was not identified. The authors were also unable to identify actual threshold shifts for the dogs, as the dogs were living in kennels and the authors could not evaluate unaffected preexposure levels (Scheifele et al., 2012). Because of the missing values for preexposure levels, they assumed that the level of threshold shift in their study was underestimated. For this reason, further studies are urgently needed to identify the nature and severity of NIHL in dogs as a result of environmental noise from kennels. This research should take into consideration both dogs that are kennelled for prolonged periods (e.g., in shelters and working dogs) and those kennelled for only a few daytime hours (day care). Design and management recommendations have been formulated for kennels; these stress that a mean sound level of 45 dB should be the norm for animal housing, following standards for human dwellings (Coppola et al., 2006; Hewison, Wright,

Table 3. Exemplary Sound Pressure Levels (at 1 m) and Recommended Exposure Levels

dB (SPL)	Duration	Sound Source
> 140	< 1 min	Firearms, (turbo) jet engines, rockets, bomb and grenades
130	> 1 min	Jackhammers, magnetic resonance imaging (peak values)
120 (threshold of pain)	> 5 min	Amplified speaker (e.g., concerts), symphonic orchestra, heavy thunder
110	> 15 min	Heavy engines (e.g., diesel truck engine, bulldozer)
100	> 1 hr	Chainsaw, car at highway speed, magnetic resonance imaging
90	> 4 hr	Motorcycle, lawn mower, air compressor, subway
85	> 8 hr	Plane cabin, heavy city traffic, kindergarten break room
80		Alarm clock, dishwasher, singing
70		Vacuum cleaner, toilet flushing, car cabin
60		Conversational speech, quiet office environment
50		Average home
40		Quiet library
30		Whispered conservation
20		Quiet bedroom
10		Rustling leaves
0		Hearing threshold (human)

Note. Adapted from Engineering Toolbox (2018); Lynch and Kil (2005); Sengpiel (2017); and Venn, McBrearty, McKeegan, and Penderis (2014).

Zulch, & Ellis, 2014). However, such standards are not yet regularly implemented or legislatively supported.

Another example of a noisy environment to which dogs may be exposed is the process of magnetic resonance imaging (MRI). It has been suggested that the MRI environment can have peak values of 120–130 dB (SPL; Venn et al., 2014). Humans are normally not exposed to MRI noise without hearing protection. This may not be common practice in veterinary work, as the animals are normally anaesthetized; however, it has been reported that the exposure of dogs to MRI noise can result in a threshold shift of up to 5 dB (SPL) for frequencies between 1000 and 7000 Hz (Venn et al., 2014). This includes the frequency range of most human speech (< 3000 Hz), and so dog–human communication may be affected following MRI assessment. Unfortunately, there are no studies assessing the influence of MRI noise on the high-frequency range above 7000 Hz, and the duration of any effect has not been established. Although the need for hearing protection for dogs in an MRI environment has been stressed (Baker, 2013; Venn et al., 2014) and should be legislatively mandated under the animal welfare regulations of those nations that highlight the need to avoid unnecessary suffering. Last but anecdotally, it has been reported that military working dogs can experience a threshold shift up to 50 dB after transportation in helicopters (S. Scheifele, personal communication, November 30, 2018). Hence, noise during the transportation of dogs — not only in helicopters or airplanes but also, for example, in trailers — should be taken into consideration as a factor influencing dog welfare. Generally, in the absence of specific research to the contrary, dogs should be given at least the same level of protection as people in noisy conditions, with a view to trying to prevent problems including complete hearing loss in the longer term.

There are anecdotal reports suggesting that, as in humans, loud noises can be painful to dogs, resulting in whining, barking, howling, or aversive responses, but no guidelines or thresholds have been formulated. Some research has been done on animal repellents providing evidence that a frequency sweep of 17000 Hz to 5000 Hz to 55000 Hz with an intensity of 120 dB is aversive to dogs (Blackshaw et al., 1990). It is likely that this might be painful and potentially harmful, but further research is needed. However, as amplification processes of the ear appear to be stronger in dogs than humans (see **Part 1** of this article), it should be noted that thresholds and guidelines made for prevention of auditory disturbances in humans will most likely be higher than the thresholds for dogs.

Mechanisms within the auditory system prevent disturbance. First, the auditory tube is involved in the equalization of pressure between the middle ear and the throat to maintain proper tension for optimal vibration of the membranes of the TM, oval and round window (Strain, 2011). In humans, the upper half of the auditory tube opens with every third or fourth swallow (Alberti, 2001; Pensak & Choo, 2015). Malfunctioning of this process can lead to effusion from the TC (Kent, Glass, de Lahunta, Platt, & Haley, 2013). The auditory tube is longer and wider in humans than dogs (~38 mm vs. 15 mm; Table 1), but functional differences have not been reported. Second, in humans, specialized cells — the mastoid cells — can be found above the tympanic cavity (Figure 1; Berghes et al., 2010). These help to compensate for pressure changes (Alberti, 2001). Such a reservoir does not appear to exist in dogs, and so it should be assumed that they are not able to so easily compensate for air pressure changes, which could be especially important to consider when dogs are worked at altitude or taken on an airplane. Third, to prevent injuries of the inner ear by, for example, high-energy sounds, the ossicles are able to limit the sound amplification for sounds above about 80 dB (SPL; Pujol, 2010) through a reflex triggering small muscles, which contract and stiffen the ossicular chain, limiting their leverage action. However, this reflex has limitations: It reduces predominantly the transmission of low-frequency sounds (i.e., below 2000 Hz) and it takes up to 50–100 ms to occur and is therefore ineffective for short pulse noises (e.g., fireworks; Pujol, 2010; Strain, 2011).

Disturbance to the auditory system can also arise from rupture of the TM from strong pressure changes. The rupture of the TM leads to a conductive hearing loss, as sounds cannot be transduced effectively via the ossicular chain anymore. A fast-rising shock, such as the abrupt change in pressure associated with an explosion, can rupture at least 50% of the TM in humans at a force of 194 dB (SPL) and 192 dB (SPL) for dogs (Richmond, Fletcher, Yelverton, & Phillips, 1989). For a static pressure exposure, the average threshold is slightly higher at 198 dB (SPL) for humans and 194 dB (SPL) for dogs (Richmond et al., 1989). Therefore, values do not differ substantially between species despite anatomical differences in the TM (see **Part 1** in this article). Still, there can be individual variation in the threshold at which the eardrum ruptures. Note that a rupture in the reported studies was described as a loss of at least 50% of the TM, and smaller ruptures can be experienced at much lower pressure levels. Existing data emphasize that dogs' TM is as sensitive to pressure changes as humans'.

It is therefore advisable to check hearing function in a dog after it has been exposed to any event that has the potential to cause damage to the TM of a human. NIHL can have a significant impact on an individual's everyday performance, and it is thought that this may be as true for dogs as it is for people. In humans, hearing loss has been associated with a decline in an individual's professional and social functioning, possibly resulting in cognitive decline, decreased physical activity, poorer health conditions, and depression (Ryan et al., 2016; Scheifele et al., 2012). Hearing acuity is also important for dogs, and hearing loss in this species has been correlated with stress-related (e.g., startle) and aggressive behaviors; dogs with a disturbance of the auditory system are also at greater risk of being involved in accidents and are harder to train (Baker, 2013; Strain, 2011; Venn et al., 2014).

Temporary Threshold Shift

A temporary threshold shift (TTS) is an acute change in the hearing ability that recovers over time. Several criteria for defining a TTS have been formulated (for a review, see Ryan et al., 2016), but a standard definition is a minimum 10 dB change in hearing threshold across the frequency range of 2000–4000 Hz, which can recover within minutes, hours, or weeks (but at most 30 days) depending on severity of exposure. It is important to appreciate that recent research stresses that even though the auditory system has been reported to recover after a TTS, repeated exposure can lead to permanent functional changes in the auditory system (Kujawa & Liberman, 2006, 2009). Ryan et al. (2016) postulated that acute threshold shifts up 50 dB after a single noise exposure are likely to recover. No distinct values have been formulated for dogs, but it can be assumed that the affected frequency range after an NIHL varies because of differences in the audible hearing range. As dogs hear better in higher frequency range and higher frequencies are most often affected by loud noises, in general NIHL could be more easily induced, and possibly more severe, in dogs compared with humans, although empirical data are missing.

A TTS can be perceived as dull hearing or tinnitus in humans. It is caused by fatigue of the ear structures (especially muscles of the ossicular chain) but also changes in metabolism along the whole auditory pathway (such as glutamate accumulation in the basilar membrane or auditory brainstem; for a review, see Pensak & Choo, 2015; Ryan et al., 2016). Some studies have demonstrated that otoprotective agents such as magnesium or glutamate antagonists can be administered to reduce the extent of a TTS, but the necessity of very high doses and individual differences complicate reliable predictions regarding efficiency (for a review, see Kujawa & Liberman, 2009; Ryan et al., 2016). There do not appear to be any studies into the use of otoprotective drugs on dogs.

Research on threshold shifts in dogs does not normally differentiate between temporary and permanent damage, as long-term measures are usually missing. For this reason, and given that TTS can cause long-term consequences, the existing literature is summarized in the next section on permanent threshold shifts, even though it has not been demonstrated that this is necessarily the case. However, the lack of data in this area underlines the necessity for further research on disturbances of the auditory system in dogs, to tease apart possible short- versus long-term dangers.

Permanent Threshold Shift

A permanent threshold shift (PTS) is a change in the hearing sensitivity upon exposure to a noise that does not recover to preexposure level. A threshold shift of greater than 50 dB from baseline has been reported to most likely be unrecoverable (Ryan et al., 2016). Typically, sustained noises cause more severe PTS than single blasts (Fausti, Wilmington, Gallun, Myers, & Henry, 2009). As with TTS, there are several definitions of PTS (for a review, see Ryan et al., 2016), but the following threshold-based definitions can be taken as a guideline for hearing loss: slight hearing loss is 16–24 dB deviation from baseline, mild is 25–40 dB, moderate is 41–55 dB, moderately severe is 56–70 dB, severe is 71–90 dB, and profound is more than 91 dB (Ryan et al., 2016). However, these definitions are for acute measurements of NIHL after exposure to a noise source and do not take preexposure hearing abilities into account; only a threshold is measured, and the actual level of hearing loss can vary with the individual. Threshold levels and guidelines for dogs have not been formulated to date.

PTS is of a sensorineural nature and therefore impacts cochlear hair cells, nerve cells, and structures of the auditory pathway. The OHC are most sensitive to damage, and this results in decreased cochlear sensitivity and selectivity from reduced cochlear amplification. The biochemical mechanisms for how this damage occurs are not known with certainty, but excitotoxicity due to antioxidants and glutamate has been reported to play an important role in cell damage and apoptosis (for a review, see Kujawa & Liberman, 2009; Puel, Ruel, Gervais d'Aldin, & Pujol, 1998; Ryan et al., 2016). Among humans, enhancement of frequencies at the highest sensitivity (4000 Hz) is common, and PTS is prevalent around this frequency, in the range of 4000–6000 Hz (Ryan et al., 2016). Therefore, it can be assumed, in the absence of data to the contrary, that a common frequency range for damage related to sounds in dogs is also at their highest sensitivity (> 8000 Hz). Anecdotally, it is the opinion of one of the authors (DSM) from his clinical behavior work, that loss of high-frequency hearing may also result in a general increase in sound-related problems, and this may be due in part to a reduced capacity for sound localizability, increasing the fear associated with loud noises.

Upon experiencing an acoustic trauma, immediate symptoms in humans are otalgia (ear pain), tinnitus, aural fullness, dizziness, noise sensitivity, or distorted hearing, which in the longer term can lead to sensorineural hearing loss accompanied by peripheral hearing loss or central auditory processing deficits. It is important to note that certain medications used for the treatment of injuries can be ototoxic and therefore may exacerbate hearing impairments following blast trauma (Fausti et al., 2009; Wilson & Mills, 2005). Symptoms of acoustic trauma are reported to frequently overlap with posttraumatic stress disorders (Fausti et al., 2009). Hence (working) dogs exposed to acoustic blast events might experience similar physical effects to humans because of their biological similarity.

Deafness

Besides partial permanent threshold shifts, connected to partial deafness, an individual can also experience total deafness, which can be unilateral (i.e., just one ear) or bilateral. There are several causes of deafness and, besides exposure to high-intensity noises, it can be congenital or caused by disease. Some dog breeds are especially at risk of congenital deafness (dalmatian, bull terrier, English setter, English cocker spaniel, Australian cattle dog, Norwegian dunkerhound, and dappled dachshund) with an estimated prevalence of up to 30% in the United States (Kemper, Scheifele, & Clark, 2013; Strain, 1999). However, in European countries prevalence rates for deafness for some of these breeds, especially dalmatians, are lower because of the prohibition of blue eyes in the breed standard, which is linked to the piebald gene and the risk of deafness (Juraschko, Meyer-Lindenberg, Nolte, & Distl, 2003; Strain, 2011). Deafness in dogs is positively associated with the Merle gene, which is also associated with ocular defects and therefore multisensory restrictions. It is advisable to avoid breeding lines that have been reported to be susceptible to deafness. Identification of congenital bilateral and especially unilateral deafness in puppies can be challenging because of the timing of development of auditory functioning, such as the opening of the EAM, and early behavioral indications within the litter may not be conspicuous. However, deaf dog puppies may be prone to excessive vocalization and startle reflexes (including snapping or biting), and play with conspecifics can be more aggressive because of the lack of auditory feedback (Kemper et al., 2013; Strain, 2011). Still, deaf animals can quickly compensate for their auditory deficits and are trainable, when using appropriate cues. Brainstem auditory evoked potentials testing is therefore recommended for objective identification (Strain, 2011).

Strain, 2011 reported anecdotally that during ontogeny, deaf dogs can develop anxious or aggressive behavioral patterns, but provided no data to support this. Later onset deafness can be caused by acoustic or physical trauma, ototoxicity, or otitis. Management of dogs with later onset deafness is normally easier, as they already have basic training and will often use visual cues as well as audible ones for human-directed actions. Still, animals with hearing difficulties are, like humans, at higher risk of accidents and more likely to get lost. Management of deaf dogs has been substantially reviewed by Strain (2011) and more recently by Becker (2017).

Presbycusis is an age-related form of hearing loss that arises due to the loss of IHC and spiral ganglion nerves, atrophy of the organ of Corti and vessels of the cochlear duct, and an age-dependent thickening of the basilar membrane. Such changes are generally more prominent at the base of the cochlea compared with the apex, resulting in a greater loss of high-frequency hearing (Shimada, Ebisu, Morita, Takeuchi, & Umemura, 1998), which gradually affects the entire frequency range (Ter Haar, 2011a). Mechanisms have been reported to be similar in dogs and humans but can vary substantially on an individual basis (Adler & Hart, 1992; Pensak & Choo, 2015; Shimada et al., 1998; Ter Haar, de Groot, Haagen, van Sluijs, & Smoorenburg, 2009). In both dogs and humans, presbycusis has been described as a cumulative effect of heredity, disease, noise, and ototoxic agents superimposed on the aging process (Ter Haar, 2011a). Presbycusis is the most common form of hearing loss in dogs, and the onset of presbycusis has been reported to be around 8–10 years of age (in mixed breeds of comparable body weight; Ter Haar, 2011a; Ter Haar, Venker-van Haagen, van den Brom, van Sluijs,

& Smoorenburg, 2008), whereas early onset in humans occurs at older than 40 years of age but typically older than 60 (Arvin, Prepageran, & Raman, 2013; Ter Haar, 2011a). Sex differences have been reported, with males suffering from an earlier onset of presbycusis than females (McFadden, 1998; Pearson et al., 1995). It has been reported that individual lifestyle and exposure to environmental noises are important predictors for presbycusis in humans (Goycoolea et al., 1986), and it is also likely that such predictions hold true for dogs, with dogs with high levels of exposure to loud environments experiencing presbycusis earlier. Presbycusis has also been reported to impact binaural localization, which subsequently causes problems in selective hearing and attention, especially in environments with background noise because of the inability to separate several auditory streams (Alberti, 2001; Fausti et al., 2009).

Other disturbances of the auditory system, such as tinnitus, diseases, and lesions, which are of less relevance to this comparative review, are discussed in the supplementary information.

Part 4: Potentially Problematic Behavior Responses Associated with the Auditory System

Acoustic Startle Response and Noise Reactivity

The acoustic startle is a reflexive response (latency 6–8 ms; Lee, Lopez, Meloni, & Davis, 1996) to a sudden noise, causing a physiological chain reaction that results in increased arousal and attention, hypervigilance, and behavioral preparation for a potential fight-or-flight response. Learning and training can be used to modify and attenuate the acoustic startle reflex (Berg & Davis, 1985; Lee et al., 1996), for example, through the use of prepulse inhibition or habituation (Valsamis & Schmid, 2011). The use of prepulse inhibition in training may be a future area of value to explore for the conditioning of individuals expected to work in environments with sudden noises, where a significant startle could inhibit functionality. In mice, pulses of 120 dB can provoke a startle response, but prepulses of varying interstimulus intervals of about 70–80 dB can reduce the intensity of this (Valsamis & Schmid, 2011). Repeated controlled exposure to prepulses and pulses can subsequently lead to long-term habituation (Valsamis & Schmid, 2011), but there are no data on the practical use of this in dogs, despite its potential clinical utility (Lindsay, 2013). Further, the failure of an individual to show prepulse inhibition could be indicative of deficits in sensorimotor processing and a variety of other disorders (Lindsay, 2013), and so a prepulse inhibition test could form a useful part of the selection process for working dogs, who need an attenuated reaction to noise. A more practical solution in some circumstances might be the use of pressure vests, which are reported to attenuate the response to sudden sounds and potentially have a calming effect in such situations (King, Buffington, Smith, & Grandin, 2014). These vests apply pressure to the torso, potentially increasing vagal tone by encouraging diaphragmatic breathing. Recovery times after exposure to noise may also be reduced by these pieces of clothing (see Buckley, 2018, for a review of their use and efficacy in dogs).

Noise reactivity can be problematic for both humans and dogs; indeed, between 40% and 50% of pet dog owners report that their dog is “scared” of some sort of noise (Beaver, 1999; Blackwell, Bradshaw, & Casey, 2013). However, the extent to which dogs affected with this problem are overly sensitive to sound, in terms of stimulus perception rather than simply reactive to them—perhaps because of learned associations—remains unknown. Noise reactivity takes many forms and can arise through various processes in both humans and dogs (Riccomini, 2011), ranging from traumatic exposure and stress-induced dishabituation to potential social transmission. A review of the development of this problem and its management is beyond the scope of this article, but see Riccomini (2011) and Sherman and Mills (2008). Repeated or continuous exposure to noise can also result in health and welfare problems in both humans (Shepherd, Welch, Dirks, & Mathews, 2010) and dogs (Mills, Karagiannis, & Zulch, 2014).

Noise sensitivity/reactivity may be specific to a particular sound or a broader behavioral trait relating to sound more generally and is quite a stable predisposition in humans (Zimmer & Ellermeier, 1999). Females, whether human or dog, may be more noise sensitive than males (McFadden, 1998; Roche, Siervogel, Himes, & Johnson, 1978; Rogers, Harkrider, Burchfield, & Nabelek, 2003; Storengen & Lingaas, 2015). Further, there is evidence that noise sensitivity increases (i.e., tolerance for loud sounds decreases; Fucci, McColl, & Petrosino, 1998) with age or due to disturbances of the auditory systems (e.g., threshold shift), although reports in dogs are anecdotal.

Hyperacusis is a frequent auditory disorder in humans and defined as a heightened aural response; sounds of normal volume are perceived as too loud or even painful. This can concern everyday environmental sounds and range from a strong dislike of sounds (mysophobia) to a fear of these sounds (phonophobia;

Sheldrake, Diehl, & Schaette, 2015). Hyperacusis can greatly impact quality of life and ability to function, as loud environments will tend to be avoided. The occurrence of hyperacusis may be associated with tinnitus and a variety of psychological disorders including bipolar disorders, obsessive compulsive disorder or posttraumatic stress disorder (Fausti et al., 2009), and there is some evidence to suggest similar associations may occur in the dog (Drobny & Miller, 2016). Although it has been suggested that the hearing ability of most sound reactive dogs is probably normal (Scheifele, Sonstrom, Dunham, & Overall, 2016), the same could be said of individuals who are "jumpy" when hearing noises, so it seems reasonable to suggest that hyperacusis may occur in dogs. Given the potential significance of this condition for both the working potential and welfare of dogs, this subject deserves specific research attention. Recently, evidence has begun to emerge of a relationship between the occurrence of sound sensitivity and musculoskeletal pain in dogs (Lopes Fagundes, Hewison, McPeake, Zulch, & Mills, 2018). Certain evidence suggests that noise sensitivity may be related to the strength of cerebral lateralization in dogs. Those without a paw preference have been shown to be more reactive toward noises compared with dogs without a paw preference (Branson & Rogers, 2006). However, the extent to which a simple test of laterality may be a useful screening test for at-risk individuals remains unknown.

Responses to Ultrasound

Ultrasound refers to frequencies above the upper limit of the human hearing range—20000 Hz (children up to 30000 Hz; Ueda, Ashihara, & Takahashi, 2016). In addition to ultrasounds originating from natural sources (e.g., some animal's communication; for further reading, see **Part 2**) everyday devices produce ultrasound (e.g., motion detectors, audio systems, humidifiers, televisions, and telephones; Wohlfahrt, Waniek, Myrzik, Meyer, & Schegner, 2017). Ultrasound diagnostic imaging is also used in medical as well as military settings for reconnaissance purposes, which function in the ultrasonic range above 20000 Hz (Ter Haar, 2011b; Watson & Gorski, 2011). Even though there is, to date, no evidence that medical diagnostic ultrasound causes harm to humans (including the developing fetus), concerns have been expressed about the potential long-term impact on hearing (Marmor, Hilerio, & Hahn, 1979; Ter Haar, 2011b). It is well established that ultrasound can have thermal and mechanical (acoustic cavitation) effects on tissue indicative of the high-energy content of these sound waves (Ter Haar, 2011b). In humans, exposure to ultrasound has been reported to be accompanied by annoyance, disorientation, tinnitus, headache, fatigue, nausea, and high arousal, producing unpleasant subjective effects (Bunker, 1997; Lawton, 2001). Airborne ultrasounds with an intensity up to 120 dB have been judged to be nonhazardous, as they do not cause temporary hearing loss (Lawton, 2001), although very high-frequency sounds have the capacity to cause cell damage and death (Marmor et al., 1979). There are strict guidelines concerning the exposure of humans to ultrasound (Lawton, 2001; Ter Haar, 2011b). By contrast, dogs can hear ultrasounds up to 45000 Hz. Ultrasound is also often used in dog whistles, with the advantage that humans are not disturbed by the whistle. Further, ultrasound is often used as an animal repellent, and high-intensity ultrasound can provoke aversive responses in many species, including dogs, and may be perceived as painful if very loud (Blackshaw et al., 1990). In an experiment on dogs, 120 dB ultrasonic sweeps were shown to effectively expel dogs from tested areas (Blackshaw et al., 1990). It was postulated that the effectiveness of such devices depends not only on their frequency range but also on the wave amplitudes alongside individual features in the dog, with reactions ranging from no reaction to surprise and curiosity to ear pricking and aversion (Blackshaw et al., 1990; Edgar, Appleby, & Jones, 2007). However, ultrasounds of 120 dB are described as nonhazardous in humans, and although there may be variation in their effect depending on the exact frequency of the ultrasound, this disparity with the response of dogs needs to be carefully considered when reviewing the environment in which human–dog teams are required to work.

Responses to Infrasound

Infrasound, defined as frequencies below 20 Hz, can travel long distances and is not easily attenuated by environmental obstacles; it is even able to penetrate buildings. Besides the many natural sources of infrasound, including storms, breaking waves, earthquakes, and volcanic eruptions there are also artificial sources, including heavy engines, windmill power plants, and ventilation systems (Leventhal, 2003). For humans, background infrasound can have significant impacts on welfare, in terms of both loss of sleep and reduced wakefulness, which can reduce task performance to a level similar to that associated with alcohol intake (Leventhal, 2003). Body organs resonate within the low-frequency range, and common complaints relating to being within environment emitting certain types of infrasound include the subjective feeling of vibrations; nausea; disorientation; and, potentially with higher intensities, organ damage or death (Bunker, 1997; Leventhal, 2003). There is much anecdotal evidence that dogs, like many other species, are able to predict natural disasters such as earthquakes or storms (Liso, Fidani, & Viotto, 2014), and they are used as part of an early warning system in some countries (Woith, Petersen, Hainzl, & Dahm, 2018). However, the way that they might be able to sense these changes has not been scientifically investigated. Studies on the consequences of urban infrasound on dog behavior and well-being are also missing. This is likely to be important, given the potentially cumulative effect of prolonged exposure on human mental health and well-being.

Part 5: Auditory Perception and Related Cognitive Processes

Auditory perception is dependent on (a) the appropriate transduction of sound waves to electrical signals, (b) the filtering of certain sounds (e.g., background noise), and (c) the identification and interpretation of sound (Carreiro, 2009). We now consider how this relates to cognition and performance. Dogs hear and respond to a different frequency range than humans, so it is important for handlers to be aware that dogs may react to sounds that humans cannot hear. Studies on discrimination, generalization, and reversal learning in dogs indicate that unlike some primates, they are very sensitive to auditory stimuli (Kowalska & Zieliński, 1980), but the extent to which this might a compensation for differences in visual acuity is unknown. However, in a practical context, some evidence suggests that when a dog makes an error in an obedience class, refocusing attention using auditory cues may be of more value than using corrections (Lynge & Ladewig, 2005).

High-frequency sounds are generally considered more salient by many species (Alberti, 2001; McDermott, 2012; Yong & Ruffman, 2014), but sounds that provide information about the sound source are also prioritized (Heffner, 1998). Natural sounds may also be more likely to catch attention, as they provide the recipient with information about their surroundings and so are generally more relevant for survival (e.g., the rattle of a rattlesnake; Alberti, 2001). Humans are generally good at differentiating and evaluating the content of dog vocal communication based on only auditory cues (Chen & Spence, 2010; Molnár, Pongrácz, Dóka, & Miklósi, 2006; Molnár, Pongrácz, & Miklósi, 2010). Like humans, dogs are reported to be able to distinguish natural from artificial sounds (Heffner, 1998) and to categorize novel sounds into previously learned categories (Heffner, 1998). Playback experiments with dogs also provide evidence that dogs not only can detect the semantic content of conspecific barks but also remember individual characteristics (Bálint, Faragó, Dóka, Miklósi, & Pongrácz, 2013; Faragó et al., 2010; Molnár, 2007). Further, they are also able to detect the difference in the non-semantic content of human speech (Albuquerque et al., 2016) and can discriminate emotionally relevant information of human communication based on auditory cues (Huber et al., 2017; Yong & Ruffman, 2014). Dogs (like humans; see Pisoni & Luce, 1987) discriminate human spoken words on the basis of their phonetic composition (Fukuzawa, Mills, & Cooper, 2005a) and can normalize spoken sounds across different individual speakers (Root-Gutteridge, Ratcliffe, Korzeniowska, & Reby, 2019). However, it has also been postulated that dog performance to cues is best under natural conditions, in which auditory and visual stimuli are combined suggesting that (possibly learned) nonverbal features moderate responsiveness to auditory cues (Fukuzawa, Mills, & Cooper, 2005b). However, some evidence suggests that dogs may be capable of some syntactic understanding (Ramos & Ades, 2012). For a wider review of dogs' understanding of words, see Mills (2005).

The proximity of a sound source may affect the level of attention given to it, and dogs may learn an auditory go/no-go procedure faster if the required response is spatially close to the signaling sound source (Dobrzecka, Szwejkowska, & Konorski, 1966). This has some implications for command-based training, which should probably begin in close proximity to the dog, even for commands that will later be given at a distance.

Preference for a sound may be based on many factors, such as its amplitude, frequency range, and composition, but also the experience of the individual. Certainly, individuals prefer sounds that are not painful (in humans < 120 dB) or distracting for them, and plenty of studies show that loud sounds can be aversive to animals (Ballantyne, 2018; Blackshaw et al., 1990; Heffner & Heffner, 1998; Job, 1999; Landsberg, Mougeot, Kelly, & Milgram, 2015). However, whether a sound is perceived as aversive may depend on other factors, such as frequency composition (McDermott, 2012) as well as learned associations (Lopes Fagundes et al., 2018) and more general previous experience. For example, an individual who has not been reared in a noisy environment will most probably prefer a quiet environment over a noisy one, and vice versa. Thus, both familiarity and habituation may play an important role in auditory preferences (Heffner & Heffner, 1998). In humans, frequencies between 2000 Hz and 4000 Hz, which is in the range of the best perceived frequencies, have the highest potential for annoyance (McDermott, 2012). If this effect also applies to dogs, then the frequencies around 8000 Hz may be the most problematic ones, but further research is needed to determine this.

In general, individuals prefer sounds of ecological relevance (i.e., they prefer natural sounds over artificial and prefer sounds that are species specific and familiar; Heffner & Heffner, 1998; Snowdon, Teie, & Savage, 2015; for a review, see McDermott, 2012). In humans, McDermott (2012) postulated that natural sounds, such as ocean waves or rainfall, are rated as pleasant; it is thought that this is due to their low-frequency components and slow temporal modulations (McDermott 2012). Further, infants prefer their mother's voice over a stranger's and the native language of the mother over a foreign one (Barker & Newman, 2004). Adults prefer frequencies that are within the fundamental frequency of human speech (i.e., approximately 200 Hz; Huber, Stathopoulos, Curione, Ash, & Johnson, 1999; Ratcliffe, 2015). Generally, humans prefer harmonic sounds over dissonance, which has the capacity to distress an individual (McDermott, 2012). In music, the composition of fundamental frequency and harmonics can modulate physiological reactions (synchronization of heart rate to the beat rate of the music) and even emotional states (Det & Fakultet, 2017; Khalfa, Isabelle, Jean-Pierre, & Manon, 2002; Paquette, Peretz, & Belin, 2013; Wang & Huang, 2014). As a consequence, music can have an intrinsic capacity to calm or excite an individual.

Less is known about auditory preferences in dogs. They can discriminate familiar from unfamiliar sounds (Pongrácz, Szabó, Anna, András, & Ádám, 2014; Quervel-Chaumette, Faerber, Faragó, Mashall-Pescini, & Range, 2016), and have been reported to recognize their handlers by their voice (Coutellier, 2006). They can match the voice of a human to age categories (Ratcliffe, 2015), but whether dogs prefer familiar over novel sounds, or harmonic sounds over dissonances, has not been investigated. It has been postulated that the same features of music (i.e., low-frequency components and slow temporal modulations) may have similar physiological effects, albeit with species-specific adaptations regarding frequency ranges (calculated on basis of species-typical fundamental frequency during communication) or tempo (calculated on basis of species-typical heart rate; Snowdon et al., 2015), that is, species-specific music. There is some research on the perception of music and species-specific music in dogs (Leeds & Wagner, 2008), where it was found that soft rock, reggae, and classical music may have positive effects, whereas heavy metal had negative effects on dogs. Surprisingly, species-specific music appears to have no effect on dog behavior (Bowman, Dowell, & Evans, 2017; Bowman, Scottish, Dowell, & Evans, 2015; Kogan, Schoenfeld-Tacher, & Simon, 2012; Wells, Graham, & Hepper, 2002), unlike the preference shown by cats and monkeys (Snowdon & Teie, 2010; Snowdon et al., 2015). In contrast, it has been claimed that the calming effect of audiobooks exceeds that of music for dogs (Brayley & Montrose, 2016), although Wells et al. (2002) previously argued that classical music may outcompete speech. These differences in the dog might reflect adaptation to the human environment or simply a familiarity effect. Nonetheless it seems reasonable to suggest that appropriate auditory enrichment can increase dog welfare and inappropriate stimulation reduce it.

Infant-directed speech and dog-directed speech ("motherese" and "dogerese") have the capacity to attract the attention of the individual; infant-directed speech, characterized by high and variable pitch as well as a slower tempo and clearer articulation, is preferred by human infants over adult-directed speech (Xu, Burnham, Kitamura, & Vollmer-Conna, 2013). Similar results have been obtained for dogs (Ben-Aderet, Gallego-Abenza, Reby, & Mathevon, 2017). However, even though dog-directed speech is used for dogs of all ages, only puppies seem to prefer this form of communication (Ben-Aderet et al., 2017; Benjamin & Slocombe, 2018).

It has been suggested that dogs can be trained faster to perform a passive action such as sit or stay when using a long note with descending fundamental frequency, whereas active actions such as approaching the trainer are more likely followed if a sequence of rapidly short notes with rising frequency is used (McConnell, 1990; McConnell & Baylis, 1985). It is thought that this might relate to some inherent bias between action and sound such that acoustic structure can bias the response of the dog. Whether this is due to an auditory preference or a general correlation with certain emotional states has not been disentangled.

In humans, Cohen, Horowitz, and Wolfe (2009) postulated that auditory memory is inferior to visual memory, that is, we are more likely to remember a scene based exclusively on visual information than one based solely on its auditory associations. No comparable experiments have been conducted with dogs, but in a learning paradigm, it was suggested that a cat is more likely to associate an auditory cue with an aversive stimulus than a visual one, as an auditory cue is more salient (Jane, Masterton, & Diamond, 1965). It is not clear whether visual or auditory cues are more salient to dogs, although visual cues may overshadow verbal ones during command learning (Skyrme & Mills, 2010). Although long-term auditory memory in dogs has been investigated (e.g., Kowalska, 1997), little is known about their short-term auditory retention. It has been stated that dogs can localize sounds depending on the memory of an auditory stimulus (Heffner, 1978) and that they learn auditory tasks relatively easily compared with monkeys (Kowalska & Zieliński, 1980). Still, in a delayed matching-to-sample test using auditory cues, it has been shown that task performance decreased gradually with an increase in delay between presentation and response; at a delay of 30s, only about 70% of responses were correct, and this fell to around 60% with a delay of 90s. Dogs' short-term auditory memory therefore appears to be more limited under experimental conditions, but the extent to which this applies to the "real world" is unclear. However, various studies have shown that context can play an important role in what appears to be learned, when training verbal–action associations (Braem & Mills, 2010; Fukuzawa et al., 2005b). It is perhaps surprising that more research has not been undertaken in this area, given the importance of verbal commands in the control of dog behavior.

Part 6: Ontogenetic and Age-Related Changes in Hearing

At birth, the level of development of the auditory system of humans and dogs differs. For human fetuses the onset of hearing has been estimated to be 27 to 28 weeks of gestation (Litovsky, 2015); by 35 weeks, fetuses can discriminate 250 and 500 Hz tones, but sensitivity to sounds of a frequency of 4000 Hz (the frequency with highest sensitivity in humans) is reached only by around 6 months of age. Frequency and intensity discrimination, as well as selective attention, mature between 3 and 6 months of age but do not reach adultlike performance (at 4000 Hz) before 12 months. Localization of sound is evident within hours after birth, but the full maturation of the orienting responses can take several years (Litovsky, 2015). By contrast, at birth, dogs' ear channels are closed, and they are considered to be largely deaf. The ear channels open at about 12–14 days of age; from this time point an acoustic startle response can be observed (Breazile, 1978). After opening of the ear, hearing matures rapidly and reaches adult sensitivity by about Day 20 (Mech & Boitani, 2003). Dogs respond to frequencies of 250–750 Hz at about Day 13–16, but sensitivity to dogs' "best-heard" frequencies of 8000 Hz is not reached until after Day 20–22 (Mech & Boitani, 2003). Orientation toward sound sources is observed from Day 18 to 25 (Beaver, 1982), with full maturity of the auditory system reached at Week 6 to 8 (Mech & Boitani, 2003; Plonek, Nicpoń, Kubiak, & Wrzosek, 2017; Wilson & Mills, 2005). For both dogs and humans, all auditory structures naturally need to grow with the individual, which can be expected to cause changes in the hearing amplification processes, the frequency ranges detected, and possibly sensitivity within them. This is potentially important to appreciate with respect to the start of the early training of working dogs, which may begin before some dog breeds (especially large dogs) have their adult size (18 months of age for some large breeds; Royal Canin, 2018) and so their perceptual responses to auditory cues may change during training as they mature.

In adult humans, body and head size are relatively consistent and the pinna has an average length of 55 mm when mature at 12–13 years of age. However, the pinna continues to increase in size until death and can reach up to 70–75 mm by the age of 80 (Brucker et al., 2003; Ito et al., 2001). It seems unlikely that this is some form of compensation for functional loss of hearing with aging, as much of the change may relate to the earlobe; also unlike humans, dogs' pinnae (and those of many other species) do not appear to show a similar size change throughout their life.

Conclusions

This review highlights extensive gaps in our knowledge concerning the hearing ability of dogs, how sound might impact the performance and the level of variation that might exist between individuals and breeds. Priority areas for future research should be those that are minimally invasive and can be broadly divided into (a) aspects that may be relatively easy to model and (b) aspects that may be possible to assess using behavioral observation. For example, it would be relatively straightforward to model some of the known physical differences between dogs and humans, such as the effects of differently shaped EAMs (ear flap and auditory canal length and dimension) on the amplification of sound across the potential hearing range spectrum of dogs, or to model the mechanical effect on force transmission of the differently shaped ear ossicles using three-dimensional models. This has the potential to transform our basic understanding of the hearing in dogs and the factors that might contribute to its variability between individuals. Priorities that might be assessed behaviorally include fundamental investigations of preferred sounds and sound qualities that attract attention, as well as the features of sound (amplitude, frequency, and composition) that can lead to avoidance. From a practical perspective, exposure to noisy environments, such as during transport and kennelling, may result in temporary or even permanent hearing loss. Therefore, there is a need to monitor dogs' hearing functionality across the spectrum on a regular basis. This process should include an assessment across the ultrasonic waveband, as it seems that this is not widely researched in the literature. For this reason, more applied behavioral work should consider the impact of different soundscapes on behavior and performance as well as the development of strategies to help dogs cope better in challenging environments, in terms of both the prevention of damage and maintaining performance. Factors related to sound interference include the effects of noise and input from other sensory modalities on a dog's performance (both positive and negative) and the dog's response to the cues used to control their behavior in the field (visual and verbal commands). Finally, it is essential that, in the absence of so much basic information on the hearing ability of dogs compared with humans, there is further investigation into the factors that might affect hearing loss in this species. This should be investigated alongside research into practical solutions to minimize the risk of hearing loss or the development of sound reactivity in dogs. In the short term, it should be assumed that dogs are at least as sensitive to hearing damage as humans in equivalent settings. In the longer term, it is clear that we need a much more comprehensive understanding of dog hearing so we can identify the source of potential issues and develop an evidence-based approach to prevention and management for both working and pet dogs.

Conflicts of Interest

No conflicts of interest are declared by the authors.

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COMPARATIVE COGNITION & BEHAVIOR REVIEWS

Supplementary Information

The Nature of Sound and Hearing

Sound refers to air vibration, a wave of pressure. The transduction of sound to a sensory signal depends on the energy transmitted from the sound wave to the sensor, and this process involves the sound wave crossing through a number of structures and materials, which affect the properties of the pressure wave. The speed of sound in air (at 20 °C) is 340 m/s, but it is about 4 times faster in water at 1500 m/s (as the particles of a fluid are closer, they more readily transmit vibrations).

Sound waves flow through different media (e.g., water vs. air) not only at different speeds but also in different ways; this determines both the level of transmission of sound waves at material boundaries and the degree of sound reflection at these points (Rossing, Wheeler, & Moore, 2002). These differences in wave flow are described in terms of their specific acoustic impedance (Pa × s/m or rayl) or acoustic impedance (Pa × s/m^2 or rayl/m^2). Thus, there is a change in the sound wave at each material interface between its source and the sensory cells, which are responsible for detecting it.

The **movement of sound waves** may be thought to be relatively slow compared with the speed of light (~300 million m/s), but from a biological perspective, this is still fast enough to allow the rapid exchange of information between individuals, compared with the potential association with some other sensory modalities (e.g., smell from chemical diffusion); an advantage of auditory signals over visual signals is that they are not blocked to the same extent by physical barriers and obstacles in the environment (Rossing et al., 2002). Accordingly, audible signals have often evolved for use in situations, where the rapid exchange of information is required, but there may be environmental constraints on the effectiveness of visual signals—for example, the presence of cover in the environment, or when individuals are separated.

The **subjective perception of the loudness** of a sound is a function of the amplitude of the sound wave, which is expressed in terms of the intensity of the sound (see also Supplementary Figure 1). The amplitude of the sound wave is commonly measured on a logarithmic scale (measured in decibels [dB]) relative to a reference value (typically a standard level of air pressure of 20 micro-Pascals [μPa]) as a measure of the sound pressure level (SPL). Thus, in the dB (SPL) scale, 0 dB is equivalent to 20 μPa (or micro-Newton/m² [μN/m^2]), a level near the human hearing threshold in air, whereas 10 dB equates a 100-fold increase in pressure. In humans, a sound at 100 Hz and 60 dB (SPL) is perceived as quieter than a sound of 1000 Hz at 60 dB (SPL). This is due to the perception of loudness being a psychological phenomenon that depends on the temporal integration of the signal (Vater & Kössl, 2011). It is unknown whether this is also the case in dogs, but it seems likely.

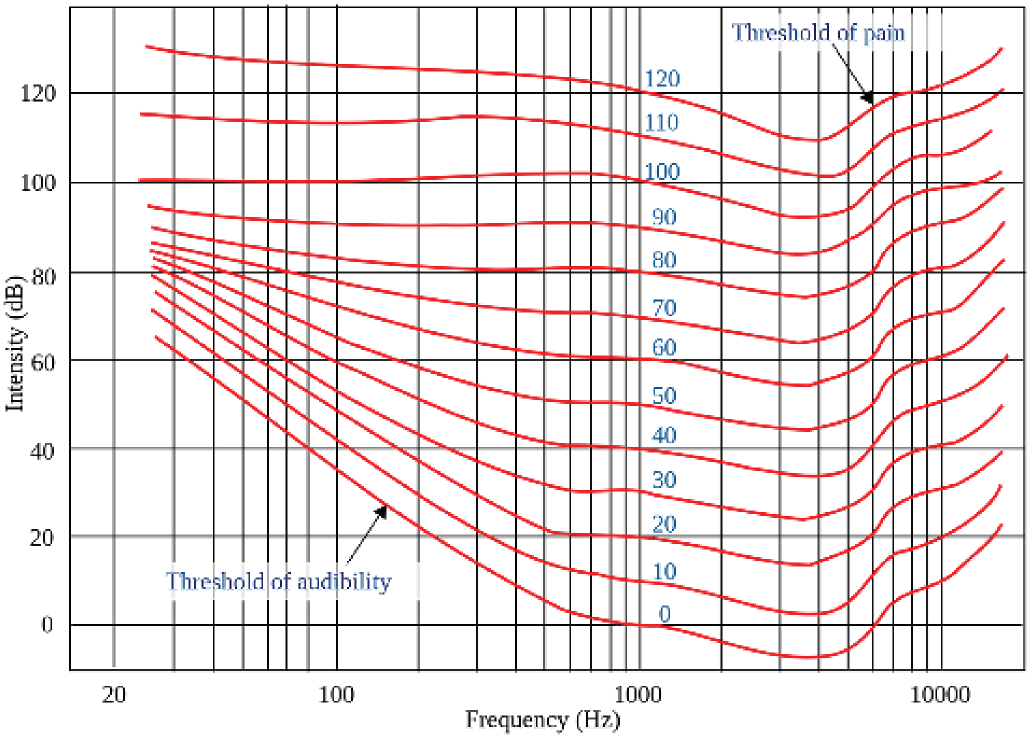
The **pitch of a sound is the subjective perception** of the frequency of the sound wave. This is commonly described in terms of the linear frequency of the sound wave—that is, the number of oscillations of the wave per unit time, typically a second, as Hertz (Hz). Frequencies below the hearing range of the human are commonly referred as infrasound (< 20 Hz) and those above it as ultrasound (> 20000 Hz). It is generally assumed that the ability to hear high frequencies declines as low-frequency hearing improves (Heffner, 1983; Packer, 1987). High- and low-frequency hearing are therefore competing abilities, and it has been reported that in mammals, low-frequency hearing is restricted to prevent low-frequency components from interfering with the analysis of high-frequency components, which are important for sound localization (Heffner, 1983; Packer, 1987). However, sensitivity to high frequencies is associated with outer and middle ear structures, whereas sensitivity to low frequencies is predominantly associated with middle ear structures (Fay & Popper, 1994). Given differences in the anatomy (see the main text), not only between dogs and humans but possibly also between dogs, it is likely that the subjective perception of sound differs differ not only between dogs and human but also between different dog breeds.

To **evaluate the hearing range** of animals, it is possible either to measure their conditioned or unconditioned behavioral response to auditory stimuli or to measure the responses physiologically—for example, through brainstem auditory evoked potentials (BAER) responses. Limitations of BAER testing in dogs include the frequency range used, which is sufficient for humans, but not covering the full range of frequency in dogs, thus hindering a reliable stimulation of the basal areas of the dog's cochlea (Strain, 2011). Regarding behavioral testing, an animal's threshold for a tone is typically defined as the probability that an animal detects it in 50% of cases (Heffner & Heffner, 2007). For this reason, it is commonly agreed that both behavioral and physiological measurements are only approximations, as the absence of a behavioral response does not mean that the animal cannot detect the sound and accordingly a neural response does not imply that an animal can perceive the sound.

Further, it is also important to consider that **frequencies that are not perceived by the brain** can still be transmitted into the ear and could cause physiological reactions, even though the sound wave is not processed as an acoustic signal. This is discussed further in the main text.

Physiological noise can influence hearing abilities in humans, but no investigations have been undertaken in dogs. An anatomical feature causing physiological noise, which can influence **low-frequency hearing**, is the internal carotid and stapedial arteries, which pass through the tympanic cavity (TC). As these structures pulse, Packer (1987) has reported that they produce volume and pressure changes in the TC and possibly produce sound waves, which could influence hearing. In humans such physiological noise causes a rise in low-frequency thresholds, when the ear is closed—for example, with headphones (i.e., closed ear effect; Packer, 1987). However,

Supplementary Figure 1. Fletcher-Munson Curve (equal loudness contours) describing the relation between frequency and intensity of a sound in humans with threshold of audibility and pain. Adapted with permission from Oarih, Wikimedia Commons under the Creative Commons Attribution-Share Alike 3.0 Unported license.



during normal hearing, this effect cannot be shown, as pressure changes caused by the arteries are most likely compensated by the outer and middle ear. There have been no reports investigating whether dog hearing is influenced by such physiological noise, but as dogs' arteries also pass through the TC, it is likely that they would be influenced in a similar way. So, if dogs are required to wear ear protection in loud environments, it should be taken into consideration that the closed ear effect might shift their low-frequency threshold.

Sound localization abilities differ between dogs and humans not only because of differences in the mobility of the pinnae (see next) but possibly also because of differences in the related brain regions. Sound localization begins centrally within the olivary nuclei of the brainstem based on interaural signal time delays and intensity comparisons. The medial superior olive differs in shape between species, being wider and U-shaped in dogs and spindle-shaped in humans (Goldberg & Brown, 1968). It is likely that differences in this structure are associated with differences in sound localization ability (for further reading, see the main text). Localization of sound is also closely associated with visual coordination, and the inferior colliculus is involved in the combination and consolidation of visual and auditory information and consequent visual-auditory-motor responses such as eye and head turning. The auditory cortex is not needed for an orienting response but is required only to integrate auditory information with other sensory abilities and consequently to identify the sound source or to modulate responses toward it (Heffner & Heffner, 2003; Heffner, 1997). Lesions of certain parts of the brain stem may disrupt sound localization, but this ability can recover over time (Heffner & Heffner, 2003).

The **mobility of a pinna** is supposed to enhance directional hearing, therefore giving animals with movable pinna advantages in sound localization over animals with fixed pinna (Njaa, Cole, & Tabacca, 2012). In humans, the muscles for pinna movements are rudimentary, and sound localization can be enhanced mainly by whole head movements. Dogs, on the other hand, possess several muscles and specialized cartilage layers to enable flexibility and movement of the ears. Unlike humans, dogs' auricular cartilage reaches far down into the ear channel, making this structure more flexible and solid during movement (Dukes & Reece, 2004). Additionally, dogs have the scutiform cartilage at the caudal base of pinna, which is an attachment point for several muscles. There are at least 10 muscles, which are organized in a caudal and a rostral group (Evans & De Lahunta, 2013; Strain, 2011). The rostral group primarily functions to medially rotate the ear and keeps the shape of the pinna in erect ears, whereas the caudal group is responsible for raising and rotating the ear. Because of variations in the outer ear of different individuals, it is difficult to generalize about the different parts and their functions (Evans & De Lahunta, 2013); however, it can be assumed that a muscle's length and strength will differ substantially between dogs with erect versus dropped ears. It has been argued that, although possibly giving advantages in the localization of sounds, a mobile pinna may interfere with the use of binaural cues, as the nervous system would have to take account of the position of the pinna to correctly calculate the sound source. There is evidence that such correction is made in the cats' auditory system (Populin & Yin, 1998) but no data for dogs. Still, it is likely that the larger pinnae of dogs are of a great value in localizing sounds but that the varying shape of the pinna between breeds will also influence this. A large upright pinna is believed to localize sound better than a dropped ear flap (for more information, see the main text). Because of fundamental differences in the auditory system between dogs and humans, conclusions regarding sound localization abilities solely on basis of the mobility of the pinna cannot be drawn. In direct comparison, dogs are poorer in sound localization compared with human even though they have a mobile pinna (see also the main text), and it remains unclear which structures or solely the link between visual acuity and sound localization abilities play an important role in this respect.

Sex differences in sound localization are known to occur in humans but not in dogs. For humans it has been reported that there are sex differences regarding sound localization abilities, with males able to pick up sounds that differ in interaural time differences by 135 μs, whereas females would need differences of 185 μs (at band noise of 600–800 Hz; McFadden, 1998). Further it has been shown that males localize sounds better with the right ear, whereas females may be more accurate with their left ear, and it has been postulated that this lateralization underpins the finding that males are better in sound localization and females perform better regarding auditory acuity (McFadden, 1998). There do not appear to be any equivalent reports for dogs. Expert echolocating blind humans can judge distances effectively within a field of up to 4 m but with decreasing precision with increasing distance (Kolarik, Cirstea, Pardhan, & Moore, 2014). Generally, humans' ability to perceive distance to sound sources within their personal space (i.e., within the reach of the arms, approx. 1 m) tends to be overestimated, whereas distance to sounds outside the personal space are underestimated; for close sounds, the distance judgment has been reported to be more accurate, when the sound is presented slightly lateral adding binaural cues to the calculation (for a review, see Kolarik, Moore, Zahorik, Cirstea, & Pardhan, 2016).

Several authors have described how high-performance audition is likely to be related to directing visual attention toward a sound source (Heffner & Heffner, 2016; Heffner & Heffner, 1992a, 1992b; Sterbing-D'Angelo, 2010). It is therefore not surprising that there is extensive **integration of auditory and visual information**. Hearing has an important function in attention and orientation responses. For humans, visual cues seem to dominate over auditory ones in bimodal spatial perception (but not temporal perception), as spatial discrimination is greater for vision (Ortega, Guzman-Martinez, Grabowecky, & Suzuki, 2014). However, this dominance can be eliminated if the sense is impaired; thus, the modality that provides greater resolution outcompetes the other. It can be assumed that auditory cues are more salient in animals with inferior vision (Heffner & Heffner, 2014; Heffner, 1997, 2004; Heffner & Heffner, 1992a, 1992b) as is the case for dogs compared with humans (for a review, see Barber et al., 2020). Such discrepancies in the relative resolution of auditory and visual cues could cause dogs to prioritize different sensory information to humans depending on the task.

The Nature of the Auditory System in Humans and Dogs

Outer Ear

Passive amplification processes occur within the outer ear—that is, sound information is modified on the basis of the selective collection and funneling of sound waves of differing frequency and/or amplitude. This begins with the structure of the outer ear, the **pinna** (auricula). The pinnae vary in shape depending on species and a range of within species factors such as breed. It consists of flexible cartilage and is coated with skin and/or fur, which will affect its acoustic properties. At its simplest, the pinna can act as a funnel, which functions like an old-fashioned ear trumpet, to selectively collect and amplify certain wavelengths (Fletcher, 1992). However, if the pinna is folded down, it will act as an acoustic barrier to this process. Likewise, if it is altered it can be expected to affect its function. Ordinarily, specific folds within the pinna function to collect and amplify high-frequency sounds (Heffner & Heffner, 2008), which may vary depending on the size and shape of the pinna.

In humans, the **external auditory meatus (EAM)** is enveloped along about half of its length by extensions of the auricular cartilage of the pinna, with the other half being surrounded by the temporal bone, a hard cavity, which absorbs little sound but directs it to the tympanum (Alberti, 2001). The EAM has a sigmoid shape, with the bend limiting intrusion into the ear by potential physical obstructions (Menner, 2003; Moore, Dalley, & Agur, 2013; Pensak & Choo, 2015).

The EAM acts as a resonating tube; for humans, it is sigmoid shaped and has been shown to amplify sounds of 2000–6000 Hz best (Alberti, 2001; Keidel & Neff, 1974; Wolfe, Kluender, & Levi, 2010). The length and diameter of the EAM have been reported to be correlated with body size, and so it is not surprising that it varies with the sex of the individual: Male EAMs are on average 2 mm longer and wider than those of females (Salvinelli et al., 1991). However, differences in the length of the ear channel may also arise from differences in the measurement method, as different studies do not agree on the measurement reference points; that is, start and end point as well as angle of measurement can vary (Staab, 2013). The EAM of dogs has a vertical and horizontal part—it is L-shaped (Strain, 2011; see Figure 2). The total length and diameter of dogs' EAM is correlated with body size (Huang, Little, & McNeil, 2009).

The relative degree of enclosure by cartilage and bone varies with both the breed and skull shape of the dog (Harvey & Ter Haar, 2017). For example, the EAM of a pit bull terrier sits "deeper" and at a different angle compared with a German shepherd EAM, so that a higher proportion of the EAM in the pit bull is embedded in the temporal bone; it has been assumed that this provides better protection, but it may have implications for the amplifications of sounds and consequently hearing sensitivity. Within the middle ear of humans, which is embedded in the temporal bone, the reflections from the bulla walls are thought to enhance the pressure drive from the tympanum and therefore sound amplification especially for higher frequencies (Bergevin & Olson, 2014). Whether a similar phenomenon applies to the EAM as a result, when there is greater bony encasement, remains unknown. This, along with other factors, should be considered when trying to evaluate the potential for breed-related differences in hearing ability.

In summary, the outer ear (i.e., pinna and EAM) of humans has been reported to amplify sounds in the frequency range of 2000–5000 Hz (up to 7000 Hz in newborns) by 10 to 20 dB (SPL; Keidel & Neff, 1974; Pensak & Choo, 2015). Although the natural resonance properties depend on the size and the shape of the EAM, it is inversely related to its length—that is, the longer and wider it is, the greater the passive amplification (Pensak & Choo, 2015). Furthermore, the shape and dimension of the pinna may influence the resonance properties to selectively amplify certain sound frequencies (Strain, 2011). It is assumed that the amplification process of the dogs' ear is greater than in humans, as they have proportionally bigger pinnae, wider concha, and wider and longer EAM compared with humans.

Middle Ear

The transduction of acoustic energy from the TM over the ossicular chain to the oval window is affected by the size ratio of the TM and the oval window; this membranous transfer of energy involves a shift from a relatively large displacement of low force at the larger TM to a smaller displacement of higher force on the small area of the oval window. For humans, it has been reported that without the transmission of the acoustic energy over the ossicular chain, 30 dB would be lost (Alberti, 2001; Pensak & Choo, 2015; Pujol, 2010).

No major differences are reported in the proportion of the sizes of the TM and oval window within dogs and humans, with ratios of 1:18 and 1:17–20 respectively. Therefore, it seems unlikely that this feature is responsible for any differences in amplification between dogs and humans (Hemilä, Nummella, & Reuter, 1995).

The size of the ossicles has been reported to vary between individuals in human, but it remains unknown whether such differences are due to physical differences (e.g., in body size). However, despite differences in the size of people, concordance with mass between the ossicles seems to be maintained, indicating no strong amplification differences between individuals (Wendell Todd & Creighton, 2013). To our knowledge, there are no comparable and comparative studies for dogs.

Inner Ear

The structures of the inner ear lie inside the temporal bone and can be divided into the bony and membranous labyrinth. The bony labyrinth includes the vestibule, semicircular channels, and the cochlea, whereas the membranous labyrinth includes, among other things, the semicircular and the cochlear ducts. The semicircular channels and ducts are involved in balance, which is outside the scope of this review.

The vestibule, a small chamber filled with perilymph (an aqueous fluid), is the entry point of vibration from the middle ear to the inner ear, separated by the oval window—a membranous structure that is set in motion by the vibration of the stapes. At this point the sound wave is translated into a slow propagating mechanical pressure wave because of its transduction into the fluid environment (henceforth the *traveling wave*; in humans approximately 2.5–20 m/s depending on frequency; Rhode & Recio, 2000; Von Békésy & Wever, 1989; Windmill, 2005). Subsequently, the pressure wave passes through to the cochlea. The cochlea is a spiral bony chamber containing three channels (scala vestibuli, scala tympani, and scala media [i.e., cochlear duct]), which are wrapped around a bony axis, narrowing toward the apex. Within the cochlea the traveling wave passes along the perilymph-filled scala vestibuli (upper chamber), from its base to the apex and over the helicotrema back through the scala tympanic (lower chamber) to a structure called the round window. The round window is the membranous exit point of the cochlea, which is positioned beneath the oval window. It can be thought of as the pressure release point for energy of the traveling waves that was not used in the frequency analysis of the cochlea. The movement of the round window is synchronous to the oval window but in the opposite phase, as fluid is relatively incompressible. This movement may cause an increase in pressure within the TC (Alberti, 2001), which may play an important role in the amplification processes, especially for higher frequencies (Bergevin & Olson, 2014). The back-reflection of traveling waves of the inner ear to the middle ear is also important for the transduction of otoacoustic emissions (OAE; Bergevin & Olson, 2014), which are discussed next and further in the main text.

The cochlear duct, between the scala vestibuli and scala tympani, contains the basilar membrane with the Organ of Corti. The Organ of Corti consists of one row of inner hair cells, attached to afferent ganglion nerve cells, and three rows of outer hair cells (OHC), attached to efferent ganglion cells. In humans, 90% of all afferent nerve fibers are connected to inner hair cells but the OHC make up 75%–80% of the total sensory cell population (Fay & Popper, 1994). The hair cells are bound by the tectorial membrane. On top of the hair cells, stereocilia are located, which are linked via tip-links to neighboring stereocilia. If a traveling wave propagates through the fluid of the scala vestibuli and scala tympani, the basilar membrane is deflected, and consequently the hair cells are bent against the tectorial membrane. Because of this movement, potassium channels in the hair cells are mechanically opened, the cell depolarizes, and an electrical signal sent to the brain via the auditory nerve. The hair cells therefore serve as mechanoreceptors converting mechanical energy (in the form of traveling waves) into electrical energy (i.e., nerve potentials; Strain, 2011). It is important to note, that because of the special structure of the basilar membrane (narrow and stiff at its base, wide and flexible at its apex), traveling waves only effectively discharge energy and deflect specific regions of the basilar membrane, causing only specific hair cells in a particular region to produce a nerve action potential; thus the basilar membrane is tonotopically organized, with high frequencies deflecting the base and lower frequencies gradually transduced more towards the apex. This frequency selectivity is discussed in more detail in the main text.

OHC have been reported to provide a feedback system and are responsible for enhancing the perceived frequencies, which unlike the outer ear structures provide an *active* amplification process. If an OHC is bent against the tectorial membrane, the hair cell's respective stereocilia become longer and reactively contract like a muscle cell. This results in movements that pull the tectorial membrane downward, while pushing the basilar membrane upward; this can also be imagined as the excited region becoming stiffer leading to enhanced displacement of this cochlear region. This mechanism, commonly referred to as the "cochlear amplifier" (Abdala & Visser-Dumont, 2001), results in an improved detection of sound and frequency resolution. However, this mechanism has been reported to only improve perception of sounds at low to moderate levels, as it is saturated by high-level input. Contraction of healthy OHC in humans has been reported to increase sensitivity around 45–50 dB (Lynch & Kil, 2005). To our knowledge, there are no investigations on dogs.

Because of the interconnection of neighboring hair cells, a whole group of hair cells always reacts together. This, in combination with the fact that there is, unlike other sensory cells, no active equalization of ionic concentrations in the hair cells, explains the rapidity and sensitivity associated with these cells (Pujol, 2010; Wolfe et al., 2010).

The stronger the amplitude of a propagating traveling wave, the greater the hair cells bend and the faster the neuron fires, which enables the brain to encode for the "loudness" of an arriving sound. Four features of the stereocilia of the hair cells make them particularly sensitive. First, they do not have to adapt to changes and therefore always register changes in the environment; second, the deflection of the ion pores needs to be as little as 1 nm for the generation of nerve potential; third, they are capable of detecting time differences as small as 10 μs; and fourth, they do not need regeneration times as no biochemical cascade mechanisms are involved in the electrical transduction process.

Also, the helicotrema (the transition point between the scala vestibuli and scala tympani of the cochlea) is known to influence the capacity for low-frequency hearing. The helicotrema acts like an acoustic shunt, reducing pressure differences between the cochlear ducts. It has been proposed that the size of it is inversely related to cochlear sensitivity to low frequencies—that is, the smaller its size, the better the low-frequency hearing (Fay & Popper, 1994; Manoussaki et al., 2008). In humans the helicotrema has an average size of 0.25 mm^2 (Littler, 1965). Systematic data on helicotrema size in dogs do not appear to exist.

Neurophysiology of Hearing

The cochlear nucleus of the brain is important for temporal and spatial coding and, like all structures of the mammalian auditory pathway, is tonotopically organized—that is, higher and lower frequencies synapse according to an orderly ascending regime (for further reading, see, e.g., Kolb & Whishaw, 2014; Roberts, 2002; Wolfe et al., 2010). The cochlear nucleus incorporates special nerve cells that are sensitive to the onset of a sound, some of which are especially tuned to certain frequencies and involved in a process of lateral inhibition and therefore frequency tuning. The inferior nucleus plays an important role in the processing of more complex aspects of sound in mammals, including frequency and amplitude, with specialized cells that respond to certain combinations of these features.

In humans, up to seven electrical waves within the brain can be measured after the onset of a signal (Boston & Møller, 1985; Markand, 1994). However, in dogs, normally only five electrical waves can be reliably measured (Kemper, Scheifele, & Clark, 2013). As the physiological structures of the auditory pathway are the same in dogs and humans, these differences of measurable waves might not be due to neurological differences but to methodological constraints (e.g., thicker cranial bones inhibiting transduction of electrical signals), and so the significance of this difference is unknown. BAER experiments on dogs have shown that the onset of a nerve signal in the auditory nerve can be measured after

1–1.5 ms and subsequent brain waves at 1 ms respectively (11 ms till Wave 5; Kemper et al., 2013). This value is similar to that reported in human BAER experiments with an onset of a signal after 1 ms and further waves after 1 ms, respectively (7 ms till Wave 5; Kemper et al., 2013; Markand, 1994). In humans it has been reported that BAER is affected by temperature (absolute and interpeak latencies longer at low body temperatures), body and head size (absolute and interpeak latency longer for bigger individuals), and the sex of the individual (absolute and interpeak latencies being shorter in females; Boston & Møller, 1985; Markand, 1994; Meij, Venker-van Haagen, & van den Brom, 1992; Wilson & Mills, 2005). In dogs, some authors report no differences in the temporal characteristics of BAER because of variations in head size but report sex differences with female dogs having shorter cochlear response times (Kemper et al., 2013). Other authors report strong influences of head size on absolute and interpeak latencies but only weak correlations with sex and age (Meij et al., 1992). Present studies differ substantially in the number, breed, and individuals used, as well as the testing parameters (see also Kawasaki & Inada, 1994; Plonek, Nicpoń, Kubiak, & Wrzosek, 2017; Wilson & Mills, 2005), and breed- or sex-related differences in the speed of auditory processing cannot be ruled out. For further reading concerning BAER experiments in humans, see Boston and Møller (1985) and Markand (1994), and for the experiments in dogs, see Marshall (1985), Plonek et al. (2017), Strain (2011), and Wilson and Mills (2005).

Otoacoustic Emissions

OAE are evidence of this active cochlear amplification and have been reported in a wide range of vertebrates, including both humans and dogs, but also in invertebrate species; this is considered a very important part of the hearing process (Abdala & Visser-Dumont, 2001; Gonçalves, McBrearty, Pratola, Calvo, Anderson, & Penderus, 2012; Kössl, Möckel, Weber, & Seyfarth, 2008; Möckel, Seyfarth, & Kössl, 2011; Pensak & Choo, 2015; Powers, Salvi, Wang, Spongr, & Qiu, 1995; Ruggero, Kramek, & Rich, 1984; Strain & McGee, 2017; Strain, Rosado Martinez, McGee, & McMillan, 2016; Venn, McBrearty, McKeegan, & Penderis, 2014). Vibrations of the OHC can be back-projected via the round window to the TC and outer ear, producing a measurable low-intensity sound, commonly named an OAE. Measurement of these emissions give insight into the unobstructed processing of traveling waves in the inner ear and are a sign of active amplification processes in the cochlea. OAE are therefore a powerful noninvasive tool in medical and research settings for screening hearing, estimating hearing sensitivity and differentiating between the sensory and neural components of hearing, especially in relation to individuals with hearing deficits or loss. They have been used to assess hearing in puppies (Schemera et al., 2011) and might be a practical way to monitor hearing in working dogs in the field, especially following exposure to extreme sounds such as explosions and gunfire by military working and police dogs. Still, the technique will need validation and good baseline measure before it is used to monitor hearing changes over time. Vibrations of the OHC have also been reported to have the ability to elevate the threshold of hearing and therefore reduce sensitivity to sounds, as the detection of “internal biological noise” degrades the ability of the sensory neuron to respond to sound (Powers et al., 1995); this could be a protective mechanism in noisy environments derived from a temporary threshold shift.

Other Disturbances of the Auditory System

Tinnitus

Tinnitus, the sensation of a high-pitched tone or hissing sound, is strongly correlated with noise-induced hearing loss and can be a source of individual distress. Tinnitus is defined as head or ear noise lasting 5 min or longer and has been reported to be a symptom of a variety of health problems (Fausti, Wilmington, Gallun, Myers, & Henry, 2009). For humans, tinnitus can be objectively measured by OAE; there are also reports of tinnitus in dogs (Norton, Schmidt, & Stover, 1990; Strain, 2011). However, as tinnitus is a subjective sensation, it remains unknown whether dogs actually perceive it or whether it impacts them. Still, tinnitus in dogs could be a sign of the ongoing development of deafness and has been reported to be associated with excessive head shaking, pawing at the ears, or sensitivity to touch around the ears (Strain, 2011). Whether tinnitus is the cause or result of some of these behaviors requires further research.

Diseases Associated With Changed Hearing Function

Several diseases have been reported to be correlated with hearing loss, which can be of a temporary or permanent nature, depending on severity and aetiopathology. Van der Gaag (1986) suggested that dogs with erect and cropped ears are at a higher risk for infections of the auditory system, as intrusions are more likely to enter the ear. However, because of a lack of ventilation, dogs with hirsute or dropped ears are also believed to be at higher risk of otitis. Otitis is a common cause of hearing loss in dogs, infants, and adult humans. Otitis can concern any part of the ear (outer, middle, inner). The inflammation causes swelling, leading to a conductive hearing loss. Normally, this will return after treatment (temporal conductive hearing loss). However, an ongoing disease without treatment can subsequently lead to cell death, which can lead to permanent hearing loss. Otitis media (middle ear inflammation) with effusion (i.e., filling with fluid) has been reported to result in temporary hearing loss of 10–50 dB and in chronic cases a loss of up to 65 dB of sensitivity (Carreiro, 2009). The consequence of this (e.g., in human children with otitis for 130 days in their 1st year of life) can be a lower score in language skills (Carreiro, 2009). The aftereffects in dogs have not been quantified.

Another cause for a temporary conductive hearing loss is the accumulation of cerumen (ear wax) in the EAM. Cerumen from sebaceous and apocrine glands prevents surface dehydration and inflammation and helps to guarantee full functioning. It functions to trap small particles but also to transport shed skin out of the ear. However, overproduction or disturbances of the transport of cerumen can lead to blockage and consequently limit ventilation of the ear. This can increase the risk for otitis externa and neoplasia (Cole, 2009; Strain, 2011; van der Gaag, 1986). The composition of dog and human cerumen has been reported to be slightly different, but there are no reports of functional differences (Stahl, Mielke, Pankow, & Kietzmann, 2013). The number of glands producing cerumen is positively correlated with the risk of otitis (Huang et al., 2009); this varies with breed but is especially high in long-haired breeds or dogs with floppy or hirsute ears (e.g., cocker spaniel, poodle).

An iatrogenic cause of temporary or permanent hearing loss in dogs and humans is ototoxicity, from certain medications used to treatment other diseases—for example, some nonsteroidal anti-inflammatory drugs or antibiotic medications (e.g., gentamicin; Fausti et al., 2009; Harvey & Ter Haar 2017; Knowles, Cash, & Blauch, 1988; Kujawa & Liberman, 2006; Ter Haar, Venker-van Haagen, van den Brom, van Sluijs, & Smoorenburg, 2008). The risk from these medications, though often very low, needs to be given careful consideration with dogs that depend on their hearing for their work (e.g., hearing alert dogs).

Lesions of the Temporal Cortex and Brainstem

Trauma or diseases, such as vascular accidents, which cause lesions of the auditory cortex, have varying impact on hearing, which depends on their position and extent. Many lesion studies are performed on animal models, whereas historical research on humans has relied on the few individuals accidentally injured. Unilateral lesions of the posterior two-thirds of the auditory cortex can cause hearing loss in the contralateral side and impact sound localization (Heffner & Heffner, 1984; Strain, 2012). However, as the detection of sound is mainly dependent on subcortical structures and as the contralateral side remains intact, some ability for sound localization remains.

Lesions to the structures of the brainstem have a greater effect on this ability. In the case of unilateral lesions, the ability to localize sound can partly recover within a few months (Heffner & Heffner, 2003); thus, a working dog suffering such trauma may be able to return to work, depending on the importance of good hearing to the tasks that it performs. In humans, the ability to localize sound is located in the right hemisphere, so only lesions to this side of the cortex will cause difficulties in sound localization (Zatorre & Penhune, 2001). Bilateral lesions of the posterior part of the auditory cortex can cause total deafness in both humans and dogs (Heffner & Heffner, 2003), but functional effects may not be as catastrophic as might be thought, because of the subcortical processing of sound.

Multimodal processing (vision and hearing) as well as speech processing can be affected in humans with bilateral lesions (Cohen, Jobert, Le Bihan, & Dehaene, 2004). In dogs, bilateral ablation of the parts of the auditory cortex results in only slight, but detectable, hearing loss (Heffner & Heffner, 1984). Processing of words/sentences is predominantly by the left hemisphere in humans and dogs (Andics, 2017; Peelle, 2012; Ratcliffe & Reby, 2014), and lesions of this region might cause problems in lexical processing. However, identification of the basic frequency, intensity, and duration as well as the vowels *a* and *i* are preserved even after bilateral removal of the auditory cortex in dogs (Baru & Shmigidina, 1977). However, a full bilateral lesion of the temporal cortex causes a complete collapse of the auditory process. Animals with full bilateral lesions can be trained to indicate whether a sound comes from the left or the right, but they are not able to localize the sound source (Heffner & Heffner, 2003) and may lack the ability to differentiate the direction of sound movement

(Baru, Kalmykova, & Shmigidina, 1986). More recently it has been shown that lesions of A1 (the primary auditory cortex) in dogs impair auditory localization abilities, whereas lesions of the belt area (secondary auditory cortex) result in deficits in auditory quality discrimination and the processing of complex sound patterns (Kuśmierek, Malinowska, & Kowalska, 2007).

Lesions of the cortex can also affect the ability to distinguish between sounds; for example, the threshold for distinguishing a sound from a higher frequency rises from 7.5 Hz to 27.5 Hz in macaques (Harrington, Heffner, & Heffner, 2001). This is an interesting finding, as the cortex is not per se involved in the discrimination of sounds in the first instance.

Recovery after lesions is possible, at least in cats, as the cortex seems to play only a minor role in this ability (Cranford, 1978). Similar effects have been reported for the discrimination of frequency sweeps, that is, the discrimination of falling and rising tones, which is impaired but not abolished by lesioning of the cortex in rats (Kelly & Whitfield, 1971). The extent to which these results apply to dogs and humans is unknown. There may be species-specific differences, but these results are of relevance when considering the prognosis of, for example, a military working dog injured in action. Injury to the lateral lemniscus has been reported, in the cat, to affect reflexive head movements toward a sound source, whereas lesions to the inferior colliculus and brachium abolish the accuracy of the sound localization in the contralateral field and increased latencies toward sound sources (Thompson & Masterton, 1978).

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