Journal of the American Association for Laboratory Animal Science
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Vol 46, No 1
January 2007
Pages 28–34

Types and Functions of Ultrasonic Vocalizations in Laboratory Rats and Mice

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Many laboratory rodents emit ultrasonic vocalizations. The purpose of this review is to highlight the types and functions of ultrasonic vocalizations emitted by laboratory rats and mice. Rats emit 3 types of ultrasonic vocalizations, depending on the animal's age, its environmental conditions, and its affective state. Rat pups emit a 40-kHz vocalization when they are separated from their mothers. Adult rats emit a 22-kHz vocalization in anticipation of inescapable aversive stimuli. These two types of vocalizations reflect a negative affective state of the animal. Rats produce a 50-kHz vocalization under nonaversive conditions, and these vocalizations reflect a positive affective state of the animal. Adult mice produce several different types of ultrasonic calls that can be classified as different syllables. Mice produce ultrasonic vocalizations during nonaggressive interactions, particularly during mating behaviors, but these vocalizations are not indicators of negative or positive affect. Therefore, the function of ultrasonic vocalizations in adult mice is likely only to facilitate or inhibit social interactions. Understanding the types and functions of ultrasonic vocalizations emitted by laboratory rodents may enable researchers and animal care personnel to use vocalizations as an indicator of an animal's behavior and affect.

Many vertebrates use species-specific vocalizations to communicate information regarding such things as identity (individual or group), their group status or mood (dominance, submissive, fear, or aggression), their next likely behavior (approach, flee, play, groom, or mount), and environmental conditions (presence of predators or location of food) and to facilitate mother–offspring interactions. The transmission of different types of information through vocalizations depends on specific frequency and temporal properties of the acoustic signals (so-called 'information-bearing parameters').[19,38] Understanding the vocalizations that an animal emits under particular physical, environmental, or social conditions can inform us about these conditions. Moreover, the vocalizations can provide an index of the affective state of the animal.[29] This information is important for understanding the behaviors of animals both in the wild and under laboratory conditions.

The acoustic signals used by animals to convey information vary from simple tonal signals to complex signals with multiple frequency components that change over time. Each species emits vocalizations with energy in frequency ranges compatible with their hearing abilities.[1,7,23] Most small rodent species, including laboratory rats and mice, emit ultrasonic (that is, above 20 kHz) vocalizations. These vocalizations are inaudible to humans without the use of specialized equipment. As a result, many researchers who work with laboratory rodents are unaware when their animals are vocalizing and that these ultrasonic vocalizations are context- and state-dependent. The purpose of this review is to highlight the types and purported functions of ultrasonic vocalizations emitted by laboratory rodents so that researchers and animal care personnel better understand how they might use vocalizations as an indicator of an animal's behaviors and affect.

Diverse rodent species use acoustic signals in social situations,[36] but most research on ultrasonic vocalizations in laboratory rodents has focused on strains of rats and mice. This review first discusses the acoustic parameters and functions of ultrasonic vocalizations emitted by laboratory rats. It then compares and contrasts ultrasonic vocalizations of mice to those in the rat. Ultrasonic vocalizations emitted by adult rats and mice differ from those emitted by pups and therefore are described in different sections of this review.

Received: 16 Aug 2006. Revision requested: 11 Sept 2006. Accepted: 8 Nov 2006.
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Emission of Ultrasonic Vocalizations by Adult Rodents

Types and functions of rat ultrasonic vocalizations. On the basis of frequency and temporal parameters, rats emit 3 distinctly different ultrasonic vocalizations.[9,29] The emission of these ultrasonic vocalizations depends on the animal's age, environmental condition, and affective state. Adolescent and adult rats emit 2 primary types of ultrasonic vocalizations that are distinguished on the basis of the frequency with peak energy. The vocalizations typically referred to as '22-kHz vocalizations' have frequencies between 18 to 32 kHz and vary in frequency by only 1 to 6 kHz in a particular animal.[36] Thus, they are minimally modulated in frequency. The calls are between 300 to 4000 ms and are emitted at a sound pressure level of 65 to 85 dB.[36,41,47] The so-called '50-kHz vocalizations' have a frequency at peak energy of 32 to 96 kHz (Figure 1). These calls also have narrow bandwidths (1 to 7 kHz) but much shorter durations (30 to 50 ms) than 22-kHz vocalizations.[26,36] Sometimes 50-kHz vocalizations are referred to as 'chirps' because of their brief duration.[33] In addition, 22-kHz and 50-kHz vocalizations are emitted in different social situations, and the occurrence of each type depends on the physical and psychological demands of the environmental situation.[29] Moreover, recent evidence suggests that these vocalizations represent different affective states of the animal.[29]

Juvenile and adult rats emit 22-kHz vocalizations in a number of aversive behavioral situations including exposure to predators,[4,12] exposure to inescapable pain such as foot shocks,[8] in response to startling noises,[27] and during male–male aggression and social defeat.[42] Moreover, 22-kHz vocalizations are emitted during distressing events and in response to stimuli associated with distressing experiences.[2,41] The behaviors the rats exhibit in these types of situations and during emission of the 22-kHz call include tense, motionless couching (also referred to as 'freez-

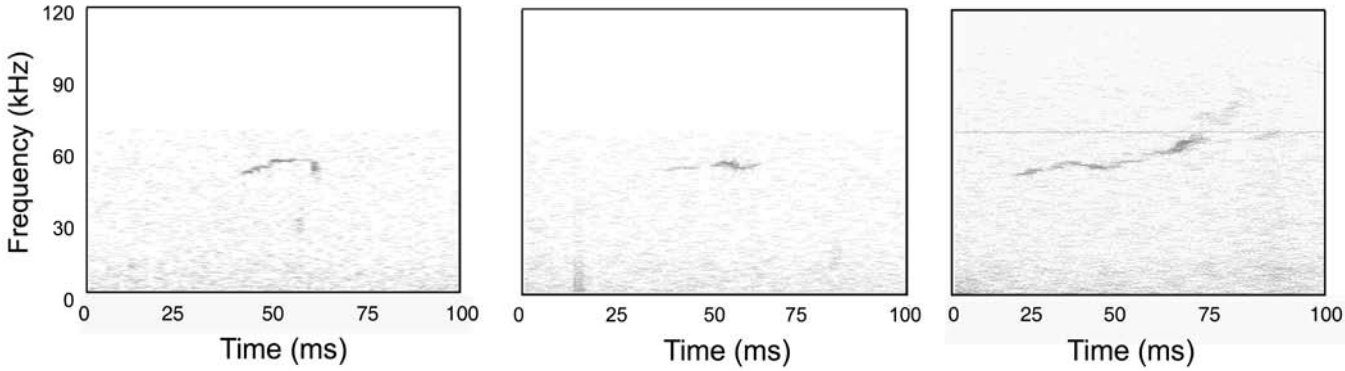

Figure 1. Sonograms of ultrasonic vocalizations produced by Sprague-Dawley rats. These 50-kHz vocalizations show slight variations in frequency modulation. Recordings were obtained from animals in their homecages placed in a sound-attenuating chamber. A ¼-in. condenser microphone was placed 10 cm above the cage, and the signals were digitized using a 16-bit analog-to-digital converter with a sampling rate of 333,333 samples/s. Sonograms were constructed after Fast Fourier transform by use of custom-designed software.

ing') and pronounced breathing.[9] Various studies suggest that 22-kHz vocalizations are emitted predominantly in anticipation of inescapable aversive stimuli[4,40] and that they reflect a negative affective state of the animal.[29]

Along with indicating a negative affective state of the animal, 22-kHz calls can communicate specific information to conspecifics. For instance, subordinate males emit 22-kHz vocalizations and display submissive postures during aggressive interactions with dominant males.[36] These calls may function to inhibit additional aggressive attacks. In addition, rats living in artificial burrows with conspecifics emit these vocalizations in the presence of a predator,[4] and playbacks of 22-kHz vocalizations evoke freezing and avoidance behaviors.[10] Therefore, 22-kHz vocalizations may function secondarily as alarm calls to warn conspecifics of predators or other potential threats.[4,12] The survival of the group may benefit from a communication system in which the presence of a potential threat is signaled to other group members. Laboratory rats also emit 22-kHz calls when handled by unfamiliar humans.[12]

The exception of the 22-kHz call reflecting negative affect is when male rats emit a vocalization with energy around 22 kHz after copulation, a behavior not normally considered aversive.[3] Postcopulatory vocalizations tend to have more frequency modulations than those emitted during threatening situations,[40] and these frequency modulations may differentiate the meanings of the calls. Additional studies are required to understand how 22-kHz vocalizations convey different information when emitted under different situations.

Rats emit 50-kHz vocalizations under nonaversive conditions. Rats emit short, chirping 50-kHz vocalization during sexual behaviors,[3,36] male agonistic behaviors during fighting,[31,36,39] juvenile play,[28,32] and manual tactile stimulation ('tickling') by experimenters.[33] During the emission of 50-kHz vocalizations, rats are engaged in locomotor activities such as approaching another rat, rearing, and exploring. These vocalizations have not been recorded during freezing behaviors as occurs with 22-kHz vocalizations. Consequently, emission of this vocalization by a rat may indicate a positive affect.[29] Because rats emit 50-kHz calls in situations that involve potential rewards (sex, play, winning a fight), these vocalizations may indicate positive affective states in the same manner as do the excitement and heightened arousal elicited by anticipation of rewards.[13]

Because the social interactions that invoke 50-kHz vocalizations are thought to be positively reinforcing, the 50-kHz vocalization has been suggested as an index of a positive affect.[29] For example, rough-and-tumble play by juvenile rats is viewed as rewarding and, during play, rats emit a large number of 50-kHz vocalizations,[28,32] in fact more than during any other normal social interaction that elicits these calls. Interestingly, the most frequent emission of 50-kHz vocalizations occurs when juvenile rats are tickled (ruffling the fur of the rat) by a human experimenter who is familiar to the rat.[14,28] This tickling appears to produce a positive affective response and to be rewarding to the rats.[33] In contrast, contact of adult rats by unfamiliar humans evokes 22-kHz vocalizations rather than 50-kHz calls.[12]

Summarizing the stimuli that elicit ultrasonic vocalizations in rats provides a general overview of the evidence that emission of ultrasonic vocalizations is an affective expression in this species. Minimally frequency-modulated 22-kHz vocalizations occur in situations that are threatening, whereas 50-kHz vocalizations occur in contexts involving potential rewards. Therefore, 22-kHz vocalizations may reflect negative affective states similar to the anxiety caused by the anticipation of noxious stimuli or punishment, whereas and 50-kHz vocalizations may indicate positive affective states similar to the excitement caused by the anticipation of pleasant stimuli or reward. Both types of ultrasonic vocalizations likely convey communication information to conspecifics as well as connoting the affective state of the animal emitting the vocalization.

Because 22- and 50-kHz vocalizations both are emitted in a variety of situations, the calls are likely to have acoustic features that are specific for a given behavioral situation and enable communication of different information to conspecifics. For example, frequency modulation in 22-kHz calls varies depending on whether the call is emitted after mating or aversive stimulation.[40] In addition, the intensity of the affective state of the animal correlates with the duration and loudness of the call.[47] Sophisticated acoustic recording and sound analysis equipment allow the analysis of more detailed frequency and time structures in ultrasonic vocalizations for determination of differences between vocalizations emitted in different situations or by different animals.

Types and functions of mouse ultrasonic vocalizations. In contrast to rats, adult mice do not produce ultrasonic vocalizations during aversive situations. Ultrasonic vocalizations have not been observed during handling, restraint, in response to noxious stimulation such as electric shock or tail pinch, or during aggressive encounters. Mice emit ultrasonic vocalizations exclusively during nonaggressive interactions and, in particular, during mating behaviors.[20,36] Also in contrast to those in rats, ultrasonic vocalizations in mice have not been shown to indicate negative or positive affect. Therefore, the function of ultrasonic vocalizations in adult mice is likely only to facilitate or inhibit social interactions.

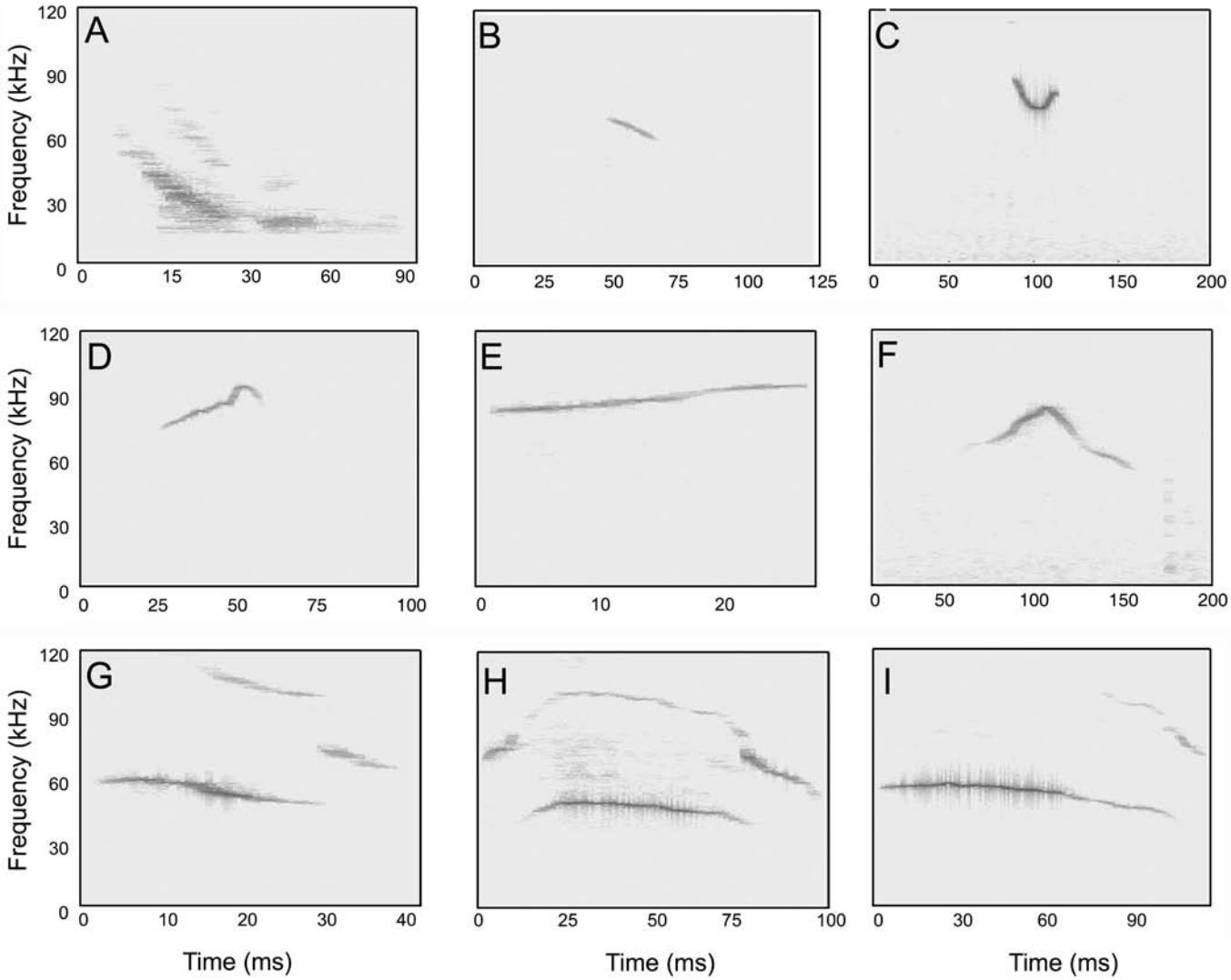

Figure 2. Sonograms of ultrasonic vocalizations produced by male adult CBA/CaJ mice. Each vocalization is considered a different syllable type based on the acoustic parameters of starting frequency, ending frequency, frequency at peak energy, bandwidth of frequency modulation and duration. (A, B) Frequency-modulated downsweeps. (C) U-shaped frequency modulation. (D) Frequency-modulated upsweep. (E) Constant frequency. (F) Hump frequency modulation. (G–I) Frequency jumps. Recordings were obtained as described in Figure 1.

Both male and female mice of strains with normal hearing emit ultrasonic vocalizations, although the majority of research has focused on the vocalizations emitted by male mice. When male mice encounter female mice or their urinary pheromones, the male mice produce ultrasonic vocalizations with frequencies ranging between 30 to 110 kHz.[20,24,48] In contrast to those in rats, ultrasonic vocalizations in mice have been described quantitatively and include several syllable types.[24] In these studies, a syllable is defined as a unit of sound separated by a silent period before another sound. Figure 2 shows sonograms of a number of different syllable types recorded from normal-hearing (CBA/CaJ strain) male mice, and series of these syllables emitted together in phrases or song are shown in Figure 3. In Figure 2, syllables were defined based on the following acoustic parameters: starting frequency, ending frequency, frequency with peak energy, frequency modulation, and duration. Male mice emit a variety of simple syllables that consist of single harmonic whistles. These syllables include frequency-modulated downsweeps (Figure 2 A, B), u-shaped modulated frequencies (Figure 2 C), frequency-modulated upsweeps (Figure 2 D), constant frequencies (Figure 2 E), and hump-shaped modulated frequencies (Figure 2 F). Male mice also emit more complex syllables that have multiple components that involve either harmonics or frequency jumps (Figure 2 G–I). The frequency jumps can either be from a low frequency to a high frequency or from a high frequency to a low frequency.[24] Although the functional significance of the different syllables is unknown, these syllables are emitted in nonrandom, repeated temporal sequences and thus have characteristics of song.[24] Figure 3 shows sonograms of complex sequences of syllable types that could be classified as male songs. All of the serial ultrasonic vocalizations in the panels of Figure 3 were produced by male mice, except for the sequence of frequency-modulated upsweeps shown in Figure 3 E, which were emitted by a female mouse when her pups were removed from the nest. Female mice produce ultrasonic vocalizations during female–female interactions and when they are alone, particularly when they have pups and the litter is removed.[15]

Therefore, both male and female laboratory mice produce ultrasonic vocalizations in specific situations. Male mice are stimulated to emit ultrasonic vocalizations in the presence of female mice (or their pheromones), whereas female mice produce these calls when alone, searching for pups, or in the presence of other females. Thus the laboratory housing environment can influence the production of ultrasonic vocalizations in mice. Standard practice for mice involves housing same-sex animals in groups of 2 to 3 in 'shoebox' (17 × 28 × 12 cm) cages (Figure

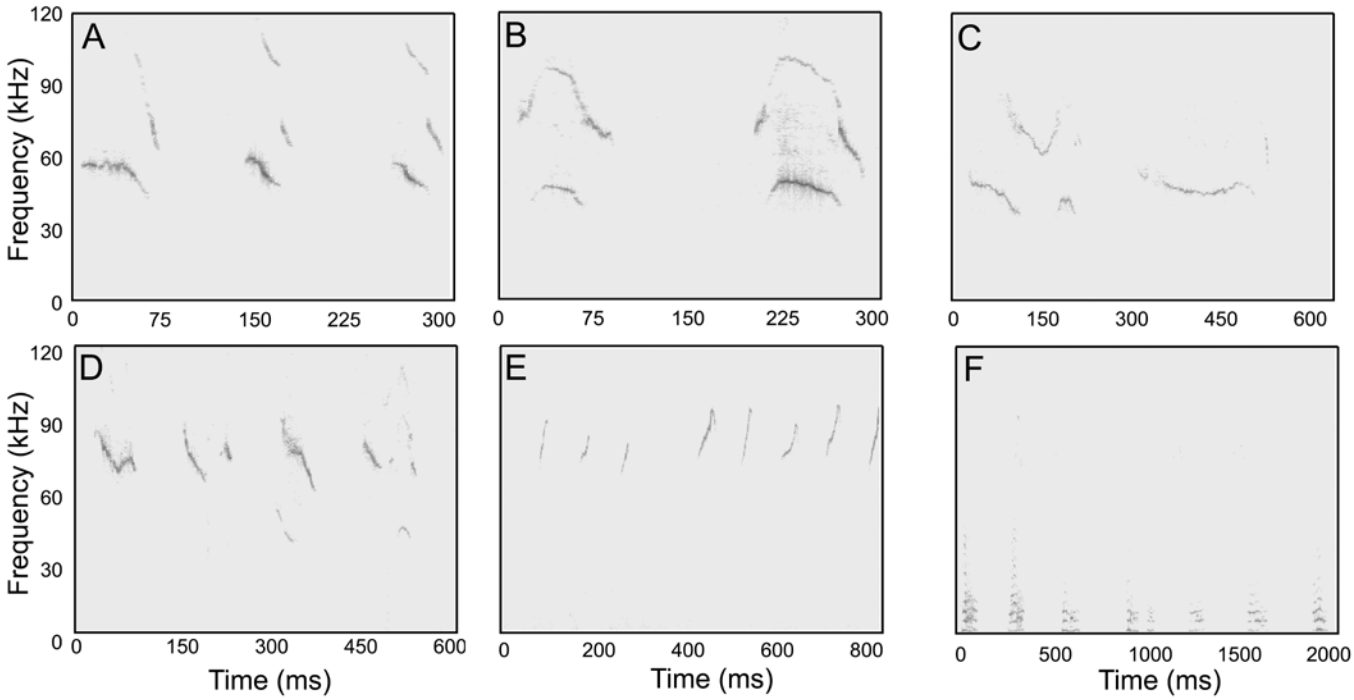

Figure 3. Sonograms illustrating series of vocalizations recorded from adult CBA/CaJ mice. (A–D) Recordings from male mice exposed to female pheromones. (E) Recording from a female mouse after her pups were removed from the nest. (F) Series of low-frequency vocalizations that are occasionally emitted by mice. Recordings were made as described for Figure 1.

4 A). In this housing environment, normal-hearing male mice do not produce ultrasonic vocalizations, and female mice produce simple frequency modulated-calls (upsweeps and u-shaped).[35] Therefore the diversity of ultrasonic vocalizations produced in these environments is low. In contrast, if mice are housed mixed-gender in large, environmentally enriched cages (60 × 60 × 30 cm; Figure 4 B), they produce a diverse repertoire of call types with much more variability in acoustic features such as frequency modulation.[35] In these experiments, recording of the vocalizations of mice in different housing environments occurred at different times during the day and over a period of 10 d to ensure that their vocalization behaviors were sampled sufficiently.

These findings suggest that mice housed in traditional same-sex laboratory cages produce less diverse and complex vocalizations than do mice that live in socially and environmentally enriched cages. The enriched housing environments I use in my lab (Figure 4 B) allow the mice to live in more natural conditions, and this arrangement stimulates the production of more naturalistic ultrasonic vocalizations and behaviors. Moreover, these animals are exposed to a wide range of diverse vocalizations during development, and this exposure may be critical to their developing neural pathways selective to these vocalizations. If these animals continually live in an acoustically impoverished environment, the way by which their auditory neurons encode subsequent vocalization stimuli may be altered, and the ways in which the animals perceive future vocalizations may change, as may their resulting behaviors. Although physiologic evidence is not yet available to support this hypothesis, animals acoustically deprived through cochlear damage, spiral ganglion lesions, or deafness show changes in their neural responses that suggest encoding of complex sounds (such as vocalizations) is impaired.[34,37,44,45]

A recent suggestion is that inbred laboratory mice may have less variation in ultrasonic vocalizations compared with wild mice.[24] Despite extensive research on ultrasonic vocalizations emitted by laboratory rodents, only 2 studies—1 in ground squirrels and 1 in mice—have documented ultrasonic vocalizations in wild rodents.[25,46] Examining the production and function of ultrasonic vocalizations in wild rodents is necessary to understand the adaptive significance of these calls in a natural context and to understand how laboratory conditions affect the diversity, complexity, and function of these vocalizations. In the only study of ultrasonic vocalizations in wild mice to date, 2 different *Peromyscus* species emitted ultrasonic calls with sizeable variation in the acoustic parameters, suggesting that the ultrasonic vocalizations emitted by wild mice are indeed more diverse and complex than in laboratory mouse strains.[25]

The function of the ultrasonic vocalizations emitted by laboratory mice during mating behaviors and the effect of these calls on other individuals is not clear. The ultrasonic vocalizations emitted by an approaching male mouse may indicate to the female mouse that the male mouse is sexually motivated rather than aggressively motivated.[36] Because mice in the wild are territorial, the ultrasonic vocalizations may communicate the intent to mate and consequently inhibit an aggressive response from the female mouse so that mating can occur successfully.[43] Male song also may be an indicator of the male mouse's fitness, and the female mouse may use this index to determine whether she will allow mating to occur or not. Further studies are necessary to establish the function of male song, both in the wild and in the laboratory.

Emission of ultrasonic vocalizations by rodent pups. Pups of a wide variety of myomorph rodents emit ultrasonic vocalizations when they are separated from their mothers. These vocalizations have been recorded from all the species that have been studied in the families Muridae and Cricetidae, indicating their ubiquitous nature among rodents. Because the majority of research has focused on laboratory rats and mice, only the ultrasonic vocalizations of these rodent pups will be discussed.

Types of ultrasonic vocalizations in rat pups. When rat pups between 4 to 16 d of age are separated from their mothers, they emit a so-called 40-kHz vocalization.[36] These isolation vocalizations are referred to as 40-kHz calls because the frequency with peak energy is approximately 40 kHz although the calls

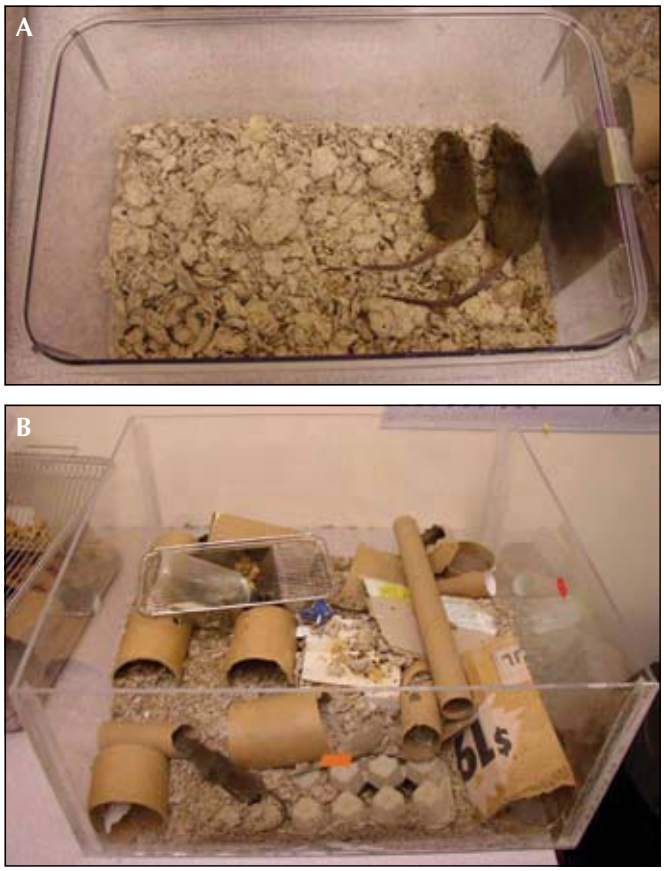

Figure 4. Housing environments for mice. (A) Standard laboratory shoebox cage housing 2 same-sex individuals. The size of this cage was 17 × 28 × 12 cm. (B) Socially and environmentally enriched cage housing multiple male and female mice. The size of this cage was 60 × 60 × 30 cm. This cage included burrows, alternate food sources, tunnels, and multiple levels. Vocalizations were recorded from animals living in both of these types of cages by placing a ¼-in. microphone 10 cm from the top of the cage. Recordings were made in a sound-attenuating chamber at different times during the day for 10 d.

tend to be frequency-modulated sweeps between 30 to 65 kHz. Moreover, the frequency sweeps tend to be U- or hump-shaped patterns.[11,22] Rat pups emit 4 different types of ultrasonic vocalizations, 3 of which have 2 or 3 components that make the syllable more complex than a simple whistle.[22]

Types of ultrasonic vocalizations in mouse pups. Mouse pups isolated from their mothers or exposed to cold emit ultrasonic vocalizations with frequencies above 35 kHz. These vocalizations fall into 2 categories, based on frequency. The energy of 1 group of ultrasonic vocalizations is around 70 kHz, and the second group of ultrasonic vocalizations shows much higher frequency ranges (around 100 kHz).[30] Figure 5 illustrates some examples of ultrasonic vocalizations in mouse pups. Most vocalizations are frequency-modulated sweeps. The ultrasonic vocalizations are most often emitted in series, with an intercall interval of about 200 ms.[30]

Although ultrasonic vocalizations of pups vary (Figure 5), their features are consistent enough so that they are not confused with calls produced by adults. Adult ultrasonic vocalizations can be distinguished from pup ultrasonic vocalizations by duration (adult ultrasonic vocalizations tend to be shorter than 25 ms), frequency range (pup calls tend to be lower in frequency than those from adults), and repetition rate (rates in adults are higher than those in pups).[30] Therefore, pup and adult ultrasonic vocalizations likely belong to different perceptual categories and consequently have different functional effects on conspecifics.

Function of ultrasonic vocalizations in mouse pups. The function of pup ultrasonic vocalizations has received considerable debate.[5,6,15,29] The traditional interpretation is that ultrasonic vocalizations are distress calls that pups emit when isolated from the nest. Because pups lack fur and subcutaneous fat, they cool rapidly and thus are in danger of death if they are not retrieved and returned to the nest quickly. Moreover, cold exposure is a potent stimulus for eliciting ultrasonic vocalizations by pups. Mother mice and rats, upon hearing the ultrasonic vocalizations from pups, rapidly investigate the sound and retrieve the pups to the nest.[16-18,21] Therefore, the pups' ultrasonic vocalizations are often thought of as 'cries for help' and have been viewed as a sign that the pup is under emotional distress. This idea facilitates the notion that ultrasonic vocalizations are communication signals produced by distressed pups that are motivated to gain the attention of the mother. However, this traditional view has been challenged recently.

Arguments by Blumberg and Sokoloff[5] support the notion that the ultrasonic vocalizations of pups are an acoustic by-product of laryngeal braking, which is caused by an abdominal compression reaction that increases blood flow return to the heart. An abdominal compression reaction occurs in response to a cold stimulus or possibly when the pups fall over when trying to right themselves or when handled roughly by human experimenters. Therefore, ultrasonic vocalizations are produced as a consequence of movement related to external stimuli and are unrelated to any motivation to communicate acoustically with the mother.[5] However, regardless of whether the pup is trying to communicate by using ultrasonic vocalizations or whether these vocalizations are merely incidental by-products, the effect of the emission of ultrasonic vocalizations by the pup is retrieval by the mother. Therefore, these vocalizations serve a communication function.

When pups emit series of ultrasonic vocalizations, mothers reliably approach the sounds. The pup ultrasonic vocalizations provide a potent stimulus for the mother's inspection as visual and olfactory cues to the pup's presence are not necessary; playbacks of a vocalizing pup through speakers elicits the same approach behavior as do calls from a live pup.[15,21] However, mothers tend to approach a variety of ultrasonic signals even if they contain acoustic features never found in pup ultrasonic vocalizations. These findings suggest that any type of ultrasonic signal is attractive to mother rats and mice, although they markedly prefer ultrasonic vocalizations with acoustic features congruent with real pup calls.[15,16] Moreover, the emotional or motivational state of the mother affects the response to ultrasonic vocalizations. Mothers that are involved in maternal behaviors at the nest (that is, they are lactating and actively caring for pups) respond to natural pup ultrasonic vocalizations faster and more often than they respond to non-pup ultrasonic vocalizations. The mother animals also respond faster than do nonlactating mothers, suggesting that hormonal changes may increase the arousal or motivational state of the animal to respond to pup vocalizations.[18] Regardless of motivational state of the mother, pup ultrasonic vocalizations function to invoke retrieval behavior in mothers.[15]

Implications for Laboratory Facilities and Personnel

An understanding of ultrasonic vocalizations in laboratory rodents can facilitate best care practices for housing laboratory rodents in animal facilities. For example, when rats are

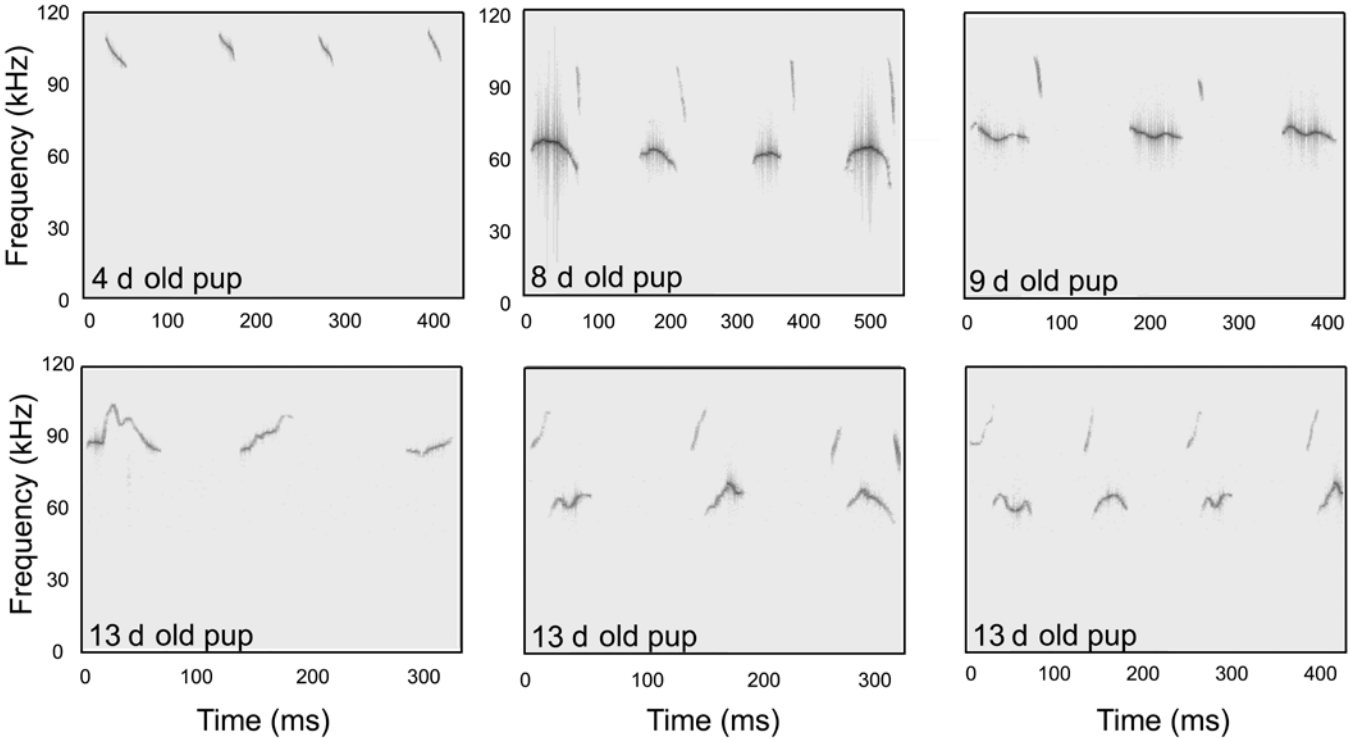

Figure 5. Sonograms of calls produced by CBA/CaJ mouse pups isolated from the nest. Recordings were obtained as described for Figure 1.

in distress or pain, they emit 22-kHz ultrasonic vocalizations. Because these vocalizations cannot be heard by humans, they go unnoticed and do not elicit attention or treatment. Likewise, juvenile rats may be engaged in rough-and-tumble play, but because laboratory personnel can't hear the associated calls, they may mistake this play for aggressive interactions. Recording of 50-kHz vocalizations would indicate that the rats are engaged in normal juvenile play.[28] Monitoring of the vocalizations of rats and mice with an ultrasonic microphone would enable monitoring of the animals' affective states.[29]

An issue that is often neglected by auditory research is the acoustic environment in which laboratory animals live. Maintaining mice in same-sex cages limits the production and diversity of ultrasonic vocalizations. Housing animals in large, socially and environmentally enriched cages allows rats and mice to engage in more natural behaviors, including producing a diverse repertoire of ultrasonic vocalizations. Because this environment may be important for shaping neural responses in the auditory system to these species-specific vocalizations, researchers should consider alternative housing arrangements for mice and rats used in studying the neural basis of sound processing.

Acknowledgments

I thank Deborah Palmer and Richard Felix II for help in recording the vocalizations of the mice, Peter Ritson (Washington State University) for critically reviewing the paper, and three anonymous reviewers for comments on a previous version. Partial support for this work was provided by grant number 04733 from the National Institute on Deafness and other Communication Disorders (National Institutes of Health, Bethesda, MD).

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