Understanding the neurophysiological basis of auditory abilities for social communication: A perspective on the value of ethological paradigms

Sharath Bennur[1,*], **Joji Tsunada**[1,*], **Yale E. Cohen**[1,2,3], and **Robert C. Liu**[4,5,6]

[1]Department of Otorhinolaryngology, University of Pennsylvania, Philadelphia, PA 19104 USA

[2]Department of Neuroscience, University of Pennsylvania, Philadelphia, PA 19104 USA

[3]Department of Bioengineering, University of Pennsylvania, Philadelphia, PA 19104 USA

[4]Department of Biology, Emory University, Atlanta, GA 30322, USA

[5]Center for Translational Social Neuroscience, Emory University, Atlanta, GA 30322, USA

[6]Center for Behavioral Neuroscience, Georgia State University, Atlanta, GA 30302, USA

Abstract

Acoustic communication between animals requires them to detect, discriminate, and categorize conspecific or heterospecific vocalizations in their natural environment. Laboratory studies of the auditory-processing abilities that facilitate these tasks have typically employed a broad range of acoustic stimuli, ranging from natural sounds like vocalizations to "artificial" sounds like pure tones and noise bursts. However, even when using vocalizations, laboratory studies often test abilities like categorization in relatively artificial contexts. Consequently, it is not clear whether neural and behavioral correlates of these tasks (1) reflect extensive operant training, which drives plastic changes in auditory pathways, or (2) the innate capacity of the animal and its auditory system. Here, we review a number of recent studies, which suggest that adopting more ethological paradigms utilizing natural communication contexts are scientifically important for elucidating how the auditory system normally processes and learns communication sounds. Additionally, since learning the meaning of communication sounds generally involves social interactions that engage neuromodulatory systems differently than laboratory-based conditioning paradigms, we argue that scientists need to pursue more ethological approaches to more fully inform our understanding of how the auditory system is engaged during acoustic communication.

Keywords

ethology; auditory; behavior; acoustic feature; categorization learning; communication; vocalization

---

Corresponding author: Robert C. Liu, Ph.D., Department of Biology, Emory University, Rollins Research Center Room 2006, 1510 Clifton Road NE, Atlanta, GA 30322, USA. Tel: +1-404-727-5274; Fax: +1-404-727-2880, robert.liu@emory.edu.
*Both authors contributed equally

1. Introduction

Acoustic communication between individuals of the same (conspecific) or different (heterospecific) species is an essential ingredient for the reproductive success and survival of many animals, yet our understanding of its underlying neurobiological mechanisms is still limited. In particular, the neural bases for the functional abilities that enable auditory communication are not fully understood. For example, in order to communicate, animals have to detect, discriminate and categorize a vocalization before being able to use it within their ecological and social contexts to guide behavior (Cheney et al., 1980; Fischer et al., 2011; Ghazanfar et al., 2004). What neural-, circuit-, and systems-level properties within the auditory pathway facilitate these abilities?

For the complex task of acoustic communication between individuals, especially in mammals, our knowledge of its neural basis is limited because of the technical and methodological challenges in designing appropriate experiments. Instead, most auditory neurobiology studies have utilized more controlled laboratory paradigms, which investigate "general" auditory processing of sounds, and use behaviors that do not involve social communication. From these studies, scientists often infer how an animal and its brain would function in natural communication contexts. Such "generalist" approaches have certainly yielded important insights into the basic mechanisms and limits of auditory processing but applying that knowledge to elucidate what occurs in the natural communication context remains an open area of investigation.

This leads to the key motivation for our review. We make two overall arguments in favor of a continued expansion of a complementary, neuroethological approach to studying auditory processing with ever-more naturalistic communication paradigms, despite their technical challenges. Indeed, a long tradition of auditory neuroethological research in model organisms like crickets, frogs, bats and songbirds (Covey et al., 1999; Gentner et al., 2003a; Hahnloser et al., 2010; Konishi, 2004; Moss et al., 2011; Neuweiler, 1990; Pollak, 1992; Razak et al., 2010; Suga, 1988; Tsuzuki et al., 1988; Woolley, 2012) has established a conceptual foundation that can be used to approach similar questions in what some have considered more generalist laboratory animal models, like non-human primates and rodents. For those studying these latter species, it may not always seem necessary to employ natural vocal stimuli and behaviors to understand the general auditory-processing abilities of sound detection, discrimination or categorization (Dylla et al., 2013; Heffner et al., 2001; Klink et al., 2004; Ohl et al., 2001; Recanzone et al., 1993; Talwar et al., 2001). Here, we first try to counter this impression by using a few recent examples to illustrate how ethologically motivated approaches using vocalizations (or other "ethologically valid" stimuli with acoustic features derived from natural sounds) can provide insights into neural mechanisms that might otherwise be difficult to uncover.

Building on this, our second main point is that an important new direction in vocalization studies is to develop experimental designs that comprehensively incorporate behavioral contexts into neurophysiological research. This is important because behavioral context can profoundly affect neural processing. Thus, if we are to make progress understanding the neural mechanisms underlying acoustic communication, we must try to study how these mechanisms are engaged in more naturalistic communication behaviors.

In making these two arguments, an important question that arises is whether the neural substrates for vocalization processing differ from those used to process other types of sounds. For example, vocalizations may be more intrinsically arousing than other sounds and, thus, increase engagement of limbic areas relative to those other sounds (Ehret, 2005). Do these differences arise from evolutionarily tuned innate mechanisms present at birth or

because of extensive experience during development and/or adulthood for ethologically important communication sounds? In other words, are vocalizations processed just like any another complex sound, or are they "special" in engaging unique (or, at least, different) processing mechanisms? Whereas recent findings begin to speak to this question, it is likely irresolvable in many species. Indeed, the ideal experiment would require the prohibitively burdensome task of providing an animal from birth as much experience hearing and responding to a category of non-vocal (e.g. synthetic) sounds as a "natural" category of species-specific vocalizations, and then performing neurophysiological studies to uncover differences.

Instead, we advocate that hearing scientists embrace the basic principle from neuroethology (Ewert et al., 1983): neural activity needs to be considered in the full context of the elicited behaviors. Following this principle, we believe that the more tractable answer to the aforementioned problem is to identify how (1) vocalizations and (2) synthetic stimuli that become behaviorally salient through operant conditioning differentially modulate neural transformations along the auditory pathway from an acoustic input to behavioral output. In fact, several studies have already suggested that the neural representations of non-vocalizations (Bieszczad et al., 2010b; David et al., 2012; Polley et al., 2006) and vocalizations (Gentner et al., 2003b) depend on the details of a trained behavioral task (e.g. contingencies, rewards, strategy). It is precisely because of the importance of such details in the manifestation of auditory processing that we argue that to truly understand how such processing proceeds in the context of real acoustic communication, we must move towards experimental designs that may capture more of this natural behavioral context (DiMattina et al., 2006; Fortune et al., 2011).

To proceed, we first adopt a framework for testing how the neural representation of an acoustic-communication signal is linked in the brain to behavior that could also be used for other sounds that are not used in vocal communication. We make no attempt to ascribe any of the subsequent processing functions to specific brain regions. Instead, we discuss the computational and processing steps that we hypothesize must take place for an animal to use a communication signal to guide behavior (Griffiths et al., 2004).

Consider an animal hearing a species-specific vocalization that signals both the presence of food and contains information about the identity of the vocalizer. The first stage of auditory processing is to transduce the vocalization's acoustic energy into a neural signal reflecting the vocalization's spectral and temporal properties. Complex sounds such as vocalizations can be thought of as specific combinations of individual features, like a call's pitch or temporal envelope. The neural representations of such acoustic features are then bound together through sequential and simultaneous grouping principles to form an "auditory object", which is the fundamental perceptual unit in audition (Griffiths et al., 2004; Shamma et al., 2011; Winkler et al., 2009). This representation must then be interpreted in a framework that converts this information into a behavioral judgment (i.e., an auditory decision). Throughout this process, the representation of the vocalization is presumably compared with memory stores to categorize this call and recognize its "meaning". Once this information has been referenced, it has to be interpreted within the context of an animal's current behavioral goals. Ultimately then, the bottom-up representation of the acoustic signal must be interpreted in the top-down framework of the animal's behavioral and social experiences.

Importantly, these hypothesized steps could relate to any auditory stimulus that has behavioral relevance to the animal (i.e., those that inform an animal's current or future behavior). As outlined above, studying these steps for acoustic communication not only provides a concrete, ethologically relevant context for elucidating functional auditory

processing abilities but also adds value to our ability to clarify neural mechanisms. To make this point explicit, we use the remainder of this review to discuss some of these general auditory steps (acoustic-feature encoding and categorization) in more detail and illustrate how ethological approaches have contributed to revealing their underlying mechanisms.

2. Value of ethological approaches to studying acoustic-feature encoding

In early stages of processing, the auditory system encodes the spectrotemporal features of a stimulus. These features include tonal components, noise components, amplitude modulations, and frequency modulations (Attias et al., 1997; Kanwal et al., 1994; Liu et al., 2003; Morton, 1977). These features, which are universally present in many species' vocalizations, are classically thought to correlate with a sender's internal motivation level arising from specific hostile or friendly contexts (August et al., 1987; Morton, 1977). For example, low-frequency noisy utterances in many species transmit information about hostility. In contrast, high-frequency tonal calls transmit information about fear. Importantly, this convergence in acoustic structure arises irrespective of whether or not non-human animals intentionally transmit motivational or other types of information (Cheney et al., 1992).

Auditory neurophysiologists have generally approached the neural encoding of such acoustic features in one of several different complementary ways. The most traditional approach is simply to define a discrete feature class, like a noise band or a tone frequency, and then acquire neural spike-count responses to systematically parameterized versions of these features (e.g., changes in frequency) to produce a tuning curve. Alternatively, without first presuming the classes of relevant features, one can use synthetic stimuli of varying mathematically parameterized complexity – like ripples (Calhoun et al., 1998; Depireux et al., 2001; Escabi et al., 2003; Kowalski et al., 1996a; Kowalski et al., 1996b) or random chords (deCharms et al., 1998; Linden et al., 2003) – to probe neural responses in a more unbiased fashion and produce spectrotemporal receptive fields (STRFs) (Ahrens et al., 2008; Calabrese et al., 2011; Holmstrom et al., 2007).

These approaches have been broadly used to test auditory sensitivity of neurons from the auditory periphery to the prefrontal cortex (Abeles et al., 1972; Cohen et al., 2007; Escabi et al., 2002; Linden et al., 2003; Miller et al., 2002; Phillips et al., 1981; Sachs et al., 1968; Temchin et al., 2005). However, in practice, they have two limitations that can impede further progress in elucidating the encoding of acoustic features. First, passively stimulating animals with just tone bursts or even band-limited noise often does not evoke strong neural responses in higher cortical areas (Rauschecker et al., 1995; Stiebler et al, 1997; Romanski and Goldman-Rakic, 2002;), making the calculation of tuning curves and STRFs difficult (Averbeck et al., 2006; Cohen et al., 2007). Interestingly though, when tone bursts are presented in the context of a behavioral task, they can actually elicit strong responses, even in the prefrontal cortex (J Tsunada and YE Cohen, unpublished observation). This emphasizes the importance of the behavioral relevance of sounds in order to evoke responses.

In this sense, ethologically valid sounds may have an advantage for probing neural encoding in an animal's auditory system, since this system has presumably evolved to more efficiently transmit information about the natural variability of acoustic features in sounds that are intrinsically relevant (Cohen et al., 2007; Margoliash, 1983; Margoliash, 1986; Ohlemiller et al., 1996; Rauschecker et al., 1995; Scheich et al., 1979; Singh et al., 2003; Woolley et al., 2005). For example, Rieke and colleagues (1995) found that the spiking activity of bullfrog auditory-nerve fibers encodes (in the information-theoretic sense) natural amplitude spectra (i.e., spectra that mimic a bullfrog call) better than spectrally matched broadband Gaussian

(random) noise. Likewise, in the cat inferior colliculus, ethologically valid amplitude-modulation rate (Attias et al., 1998) and amplitude-contrast distributions (Escabi et al., 2003) also yield better information transmission than non-natural distributions. In the auditory cortex, the natural rhythm of vocalizations generally evokes stronger responsiveness than temporally compressed or expanded versions of calls (Carruthers et al., 2013; Chandrasekaran et al., 2009; Wang et al., 1995). A bias for the ethologically valid range of temporal modulation may also explain why it is easier to drive certain forms of auditory cortical plasticity for sound rhythms that are typically found in natural vocalizations (Chandrasekaran et al., 2009; Kim et al., 2009; Liu et al., 2006). These data reinforce the idea that the auditory system is adapted to the statistical structure of acoustic features that are present in natural stimuli, including vocalizations.

A second limitation of the standard approaches to characterizing auditory neurons stems from the fact that auditory neurons exhibit substantial nonlinearities in the time and frequency domains, thereby diminishing the predictive ability of the linear STRF or tuning curve to explain auditory encoding (Bar-Yosef et al., 2002; Carruthers et al., 2013; Cohen et al., 2007; Escabi et al., 2002; Machens et al., 2004; Theunissen et al., 2000). Whereas findings have identified methods to describe the multiple acoustic dimensions that drive neural activity and their associated nonlinearities (Atencio et al., 2008), these methods are often too computationally intensive to be widely used.

Instead, ethological approaches that explicitly test for nonlinear sensitivities to naturally arising combinations of ethologically valid acoustic features (Arnold et al., 2006; Balaban, 1988; Holy et al., 2005) have proven to be informative. Neurons in multiple brain regions have been found to be more responsive to combinations of acoustic features than to the individual contributions of each feature (Fuzessery et al., 1983; Kanwal et al., 2007; Leppelsack, 1978; Margoliash, 1983; Margoliash et al., 1992; Portfors, 2004; Portfors et al., 1999; Rauschecker et al., 2000; Rauschecker et al., 1995; Suga, 1978). For example, in the bat auditory cortex, neural activity in response to a sequence of stimuli that simulate an echolocation pulse and its reflection exceeds the sum of the responses to the individual stimuli when the sequence is presented within an ethologically appropriate temporal window (Suga et al., 1979). Similarly, neurons in the auditory cortex have been reported to be more responsive to a species-specific vocalization when it is presented in the normal forward direction than when it is presented backwards (Rauschecker et al., 1995; Wang et al., 1995). Both of these examples highlight the fact that the auditory system not only cares about the spectral content of acoustic features but also their non-linear temporal organization. More importantly, they demonstrate a neural sensitivity to the natural complexity of behaviorally relevant sounds, which motivates studying acoustic feature encoding with ethologically valid stimuli.

3. Value of ethological approaches to studying acoustic categorization

The neural representation of acoustic features enables functional auditory decisions to be made to guide behavior, including the detection, discrimination and categorization of sounds. Here, we discuss categorization in more detail and again argue that ethological approaches may offer advantages for revealing underlying neural mechanisms.

The need to categorize sounds arises because discriminating acoustic variability may not always be necessary or desirable for a required behavioral judgment. In the context of communication, this variability may appear due to intrinsic differences in the vocalizer, such as male vs. female, large vs. small or young vs. old (Liu et al., 2003; Peterson et al., 1952; Riede et al., 1999); the vocalizer's emotional state, such as stressed vs. relaxed (Bachorowski et al., 1995; Streeter et al., 1983); or simply environmental conditions like

room reverberation (Houtgast et al., 1980). Depending on the behavioral situation, variability could be important for guiding differential responses or should be ignored to drive a specific stereotyped response triggered by the sound category.

Progress in understanding the neural basis of acoustic categorization has typically used sounds that are *not* ethologically relevant for the species being studied. In particular, speech phonemes, which humans perceive categorically (Harnad, 1987), have been used in many auditory neurophysiological studies conducted in animals from rodents to non-human primates (Engineer et al., 2008; Lee et al., 2009; Mesgarani et al., 2008; Russ et al., 2007; Russ et al., 2008; Steinschneider et al., 2003; Tsunada et al., 2011; Tsunada et al., 2012). The assumption has been that basic auditory mechanisms shared across species contribute to this ability (Kuhl, 1981). For example, once trained to discriminate speech sounds, monkeys can readily categorize their morphs (Lee et al., 2009; Russ et al., 2007; Tsunada et al., 2011; Tsunada et al., 2012). These categories are represented in the ventral prefrontal cortex. Importantly, neural activity in the prefrontal cortex during categorization also predicts behavioral choice (Russ et al, 2008). Earlier in the stimulus-behavior transformation, these categories are differentially represented between interneurons and pyramidal neurons in the belt region of the auditory cortex (Tsunada et al., 2012), but this belt activity is not modulated by the monkey's categorical choices. (Tsunada et al., 2011). Finally, a study in mongolian gerbils even suggests that primary auditory cortex can exhibit categorical neural activity after animals learn to categorize frequency sweeps (Ohl et al., 2001).

Whereas these studies provide some important insights into neural mechanisms for acoustic categorization, they are limited by the fact that the sounds do not have intrinsic meaning for the animals. To further advance our understanding of brain mechanisms for categorization in the context of acoustic communication, the communication stimuli used and the behaviors studied should be species-specific. This helps ensure that the animals have been exposed to the natural acoustic variability that triggers the natural, stereotyped response (although the range of exposure of animals raised in a laboratory-based vivarium may be more limited than their wild counterparts). In contrast, most of the paradigms described above using human speech sounds in animals require explicit training (often with considerable time and effort) in a new behavior so that experimenters can infer perception. Such paradigms generally involve instrumental conditioning rather than social interactions for learning the meaning of a sound category. This could alter the nature of the learned categorical representations, as other studies have shown that the way in which stimuli are learned affects how they are encoded (Bieszczad et al., 2010a; David et al., 2012; Gentner et al., 2003b; Polley et al., 2006). Finally, the range of stimuli is more limited than would naturally be encountered if those stimuli were part of a natural communication repertoire, potentially affecting the way in which categorization is achieved.

The strategy of using species-specific vocalizations has led to important progress understanding the neural basis of human speech categorization (Chang et al., 2010), but so far only at the level of local field potentials. A clearer picture at the single neuron level will, practically speaking, require animal models. Thus, developing ethological paradigms using species-specific vocalization categories that elicit stereotyped responses is essential. Some intriguing approaches are antiphonal calling in non-human primates (Miller et al., 2009), spontaneous categorization of food vocalizations in non-human primates (Gifford et al., 2005), and dueting in songbirds (Fortune et al., 2011), wherein animals respond to hearing conspecific vocalizations by vocalizing themselves.

Another paradigm being actively pursued is the maternal response to infant vocalizations in rodents, particularly mice (Cohen et al., 2011; Fichtel et al., 1999; Liu et al., 2006; Liu et al., 2003). Mouse pups emit ultrasonic calls when isolated from their nest; these calls elicit a

search and retrieval behavior in mothers (Ehret, 2005). This behavior likely involves some experience-dependent acquisition, since virgin females begin preferring calls after helping to raise pups (Ehret et al., 1987; Lin et al., 2013). In terms of acoustic categorization, the pup calls form a natural acoustic category in the frequency and duration domains that can be discriminated from other mouse ultrasonic vocalizations (Liu et al., 2003), and mouse mothers actually perceive ultrasonic sound frequency, bandwidth and duration categorically (Ehret, 1992; Ehret et al., 1981).

The behavioral findings have motivated the use of the maternal model to explore how the ultrasonic pup call category is represented in the auditory cortex (Liu et al., 2007; Liu et al., 2006). This has helped uncover novel mechanisms, like inhibitory plasticity (Galindo-Leon et al., 2009; Lin et al., 2013; Vogels et al., 2013) and multimodal olfactory-auditory integration (Cohen et al., 2011). In the latter result, pup-naïve virgin females exhibited only minimal multimodal integration in contrast to mothers, thereby emphasizing the importance of using behaviorally relevant, species-specific communication sound categories to reveal novel neural mechanisms.

4. Do vocalizations engage "special" processing or plasticity mechanisms?

Given our argument for the use of ethological paradigms to study communication, it may seem that we advocate the position that the auditory system has a preferential bias towards a *specific* class of acoustic stimuli, namely vocalizations. In fact, though, whether vocalizations have some sort of processing or plasticity "privilege" above and beyond other natural stimuli is still an active debate, and we cannot make any definitive conclusions. Nevertheless, there is some evidence in favor of preferential processing. For example, behavioral studies in non-human primates point to preferential processing of vocalizations over other natural sounds: a monkey's performance during a working-memory task is better when he is required to remember a species-specific vocalization than when he is required to remember other sounds, like human voices and music (Ng et al., 2009).

Perhaps, the best evidence for vocalization specialization comes from work showing that in the primate, regions in the anterior portion of the temporal lobe respond selectively not only to vocalizations but also to the identity of the vocalizer (Perrodin et al., 2011; Petkov et al., 2008). Consistent with these findings, human patients with damage in the temporal and parietal cortices have deficits in voice recognition and discrimination (i.e., phonagnosia) (Van Lancker et al., 1982; Van Lancker et al., 1988). However, this kind of selectivity lies at the apex of a series of computational steps that have yet to be fully identified, including the learning of perceptual categorization and computations that create neural invariance (tolerance) to "identity-preserving" (e.g., changes in loudness, location etc.) changes in a sound. It may be that those same steps are employed for general auditory processing of sound categories that are not vocalizations, albeit potentially in other brain areas. In the case of either vocal or non-vocal stimuli though, to better understand the nature of category specialization, it will be important to differentiate between neural variability that is elicited by different vocalizers or sources producing the same sound (i.e., inter-source variability) from variability that is elicited by the same source producing different sounds (intra-source variability).

This prompts one to ask whether there might be a progression along the ascending auditory system in the weighting of different classes of acoustic communication stimuli, so that neurons in certain auditory regions begin showing greater (or perhaps exclusive) selectivity for the natural acoustic structure of vocalizations over that of other natural valid stimuli. Indeed, Woolley et al (2005) (Woolley et al., 2005) found that the spectrotemporal tuning of neurons in the avian analogues of the auditory thalamus and cortex deemphasizes the

spectrotemporal modulations that are common to most natural stimulus classes and, instead, accentuates those unique modulations that allow a listener to discriminate between different stimulus classes. Importantly, though, at this level, there is no *exclusive* responsiveness to the spectrotemporal features of vocalizations: this exclusivity emerges in the sensorimotor-integration areas of the songbird's song-production system.

If vocalizations are indeed privileged, it is still an open question whether this specialization is genetically "hard wired" or arises from learning or the animal's "overexposure" to these behaviorally salient stimuli (Egnor et al., 2004); most likely, it is a combination of both. Recent research has begun to address such questions through the use of neurophysiology in scenarios where vocalizations *acquire* salience through natural social interactions. For instance, songbird research has begun exploring the neural changes in the auditory forebrain of females as they learn the "meaning" of different male songs. Woolley and Doupe (Woolley et al., 2008) found that female zebra finches prefer their mate's song more than an unfamiliar conspecific's song. Moreover, the expression of the immediate early gene *zenk* in the caudomedial nidopallium (NCM), which is an analog of the belt auditory cortex, is higher when female finches listen to their mate's song than when they listen to an unfamiliar conspecific's song. The songbird NCM also happens to be a site where estrogen, a so-called social neurochemical (Choleris et al., 2003) that is upregulated during mating season, can modulate neural activity and plasticity in response to songs (Maney et al., 2006; Remage-Healey et al., 2012; Tremere et al., 2011; Tremere et al., 2009; Tremere et al., 2012). This further emphasizes the importance of exploiting the natural ethological context to study auditory processing, since the involvement of these hormonal neurochemicals could well be different in processing sounds that are not behaviorally salient (Maney et al., 2006).

The importance of hormones in plasticity and the processing of communication signals is also beginning to be implicated in the maternal communication system between mouse pups and their mothers (Ehret et al., 2009; Lin et al., 2013; Miranda et al., 2009). Overall, research in this area is now turning to the roles of social experience with pups and maternal hormonal modulation in mediating neural coding changes, directions that may one day inform strategies to ameliorate deficits in real-life communication learning.

5. Conclusions

If a primary goal of hearing scientists is to elucidate the neural mechanisms for many of the auditory abilities that contribute to natural acoustic communication, then we advocate that research efforts should more fully embrace ethological paradigms that involve species-specific communication sounds and actual communication behavior. While recent ethologically motivated studies outlined here have made great strides on the stimulus side, much more still needs to be done to realize the natural behavioral side. We, therefore, end by briefly considering advances still needed that could help natural ethological paradigms for communication overcome the practical difficulties of its laboratory study. For example, the development of newer wireless neural recording techniques (Roy et al., 2012; Szuts et al., 2011) in non-human primates would allow freer and more natural movement during neural recordings. Second, even though behavior may become less restricted, trial-by-trial behavioral variability would likely persist, motivating the need to be able to derive neural results from individual behavioral trials. Improving the ability to record a greater number of neurons and to apply statistical and computational methods for single-trial analyses would therefore be important (Kass et al., 2005; Yu et al., 2009). The discussion above suggests that adopting natural communication stimuli and natural behavioral paradigms for auditory research would be desirable for studying how the auditory system normally functions and learns to guide behavior. Indeed, the neural basis for action selection is poorly understood

for auditory-evoked behaviors in general, and robust natural tasks would, in principle, be greatly advantageous.

Acknowledgments

Abbreviations

A1	primary auditory cortex
NCM	caudomedial nidopallium
STRF	spectrotemporal receptive field

References

Abeles M, Goldstein MH Jr. Responses of single units in the primary auditory cortex of the cat to tones and to tone pairs. Brain Res. 1972; 42:337–352. [PubMed: 5050171]

Ahrens MB, Linden JF, Sahani M. Nonlinearities and Contextual Influences in Auditory Cortical Responses Modeled with Multilinear Spectrotemporal Methods. J. Neurosci. 2008; 28:1929–1942. [PubMed: 18287509]

Arnold K, Zuberbuhler K. Language evolution: semantic combinations in primate calls. Nature. 2006; 441:303. [PubMed: 16710411]

Atencio CA, Sharpee TO, Schreiner CE. Cooperative nonlinearities in auditory cortical neurons. Neuron. 2008; 58:956–966. [PubMed: 18579084]

Attias, H.; Schreiner, CE. Temporal low-order statistics of natural sounds. In: Mozer, MC.; Jordan, MI.; Petsche, T., editors. Advances in Neural Information Processing Systems 9. Vol. Vol. 9. Denver, CO: MIT Press; 1997. p. 27-33.

Attias, H.; Schreiner, CE. Coding of Naturalistic Stimuli by Auditory Midbrain Neurons. In: Jordan, MI.; Kearns, MJ.; Solla, SA., editors. Advances in Neural Information Processing Systems 10. Vol. Vol. 10. Denver, CO: MIT Press; 1998. p. 103-109.

August PV, Anderson JGT. Mammal Sounds and Motivation-Structural Rules: A Test of the Hypothesis. Journal of Mammalogy. 1987; 68:1–9.

Averbeck BB, Romanski LM. Probabilistic encoding of vocalizations in macaque ventral lateral prefrontal cortex. J Neurosci. 2006; 26:11023–11033. [PubMed: 17065444]

Bachorowski J-A, Owren MJ. Vocal Expression of Emotion: Acoustic Properties of Speech Are Associated With Emotional Intensity and Context. Psychological Science. 1995; 6:219–224.

Balaban E. Bird song syntax: learned intraspecific variation is meaningful. Proceedings of the National Academy of Sciences. 1988; 85:3657–3660.

Bar-Yosef O, Rotman Y, Nelken I. Responses of neurons in cat primary auditory cortex to bird chirps: effects of temporal and spectral context. J Neurosci. 2002; 22:8619–8632. [PubMed: 12351736]

Bieszczad KM, Weinberger NM. Remodeling the cortex in memory: Increased use of a learning strategy increases the representational area of relevant acoustic cues. Neurobiol Learn Mem. 2010a

Bieszczad KM, Weinberger NM. Learning strategy trumps motivational level in determining learning-induced auditory cortical plasticity. Neurobiol Learn Mem. 2010b; 93:229–239. [PubMed: 19853056]

Calabrese A, Schumacher JW, Schneider DM, Paninski L, Woolley SM. A generalized linear model for estimating spectrotemporal receptive fields from responses to natural sounds. PLoS ONE. 2011; 6:e16104. [PubMed: 21264310]

Calhoun BM, Schreiner CE. Spectral envelope coding in cat primary auditory cortex: linear and non-linear effects of stimulus characteristics. Eur J Neurosci. 1998; 10:926–940. [PubMed: 9753160]

Carruthers IM, Natan RG, Geffen MN. Encoding of ultrasonic vocalizations in the auditory cortex. J Neurophysiol. 2013; 109:1912–1927. [PubMed: 23324323]

Chandrasekaran C, Trubanova A, Stillittano S, Caplier A, Ghazanfar AA. The Natural Statistics of Audiovisual Speech. PLoS Comput Biol. 2009; 5:e1000436. [PubMed: 19609344]

Chang EF, Rieger JW, Johnson K, Berger MS, Barbaro NM, Knight RT. Categorical speech representation in human superior temporal gyrus. Nat Neurosci. 2010; 13:1428–1432. [PubMed: 20890293]

Cheney DL, Seyfarth RM. Vocal recognition in free-ranging vervet monkeys. Animal Behaviour. 1980; 28:362–367.

Cheney, DL.; Seyfarth, RM. How Monkeys See the World: Inside the Mind of Another Species. University of Chicago Press; 1992.

Choleris E, Gustafsson JA, Korach KS, Muglia LJ, Pfaff DW, Ogawa S. An estrogen-dependent four-gene micronet regulating social recognition: a study with oxytocin and estrogen receptor-alpha and -beta knockout mice. Proc Natl Acad Sci U S A. 2003; 100:6192–6197. [PubMed: 12730370]

Cohen L, Rothschild G, Mizrahi A. Multisensory integration of natural odors and sounds in the auditory cortex. Neuron. 2011; 72:357–369. [PubMed: 22017993]

Cohen YE, Theunissen F, Russ BE, Gill P. Acoustic features of rhesus vocalizations and their representation in the ventrolateral prefrontal cortex. J Neurophysiol. 2007; 97:1470–1484. [PubMed: 17135477]

Covey E, Casseday JH. Timing in the auditory system of the bat. Annual review of physiology. 1999; 61:457–476.

David SV, Fritz JB, Shamma SA. Task reward structure shapes rapid receptive field plasticity in auditory cortex. Proc Natl Acad Sci U S A. 2012; 109:2144–2149. [PubMed: 22308415]

deCharms RC, Blake DT, Merzenich MM. Optimizing sound features for cortical neurons. Science. 1998; 280:1439–1443. [PubMed: 9603734]

Depireux DA, Simon JZ, Klein DJ, Shamma SA. Spectro-temporal response field characterization with dynamic ripples in ferret primary auditory cortex. J Neurophysiol. 2001; 85:1220–1234. [PubMed: 11247991]

DiMattina C, Wang X. Virtual vocalization stimuli for investigating neural representations of species-specific vocalizations. Journal of neurophysiology. 2006; 95:1244–1262. [PubMed: 16207780]

Dylla M, Hrnicek A, Rice C, Ramachandran R. Detection of tones and their modification by noise in nonhuman primates. J Assoc Res Otolaryngol. 2013; 14:547–560. [PubMed: 23515749]

Egnor SE, Hauser MD. A paradox in the evolution of primate vocal learning. Trends Neurosci. 2004; 27:649–654. [PubMed: 15474164]

Ehret G. Categorical perception of mouse-pup ultrasounds in the temporal domain. Anim Behav. 1992; 43:409–416.

Ehret G. Infant rodent ultrasounds -- a gate to the understanding of sound communication. Behav Genet. 2005; 35:19–29. [PubMed: 15674530]

Ehret G, Haack B. Categorical perception of mouse pup ultrasound by lactating females. Naturwissenschaften. 1981; 68:208–209. [PubMed: 7278997]

Ehret G, Schmid C. Reproductive cycle-dependent plasticity of perception of acoustic meaning in mice. Physiol Behav. 2009; 96:428–433. [PubMed: 19061908]

Ehret G, Koch M, Haack B, Markl H. Sex and parental experience determine the onset of an instinctive behavior in mice. Naturwissenschaften. 1987; 74:47. [PubMed: 3561521]

Engineer CT, Perez CA, Chen YH, Carraway RS, Reed AC, Shetake JA, Jakkamsetti V, Chang KQ, Kilgard MP. Cortical activity patterns predict speech discrimination ability. Nat Neurosci. 2008; 11:603–608. [PubMed: 18425123]

Escabi MA, Schreiner CE. Nonlinear spectrotemporal sound analysis by neurons in the auditory midbrain. J Neurosci. 2002; 22:4114–4131. [PubMed: 12019330]

Escabi MA, Miller LM, Read HL, Schreiner CE. Naturalistic auditory contrast improves spectrotemporal coding in the cat inferior colliculus. J Neurosci. 2003; 23:11489–11504. [PubMed: 14684853]

Ewert, J-P.; Capranica, RR.; Ingle, DJ. Scientific Affairs Division. New York: Advances in vertebrate neuroethology Plenum Press; 1983. North Atlantic Treaty Organization.

Fichtel I, Ehret G. Perception and recognition discriminated in the mouse auditory cortex by c-{F}os labeling. Neuroreport. 1999; 10:2341–2345. [PubMed: 10439460]

Fischer J, Hammerschmidt K. Ultrasonic vocalizations in mouse models for speech and socio-cognitive disorders: insights into the evolution of vocal communication. Genes, Brain and Behavior. 2011; 10:17–27.

Fortune ES, Rodriguez C, Li D, Ball GF, Coleman MJ. Neural mechanisms for the coordination of duet singing in wrens. Science. 2011; 334:666–670. [PubMed: 22053048]

Fuzessery Z, Feng A. Mating Call Selectivity in the Thalamus and Midbrain of the Leopard Frog (rana-P-Pipiens) - Single and Multiunit Analyses. Journal of Comparative Physiology. 1983; 150:333–344.

Galindo-Leon EE, Lin FG, Liu RC. Inhibitory Plasticity in a Lateral Band Improves Cortical Detection of Natural Vocalizations. Neuron. 2009; 62:705–716. [PubMed: 19524529]

Gentner, TQ.; Margoliash, D. The Neuroethology of Vocal Communication: Perception and Cognition. In: Simmons, A.; Fay, RR., editors. Acoustic Communication. Vol. Vol. 16. New York: Springer; 2003a. p. 324-386.

Gentner TQ, Margoliash D. Neuronal populations and single cells representing learned auditory objects. Nature. 2003b; 424:669–674. [PubMed: 12904792]

Ghazanfar AA, Santos LR. Primate brains in the wild: the sensory bases for social interactions. Nature Reviews Neuroscience. 2004; 5:603–616.

Gifford GW 3rd, MacLean KA, Hauser MD, Cohen YE. The neurophysiology of functionally meaningful categories: macaque ventrolateral prefrontal cortex plays a critical role in spontaneous categorization of species-specific vocalizations. J Cogn Neurosci. 2005; 17:1471–1482. [PubMed: 16197700]

Griffiths TD, Warren JD. What is an auditory object? Nature Reviews Neuroscience. 2004; 5:887–892.

Hahnloser RHR, Kotowicz A. Auditory representations and memory in birdsong learning. Current opinion in neurobiology. 2010; 20:332–339. [PubMed: 20307967]

Harnad, SR. Categorical perception: the groundwork of cognition. New York: Cambridge University Press; 1987.

Heffner RS, Koay G, Heffner HE. Audiograms of five species of rodents: implications for the evolution of hearing and the perception of pitch. Hear Res. 2001; 157:138–152. [PubMed: 11470193]

Holmstrom L, Roberts PD, Portfors CV. Responses to social vocalizations in the inferior colliculus of the mustached bat are influenced by secondary tuning curves. J Neurophysiol. 2007; 98:3461–3472. [PubMed: 17928559]

Holy TE, Guo Z. Ultrasonic songs of male mice. PLoS Biol. 2005; 3:e386. [PubMed: 16248680]

Houtgast T, Steeneken HJM, Plomp R. Predicting Speech Intelligibility in Rooms from the Modulation Transfer Function. I. General Room Acoustics. Acta Acustica united with Acustica. 1980; 46:60–72.

Kanwal JS, Rauschecker JP. Auditory cortex of bats and primates: managing species-specific calls for social communication. Frontiers in bioscience: a journal and virtual library. 2007; 12:4621–4640. [PubMed: 17485400]

Kanwal JS, Matsumura S, Ohlemiller K, Suga N. Analysis of acoustic elements and syntax in communication sounds emitted by mustached bats. J Acoust Soc Am. 1994; 96:1229–1254. [PubMed: 7962992]

Kass RE, Ventura V, Brown EN. Statistical Issues in the Analysis of Neuronal Data. Journal of Neurophysiology. 2005; 94:8–25. [PubMed: 15985692]

Kim H, Bao S. Selective increase in representations of sounds repeated at an ethological rate. J Neurosci. 2009; 29:5163–5169. [PubMed: 19386912]

Klink KB, Klump GM. Duration discrimination in the mouse (Mus musculus). J Comp Physiol A Neuroethol Sens Neural Behav Physiol. 2004; 190:1039–1046. [PubMed: 15480703]

Konishi M. The role of auditory feedback in birdsong. Annals of the New York Academy of Sciences. 2004; 1016:463–475. [PubMed: 15313790]

Kowalski N, Depireux DA, Shamma SA. Analysis of dynamic spectra in ferret primary auditory cortex. I. Characteristics of single-unit responses to moving ripple spectra. J Neurophysiol. 1996a; 76:3503–3523. [PubMed: 8930289]

Kowalski N, Depireux DA, Shamma SA. Analysis of dynamic spectra in ferret primary auditory cortex. II. Prediction of unit responses to arbitrary dynamic spectra. J Neurophysiol. 1996b; 76:3524–3534. [PubMed: 8930290]

Kuhl PK. Discrimination of speech by nonhuman animals: {B}asic auditory sensitivities conducive to the perception of speech-sound categories. J Acoust Soc Am. 1981; 70:340–349.

Lee JH, Russ BE, Orr LE, Cohen YE. Prefrontal activity predicts monkeys' decisions during an auditory category task. Front Integr Neurosci. 2009; 3:16. [PubMed: 19587846]

Leppelsack HJ. Unit responses to species-specific sounds in the auditory forebrain center of birds. Federation Proceedings. 1978; 37:2336–2341. [PubMed: 354969]

Lin FG, Galindo-Leon EE, Ivanova TN, Mappus RC, Liu RC. A role for maternal physiological state in preserving auditory cortical plasticity for salient infant calls. Neuroscience. 2013; 247:102–116. [PubMed: 23707982]

Linden JF, Liu RC, Sahani M, Schreiner CE, Merzenich MM. Spectrotemporal structure of receptive fields in areas AI and AAF of mouse auditory cortex. J Neurophysiol. 2003; 90:2660–2675. [PubMed: 12815016]

Liu RC, Schreiner CE. Auditory cortical detection and discrimination correlates with communicative significance. PLoS Biology. 2007; 5:e173. [PubMed: 17564499]

Liu RC, Linden JF, Schreiner CE. Improved cortical entrainment to infant communication calls in mothers compared with virgin mice. Eur J Neurosci. 2006; 23:3087–3097. [PubMed: 16819999]

Liu RC, Miller KD, Merzenich MM, Schreiner CE. Acoustic variability and distinguishability among mouse ultrasound vocalizations. J Acoust Soc Am. 2003; 114:3412–3422. [PubMed: 14714820]

Machens CK, Wehr MS, Zador AM. Linearity of cortical receptive fields measured with natural sounds. J Neurosci. 2004; 24:1089–1100. [PubMed: 14762127]

Maney DL, Cho E, Goode CT. Estrogen-dependent selectivity of genomic responses to birdsong. Eur J Neurosci. 2006; 23:1523–1529. [PubMed: 16553615]

Margoliash D. Acoustic parameters underlying the responses of song-specific neurons in the white-crowned sparrow. J Neurosci. 1983; 3:1039–1057. [PubMed: 6842281]

Margoliash D. Preference for autogenous song by auditory neurons in a song system nucleus of the white-crowned sparrow. J Neurosci. 1986; 6:1643–1661. [PubMed: 3712002]

Margoliash D, Fortune ES. Temporal and harmonic combination-sensitive neurons in the zebra finch's HVc. The Journal of neuroscience: the official journal of the Society for Neuroscience. 1992; 12:4309–4326. [PubMed: 1432096]

Mesgarani N, David SV, Fritz JB, Shamma SA. Phoneme representation and classification in primary auditory cortex. J Acoust Soc Am. 2008; 123:899–909. [PubMed: 18247893]

Miller C, Beck K, Meade B, Wang X. Antiphonal call timing in marmosets is behaviorally significant: interactive playback experiments. Journal of Comparative Physiology A. 2009; 195:783–789.

Miller LM, Escabi MA, Read HL, Schreiner CE. Spectrotemporal receptive fields in the lemniscal auditory thalamus and cortex. J Neurophysiol. 2002; 87:516–527. [PubMed: 11784767]

Miranda JA, Liu RC. Dissecting natural sensory plasticity: hormones and experience in a maternal context. Hear Res. 2009; 252:21–28. [PubMed: 19401225]

Morton ES. On the Occurrence and Significance of Motivation-Structural Rules in Some Bird and Mammal Sounds. The American Naturalist. 1977; 111:855–869.

Moss CF, Chiu C, Surlykke A. Adaptive vocal behavior drives perception by echolocation in bats. Current opinion in neurobiology. 2011; 21:645–652. [PubMed: 21705213]

Neuweiler G. Auditory adaptations for prey capture in echolocating bats. Physiol Rev. 1990; 70:615–641. [PubMed: 2194220]

Ng CW, Plakke B, Poremba A. Primate auditory recognition memory performance varies with sound type. Hear Res. 2009; 256:64–74. [PubMed: 19567264]

Ohl FW, Scheich H, Freeman WJ. Change in pattern of ongoing cortical activity with auditory category learning. Nature. 2001; 412:733–736. [PubMed: 11507640]

Ohlemiller KK, Kanwal JS, Suga N. Facilitative responses to species-specific calls in cortical FM-FM neurons of the mustached bat. Neuroreport. 1996; 7:1749–1755. [PubMed: 8905657]

Perrodin C, Kayser C, Logothetis NK, Petkov CI. Voice cells in the primate temporal lobe. Current biology: CB. 2011; 21:1408–1415. [PubMed: 21835625]

Peterson GN, Barney HL. Control methods used in a study of the vowels. J Acoust Soc Am. 1952; 24:175–184.

Petkov CI, Kayser C, Steudel T, Whittingstall K, Augath M, Logothetis NK. A voice region in the monkey brain. Nature Neuroscience. 2008; 11:367–374.

Phillips DP, Irvine DR. Responses of single neurons in physiologically defined primary auditory cortex (AI) of the cat: frequency tuning and responses to intensity. J Neurophysiol. 1981; 45:48–58. [PubMed: 7205344]

Pollak, GD. Adaptations of Basic Structures and Mechanisms in the Cochlea and Central Auditory Pathway of the Mustache Bat. In: Webster, DB.; Fay, RR.; Popper, AN., editors. The Evolutionary Biology of Hearing. New York: Springer; 1992. p. 751-778.

Polley DB, Steinberg EE, Merzenich MM. Perceptual learning directs auditory cortical map reorganization through top-down influences. J Neurosci. 2006; 26:4970–4982. [PubMed: 16672673]

Portfors CV. Combination sensitivity and processing of communication calls in the inferior colliculus of the Moustached Bat Pteronotus parnellii. An Acad Bras Cienc. 2004; 76:253–257. [PubMed: 15258635]

Portfors CV, Wenstrup JJ. Delay-tuned neurons in the inferior colliculus of the mustached bat: implications for analyses of target distance. J Neurophysiol. 1999; 82:1326–1338. [PubMed: 10482752]

Rauschecker JP, Tian B. Mechanisms and streams for processing of "what" and "where" in auditory cortex. Proceedings of the National Academy of Sciences of the United States of America. 2000; 97:11800–11806. [PubMed: 11050212]

Rauschecker JP, Tian B, Hauser M. Processing of complex sounds in the macaque nonprimary auditory cortex. Science (New York, N.Y.). 1995; 268:111–114.

Razak KA, Fuzessery ZM. Experience-dependent development of vocalization selectivity in the auditory cortex. The Journal of the Acoustical Society of America. 2010; 128:1446–1451. [PubMed: 20815478]

Recanzone GH, Schreiner CE, Merzenich MM. Plasticity in the frequency representation of primary auditory cortex following discrimination training in adult owl monkeys. J Neurosci. 1993; 13:87–103. [PubMed: 8423485]

Remage-Healey L, Dong SM, Chao A, Schlinger BA. Sex-specific, rapid neuroestrogen fluctuations and neurophysiological actions in the songbird auditory forebrain. J Neurophysiol. 2012; 107:1621–1631. [PubMed: 22190616]

Riede T, Fitch T. Vocal tract length and acoustics of vocalization in the domestic dog (Canis familiaris). J Exp Biol. 1999; 202:2859–2867. [PubMed: 10504322]

Roy S, Wang X. Wireless multi-channel single unit recording in freely moving and vocalizing primates. J Neurosci Methods. 2012; 203:28–40. [PubMed: 21933683]

Russ BE, Lee YS, Cohen YE. Neural and behavioral correlates of auditory categorization. Hear Res. 2007; 229:204–212. [PubMed: 17208397]

Russ BE, Orr LE, Cohen YE. Prefrontal neurons predict choices during an auditory same-different task. Curr Biol. 2008; 18:1483–1488. [PubMed: 18818080]

Sachs MB, Kiang NY. Two-tone inhibition in auditory-nerve fibers. J Acoust Soc Am. 1968; 43:1120–1128. [PubMed: 5648103]

Scheich H, Bonke BA, Bonke D, Langner G. Functional organization of some auditory nuclei in the guinea fowl demonstrated by the 2-deoxyglucose technique. Cell Tissue Res. 1979; 204:17–27. [PubMed: 527021]

Shamma SA, Elhilali M, Micheyl C. Temporal coherence and attention in auditory scene analysis. Trends Neurosci. 2011; 34:114–123. [PubMed: 21196054]

Singh NC, Theunissen FE. Modulation spectra of natural sounds and ethological theories of auditory processing. J Acoust Soc Am. 2003; 114:3394–3411. [PubMed: 14714819]

Steinschneider M, Fishman YI, Arezzo JC. Representation of the voice onset time (VOT) speech parameter in population responses within primary auditory cortex of the awake monkey. J Acoust Soc Am. 2003; 114:307–321. [PubMed: 12880043]

Streeter LA, Macdonald NH, Apple W, Krauss RM, Galotti KM. Acoustic and perceptual indicators of emotional stress. J Acoust Soc Am. 1983; 73:1354–1360. [PubMed: 6853847]

Suga N. Specialization of the auditory system for reception and processing of species-specific sounds. Federation proceedings. 1978; 37:2342–2354. [PubMed: 354970]

Suga, N. Neuroethology and speech processing: Complex sound processing by combination-sensitive neurons. In: Edelman, GW.; Gall, WE.; Cowan, WM., editors. Auditory Function: Neurobiological Bases of Hearing. New York: John Wiley and Sons; 1988. p. 679-719.

Suga N, O'Neill WE. Neural axis representing target range in the auditory cortex of the mustache bat. Science. 1979; 206:351–353. [PubMed: 482944]

Szuts TA, Fadeyev V, Kachiguine S, Sher A, Grivich MV, Agrochao M, Hottowy P, Dabrowski W, Lubenov EV, Siapas AG, Uchida N, Litke AM, Meister M. A wireless multi-channel neural amplifier for freely moving animals. Nat Neurosci. 2011; 14:263–269. [PubMed: 21240274]

Talwar SK, Musial PG, Gerstein GL. Role of mammalian auditory cortex in the perception of elementary sound properties. Journal of Neurophysiology. 2001; 85:2350–2358. [PubMed: 11387381]

Temchin AN, Recio-Spinoso A, van Dijk P, Ruggero MA. Wiener kernels of chinchilla auditory-nerve fibers: verification using responses to tones, clicks, and noise and comparison with basilar-membrane vibrations. J Neurophysiol. 2005; 93:3635–3648. [PubMed: 15659530]

Theunissen FE, Sen K, Doupe AJ. Spectral-temporal receptive fields of nonlinear auditory neurons obtained using natural sounds. J Neurosci. 2000; 20:2315–2331. [PubMed: 10704507]

Tremere LA, Pinaud R. Brain-generated estradiol drives long-term optimization of auditory coding to enhance the discrimination of communication signals. J Neurosci. 2011; 31:3271–3289. [PubMed: 21368039]

Tremere LA, Jeong JK, Pinaud R. Estradiol shapes auditory processing in the adult brain by regulating inhibitory transmission and plasticity-associated gene expression. J Neurosci. 2009; 29:5949–5963. [PubMed: 19420261]

Tremere LA, Kovaleski RF, Burrows K, Jeong JK, Pinaud R. Mechanistic basis and functional roles of long-term plasticity in auditory neurons induced by a brain-generated estrogen. J Neurosci. 2012; 32:16478–16495. [PubMed: 23152630]

Tsunada J, Lee JH, Cohen YE. Representation of speech categories in the primate auditory cortex. Journal of Neurophysiology. 2011; 105:2634–2646. [PubMed: 21346209]

Tsunada J, Lee JH, Cohen YE. Differential representation of auditory categories between cell classes in primate auditory cortex. J Physiol. 2012; 590:3129–3139. [PubMed: 22570374]

Tsuzuki K, Suga N. Combination-sensitive neurons in the ventroanterior area of the auditory cortex of the mustached bat. J Neurophysiol. 1988; 60:1908–1923. [PubMed: 3236055]

Van Lancker DR, Canter GJ. Impairment of voice and face recognition in patients with hemispheric damage. Brain and cognition. 1982; 1:185–195. [PubMed: 6927560]

Van Lancker DR, Cummings JL, Kreiman J, Dobkin BH. Phonagnosia: a dissociation between familiar and unfamiliar voices. Cortex; a journal devoted to the study of the nervous system and behavior. 1988; 24:195–209.

Vogels TP, Froemke RC, Doyon N, Gilson M, Haas JS, Liu R, Maffei A, Miller P, Wierenga C, Woodin MA, Zenke F, Sprekeler H. Inhibitory Synaptic Plasticity - Spike timing dependence and putative network function. Frontiers in Neural Circuits. 2013; 7:119. [PubMed: 23882186]

Wang X, Merzenich MM, Beitel R, Schreiner CE. Representation of a species-specific vocalization in the primary auditory cortex of the common marmoset: temporal and spectral characteristics. J Neurophysiol. 1995; 74:2685–2706. [PubMed: 8747224]

Winkler I, Denham SL, Nelken I. Modeling the auditory scene: predictive regularity representations and perceptual objects. Trends Cogn Sci. 2009; 13:532–540. [PubMed: 19828357]

Woolley SC, Doupe AJ. Social context-induced song variation affects female behavior and gene expression. PLoS Biol. 2008; 6:e62. [PubMed: 18351801]

Woolley SMN. Early experience shapes vocal neural coding and perception in songbirds. Developmental psychobiology. 2012; 54:612–631. [PubMed: 22711657]

Woolley SMN, Fremouw TE, Hsu A, Theunissen FE. Tuning for spectro-temporal modulations as a mechanism for auditory discrimination of natural sounds. Nature Neuroscience. 2005; 8:1371–1379.

Yu BM, Cunningham JP, Santhanam G, Ryu SI, Shenoy KV, Sahani M. Gaussian-Process Factor Analysis for Low-Dimensional Single-Trial Analysis of Neural Population Activity. Journal of Neurophysiology. 2009; 102:614–635. [PubMed: 19357332]

Highlights

1. Processing communication sounds depends on general auditory abilities

2. Advantages to ethological paradigms to study general auditory abilities

3. Neuroethology has elucidated higher-order processing and nonlinear sensitivity

4. Neuroethology can help elucidate categorization of naturally variable calls

5. To test vocalization specialization, must study call-to-behavior transformations