

Animal Psychoacoustics

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Animal psychoacoustics is an instrumental tool for our understanding of how nonhumans perceive the world around them.

Acoustic communication is vital for any living being. An antelope unable to hear a lion pride sneaking up on it (**Figure 1**) will be dinner for those lions, especially at night when visual cues are minimal. On the other side of the coin, predators unable to hear the rustling of prey will go hungry for a long time, likely leading to starvation. Across the animal kingdom, acoustic communication is also used for mate attraction, courtship rituals, offspring detection and recognition, territoriality, conflict resolution, coordinating hunts, and alarm signaling. Although some animals will use multiple sensory modalities across these communication contexts, acoustic communication has the benefit of traveling long distances, not requiring a direct line for communication, and working day, night, or in dense environments. Acoustic signals can also be cryptic, such as narrowband high-frequency predator detection signals, which can be sent to warn conspecifics about danger without giving away the sender's location (Bradbury and Vehrencamp, 2011).



Figure 1. Lions (*Panthera leo*). Photo courtesy of Barry E. Hill, used with permission.

Acoustic communication can be broken down into several components, each of which can be studied independently but all of which are critical for the communication process: signals, environments, and receivers (Bradbury and Vehrencamp, 2011). Different signals are generally effective in their transmission through the environment (Wiley and Richards, 1978). Low-frequency signals travel farther, but small animals often cannot generate low-frequency signals. The environment can impose a number of other constraints on acoustic signals, including changing the temporal and spectral properties of a signal as it travels from the sender to the receiver. Sounds propagating in the real world can be affected by reflections, scattering, refraction, attenuation, absorption, reverberations, and noise. Receiv-

ers must estimate the distance to a sender to know whether an intruder is located within or outside their territory or to be able to locate a potential mate.

Ambient (or environmental) noise is a particularly interesting problem in acoustic communication by animals (e.g., Wiley, 2015). Whether it comes from other animals, weather, or humans, it is clear that at least some animals adjust their communications based on the levels and spectral features of the ambient noise when they emit signals (e.g., Brown et al., 1995). Several field studies have shown that animals have adjusted their communication signals over the past few years or decades to compensate for either anthropogenic or other noise sources (reviewed in Wiley, 2015). From many studies, we can see the clear influence that humans are having on the lives of animals (e.g., Wiley, 2015). It would be of great importance, therefore, to know as much as we possibly can about what animals can and cannot hear, how noise affects their ability to communicate, and exactly how detrimental environmental disruptions of communication can be to an animal's life. Very important, results from such animal bioacoustics studies are used to implement environmental standards for noise and human involvement in animal populations.

Thus, to survive and thrive, animals need to be able to detect, discriminate, localize, identify, and categorize all types of sounds to navigate their complex acoustic world effectively (Bradbury and Vehrencamp, 2011). To determine an animal's perception of the world, it is first important to understand simple hearing abilities under controlled laboratory conditions before one can begin to speculate about their communication strategies and abilities under more natural settings using more natural stimuli.

Psychophysics is a method of presenting stimuli to an organism to “determine the limits and dimensions of its sensory experience” (Stebbins, 1970). Psychoacoustics is a subfield of psychophysics where the stimuli are presented in the auditory domain. In animals, psychoacoustic experiments are often lengthy and difficult behavioral experiments to conduct, but they are considered the “gold standard” by most researchers in the field of audition (Klump et al., 1995). Reliable, trained, awake, behaving animals are telling the researcher how they perceive the world: whether a sound came from the left or the right, whether a sound was from a partner or a stranger, or what exactly the signal was that was obscured by noise. Psychoacoustic experiments have been

used for many years to answer questions such as these (Fay, 1988), and the more data obtained from such experiments, the better understanding we have of the communication behavior of a given species.

Psychoacoustics has been used to determine an animal's sensory-processing acuity for decades (e.g., Stebbins, 1970). Early studies on an animal species typically vary acoustic stimuli along one dimension (e.g., frequency, duration, intensity) at first and then move on to more complex, naturalistic stimuli varying in multiple dimensions (Fay, 1992). Just noticeable differences or the smallest change in an object that can be noticed about 50% of the time can be determined for both barely detectable and much louder stimuli. Typically, signal detection theory techniques are employed to calculate thresholds (Green and Swets, 1966). Stimuli with changes the animals can detect and changes they cannot detect are presented to the animals for numerous trials, and the rate of “hits” is compared with the rate of “misses.” On other trials, no change occurs in the stimulus presentation and the animal is typically required to withhold responding for a “correct reject.” If they respond on those no-change trials, a “false alarm” is recorded. Hits, misses, false alarms, and correct reject rates are all used to determine whether the animals are under stimulus control and actually responding to the experimental task in the way they were trained to respond. Importantly, these are also used to determine thresholds for each experimental condition by separating response biases the animals may have (animals, like humans, may be more or less conservative) from their sensitivity.

The various psychophysical methods used to determine auditory acuity in humans (Zwicker and Fastl, 1999) have various levels of success when used with animal subjects (summarized in Klump et al., 1995). In humans, popular psychophysical approaches include the method of constant stimuli, where a set of stimuli is presented both above and below the estimated threshold randomly for many hundreds or thousands of trials. Subjects respond “yes, I hear it” or “no, I do not hear it,” and then the thresholds are determined from an average response of the many repetitions of those trials.

Adaptive tracking procedures, where a sound characteristic (e.g., intensity) is incrementally lowered until a subject no longer reports hearing it and then is raised and lowered several more times until a mean threshold value of the reversals is obtained, are also widely used in humans and animals.

Adaptive tracking is much quicker than the method of constant stimuli, although thresholds have been found to be unstable using the former method in some species of animals such as mice (Klink et al., 2006).

Human psychoacousticians also widely use the method of adjustment, where listeners turn a dial until two sounds match along a certain dimension. Although it is fairly easy to instruct a human to move a dial to equate the levels of two sounds, such instructions are probably impossible to give to nonhuman subjects.

Another common human technique that does not translate well to animal psychophysics is magnitude estimation, where stimuli are labeled along some dimension, such as loudness. Thus, the method of constant stimuli and adaptive tracking procedures are more common in animal psychophysics than the method of adjustment or magnitude estimation (although response latencies are often used to infer magnitude across stimulus types).

In operant experiments, animals are typically shaped (trained) to respond, with successive stages of the shaping process requiring more and more of the subject. Classical conditioning experiments can be just as useful for determining stimulus properties that differ along certain dimensions for different animal species. Finding the appropriate task type for each animal species can be a major challenge. Small birds such as budgerigars (*Melopsittacus undulatus*) can be trained to peck light-touch microswitch keys (Dooling and Okanoya, 1995; **Figure 2**) even when wearing headphones (Welch and Dent, 2011; **Figure 3**), whereas larger birds such as barn owls (*Tyto alba*) are better suited to a looking (e.g., Johnen et al., 2001) or a flying (Dyson et al., 1998; **Figure 4**) task. Cats (*Felis catus*) also respond well to a visual fixation paradigm (Populin and Yin, 1998) or to releasing a lever with their paw (May and Huang, 1996). Bottlenose dolphins (*Tursiops truncatus*) and killer whales (*Orcinus orca*) can push paddles or levers (Hall and Johnson, 1971) or produce a whistle (Houser and Finneran, 2006). Fishes such as goldfish (*Carassius auratus*) suppress their respiration in a classical conditioning task (Fay, 1995). Rodents such as mice (*Mus musculus*) are good at nose (snout) poking (Radziwon et al., 2009), continuously drinking from a spout (Heffner and Heffner, 2001), or running around an arena (Klink and Klump, 2004). Next, other considerations need to be made, such as deciding what time of day to test animal subjects (owls and mice work best at night, whereas songbirds prefer the daylight hours) and what reinforcement type (food, water, shock, timeout) should be used.



Figure 2. Budgerigar (*Melopsittacus undulatus*) facing two keys in an operant chamber in the Dent laboratory. The bird is required to peck a left key to start a variable waiting interval and to peck the right key when it detects a signal presented from an overhead speaker for a millet reinforcer.



Figure 3. Budgerigar wearing headphones. This bird from the Dent laboratory ran the same task as described in **Figure 2** but had stimuli presented through the headphones instead of from the overhead loudspeaker.



Figure 4. Barn owl (*Tyto alba*) in an operant setup in the laboratory of Dr. Georg Klump at the Technical University of Munich. The owl sitting on the rear perch is breaking an infrared beam (left). When it discriminates a change in the repeating background sound, it is required to fly to the front perch (right), breaking another infrared beam for a food reinforcement. Photo courtesy of Willi Maile, used with permission.

Psychoacoustics studies have revealed interesting trends in animal hearing, with some studies showing a remarkably conserved evolution of auditory processing across vertebrates and others showing unique adaptations for animals to thrive in specific environments. Samples of some interesting findings obtained using animal psychoacoustics are presented in the sections below. The studies presented span the various psychoacoustic techniques used by researchers interested in knowing more about the auditory world of animals. These are not meant to be exhaustive; they are simply interesting to the author and hopefully to the reader. Where possible, the original or most complete measures have been presented instead of the most recent findings in order to highlight the pioneering investigators of this field.

Audiograms

Arguably, the most common measure of hearing in animals is the audiogram. Animals are placed in soundproof chambers lined with echo-reducing foam and presented with sounds of various frequencies and intensities from a calibrated loudspeaker. After hundreds or thousands of trials to control for variation in responding and to confirm that the animal has given its most accurate results, the threshold, often the lowest intensity an animal can hear 50% of the time at a given frequency, is mapped across several frequencies, and the audiogram is generated (Figure 5).

Across the animal kingdom, audiograms show great variability that can take the form of differences in how well animals hear overall (sensitivity), the frequency at which they hear best, the highest and lowest frequency they can hear, and how many frequencies they can hear. In air, larger animals like elephants (*Elephas maximus*) tend to have better low-

frequency hearing than smaller animals such as mice have (Ehret, 1974; Heffner and Heffner, 1982). Moreover, predators such as cats and barn owls tend to hear better than prey animals such as European starlings (*Sturnus vulgaris*; Neff and Hind, 1955; Konishi, 1973; Dooling et al., 1986). European starlings and Cumberland turtles (*Pseudemys scripta*) hear a narrower range of frequencies than mammals.

The frequency of best sensitivity in birds like the budgerigar, the European starling, and several other songbirds is correlated with the frequencies contained in the birds' vocalizations (Dooling, 2004). The same is true of mice (Ehret, 1989) and bats (Bohn et al., 2006), although for both groups, the tuning seems to be more correlated with infant than with adult calls so that mothers could more easily hear their own offspring calling. Bats such as the big brown bat (*Eptesicus fuscus*) and greater horseshoe bat (*Rhinolophus ferrumequinum*) also have very good high-frequency hearing, linked to the detection and localization of their echolocation signals used for navigation and prey capture (e.g., Koay et al., 1997).

Underwater audiograms for different animals show similar variations. Goldfish (*Carassius auratus*) are amenable to the respiratory conditioning technique, which has been

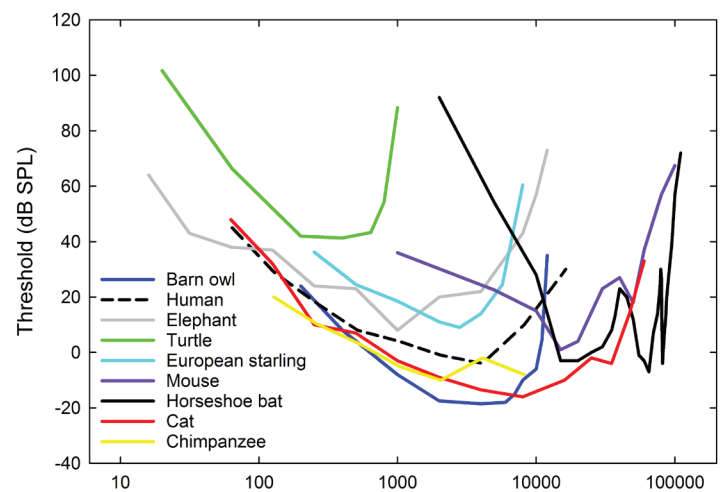


Figure 5. Sample behavioral audiograms from barn owls (blue line; Konishi, 1973), humans (dashed black line; Sivian and White, 1933), elephants (*Elephas maximus*, gray line; Heffner and Heffner, 1982), turtles (*Pseudemys scripta*, green line; Patterson, 1966), European starlings (*Sturnus vulgaris*, cyan line; Dooling et al., 1986), mice (purple line; Ehret, 1974), horseshoe bats (*Rhinolophus ferrumequinum*, black line; Long and Schnitzler, 1975), cats (*Felis catus*, red line; Neff and Hind, 1955) and chimpanzees (*Pan troglodytes*, yellow line; Elder, 1935).

used for decades with success across several psychophysical methods (e.g., Fay, 1995). Killer whales (*Orcinus orca*) and bottlenose porpoises (*Tursiops truncatus*), like bats, are known to use echolocation for navigation and prey capture and are more sensitive at high frequencies than many other animals (Johnson, 1967; Hall and Johnson, 1971). California sea lions (*Zalophus californianus*) and cormorants (*Phalacrocorax carbo*) are sensitive to both underwater and airborne sounds, although both seem to be better suited for underwater listening than airborne listening (Schusterman et al., 1972; Schusterman, 1974; Johansen et al., 2016).

Once baseline audiograms are obtained for animals, comparisons can be made for different strains, species, sexes, and ages. In the cat, the shape of the audiogram changes remarkably through development (Ehret and Romand, 1981). Behavioral audiograms from very young animals are extremely difficult to obtain, making this a relatively underexplored field of study.

Auditory threshold sensitivities from aged animals also show differences across species. Aged mice of the C57BL/6J strain show a progressive hearing loss from high to low frequencies, as in humans, whereas mice of the CBA/CaJ strain showed no significant hearing loss within the same time period (Prosen et al., 2003). CBA/CaJ mice do lose their high-frequency hearing; it just occurs at a later point in their life span (Kobrina and Dent, 2016). Strain differences are thus an important consideration not just for hearing but also for changes in auditory acuity across the life span.

The ability to regenerate sensory hair cells of the inner ear (the cells that convert sound energy into electric signals that go to the brain) has made birds an interesting model for studies of hearing and hearing loss over the years. In one study by Langemann and colleagues (1999), European starlings well past their typical life spans (8-13 years old) showed hearing comparable to that found in young starlings (6-12 months old). This demonstrates that the regenerating sensory epithelium of birds, typically attributed to repairing damaged hair cells, protects birds from the typical hearing loss such as that seen in mammals like the rhesus macaque (*Macaca mulatta*; Bennett et al., 1983), false killer whale (*Pseudorca crassidens*; Klopper et al., 2010), and human (reviewed in Gates and Mills, 2005). Advances have been made in recent years to extend the nonmammalian hair cell regeneration capacity to mammals in attempts to eliminate presbycusis (reviewed in Rubel et al., 2013; Lewis et al., 2016).

The audiogram is an important first step in cataloging the acoustic world of an animal. However, the detection of simple stimuli in completely quiet environments tells us little about the everyday life of most animal species. Animal bioacoustics researchers are also interested in knowing how animals can (or cannot) discriminate between sounds, categorize sounds, and localize sounds in their environments. A wide variety of animals have been tested on these tasks using animal psychophysics, and they complement the audiogram in rounding out what is known about the acoustic world of many species.

Discrimination of Complex Signals

Animals that use acoustic signals for communication often must judge one signal against another for evaluating potential mates or to determine if a nearby animal is familiar or unfamiliar. In birds, females are known to prefer males with larger song repertoires over those with smaller song repertoires, songs produced at a fast rate over slower songs, songs with broader bandwidths than with narrower bandwidths, and songs with very little variation from rendition to rendition over songs with more variation (reviewed in Searcy and Yasukawa, 1996).

Species-specific acoustic signal preferences like these are seen across the animal kingdom. Presumably, then, animals must be able to discriminate between different acoustic signals to aid in the mate choice process. Psychophysical studies measuring the discrimination of natural vocalizations by birds have shown that they can discriminate among calls from their own species better than calls from another species (Dooling et al., 1992), that some birds are capable of discriminating extremely small differences in signals differing in temporal fine structure (reviewed in Dooling, 2004), that males learn to discriminate between familiar songs at a faster rate than they learn to discriminate between unfamiliar songs, and that call discrimination can differ across seasons (Cynx and Nottebohm, 1992). Normal social development has also been shown to be important for vocalization discrimination by birds (Sturdy et al., 2001).

Psychophysical studies on the perception of vocalizations have not been limited to birds. Four species of macaque monkeys (*Macaca* sp.) discriminate between vocalizations using different acoustic cues depending on their experience with the vocalizations, paralleling humans on speech perception tasks (Zoloth et al., 1979). Human speech perception has been measured in several animal species. Animals such as chinchillas (*Chinchilla lanigera*) have been found to have similar categorical boundaries as humans (reviewed in Kuhl, 1981).

Perception of the Auditory Scene

Like humans, animals are often bombarded by signals coming from multiple directions, all hitting the auditory system at the same time and often obscured by noise. They must extract separate auditory objects from the complex acoustic waveform on the basilar membrane. Humans have no problem telling you that a clock is ticking to the left, a fan is whirring overhead, and a person is talking to them from the other room, even though these signals overlap in time, space, and frequency. We would call these objects separate auditory “streams.” We know less about how animals do this sort of segregation of auditory objects, but researchers are interested in whether this is common across animals. The techniques used are often more complicated than simply asking an animal if something is there or not, as in a detection task, or to discriminate between two sounds. Often, animals are trained to identify one stimulus or two (Christison-Lagay and Cohen, 2014), whether the sounds are overlapping or alternating (Neilans and Dent, 2015), or, in the case of bottlenose dolphins, to identify an object.

Bottlenose dolphins can recognize objects using “intersensory recognition.” That is, when a sample object is visually presented to them, they can use their echolocation signals to match the object they saw. Conversely, if an auditory echolocation signal is presented to them and then the sample objects are acoustically shielded, they can use their vision to identify the object they heard (Pack and Herman, 1995). This intersensory recognition ability is likely prevalent in echolocating bats (e.g., Eklof and Jones, 2003), but complementary studies have not yet been conducted.

Goldfish use frequency differences in stimuli for separating auditory objects into separate acoustic streams (Fay, 2000). Gray treefrogs (*Hyla chrysoscelis*) segregate frog advertisement calls from a chorus of other calls using spatial cues, much in the way humans are able to hear a signal at a cocktail party (Bee, 2007). These studies and many others tell us about the limits of the resolving power of animals in complex listening environments and suggest that animals organize their world in similar ways as humans.

Localization

To learn about sound localization in animals, another common animal psychoacoustics measure, see the recent article in *Acoustics Today* by Heffner and Heffner (2016). Sound localization is extremely important for survival in the animal

world. Prey need to know which direction the predator is coming from in order to escape capture. Predators need to be able to pinpoint a prey item quickly and accurately before they are noticed or they will not eat. As with audiogram variability across vertebrates, localization acuity also varies widely across the animal kingdom and has been the subject of many animal psychophysical experiments.

Conclusions

Although some measures such as auditory brainstem responses, single-cell recordings, and acoustic startle are much quicker than animal psychophysical studies (which can take weeks, months, or even years to complete), many studies have found large differences between results from operant and untrained indirect reflexive measures of hearing like the startle response (e.g., Lauer et al., 2017) and evoked physiological and operant thresholds (e.g., Sisneros et al., 2016). These differences suggest that researchers should take the time to conduct psychoacoustic experiments in awake, behaving, trained, and reliable animal observers to assess the auditory world of animals with accuracy. Furthermore, although measurements of hearing in complex acoustic environments may seem daunting to some, they are important for helping us create scientifically backed decisions for environmental noise control and development.

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Biosketch



Micheal Dent is a professor in the Department of Psychology at the University at Buffalo, State University of New York. After obtaining a PhD in integrative neuroscience from the University of Maryland at College Park, she worked as a postdoctoral research scientist at the

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