Discrimination of frequency modulated sweeps by mice

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Mice often produce ultrasonic vocalizations (USVs) that sweep upwards in frequency from around 60 to around 80 kHz and downwards in frequency from 80 to 60 kHz. Whether or not these USVs are used for communication purposes is still unknown. Here, mice were trained and tested using operant conditioning procedures and positive reinforcement to discriminate between synthetic upsweeps and downsweeps. The stimuli varied in bandwidth, duration, and direction of sweep. The mice performed significantly worse when discriminating between background and test stimuli when the stimuli all occupied the same bandwidths. Further, the mice's discrimination performance became much worse for stimuli that had durations similar to those natural vocalizations of the mice. Sweeps composed of different frequency ranges and longer durations had improved discrimination. These results collected using artificial stimuli created to mimic natural USVs indicate that the bandwidth of the vocalizations may be much more important for communication than the frequency contours of the vocalizations. © 2016 Acoustical Society of America.

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I. INTRODUCTION

A model commonly used for understanding auditory perception and communication in humans is the laboratory mouse (*Mus musculus*). Mice are used as a model because their auditory systems are similar to those of humans (Henry and McGinn, 1992). Despite the widespread use of laboratory mice as models for communication, however, there is still not a complete understanding of how mice use their vocalizations for communication (e.g., Portfors, 2007). It is, therefore, critical to determine whether or not mice use auditory signals as a form of communication, and if so, how exactly these signals are used.

Mice emit ultrasonic vocalizations (USVs) in a multitude of both inter- and intrasexual situations. Male–male, male–female, and female–female pairings, as well as pups removed from their mother (Sewell, 1972; Hammerschmidt *et al.*, 2009; Portfors, 2007; Scattoni *et al.*, 2011), all elicit vocalizations from mice. Despite the fact that USVs are most often associated with social and courtship behavior, it has yet to be shown that they are actually required for these interactions.

Mice produce USVs that vary in duration, intensity, and frequency. These vocalizations have been parsed into various categories, typically based on the frequency parameters of the call. There is, however, a wide range in how many categories scientists think the mice produce (Portfors, 2007; Grimsley *et al.*, 2011; Grimsley *et al.*, 2012; Kikusui *et al.*, 2011; Mahrt *et al.*, 2013), and almost no work has attempted to determine whether the mice actually perceive distinct categories (but see Neilans *et al.*, 2014). Certain USVs are used more often than others; in adults, frequency modulated (FM)

upsweep USVs (upsweeps) appear to be used the most often of all the USVs in their vocal repertoire (Grimsley *et al.*, 2011; Hanson and Hurley, 2012). These upsweep calls are typically around 20 ms in duration, sweep from 60 to 80 kHz [Fig. 1(A)], and are within their auditory range for detection (Radziwon *et al.*, 2009) and discrimination (Radziwon and Dent, 2014).

A clear indication that USVs carry meaning in a context-specific way as they have often been described would be that particular calls are emitted in specific situations. Historically, it was believed that mouse USVs were not context-specific and the various call types the mice produce were not correlated with any particular behavior (e.g., Hanson and Hurley, 2012). Recently, however, it has been shown that male mice do produce specific call types throughout the duration of the courtship sequence (Matsumoto and Okanoya, 2016) and during investigatory behavior (Mun *et al.*, 2015). Context-specific vocalizations are believed to communicate important information to conspecifics, as seen in other animals that have been found to have calls that correspond to behavior. Vervet monkeys (*Chlorocebus pygerythrus*), for example, have been shown to have particular calls associated with avoidance behavior for specific predators (Seyfarth *et al.*, 1980). Additionally, the Australian frog (*Uperoleia rugosa*) has three specific calls that it uses in distinct situations. Their advertisement, encounter, and courtship calls differ based on several factors, including duration and pulse rate (Robertson, 1986). Furthermore, emitted vocalizations are found to be related to emotional state in big brown bats (*Eptesicus fuscus*), where the level of aggression of the bats will influence what vocalizations they produce (Gadziola *et al.*, 2012). Preliminary work does suggest that mice can discriminate between natural vocalizations differing significantly in spectrotemporal features (Neilans *et al.*, 2014), indicating that USVs could be important for

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A. Sonogram of natural upsweeps

B. Schematic of apparatus

C. Upsweeps varying in bandwidth

D. Upsweeps varying in duration

FIG. 1. (A) Upsweep bout recorded from an adult male. (B) Schematic of the operant apparatus depicting the locations of the nose-poke holes, loud-speaker, and dipper. (C) Example of the bandwidth manipulation for upsweep test stimuli where frequency ranged within each condition from 35–80 kHz to 60–80 kHz. (D) Example of the duration manipulation for upsweep stimuli where duration changed between conditions, having lengths of 20, 50, 100, 150, and 200 ms, respectively.

communication. Currently, the connection between USVs and behavior is still in its infancy and more work must be done to fully understand their relationship.

A characteristic of the vocalizations of many species, both mammalian and avian, is frequency modulation. Frequency modulation can vary over several parameters, including direction, rate, bandwidth, and duration. It has been shown in Mongolian gerbils (*Meriones unguiculatus*, Wetzel *et al.*, 1996), rats (*Rattus norvegicus*, Mercado *et al.*, 2005; Gaese *et al.*, 2006), and humans (*Homo sapiens*, Orduña *et al.*, 2012), to name just a few, that discrimination of frequency modulation direction is possible. Most notably, echolocating bats locate prey by emitting and discriminating between minute

changes in frequency modulated vocalizations that enable them to capture insects (Schnitzler *et al.*, 1983). Given that mice produce ultrasonic upsweeps so often, we hypothesized they would also have the ability to discriminate upsweeps from a lesser used vocalization, downsweeps.

In the present study, we investigated how well mice are able to discriminate between two common USVs that adults produce, upsweeps and downsweeps. The upsweep and downsweep stimuli used in the present experiment were synthetically produced in order to eliminate any variables aside from frequency modulation that could aid in discrimination. Mice were trained to discriminate upsweep test stimuli from a repeating downsweep background, and vice versa. This was done using operant conditioning techniques similar to those used by Neilans *et al.* (2014) and Holfoth *et al.* (2014). Given that USVs are inferred to have communicative function and that sweeps are a large part of the vocal repertoire of these animals, we expected that the sweeps would be easily discriminated from one another, even at very short durations similar to their natural vocalization durations.

II. METHODS

A. Subjects

Eight adult CBA/CaJ mice (*Mus musculus*), four male and four female, were used as subjects in this experiment. Mice began training at approximately 2 mo of age and testing lasted approximately 6 mo. The mice were housed individually on a reversed day/night cycle (lights off at 6 a.m. and on at 6 p.m.). The mice were tested during the dark portion of their cycle. All of the mice were water restricted and maintained at approximately 85% of their free-drinking weight during the course of the experiment. Food was available *ad libitum*, except during testing sessions. The mice were bred at the University at Buffalo, State University of New York (SUNY) and all procedures were approved by University at Buffalo, SUNY's Institutional Animal Care and Use Committee.

B. Apparatus

The mice were tested in a wire cage (23 cm × 39 cm × 15.5 cm) placed in a sound attenuated chamber (53.3 cm × 54.5 cm × 57 cm) lined with 4-cm thick Sonex sound attenuating foam (Illbruck, Inc., Minneapolis, MN). The chamber contained an overhead web camera (Logitech QuickCam Pro, model 4000) and a small 25-W white light to monitor animals during test sessions. Sounds were played from an electrostatic speaker [Tucker-Davis Technologies (TDT), Gainesville, FL, Model ES1]. The cage also contained two nose-poke holes surrounded by infrared sensors (Med Associates Model ENV-254), and a response dipper [Med Associates Model ENV-302 M-UP, see Fig. 1(B)].

The experiments were controlled by Dell Optiplex 580 computers operating TDT modules and software. Stimuli were sent through an RP2 processor, an SA1 power amplifier, a PA5 programmable attenuator, and finally to the speaker. Inputs to and outputs from the testing cages were controlled via RP2 and RX6 processors. Power supplies

were used to drive the dipper (Elenco Precision, Wheeling, IL, Model XP-603) and infrared sensors (Elenco Precision, Model XP-605). Custom MATLAB and TDT RPDs software programs were used to control the hardware.

C. Test Stimuli

All stimuli were generated using Adobe Audition. The background stimulus was always either an artificially generated upswing or downswing with a frequency range of 60–80 kHz. Within a session, the mice were required to discriminate this background stimulus from one of seven test stimuli that were presented when an animal initiated a trial. The test stimuli were artificially generated upswings or downswings, always in the opposite direction of the background stimulus. The frequencies of the test stimuli occupied increasingly larger bandwidths. The bandwidths tested included 60–80 kHz, 55–80 kHz, 50–80 kHz, 45–80 kHz, 40–80 kHz, and 35–80 kHz [Fig. 1(C)]. These different bandwidths were included to ensure the mice were able to discriminate at least a portion of the test stimuli, guaranteeing reinforcement for those targets. Additionally, frequency-shifted test stimuli, which had a frequency range of 40–60 kHz, were included on some of the sessions.

Within a testing session, the test and background stimuli were always the same duration. Five durations were tested in all: 20, 50, 100, 150, and 200 ms [Fig. 1(D)]. Animals were trained and tested on all durations in a random order, and a different random order was used for each subject.

Stimuli were presented at 65 dB sound pressure level (A scale), measured at the position where the mouse's head would normally be during testing. Stimuli were roved by ± 3 dB from presentation to presentation. Data collection began when the mice were consistently able to correctly discriminate over 80% of the targets and had a false alarm rate of lower than 20%. Sound pressure levels were calculated using an ultrasound recording system (Avisoft Model USG 116-200) and Raven Pro (v 1.3, Cornell University).

D. Procedure

The mice were trained using a go/no-go operant conditioning procedure on a discrimination task. The mice were tested in two 30-min sessions or one 60-min session, 5 d per week. The mice typically ran between 50 and 200 trials per session. Each mouse was tested on every duration for either upswing or downswing targets.

During testing, the mouse began a trial by nose poking through an observation nose-poke hole, which initiated a variable waiting interval ranging from 1 to 4 s. During this time, a repeating background of either the upswing or downswing was presented (background stimulus). The interstimulus interval was twice the length of the stimuli. After the waiting interval, a sweep in the opposite direction as the background (test stimulus) was presented, alternating with the background two times. If the mouse discriminated the change between the background and the test stimuli, it was required to nose poke through the report nose-poke hole within 2 s of the onset of the test stimulus. In this trial type, a "hit" was recorded if the mouse correctly responded within

the response window and the animal received 0.01 ml of Ensure as reinforcement. A "miss" was recorded if the mouse failed to nose poke through the report nose-poke hole during the waiting interval, the trial was aborted, and the mouse was able to move on to the next trial immediately.

Experimental sessions consisted of multiple randomized blocks of 10 trials each, and mice completed between one and 20 blocks per session. Within each block of 10 trials, seven were "go" trials, and three were sham "no-go" catch trials. Each block was randomly generated so that no more than two sham trials could be presented in a row. In the sham trials, the repeating background continued to be presented during the response phase. These trials were required to measure the false alarm rate and calculate the animal's response bias. If the subject nose poked in the report hole during a catch trial, a "false alarm" was recorded and the mouse was punished with a 3-s timeout interval. During the timeout period, animals were not able to initiate another trial until the period ended. However, if the subject continued to nose poke into the observation hole, a "correct rejection" was recorded, and the next trial would begin immediately. In either case, no reinforcement was given. Chance performance was represented by the animal's false alarm rate. Sessions were excluded from analysis if the percentage of false alarms exceeded 20%. Using this criterion ensures the mice were under stimulus control. Approximately 15% of sessions were discarded due to high false alarm rates. These sessions were randomly interspersed throughout testing, with no discernible pattern of their occurrence.

In the "go" condition, the seven target trial types remained the same for each block in an experimental session (although trials were presented in a random order, and a different random order of 10 trials was generated for each block). Two or three of the target trials were considered to be the most difficult and occupied the same frequency range as the background stimulus (60 to 80 kHz), the remaining trials were easier in order to keep motivation high and to ensure that reinforcement rates remained similar from session to session.

E. Statistical Analyses

At least 200 trials were obtained for each condition from each mouse. Upswing and downswing background conditions were found to be statistically similar ($p > 0.05$) for all durations by two-way analysis of variance (ANOVA) tests (duration $\times$ bandwidth) so results were combined for all further figures and analyses. For the conditions without a frequency shifted target, a two-way repeated-measures ANOVA was used to analyze discrimination performance (duration $\times$ bandwidth). A Bonferroni *post hoc* analysis was conducted to examine the significant interaction. Bonferroni was selected due to the large number of observations and conditions being compared in this analysis.

For the conditions that included a frequency shifted target, another two-way repeated-measures ANOVA was conducted, also using duration and bandwidth as the within-subjects factors. A Holm-Sidak *post hoc* analysis was conducted to interpret the significant interaction. In this case,

Holm-Sidak was selected *a priori* due to its increased power compared to the Bonferroni test because only seven subjects completed this condition.

III. RESULTS

The mice varied in their ability to discriminate upsweeps from downsweeps across conditions, with percent corrects ranging from as low as 5% to as high as 100%

across durations and bandwidths. Figure 2 shows individual functions for mice tested on upsweep backgrounds and downsweep targets (black symbols) and those tested on downsweep backgrounds and upsweep targets (white symbols) for durations ranging from 200 down to 20 ms.

In order to examine how the mice's discrimination performance was affected by both duration and bandwidth, a two way repeated measures ANOVA was conducted. Results revealed a significant main effect for the bandwidth

FIG. 2. Percent hits as a function of bandwidth for test stimuli of varying duration for individual subjects. The background stimuli always had a bandwidth of 20 kHz. Stimuli were (A) 200 ms, (B) 150 ms, (C) 100 ms, (D) 50 ms, and (E) 20 ms in duration. White symbols indicate an upsweep test stimulus; black symbols indicate a downsweep test stimulus.

manipulation, $F(5,35) = 69.6$, $p < 0.001$, but no significant main effect of duration, $F(4,28) = 1.9$, $p = 0.132$. There was, however, a significant interaction between bandwidth and duration, $F(20,140) = 14.8$, $p < 0.001$. Overall, the mice were better able to discriminate targets that occupied a wider frequency range than the background, and this differed across durations such that discrimination was better for long duration broad bandwidths than it was for short duration broad bandwidths.

Bonferroni *post hoc* analyses revealed that mice showed significantly worse discrimination performance for the 60–80 kHz target (the same bandwidth as the background) relative to almost all other targets covering wider frequency ranges ($p < 0.05$). Performance increased significantly for targets that had a wider bandwidth than the background, including for targets only 5 kHz wider than the background for all durations that were tested, except for the longest duration of 200 ms. Discrimination performance for the 20 kHz

bandwidth targets was higher at 200 and 150 ms than it was at shorter durations of 100, 50, and 20 ms, and higher at 100 ms than at both 50 and 20 ms. Taken together, these results show the mice found it more difficult to discriminate the 60–80 kHz target from background for shorter versus longer durations, but had no trouble discriminating between all other targets that were wider in bandwidth, regardless of duration.

Figure 3 shows results from seven subjects (one subject, Hagrid, did not complete this condition) on sessions where two of the targets were 20 kHz bandwidth, but one of those targets was shifted down to 40–60 kHz. Again, results varied across trial types and performance ranged from ~5% to almost 100%. We performed a two-way repeated measures ANOVA comparing bandwidth and duration. Percent corrects were significantly higher for shifted targets relative to unshifted targets, $F(1,6) = 174.9$, $p < 0.001$, significantly higher for longer durations than short durations, $F(2,12) = 19.3$, $p < 0.001$, and there was a significant interaction between frequency range and

FIG. 3. Percent hits for 20 kHz bandwidth stimuli when the test stimuli were the same frequencies as the background (60–80 kHz, white bars) or when the test stimuli were shifted in frequency (40–60 kHz, black bars) for individual subjects tested on three durations: (A) 200 ms, (B) 100 ms, and (C) 50 ms. All mice were tested on the same upswing/downswing testing configuration as they were in the other experiment.

duration, $F(2,12) = 21.0$, $p < 0.001$. Holm-Sidak *post hoc* analyses found no significant differences in duration within the frequency shifted results ($p > 0.05$), but all durations were significantly different from each other within the unshifted results ($p < 0.05$), similar to above. Within each duration, discrimination of the shifted stimuli was significantly better than discrimination of the unshifted stimuli ($p < 0.05$). Thus, it is not simply that the background and test stimuli both have a 20 kHz bandwidth that hindered discrimination, but the background and test stimuli occupying the same frequency range that caused the observed decrease in discrimination performance.

IV. DISCUSSION

The present experiment investigated if mice were able to discriminate between artificial upsweeps and downsweeps that varied in bandwidth across several duration conditions. We still do not know much about USV discrimination in CBA/CaJ mice, despite the belief that mice are using these USVs to communicate. One recent study on USV discrimination by mice found that the spectrotemporal characteristics of calls influenced their ability to discriminate, where calls that were spectrotemporally similar were more difficult to discriminate, and calls that have very different spectrotemporal parameters were easy to discriminate (Neilans *et al.*, 2014). The results of that experiment were based on only one call per defined “category,” therefore, it is necessary to include more than one call per category in the future. The current study found that both bandwidth and duration have effects on the discriminability of artificial sweeps by mice. When the stimuli were 200 ms in duration, much longer than the natural vocalization duration of ~ 20 ms, the mice easily discriminated between the background stimulus, sweeping in one direction and ranging from 60 to 80 kHz, and target stimuli sweeping in the opposite direction and spanning 35–80 kHz to 55–80 kHz. Even for long durations, there was significant degradation of discrimination ability when the target and background stimuli both occupied the 60–80 kHz range. The interaction between bandwidth and duration indicates that as duration became shorter, the mice’s performance worsened *only* for the test stimulus that was 60–80 kHz, regardless of the sweep direction. The performance for all other stimuli, including the target that was just 5 kHz wider in bandwidth (55–80 kHz), was not significantly affected by the duration manipulation, with performance remaining high for these test stimuli.

Although one interpretation of the results is that there could have been an auditory streaming influence due to changes in presentation rate across the conditions, we do not believe this would explain the effects found in these experiments. A streaming effect would cause the test stimuli of a larger bandwidth to “pop out” against the repeating background stimulus, while this would not occur for the 60–80 kHz test stimulus (having the same bandwidth as the background). The discrimination performance for all test stimuli with bandwidths larger than 20 kHz was not significantly better for the 20 ms condition than in conditions with longer durations. If there was a streaming effect, as the rate

of presentation increased, a trend would emerge that would show an increase in discrimination ability for the larger bandwidth targets. We did not see this trend (e.g., the 30 kHz bandwidth results do not differ for the 20 and 150 ms conditions).

The change in performance for only the 60–80 kHz stimuli indicated the mice were simply using the bandwidth of the test stimuli to help them discriminate between the sweep direction of the test stimulus and background stimuli, given the background always had a 20 kHz bandwidth. To rule out this possibility, we introduced a frequency-shifted test stimuli into some trials. This test stimulus also had a 20 kHz bandwidth, but occupied the 40–60 kHz frequency range. If the mice were only using the bandwidth as a cue for discrimination, their performance on the frequency shifted test stimulus would be similar to that of the 60–80 kHz test stimulus. In contrast with the original 20 kHz bandwidth test stimulus, however, discrimination of the frequency shifted test stimulus was unaffected by the duration manipulation, with performance similar to the other, wider bandwidth targets. This indicates that mice are not using bandwidth as a cue, easily discriminating between targets occupying a wider bandwidth than the background and not attending to the direction of the sweep, but instead are unable to discriminate between the test and background stimuli because they occupy the same frequency range.

It was surprising that the mice were unable to discriminate between the 60–80 kHz upswing and downswing test and background stimuli in the 20 ms condition because these are the same frequencies and durations as their natural vocalizations. We believed that the mice would be able to discriminate between these two USVs because the mice produce upsweeps more than all the vocalizations in their repertoire (Grimsley *et al.*, 2011). It is possible that the mice had so much difficulty discriminating between these USVs because the artificial stimuli used in this experiment were lacking in important characteristics that aid in their recognition of natural USVs. Figure 1(A) shows a natural bout of upsweeps recorded from an adult male mouse, and these natural upsweeps show very clear variability in their spectrotemporal parameters and these natural variations in their USVs may play a crucial role in enabling the mouse to discern which USV is being emitted. Alternatively, the mice may have difficulty in discriminating upswing from downswing USVs because these calls are spectrotemporally too similar to each other. The findings from Neilans *et al.* (2014) emphasize the importance of spectrotemporal dissimilarity for discrimination of USVs, indicating that their inability to discriminate could stem from this relationship. Due to their similarity, it may be necessary to place upsweeps and downsweeps within the same category of USV. A third alternative is that the mice are unable to discriminate between their USVs because they are not using their USVs for communication purposes, or that the spectrotemporal characteristics of the USVs are not important for communication. Rather, spectral content or rate of USV production is important and the different spectrotemporal shapes of the calls have no real meaning or purpose. More research is needed to determine which of these proposals is true.

The current study adds to the growing body of literature on mouse communication and auditory perception. Mouse USVs have not yet been found to actually be necessary for communication purposes, despite their emission during many social and courtship interactions. In order to determine whether or not USVs are being used for communication, and whether the spectrotemporal characteristics of the calls actually translate to information content, it is necessary to further determine whether the mice are able to discriminate between their natural USVs, both sweeps and other call types.

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