Springer Handbook of Auditory Research

Arthur N. Popper
Richard R. Fay
Editors

Perspectives on Auditory Research

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Perspectives on Auditory Research

With 82 Illustrations

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Series Preface

The following preface is the one that we published in Volume 1 of the Springer Handbook of Auditory Research back in 1992. As anyone reading the original preface, or the many users of the series, will note, we have far exceeded our original expectation of eight volumes. Indeed, with books published to date, and those in the pipeline, we are now set for more than 60 volumes in SHAR, and we are still open to new and exciting ideas for additional books.

We are very proud that there seems to be consensus, at least among our friends and colleagues, that SHAR has become an important and influential part of the auditory literature. While we have worked hard to develop and maintain the quality and value of SHAR, the real value of the books is very much because of the numerous authors who have given their time to write outstanding chapters and to our many coeditors who have provided the intellectual leadership to the individual volumes. We have worked with a remarkable and wonderful group of people, many of whom have become great personal friends of both of us. We also continue to work with a spectacular group of editors at Springer, currently Melissa Higgs and formerly Ann Avouris. Indeed, several of our past editors have moved on in the publishing world to become senior executives. To our delight, this includes the current president of Springer US, Dr. William Curtis.

But the truth is that the series would and could not be possible without the support of our families, and we dedicate all of the SHAR books, past and future, to them. Our wives, Catherine Fay and Helen Popper, and our children, Michelle Popper Levit, Melissa Popper Levinsohn, Christian Fay, and Amanda Fay, have been immensely patient as we developed and worked on this series. We thank them and state, without doubt, that this series could not have happened without them. We also dedicate the future of SHAR to our next generation of (potential) auditory researchers—our grandchildren—Ethan and Sophie Levinsohn; Emma Levit; and Nathaniel, Evan, and Stella Fay.

Preface 1992

The Springer Handbook of Auditory Research presents a series of comprehensive and synthetic reviews of the fundamental topics in modern auditory research. The volumes are aimed at all individuals with interests in hearing research including advanced graduate students, postdoctoral researchers, and clinical investigators. The volumes are intended to introduce new investigators to important aspects of hearing science and to help established investigators to better understand the fundamental theories and data in fields of hearing that they may not normally follow closely.

Each volume presents a particular topic comprehensively, and each serves as a synthetic overview and guide to the literature. As such, the chapters present neither exhaustive data reviews nor original research that has not yet appeared in peer-reviewed journals. The volumes focus on topics that have developed a solid data and conceptual foundation rather than on those for which a literature is only beginning to develop. New research areas will be covered on a timely basis in the series as they begin to mature.

Each volume in the series consists of a few substantial chapters on a particular topic. In some cases, the topics will be ones of traditional interest for which there is a substantial body of data and theory, such as auditory neuroanatomy (Vol. 1) and neurophysiology (Vol. 2). Other volumes in the series deal with topics that have begun to mature more recently, such as development, plasticity, and computational models of neural processing. In many cases, the series editors are joined by a coeditor having special expertise in the topic of the volume.

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15.1 Introduction

Modern auditory research had its beginnings in the late 1940s, at which time a general review of auditory research could be accomplished in four chapters (Stevens, 1951). The subsequent expansion of auditory research led to the Springer Handbook of Auditory Research series that began to appear in 1992. It is interesting to consider what advances have been made since then and whether the advances have been new discoveries or refinements of previous ones.

Our study of the auditory abilities of mammals started in the laboratory of Bruce Masterton, first at Vanderbilt University and then at Florida State University. It began as the study of auditory cortex using the ablation-behavior procedure (Masterton, 1997). Coming from Irving Diamond's laboratory at Duke University, Bruce was interested in the evolution of auditory cortex and wanted to observe the effect of auditory cortex lesions in animals approximating the human phyletic lineage: opossum (marsupial), hedgehog (insectivore), tree shrew (classified at that time as a primate), and bushbaby (prosimian). The first step was to establish the preoperative auditory abilities of these species beginning with their audiograms (Masterton et al., 1969). It soon became apparent, however, that the animals varied in their high-frequency hearing, and that this variation was systematically related to the availability of cues to localize sound. This was an unexpected finding that sent the lab on an exploration of the audiograms and later sound-localization thresholds in a larger sample of mammalian species.

The following is a description of two areas of research: The first is the comparative approach to understanding the selective pressures on mammalian hearing and sound localization; the second is the role of auditory cortex, as determined by the ablation-behavior procedure, in absolute sensitivity, sound localization, and more complex discriminations. Underlying both of these areas of research is a third—the development of behavioral tests for determining the auditory abilities of animals—and it is there that we begin.

15.2 The Evolution of Animal Psychophysics

The advances in animal psychophysical procedures have been largely conceptual. Although advances in electronics and computers have been helpful in generating auditory stimuli and recording behavioral responses, modern behavioral procedures for testing animals could have been conducted with the equipment available over half a century ago; computers make it all easier and certainly more compact, but the procedures could have been instrumented with the relay racks that were in use at that time. Instead it was the advances in behavioral conditioning techniques and refinements in the contingencies of reinforcement that led to faster and more accurate ways to determine an animal's sensory abilities.

15.2.1 The Early Years

The period prior to 1992 was one in which new animal psychophysical procedures were being developed and old ones improved. In the 1950s, there were two behavioral procedures employed by W. D. Neff and his students for testing hearing in animals (Neff et al., 1975). One was a sound-localization procedure in which a cat was placed in a start box facing two or more goal boxes that contained food; a buzzer was sounded over the one goal box that was unlocked and the cat was trained to go to the source of the sound to obtain the food. After it finished eating, it was picked up by the experimenter, who was in the test room, and returned to the start box for another trial. The other procedure used a double grill box in which an animal was trained to move from one compartment to the other when it detected a sound, or a change in an ongoing sound, to avoid a shock delivered through the floor bars. Although both procedures worked with cats, there were some limitations. For example, the sound-localization box could be used only with tame animals that could be picked up and returned to the start box, and of course, the person doing this could also present distractions and potential cues. With the double grill box, an animal's head position in the sound field varied introducing error in the measurement of absolute thresholds.

By the 1960s, new animal psychophysical procedures were appearing, many of which are described in the book, *Animal Psychophysics*, edited by W. C. Stebbins (1970). The book contains two chapters on the method of conditioned suppression, one by Barbara Ray, the other by James Smith. The conditioned suppression procedure differed from others in that instead of training an animal to make a response when it hears a particular sound, the animal was trained to make a steady response, such as licking a water spout, but to stop (suppress) responding when it heard a sound that signaled shock. This is a cognitively simple task, much like that of an animal at a water hole that stops drinking when it detects danger. Moreover, by having an animal respond by licking a water spout, its head was fixed within the sound field, making precise measurement of the sound at its ears possible.

We adopted conditioned suppression in the 1960s, having learned of it from Jim Smith at Florida State University. Since then we have made several modifications to simplify training and accelerate testing, the details of which can be found elsewhere (Heffner & Heffner, 1995; Heffner et al., 2006). Among the changes were (1) allowing an animal to make steady contact with a water or food spout instead of requiring it to make discrete licks on the spout which some species find difficult to do, (2) shortening the trial duration from 10 s to 2–3 s, (3) lowering the response cost by requiring an animal to break contact with the spout for only 150–200 ms, (4) changing how false positives were incorporated into the performance measure, and (5) making the shock avoidable. This last change, in which an animal avoids the shock by breaking contact with the spout when it hears a sound, greatly reduced the number of shocks the animal actually received thus increasing the number of trials that could be obtained in a session. However, it also changed the procedure from conditioned suppression to an avoidance task, one that behaviorists refer to as "discriminated punishment," and we have long struggled to find a good name for it.

Because the key feature is that an animal stop or suppress what it is doing when it detects a signal, we currently refer to it as "conditioned suppression/avoidance" (Heffner et al., 2012). Naming aside, it was this application of conditioned suppression that allowed us not only to test many different species of animals, but, because it is such a robust procedure, also enabled us to test hearing in animals with brain lesions and debilitating genetic defects.

During the early years we also explored procedures that did not use electric shock but relied instead on positive reinforcement. The first was Neff's two-choice procedure that we initially used for sound localization. We automated that procedure by having an animal lick a start spout to center its head between the loudspeakers (a "ready" or "observing" response), and using water reward that was automatically dispensed from a water spout under the active loudspeaker. The animal returned to the observing spout on its own thus eliminating the experimenter from the test room. In addition to sound localization, the two-choice procedure has also been used to determine detection and discrimination abilities. In each case, animals made an observing response to indicate their readiness to perform the discrimination. For sound localization, the animal responded left or right to left and right sounds, respectively; for detection, the animal responded to one side if it detected a sound and to the other side if it did not; for auditory discriminations, the animal would respond left to one type of sound and right to another, permitting the testing of fairly complex distinctions, such as between different categories of vocalizations. Correct responses were rewarded with either food or water and errors were punished with a short wait or time out. The two-choice procedure worked well with cats, monkeys, dogs, and an elephant. However, there were some species that did not perform consistently well on the two-choice sound-localization task; specifically, some horses and cattle did not perform at a high level when tested on easily discriminated angles and none of the rats we tested would consistently perform above 90% correct even at large angles of separation.

The second reward procedure was a go/no-go procedure that we used to determine the audiograms of horses and cattle; this procedure was patterned after those developed by John Dalland, who obtained the first behavioral audiograms of bats, and Bill Stebbins who tested hearing in monkeys (Dalland, 1965; Stebbins, 1970). In our tests, an animal was required to place its mouth on an observing plate to initiate testing and to contact a reporting plate with its mouth when it detected a sound. Correct detections were rewarded with water while false positives were punished with an error time out. Although the procedure worked fairly well, false positives easily intruded, especially if an animal was rewarded for making a chance response to a subthreshold tone; in the case of a pony, it was necessary for the experimenter to stand behind the animal with a switch, which quickly eliminated false positives.

15.2.2 The Past 20 Years

Since 1992, there have been both refinements and new developments in animal psychoacoustic procedures, some of which can be found in *Methods in Comparative*

Psychoacoustics (edited by Klump et al., 1995). There are three that we would like to note. The first is the use of the reflex inhibition procedure, which has been used to obtain auditory thresholds in a variety of animals including amphibians for which there are currently no operant procedures (e.g., Simmons & Moss, 1995). The reflex inhibition procedure is based on the observation that the magnitude of an animal's startle response to a stimulus, such as a loud sound or electric shock, can be reduced by preceding the startle stimulus with a low-level sound. Absolute thresholds are obtained by reducing the amplitude of the preceding sound until it no longer has a detectable effect on the magnitude of the startle response as compared to its magnitude when there is no preceding sound. The great advantage of this procedure is that the animals do not require any training beyond acclimation to the test box. However, because operant procedures often show that it is necessary for an animal to "learn to listen" to low-level sounds, it is likely that an audiogram obtained with the startle reflex will be less sensitive than those obtained with operant procedures.

A second advance has been the recognition of species differences in tolerating the negative consequences of errors when performing a sensory discrimination. For example, when testing monkeys, cats, and dogs in a two-choice auditory discrimination, rewarding correct responses with food or water and punishing errors with a short error time out of 3–5 s is often sufficient to maintain a high level of performance. Rats and hamsters, on the other hand, do not find an error time out sufficiently aversive and are content with the thinner reward schedule that accompanies errors and the consequent delays. However, we now know that if errors are punished by even mild shock, rats and hamsters will perform a two-choice auditory task at asymptotic levels as high as that of any other animal. As a result, it is now possible to use the two-choice procedure on these species to do equivalence testing (Heffner, 2011), a procedure that cannot easily be done with conditioned suppression. In short, there must be aversive consequences for making errors. For some animals, a short error time out is psychologically aversive enough to cause them to minimize their errors. For others, it is necessary to add a physically aversive stimulus to obtain good performance.

The third area in which there have been new advances has been the application of behavioral tests for detecting tinnitus in animals (for a review, see Heffner & Heffner, 2012). Such tests are inherently difficult because, unlike other auditory tests, the experimenter does not have direct control over the stimulus of interest; that is, there is no guarantee that administering a tinnitus-inducing agent to an animal will actually cause it to have tinnitus because significant individual variation in susceptibility to tinnitus has been observed in humans. Other difficulties arise from the need to tease out the effects of tinnitus from the effects of other auditory changes that often accompany it such as hearing loss and hyperacusis. The tests for tinnitus can be divided into three general types. The first has been to train animals to discriminate the presence of sound from its absence, such as training them to stop drinking when a background sound is turned off. The animals are then given a tinnitus-inducing agent, such as salicylate or exposure to loud sound, and tested in the absence of any physical sound to determine if they behave as though a sound is still present. The second type of test involves looking for interactions between tinnitus and physical sounds—interactions in which tinnitus might fill in a gap in a sound that is similar in pitch to the tinnitus or in which the tinnitus might change the perception of a physical sound. The third has been to train an animal on a left–right sound-localization task, expose one ear to a loud sound, and test to see if the animal responds as though it hears a sound in the exposed ear when no physical sounds are presented. The various tinnitus test procedures differ in the degree to which their validity has been assessed. One type of validation is to determine how the animals would perform when tinnitus is simulated by physical sounds. Another is to consider whether alternative explanations of the results are plausible such as the hearing loss and hyperacusis that are also caused by tinnitus-inducing agents. Finally, and most fundamentally, we should ask whether a particular test would detect tinnitus in humans.

15.3 Comparative Mammalian Hearing

The simplicity, accuracy and reliability of behavioral tests of hearing made it possible to study hearing in an astonishing variety of mammals. Species that differ in their size (bats to elephants), body configuration (horse to primate), motor abilities (blind mole rats, squirrels, mice with genetic movement disorders), and lifestyle (underground in deserts to aquatic) have been tested (Heffner & Heffner, 1998, 2003). The most interesting findings so far have centered on simple pure-tone sensitivity (the audiogram) and sound localization.

15.3.1 The Early Years

In the late 1960s we came to recognize that the variation in mammalian high-frequency hearing was linked to sound localization. Because both binaural cues for sound location, the difference in the time of arrival of a sound at the two ears and the difference in the frequency-intensity spectra reaching the two ears, are affected by head size, animals with small heads may have smaller binaural cues available to them. Time delays can be well below 100 μs, and, because small heads and pinnae do not block low frequencies as effectively as they block higher ones, small animals must hear higher frequencies than large animals to use the spectral-difference cue. Defining head size functionally as the maximum difference in the time of arrival of a sound at the two ears (i.e., the maximum time difference available to an animal), it was found that the high-frequency hearing limit correlated closely with functional head size. Indeed, this relationship accommodates species ranging in size from wild mice and bats to humans and elephants. However, with the testing of additional species, some exceptions began to appear. For example, there were some mammals that did not use the binaural spectral-difference cues and others that did not hear as high as predicted by their functional head size. These exceptions had to be explained.

The sound-localization tests given to the various species typically consisted of two types. The first was the determination of the minimal audible angle for noise bursts from azimuthal locations to the left and right of the animal's midline.

The second test examined the localization of pure tones—the ability to localize low-frequency tones indicating that an animal could use the binaural phase cue (a subset of the binaural time cue), and the ability to localize high-frequency tones indicating that it could use the binaural intensity-difference cue (a subset of the binaural spectral-difference cue). At the time, we expected that all animals would localize sound as accurately as the physical locus cues available to them permitted, so we were surprised when horses and cattle proved to be far less accurate than much smaller animals such as laboratory rats. We also found that these large animals could not localize high-frequency tones, indicating that they made little or no use of the binaural spectral-difference cue; yet they still heard high-frequency sounds as predicted by the relationship between functional head size and high-frequency hearing. Both of these discoveries had to be explained.

15.3.2 The Past 20 Years

Recent research has answered the questions concerning both high-frequency hearing and sound localization. It has also revealed large variation in mammalian low-frequency hearing.

15.3.2.1 High-Frequency Hearing

The relationship between functional head size and high-frequency hearing was initially based on only seven species; with an increase of the number of species in the sample by almost 10-fold, the relationship continues to account for about 80% of the variance in high-frequency hearing (Heffner & Heffner, 2008). The original explanation for this relationship was based on the view that high frequencies are necessary for sound localization because they provide the binaural spectral-difference cue. This is supported by the observation that filtering out high frequencies from a broadband noise reduces the performance of animals such as monkeys, humans, and chinchillas, on discriminating left from right sound sources. However, there are other mammals that are either partially or completely unable to localize high-frequency pure tones, indicating that their ability to hear high frequencies cannot be accounted for by the need to use the binaural spectral-difference cue. Specifically, the Indian elephant and domestic goat are unable to localize pure tones in the upper end of their hearing range and domestic pigs, horses, and cattle cannot localize tones that are too high to be localized using the binaural phase cue. However, it soon became apparent that these animals required high-frequency hearing to localize sound using pinnae cues (Heffner & Heffner, 2008).

Although the role of the pinna in sound localization has long been known, most human research has focused on the binaural locus cues, often using headphones that eliminated any contribution from the pinna. However, the work of Robert Butler and others had demonstrated that the directionality of the pinna not only provides the primary cues for vertical localization and for preventing front–back confusions, the pinnae also provide effective cues for localizing sound in the horizontal plane. Building on this work, we found that horses, which do not use the binaural spectral-difference cue, nevertheless require high frequencies to use pinnae cues for front–back localization.

A marked exception to the relationship between functional head size and high-frequency hearing was the discovery that subterranean mammals, specifically the pocket gopher, naked mole rat, and blind mole rat, did not hear nearly as high as their small functional head sizes predicted. Subsequent testing revealed that these animals also could not localize sound. Indeed, they are not only virtually unable to distinguish left sounds from right sounds, but they also lack pinnae and therefore are not under selective pressure to hear high frequencies to make front–back distinctions (Heffner & Heffner, 2008). Evidently, sound localization is of little use to animals living underground in a one-dimensional world. The observation that mammals that do not hear high frequencies as predicted by their functional head size also lack the ability to localize sound further supports the contention that high-frequency hearing is closely linked in mammals to sound localization.

Appreciating the importance of high-frequency hearing for generating pinna locus cues has implications for the evolution of the mammalian ear. One of the hallmarks of mammals is the three-boned middle ear, which appears to have evolved to enable them to hear high-frequency sounds. Indeed, fossils are often identified as mammalian based on the presence of the mammalian ear. However, it seems likely that the high-frequency mammalian ear evolved in conjunction with the pinnae, which improve left–right localization, allow for better localization within the lateral hemifield of sounds including those so faint that they are audible in only one ear, and reduce front–back confusions. This implies that birds, at least those that have not evolved a pinna-like facial ruff like the barn owl, are probably unable to determine whether a sound is coming from in front or behind them.

Another question that arose is whether selective pressure for echolocation has caused bats to increase their high-frequency hearing beyond that required for passive sound localization. Comparing bats with other mammals, it appears that echolocating bats do hear about 0.7 octaves higher than predicted for a similar-size non-echolocating mammal. Interestingly, non-echolocating bats do not appear to have extended their high-frequency hearing at all beyond that expected for passive sound localization.

15.3.2.2 Sound Localization

The discovery that horses and cattle, with their relatively large heads and pinnae, did not localize sound as accurately as much smaller animals came as a surprise. Until then, we had believed that animals would localize sound as accurately as permitted by the physical cues available to them. Only after several replications on additional individual animals and using different test procedures did we come to accept that these species were poor localizers.

In looking to explain this unexpected variation in mammalian sound-localization acuity, we examined seven potential factors (Heffner & Heffner, 1992). The first three were functional head size, trophic level (the degree to which a species is predatory or itself preyed upon), and activity cycle (whether a species is nocturnal, diurnal, or crepuscular). The other four were visual factors: visual acuity, width of the binocular visual field, width of the panoramic visual field, and width of the field of best vision. Examining visual factors proved interesting and required one of us (RH) to learn how to process retinal whole mounts to estimate visual acuity and width of the field of best vision—this latter we defined anatomically as the horizontal width (in degrees) of the retinal area encompassing ganglion cell densities at least 75% of maximum.

The results of our multiple correlation study revealed that sound-localization acuity is most closely related to the width of the field of best vision. Indeed, the current correlation coefficient is $r = .89$. We have interpreted this to mean that the primary function of sound localization is to direct the eyes to the source of a sound. Just how accurate sound localization must be to do this depends on the width of an animal's field of best vision. Animals with a narrow field of best vision, such as humans, require good sound-localization acuity to direct their eyes so that the image of the sound source falls within that narrow region, which in the case of humans is our fovea. Animals with broad fields of best vision do not require good localization acuity to direct their gaze as their field of best vision can encompass nearly the entire horizon as is the case with visual streaks.

One question that arises is how bats fit the relationship between sound-localization acuity and width of the field of best vision, given the exquisite ability of most bats to use echolocation to detect and even discriminate objects in their environment. Because bats are thought to essentially replace vision with echolocation, it was conceivable that vision and sound localization might have become decoupled. As it turns out, however, the ability of bats to *passively* localize sound is not unusual—they localize sound as expected based on the width of their field of best vision. Thus, their development of echolocation has not detectably affected their passive sound-localization ability, at least among those bats examined so far.

A final discovery has to do with the use of the two binaural locus cues (Heffner & Heffner, 2003). Over the years it has become apparent that the binaural locus cues are not both used universally. A small number of mammals do not use the binaural time cue and others do not use the binaural spectral-difference cue, and the subterranean rodents appear to use neither. Moreover, among the mammals that use the binaural time cue in the form of the phase cue, there is systematic variation in the highest frequency at which they can use it. For example, cattle appear able to use the binaural phase cue up to 500 Hz whereas the Jamaican fruit bat can use it up to 6.3 kHz, a span of more than 3 octaves. Moreover, this variation in the upper limit of binaural phase is closely related to the maximum time difference available to an animal such that the smaller the available time difference, the higher the upper limit of binaural phase ($r = -0.85$). This is because the smaller an animal's head size, the higher the frequencies for which the binaural phase cue remains unambiguous, although other factors may be involved. Because the use of the binaural phase cue presumably requires phase locking in the auditory system, one might expect there to be species differences in phase locking with smaller species phase locking to higher frequencies than larger animals.

15.3.2.3 Low-Frequency Hearing

The range of variation in mammalian low-frequency hearing is now known to be greater than that for high-frequency hearing. Using the lowest frequency audible at a level of 60 dB, low-frequency hearing limits extend from 17 Hz (Indian elephant) to 10.3 kHz (little brown bat), a range of 9.2 octaves, almost twice the 4.7-octave range in high-frequency hearing limits (Heffner et al., 2001). Moreover, the distribution of low-frequency hearing limits appears to be bimodal with some mammals falling into a group with good low-frequency hearing (i.e., those that hear 125 Hz and lower), and others forming a group with poor low-frequency hearing (i.e., those that do not hear below 250 Hz). There is a loose relationship between high- and low-frequency hearing such that animals with good high-frequency hearing often have poor low-frequency hearing. However, high-frequency hearing accounts for less than half of the variance in low-frequency hearing and there are many species from several different orders, including rodents and carnivores, that are quite sensitive to both high and low frequencies—with audiograms in some cases spanning over 13 octaves. There is currently no selective pressure that has been proposed to account for these unusual features of low-frequency hearing.

15.4 Auditory Cortex

The use of ablation-behavior experimentation to study auditory cortex dates back to the late 19th century after it was found that sensory and motor functions could be localized to different parts of the cortex. The modern study of this field began in the late 1940s with W. D. Neff and his students being major contributors (Masterton, 1997). Improvements in the behavioral test procedures discussed earlier have helped advance this area of auditory research.

15.4.1 The Early Years

The view that the cerebral cortex is, if not the seat of the soul, at least the seat of consciousness led 19th century researches to believe that ablation of auditory cortex would abolish the ability to respond to sound. Although initial studies indicated that this was so, other studies failed to find “cortical deafness” and in spite of sporadic reports of cortical deafness in human patients, animal researchers were unanimous in dismissing the possibility. Thus, when we found that ablation of auditory cortex in macaques caused a substantial hearing loss (Heffner, 2005), it was months before we dared tell colleagues of our discovery. That other researchers failed to find cortical deafness in animals is because they were working with cats and it has only been observed in primates so far (humans and macaques).

The role of auditory cortex in discriminating frequency has also been studied, motivated by the discovery that it is tonotopically organized. Results showed that ablation of auditory cortex does not abolish the ability to discriminate frequency, but it does increase discrimination thresholds.

Perhaps Neff's most famous finding was that ablation of auditory cortex abolishes the perception of locus. Further, this appears to be a perceptual deficit because an animal with bilateral auditory cortex lesions is able to discriminate left sounds from right sounds, but no longer associates a sound with a location in space. This finding has stood unmodified since Neff first reported his discovery in 1948 (Heffner & Heffner, 2003).

One other discovery, which was difficult to classify as sensory or perceptual, was the finding in the 1980s that bilateral ablation of auditory cortex abolishes the ability of Japanese macaques to discriminate two forms of their coo vocalizations. On one hand, it suggested an aphasia-like deficit in macaques following auditory cortex ablation. However, because the coos differed acoustically with one rising in frequency and the other falling, it was possible that the monkeys had a sensory deficit that affected their ability to determine if a sound was changing in frequency.

15.4.2 The Past 20 Years

Recent behavioral studies of auditory cortex have both refined previous discoveries and made new ones.

15.4.2.1 Cortical Hearing Loss

It had been known that the cortical hearing loss that occurs in macaques following bilateral ablation of auditory cortex—a loss that may begin as a complete inability to respond to sound—shows substantial recovery during the first 1–2 months postoperatively, though the animals still have a moderate hearing loss. However, longitudinal studies have shown that recovery continues 3–5 years after surgery with thresholds returning to normal levels at low frequencies and to near normal levels in the midrange of the animals' audiograms. There are at least two possible explanations for the recovery of hearing. One is that cortical areas outside auditory cortex are mediating the function of auditory cortex in detecting sound. Another possibility is that the hearing loss is due to the disruption of the lower auditory centers caused by the sudden loss of descending cortical input and that thresholds improve as the lower centers adapt to the loss. One way to investigate these possibilities would be to examine the remaining cortical areas and the lower auditory centers using electrophysiological and functional MRI techniques to determine how their functions change as a result of ablation of auditory cortex.

It was also discovered that unilateral ablation of auditory cortex in macaques results in a hearing loss in the ear opposite the lesion. The hearing loss is not permanent and thresholds quickly recover to normal or near-normal levels in a matter of weeks. This effect, which was found by testing each ear independently using earphones, can help explain some of the initial effects of damage to auditory cortex in humans.

15.4.2.2 Intensity Discrimination

Although early studies did not suggest a role for auditory cortex in discriminating changes in the intensity of a sound, recent studies have indicated that auditory cortex ablation does affect intensity discrimination. Specifically, although bilateral ablation in macaques may result in at most a slight increase in thresholds for detecting an *increase* in intensity, it results in a large threshold increase for detecting a *decrease* in the intensity of a sound. Currently, there is no theory to explain this result, although it brings to mind the Neff Neural Model that animals without auditory cortex can detect an increase in neural activity.

15.4.2.3 Frequency Discrimination

The ability to discriminate frequency has classically been tested by training animals to discriminate a train of tone pips of the same frequency from a train of tone pips that alternate in frequency. Thresholds obtained by reducing the difference between the two frequencies indicate that ablation of auditory cortex results in a small but consistent increase in thresholds in both monkeys and cats. However, presenting tone pips is only one way to test frequency discrimination; another way is to modulate the frequency to determine an animal's ability to detect when a steady tone is replaced by one that is changing in frequency. One common way is to train an animal to discriminate tones that are rising in frequency from those that are falling in frequency, that is, frequency ramps.

Frequency ramps are of special interest to auditory researchers for several reasons. First, many neurons in auditory cortex are sensitive to the direction of frequency change; a cell that responds to a rising frequency ramp may not respond to a falling ramp over the same frequency range, a discovery reported by Whitfield and Evans in 1965. Second, it is relatively easy for animals to learn to discriminate rising from falling ramps, suggesting that is a more natural discrimination than discriminating tone pips, which is more difficult for an animal to learn. Finally, discriminating rising from falling frequency ramps forms the sensory basis for discriminating the two forms of the Japanese macaque coo calls, a discrimination that is abolished in macaques by auditory cortex lesions. Indeed, frequency modulation is an important component of both language and echolocation, making this acoustic feature very common in nature.

The major discovery in this field was that auditory cortex lesions abolish the ability of monkeys to determine if a sound is changing in frequency (Heffner, 2005). Specifically, they can no longer discriminate a steady tone from one that is either rising or falling in frequency. However, to demonstrate this deficit, it is necessary to randomize the frequency of the steady tone from trial to trial to prevent animals from performing the discrimination on the basis of absolute frequency. This finding has two interesting consequences. First, it indicates that a deficit in the ability to discriminate the coo vocalizations, shown by Japanese macaques following auditory cortex ablation, is a sensory deficit. Second, it is an example of an electrophysiological observation that correctly identified a function of auditory cortex; whereas the view that auditory cortex might be necessary for frequency discrimination, based on the finding of tonotopic maps, turned out not to be true, the discovery by Whitfield and Evans that some auditory neurons were responsive to the direction of a change in frequency did foreshadow the discovery that auditory cortex is necessary for detecting if a sound is changing in frequency.

15.4.2.4 Functional Differences Between Areas of Auditory Cortex

Auditory cortex can be divided into different areas on the basis of the electrophysiological and anatomical properties leading to the question of whether different areas have different behavioral functions. Based on electrophysiological studies, it has been suggested that, in macaques, the identification of complex sounds is processed in the rostral portion of auditory cortex and that the localization of sound is processed in the caudal portion. Indeed, this view has been at least partially supported by ablation studies. Specifically, the ability of macaques to determine if a sound is changing in frequency is abolished by removal of either the rostral or core portions of auditory cortex, but not by removal of the caudal portion. On the other hand, the ability to localize sound is impaired (though not completely abolished) by removal of the caudal or core portions of auditory cortex, with the caudal lesion resulting in the largest impairment, but ablation of the rostral portion has no effect. Thus, it appears that we are making progress in determining the behavioral functions of the subareas of auditory cortex.

15.5 Future Perspectives

There are a number of directions in which future research can go, depending on the technical skills and interests of investigators in different disciplines.

15.5.1 The Comparative Study of Hearing

There are unanswered questions and unexplored areas in our knowledge of the hearing abilities of animals. With regard to mammals, one question concerns the wide variation in low-frequency hearing limits and their remarkable bimodal distribution, for which there is currently no explanation. Is low-frequency hearing the result of a single source of selective pressure, as seems to be the case for sound localization driving high-frequency hearing, or is it due to adaptations to specific conditions in which low-frequency hearing is used for different functions by different species? On the other hand, perhaps some mammals do not hear low frequencies because they would interfere with the reception of high-frequency sounds that are important to them. An area currently receiving little attention is the ability of mammals to resolve differences in intensity and frequency; one reason for this is that the standard procedure has been to train animals to indicate whether a train of tone pips is alternating in frequency or intensity, a task that most animals find difficult. There may yet be interesting findings of evolutionary relevance in these abilities; the use of tests in which a sound is modulated (rather than discrete tone pips) may reveal important species differences. Finally, there is the unexplored area of auditory perception, which includes the ability of animals to recognize objects, usually other animals, by the sounds they make.

The auditory abilities of other vertebrate classes also await exploration. In the case of birds, although high-frequency hearing shows little variation, there may be significant variation in low-frequency hearing, as suggested by the fact that pigeons, and perhaps other birds, are able to hear lower-frequency sounds than humans (infrasound). Even less is known about the behavioral hearing abilities of amphibians and reptiles, which, with the anatomical variety of their ears, make relevant subjects for both physiological and evolutionary theory.

Finally, the results of anatomical and neurophysiological studies are sometimes used to infer the sensory abilities of species whose hearing has not been studied behaviorally. Behavioral assessment in these species would help understand the significance of the results of those studies.

15.5.2 Behavioral Study of Auditory Cortex

There are also many directions in which ablation-behavior studies can reveal more about auditory cortex, of which two are mentioned here. The first has to do with the species variation in the effect of cortical ablation on hearing. It is well established that removal of auditory cortex has little effect in the rat, a greater effect in cats where sound localization and the ability to determine if a sound is changing in frequency are affected, and an even greater effect in macaques where, in addition to the deficits observed in cats, the ability to detect sound is affected. Although Bruce Masterton originally set out to determine the evolution of auditory cortex by studying the effect of cortical ablation in species that approximated the human evolutionary line, this work is far from complete. In addition to showing the evolutionary changes in the function of auditory cortex, knowledge of the variation of its role in different species could serve as a basis for comparative electrophysiological studies of auditory cortex to determine the neurological correlates of the differences in function.

A second line of inquiry, one that shows great promise, is the use of reversible lesions made by inactivating an area either by cooling it or by applying transmitter antagonists. One advantage of this technique is the ability to repeat the lesions in the same animals, thereby reducing variation due to individual differences. Another important advantage is that the effect of inactivating an area may be determined before any compensation by other areas can occur. However, in conducting these experiments, it is important that investigators conduct the necessary control tests to rule out alternative explanations. For example, although ablation of auditory cortex does not cause a hearing loss in rats and cats when they are tested after recovering from the surgery, it is conceivable that a hearing loss could result from sudden inactivation of auditory cortex, which would then confound the results of other auditory tests. Given the behavioral procedures currently available, it is possible to shift a well-trained animal from one auditory discrimination to another within a session, a situation that would allow the effect of reversible lesions to be determined on multiple auditory discriminations in the same animals.

15.5.3 Advances in Behavioral Procedures

Advances in behavioral procedures are the most difficult to foresee, perhaps because they tend to be conceptual in nature. For example, the improvements in the method of conditioned suppression made over the years could have been made when the procedure was first used for sensory testing. The reason they were not made then is because people tend to be conservative; after all, why change something that works? The reason we made the changes we did is because we were often the ones doing the actual testing and wanted to speed up the procedure. We were also testing non-standard species, often ones with different behavioral strategies and motor capacities, that didn't work well in tests designed for rats or monkeys. Other advances, such as the use of reversible lesions, had to await technological improvements. Nevertheless, some trends in behavioral procedures are apparent.

The latest behavioral procedure to be developed is the previously mentioned reflex modification in which the detectability of a sound can be demonstrated by showing that it reduces the amplitude of an animal's reaction to a startling stimulus. Although it has the advantage of using an animal's unconditioned startle response, and thus requiring no training of the animal, it is likely to be 10–15 dB less sensitive than tests in which an animal is trained to listen for low-intensity sounds. Where this technique could use improvement is in reducing the variability of the results. One step would be to fix an animal's head in the sound field, for example, by having it drink from a water spout, so that the amplitude of the sound at its head can be accurately measured. Another source of variation is in the startle response itself, which can vary greatly in size from one trial to the next for the same stimulus. This variation may be due to changes in an animal's muscle tension and/or its level of arousal; this technique would be improved if the variability of its results could be reduced. It would also be helpful to know how closely thresholds obtained with this technique by different laboratories agree. A second trend that can be seen is in the use of electrophysiological measures, such as the auditory brain stem response, for measuring thresholds and changes in thresholds. However, as human research has shown, electrophysiological measures are no substitute for pure-tone audiograms and there is little evidence that they can accurately indicate threshold shifts caused by either a sensorineural or a conductive hearing loss. Indeed, it is unlikely we would have discovered the comparative relationships we did had we used physiological measures of hearing. However, whereas obtaining a behavioral audiogram on an animal can take weeks or even months in some species, an electrophysiological audiogram can be obtained in less than a day, making it much cheaper to obtain. As reviewers and editors come increasingly to accept electrophysiological measures as equivalent to behavioral thresholds, then behavioral studies of hearing will become scarce, demonstrating that Gresham's Law also applies to science.

Finally, the future of this research may depend most of all on the limitations put on it by others. When pressure to restrict animal research began in earnest several decades ago, scientific organizations made two crucial decisions. One was that their organizations would not defend other users of animals, such as ranchers, fishermen, and hunters. Indeed, those opposed to animal research offered to go easy on researchers if they did not support other groups, a divide and conquer strategy. The second decision was to defend animal research by ceding that while it was bad for animals, the benefits to humans outweighed the harm done to the animals. Yet not only is this position difficult to defend, it is unnecessary. The use of animals by humans results in symbiotic relationships in which animals benefit by achieving an environment that is superior to life in the wild. However, this fact is rarely noted. Indeed, a manuscript pointing out the symbiotic nature of animal research was rejected by psychological journals before finally finding publication in a journal oriented toward biology and medicine (Heffner, 1999). The continued well-being of animal research depends on whether the nature of our interactions with animals, and the benefits to both humans and animals, are understood.

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