



Published in final edited form as:

Curr Opin Neurobiol. 2014 October ; 0: 115–120. doi:10.1016/j.conb.2014.07.002.

The role of ultrasonic vocalizations in mouse communication

Christine V. Portfors¹ and David J. Perkel²

¹School of Biological Sciences, Washington State University, Vancouver, WA 98686

²Depts. Biology & Otolaryngology, University of Washington, Seattle, WA 98195-6515

Abstract

Human speech and language underlie many aspects of social behavior and thus understanding their ultimate evolutionary function and proximate genetic and neural mechanisms is a fundamental goal in neuroscience. Mouse ultrasonic vocalizations have recently received enormous attention as possible models for human speech. This attention has raised the question of whether these vocalizations are learned and what roles they play in communication. In this review, we first discuss recent evidence that ultrasonic vocalizations are not learned. We then review current evidence addressing how adult vocalizations may communicate courtship, territorial and/or other information. While there is growing evidence for these signals to play important roles in communication, many important questions remain unanswered.

Keywords

vocal learning; courtship

Introduction

Many animals, including humans, live in complex social structures that are developed and maintained through the use of communication. Communication is the process by which an individual sends a signal that alters the receiver's behavior. These signals are important for conveying diverse types of information, including membership in a group, social status, predator presence, fitness and willingness to mate. In addition, communication is important for facilitating cooperative behavior. This is particularly true in human language, which is an extreme example of the richness of communication signals that underlie social behavior. Because communication underlies so much of social behavior, understanding its underlying evolutionary, genetic and neural mechanisms is a fundamental scientific goal.

Communication can employ all sensory modalities, yet acoustic communication is one of the most ubiquitous and important across animal species. Many animals use a rich repertoire of

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Correspondence to: Christine V. Portfors, Portfors@vancouver.wsu.edu.

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vocalizations to communicate different types of information. In humans, speech and language are so fundamental for communication that speech and/or language disorders can have dramatic impact on the social behavior and well being of those afflicted and their families [reviewed in 1]. Thus, understanding the mechanisms underlying human speech and communication disorders is a key focus of current research in neuroscience.

Addressing the proximate mechanisms underlying the learning, production and processing of communication signals requires an animal model that can be manipulated in ways that are impossible or unethical in humans. Diverse rodent species use acoustic signals in social settings [2], but because of the power of genetics, mice (*Mus musculus*) have become one of the most important laboratory models for exploring the genetic and neural mechanisms underlying acoustic communication and associated disorders [3]. Mice emit a variety of vocalizations in different social contexts [reviewed in 4] and these change with particular social and genetic manipulations. For example, mutating particular genes related to autism spectrum disorder leads to altered vocalization behavior [5–9]. These studies provide intriguing evidence that mice can indeed be good models for understanding mechanisms of human communication and associated disorders. However, there is still some debate as to which areas of communication research will most benefit from studies using mice, and which areas may require other model systems. In this review, we first address the question of vocal learning in mice and then address the role of mouse vocalizations in communication.

Are mouse vocalizations learned?

A fundamental feature of human speech is that it is learned through imitation, one of several types of vocal learning [10]. Humans copy the sounds made by other individuals, underlying the cultural transmission of language and accents. There is evidence against imitative vocal learning in non-human primates [reviewed in 11] and some evidence for imitative vocal learning in a small number of non-human mammalian groups (see other chapters in this issue). On the other hand, thousands of species of songbirds exhibit imitative vocal learning of their songs [12–14]. While it has been known for several decades that male mice make ultrasonic vocalizations during social interactions [2,15,16], Holy and Guo [17] were the first to describe them as “song”. The use of this term catalyzed the study of whether those vocalizations are learned in a fashion similar to bird songs.

In evaluating the capacity for various species to learn their vocalizations, it is important to consider the types of experimental evidence that bear most strongly on this question. The strongest evidence that would *support* imitative learning comes from imitation of arbitrary sounds experienced earlier in life. Experimentally, this can be tested by rearing mice with foster parents of a different strain (cross-fostering) or co-housing adults of different strains. Two experiments have taken this approach, with conflicting results. Housing different strains of adult mice together led to small shifts in the frequency of some syllables emitted by C57Bl/6J mice toward those of a cagemate male of the B6D2F1/J [BxD] strain [18]. Considering that the shifts in frequency observed were small and could have occurred in response to aggressive or other social cues, this study does not provide convincing evidence for imitative vocal learning in mice. Kikusui et al. [19] cross-fostered two strains of mice

with different vocal parameters and found that the mice reared in this fashion emitted vocalizations with acoustic parameters characteristic of their own strain. Thus, neither of these studies provided evidence for vocal imitation in mice.

Because any imitation of acoustic behaviors would, by definition, require hearing, the strongest evidence *against* vocal learning would come from denying animals acoustic experience and finding that their vocalizations are normal. Two recent studies obtained this result in mice. Hammerschmidt et al., [20] showed that vocalizations emitted by mice lacking the gene for otoferlin, (a protein essential for synaptic transmission in hair cells and thus for hearing) were not acoustically different from those emitted by normal hearing mice. Mahrt et al. [21] also compared acoustic parameters of vocalizations emitted by deaf and normal hearing male mice. They used a strain of transgenic mice in which hair cells could be killed prior to the onset of hearing. Selectively preventing acoustic experience did not affect the acoustic features of different syllable types or the temporal features of sequences of vocalizations. Examples of vocalizations from hearing and deaf mice (Fig. 1) illustrate that hearing experience is not required for the production of normal vocalizations as adults.

In contrast, Arriaga et al. [18] suggested that there is vocal learning in mice based on two results with deaf mice. They found that vocalizations from surgically-deafened adult mice gradually increased in frequency over eight months, and that vocalizations from congenitally deaf mice (due to caspase-3 gene knock-out) were somewhat altered. Each of these hints of vocal learning, however, comes with major issues of interpretation. Shifts in acoustic parameters with age or other types of learning such as operant conditioning occur in non-vocal learners [22] and do not provide evidence for imitative vocal learning. In addition, caspase-3 knockout animals have abnormal brain morphology [23,24], which could itself lead to altered vocalizations, independent of any possible vocal learning.

Overall, there is convincing evidence that mice are not imitative vocal learners. Consequently, mice are not a good model for studying the mechanisms of vocal learning. Their lack of learning, however, makes them a potentially strong model system for studying the genetic basis of vocal communication. Specifically, mice will provide insights into the circuitry underlying normal vocal production and processing. They may also shed light on the genetic basis of human communication disorders, for example, autism spectrum disorder [5,9,25]. A critical question that needs to be addressed to increase the utility of such studies is what roles mouse ultrasonic vocalizations play in communication.

What roles do ultrasonic vocalizations play in communication?

It is well documented that rodents emit a diverse repertoire of ultrasonic vocalizations in different social contexts. Pups emit a large number of ultrasonic vocalizations when isolated from the nest [26–31]. Because these isolation calls elicit retrieval behavior in the mother [33–35], it is clear that they are communication signals that serve a particular purpose. The communicative role of adult mouse ultrasonic vocalizations, however, is less clear. A number of hypotheses have been proposed, with varying degrees of support. The vocalizations emitted by female mice when they encounter an unknown female intruder and

by socially isolated males when they encounter a male intruder may function in determining social hierarchy and/or territorial boundaries [36–39].

The ultrasonic vocalizations emitted by males in the presence of a female, or female pheromones in urine, have been recorded for decades and ascribed a role in courtship [2,15,17,40–42]. However, recently these male-emitted vocalizations have also been ascribed a territorial function [9,43] suggesting that these vocalizations may be important in a variety of different social contexts.

The evidence that male-emitted vocalizations are signals important for courtship comes from 1) patterns of emission by males and 2) behavioral responses of females. First, vocalizations emitted by males are more abundant in the presence of a female or female urine than in the presence of a male or male urine [42,44]. Moreover, there are changes in male-emitted vocalizations depending on the relative location of the male to the female [45–47]. In particular, when the male is close to or mounting the female, the number of vocalizations increases [40,48] and the syllable types change to include a higher proportion of complex, frequency-jump syllables [45,46]. These changes in the vocalizations during specific behaviors related to courtship may indicate a communicative function during courtship.

Second, phonotaxis experiments have shown that behavioral responses of females are affected by male vocalizations. Pomerantz et al. [49] showed that females spend more time with a vocalizing male than with a devocalized male. In addition, females preferentially approach a speaker playing male vocalizations rather than pup isolation calls or whistle-like sounds [50]. Females also preferentially move to a location to elicit playback of male vocalizations rather than a location eliciting silence [51]. In addition, wild female house mice (genus *Mus*) preferentially approach a speaker playing non-kin vocalizations rather than kin vocalizations [52]. In Neotropic singing mice (genus *Scotinomys*) females prefer male vocalizations that have fast temporal features [53]. Overall, the changes in male vocalizations in the presence of females, and the female behavioral responses to those sounds are consistent with the hypothesis that male mouse vocalizations are courtship signals.

In contrast to the idea that male mouse ultrasonic vocalizations are courtship signals, two recent studies have suggested that these vocalizations could be territorial signals. Using the standard intruder paradigm, Hammerschmidt et al., [54] found that the acoustic structure of vocalizations emitted by males in response to an intruder female were not significantly different from those emitted by females in response to a female intruder. Ey and colleagues [9] also found minimal acoustic differences in vocalizations emitted by male and female mice. These similarities suggest that the ultrasonic vocalizations emitted by males are used for more than just courtship and could have different meanings in different social contexts.

It is currently unclear how the vocalizations signal different meaning in different social contexts. One possibility is that there are actual differences in vocalizations emitted in different contexts, but they have not yet been fully identified. Parsing vocalizations based on what the male mouse is doing (e.g. approaching versus mounting a female) has begun to identify differences in acoustic features that may otherwise have been missed [45,46]. Thus,

it is vital to continue and extend this combined approach of acoustic and comprehensive behavioral analysis [55,56] in future studies. In addition, detailed examination of the temporal and sequencing aspects of vocalizations bouts could provide insight into how particular patterns of vocalizations have different meanings [57].

A second possibility is that other types of communication signals alter the meaning of a given vocalization. For example, chemosensory cues are used by mice to identify individuals and attract females [58–61], and it is possible that other types of sensory cues could modulate the meaning of particular vocalizations to a receiver. Understanding such multisensory communication will require expanded use of interdisciplinary approaches.

Avenues for Future Studies

There are still many unanswered questions about the communication function of mouse vocalizations. While there is mounting evidence that males use ultrasonic vocalizations for communication, each piece of evidence is correlative. To make a rigorous cause-and-effect link, there needs to be evidence that these vocalizations actually change the behavior of the individual receiving the signal. For example, a strong test of the role of vocalizations in courtship, though difficult, would involve assaying mating behavior in a large arena in which females have choice over with which male they mate. Another approach would be to explore the possibility of eliciting a behavioral response in female mice corresponding to the copulation solicitation display of birds [62,63], which allows direct assessment of which sounds are effective in promoting sexual receptivity.

Another unanswered question is which features of different vocalizations are attractive to females. Previous phonotaxis experiments have provided evidence for female preference for male-emitted vocalizations over silence or whistle-like artificial sounds [50,51] and for non-kin vocalizations over kin vocalizations [52]. An exciting avenue of future research would be to manipulate the features of the vocalizations (including timing and syllable sequences) to determine which parameters females prefer. It may also be important to explore different assays for female preference. For example, with phonotaxis experiments, it is not clear whether moving towards a sound indicates attraction to that sound or aversion to the other. One alternative approach could involve active playback, extending the approach used in [51], in which the animal actively makes one movement to trigger the playback of one sound and another movement to trigger playback of a different sound. The requirement for active participation of the animal would help to reduce possible alternative interpretations of results from phonotaxis experiments.

As existing technologies are applied to these problems in new combinations, and the power of genetics creates lines of mice with new traits, we anticipate accelerating progress toward understanding the evolutionary, genetic and neural mechanisms underlying acoustic communication and disorders of speech and language.

Acknowledgments

This work was supported by NSF IOS 1257768 to CVP and NIH R01 MH066128 to DJP.

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Highlights

- Mice do not show evidence of imitative vocal learning.
- The lack of vocal learning makes the mouse an excellent model system for understanding the genetic basis of human communication disorders.
- Mouse ultrasonic vocalizations likely play a role in both courtship and territorial interactions.

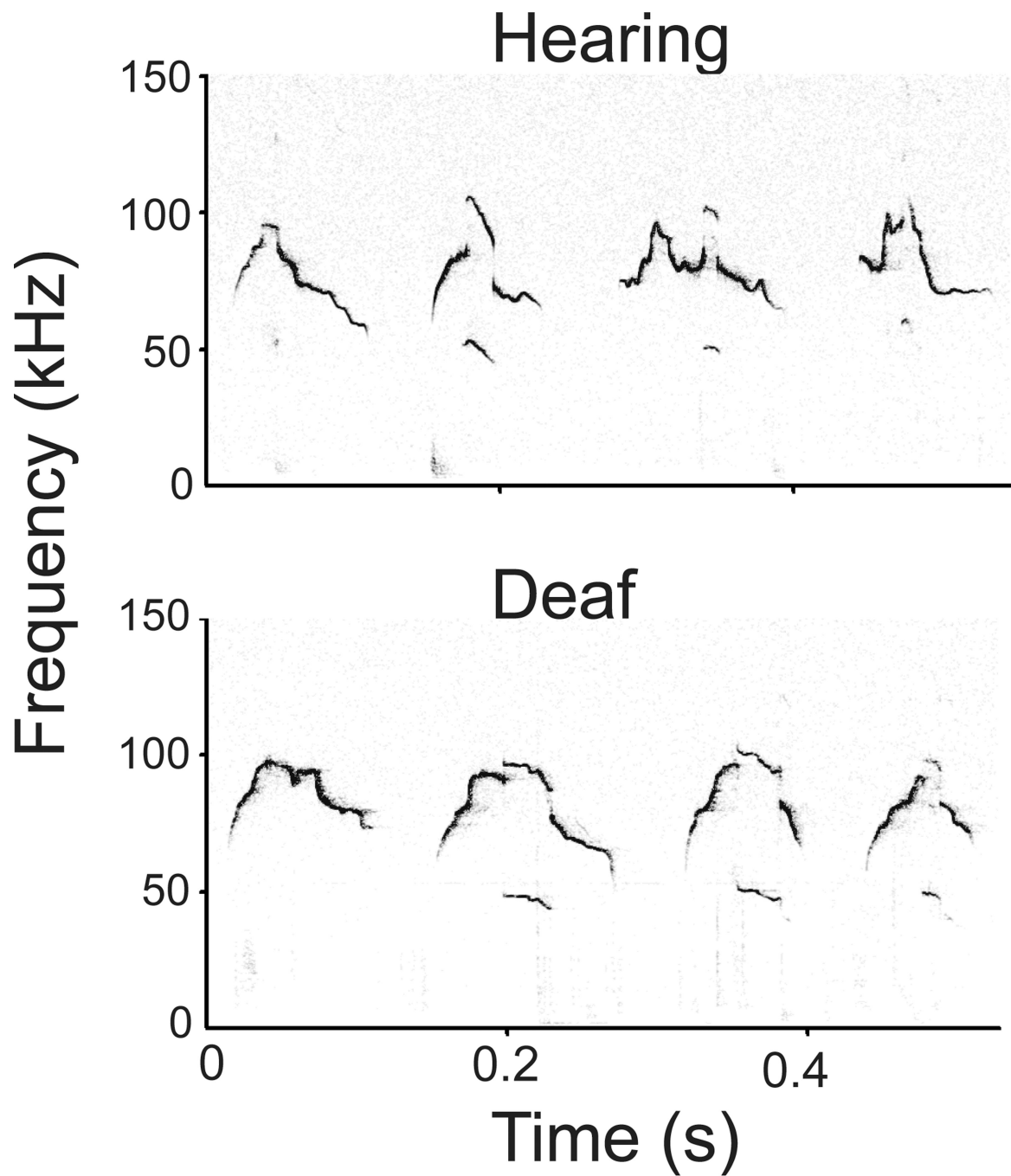


Figure 1.

Example spectrograms of vocalizations emitted by hearing and deaf adult male mice during interactions with a female. The vocalizations produced by hearing and deaf mice are similar, both qualitatively, and quantitatively as demonstrated by Mahrt et al., (2013).