Published in final edited form as:

J Comp Physiol A Neuroethol Sens Neural Behav Physiol. 2009 October ; 195(10): 923–934. doi:10.1007/s00359-009-0468-x.

Context-dependent effects of noise on echolocation pulse characteristics in free-tailed bats

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Abstract

Background noise evokes a similar suite of adaptations in the acoustic structure of communication calls across a diverse range of vertebrates. Echolocating bats may have evolved specialized vocal strategies for echolocating in noise, but also seem to exhibit generic vertebrate responses such as the ubiquitous Lombard response. We wondered how bats balance generic and echolocation-specific vocal responses to noise. To address this question, we first characterized the vocal responses of flying free-tailed bats (*Tadarida brasiliensis*) to broadband noises varying in amplitude. Secondly, we measured the bats' responses to band-limited noises that varied in the extent of overlap with their echolocation pulse bandwidth. We hypothesized that the bats' generic responses to noise would be graded proportionally with noise amplitude, total bandwidth and frequency content, and consequently that more selective responses to band-limited noise such as the jamming avoidance response could be explained by a linear decomposition of the response to broadband noise. Instead, the results showed that both the nature and the magnitude of the vocal responses varied with the acoustic structure of the outgoing pulse as well as non-linearly with noise parameters. We conclude that free-tailed bats utilize separate generic and specialized vocal responses to noise in a context-dependent fashion.

Keywords

Echolocation; Vocalization; Noise; Lombard response; Vocal plasticity; Jamming avoidance response

Introduction

A diverse range of animals alter the acoustic structure of their vocalizations in the presence of background noise. The nature and magnitude of these voice changes are interesting in both an ecological context (Brumm and Slabbekoom 2005) and in a neurobiological context, particularly as it relates to the evolution of speech and language (Sinnot et al. 1975). Experiments with animals that can change the sound of their voice may offer insight into the neural basis of human speech. In every animal so far tested, vocalization amplitude was elevated by noise, syllable durations are often lengthened, and vocal pitch is sometimes elevated. This suite of changes in acoustic structure is likely to be biomechanically linked in most animals, driven principally by increases in call amplitude (Lane and Tranel 1971), and collectively may be viewed as generic adaptations that promote signal transmission in noise.

The most common way animals improve the propagation of their communication signals in noise is by increasing signal amplitude. The human Lombard response (Lombard 1911), characterized by increased voice amplitude in noise, has also been observed in frogs (Lopez et al. 1988; Penna et al. 2005), several species of birds (Potash 1972; Manabe et al. 1998; Cynx and Von Rad 2001; Brumm and Todt 2002; Pytte et al. 2003; Leonard and Horn 2005), and many mammals, including cats (Nonaka et al. 1997), whales (Foote et al. 2004; Scheifele et al. 2005; Holt and Noren 2009), and primates (Sinnot et al. 1975; Brumm et al. 2004; Egnor and Hauser 2006). Echolocating bats tightly regulate the amplitude of their echolocation pulses (Kobler et al. 1985; Hiryu et al. 2007) and they call louder in the presence of echolocating conspecifics (Schmidt and Joermann 1986) and broadband noise (Simmons et al. 1978; Bates et al. 2008).

Increasing pulse amplitude carries with it some ecological disadvantages, including increased energy expenditure and the potential for attracting predators (Dabelsteen et al. 1988; Brumm and Todt 2002). Thus, there are selective pressures favoring the use of other vocal adaptations. Animals may also compensate for background noise by increasing syllable duration (Lane and Tranel 1971; Picheny et al. 1986; Brumm et al. 2004; Foote et al. 2004; Leonard and Horn 2005; Penna et al. 2005; Egnor and Hauser 2006), adjusting call timing (Brumm 2006; Egnor et al. 2007), and shifting pitch (Ulanovsky et al. 2004; Gillam et al. 2007; Bates et al. 2008). Big brown bats (*Eptesicus fuscus*) lengthened their pulses in broadband noise but not in the presence of a tonal interfering stimulus (Bates et al. 2008). In many species of bat, an inverse relationship exists between pulse duration and bandwidth (Jones 1999; Schnitzler and Kalko 2001) making it difficult to know the extent to which a bat can make changes in pulse intensity, duration, and frequency independent of one another. Elucidating the degree of coupling between pulse parameters would provide insight into how vocal motor pathways are controlled.

Echolocation behavior is particularly sensitive to the degrading effects of background noise, and animals that echolocate may be expected to display specialized vocal responses in addition to or in place of the generic vertebrate response to noise. The so-called jamming avoidance response (or JAR) exhibited by bats appears to be one such specialized behavior wherein the bats reportedly shift the frequency of their echolocation pulses to minimize overlap with interfering noises (Ulanovsky et al. 2004; Gillam and McCracken 2007; Gillam et al. 2007; Bates et al. 2008). Yet many previous studies in other vertebrates have reported that the most effective stimulus for eliciting vocal changes were noise stimuli overlapping in frequency with an animal's own communication sounds (Sinnot et al. 1975; Schwartz and Wells 1983; Brumm and Todt 2002), and in several studies the vocal response to interfering noises included an elevation in vocal pitch (Lombard 1911; Lane and Tranel 1971; Van Summers et al. 1988; Nelson 2000; Leonard and Horn 2005). Field studies on free-tailed bats (*Tadarida brasiliensis*) reported that the JAR occurred in the absence of changes in amplitude (Ulanovsky et al. 2004; Gillam and McCracken 2007; Gillam et al. 2007), but accurate measures of echolocation pulse amplitude are difficult to obtain in the field. These field studies also reported several other concurrent changes in pulse structure not directly associated with jamming avoidance, such as changes in duration and bandwidth, leaving open the possibility that the recorded changes in pulse pitch were byproducts of a more generalized response to noise.

To test whether the free-tailed bats' JAR is indeed a context-dependent behavior that is distinguishable from the generic vertebrate response to noise, a thorough analysis of how they manipulated pulse acoustics in response to broadband noises versus band-limited noises was required. Since pulses uttered in the lab have a broader bandwidth, emphasize higher frequencies, and are less than half as long as the average search pulse uttered outside (Schwartz et al. 2007), it was also possible to assess whether the vocal responses to noise would be dependent on the pulse type emitted. We hypothesized that the most effective frequency for

evoking the JAR in the lab would be shifted upward to correspond to the elevated frequencies emphasized by the bats in the laboratory. The results of these studies indicate that the JAR behavior exhibited by free-tailed bats appears to be a flexible context-dependent vocal behavior and neither an extension of the generic vertebrate response to noise nor a simple acoustic reflex.

Methods

Animal husbandry

Twenty Mexican free-tailed bats, *Tadarida brasiliensis mexicana*, were caught wild from a year round roost on the campus of Texas A&M University and housed in the Texas A&M Department of Biology vivarium facility. Bats were kept on a phase-shifted 12/12 day/night cycle, with vivarium lights turning off at 12:00 p.m. The bat vivarium was a temperature- and humidity-controlled room that was large enough to allow the bats to fly freely. Bats were trained to feed themselves and had to fly daily to obtain food. The bats were fed a diet of mealworms supplemented with vitamins, minerals, and essential fatty acids.

Acoustic stimuli

Acoustic stimuli consisting of either broadband or band-limited noise was generated digitally with Tucker-Davis Technology (TDT) system III hardware and the openEX software v5.4. The broadband noise was digitally filtered to present a total signal bandwidth spanning a range of 15–100 kHz, which covered the entire range of the two loudest harmonic components of *Tadarida brasiliensis*' echolocation pulses. The band-limited noises were generated by digitally bandpass filtering white noise down to a bandwidth of 5 kHz. A 5-kHz stimulus bandwidth was chosen based on pilot data indicating that this was the smallest bandwidth that reliably evoked consistent changes in pulse structure. Pure tones such as those used by Bates et al. (2008) had no significant effects on pulse parameters. We tested a frequency range of 5-kHz bandwidth signals that spanned from approximately 10 kHz below to 10 kHz above the average lowest and highest frequencies, respectively, of the principal harmonic component of the bat's echolocation pulses. These 5-kHz bandwidth stimuli were centered at 17.5, 22.5, 27.5, 32.5, 37.5, 42.5, 47.5, 52.5, or 57.5 kHz. All stimuli were played through a Sony amplifier (model # STR-DE598) driving a four-speaker array consisting of two Pioneer Ribbon Tweeters (ART-55D/301080) and two Pioneer Rifle Tweeters (ART-59F/301081), arranged to project across the flight path and in both directions along the length of the tunnel. Each speaker provided a flat (± 3 dB) output at a maximum of 85-dB SPL across the principal frequency range of interest, roughly 15–60 kHz. In order to test the effects of broadband stimulus intensity on echolocation pulse structure, broadband noise amplification was reduced by 10, 20, and 30 dB relative to the maximum. The bats' echolocation pulses ranged in intensity from 80- to 115-dB SPL during flight, as measured by a microphone placed in the center of the room. All experiments were performed with flying bats rather than stationary bats because echolocation pulses from flying bats were observed to be less variable than those emitted by stationary bats, and because it was assumed that flying bats would be more likely to exhibit a robust vocal response to noise than stationary bats.

All experiments were performed in an 8-m long by 2-m wide by 3-m high flight tunnel lined with sound-absorbing 4-inch acoustic foam (Sonex[®], model UNX-4), with the lights off. Recordings of flying bats were made using a Bruel & Kjaer Free-field ¼ inch microphone (Type 4939) placed in the center of the room. The placement of the microphone was coordinated with the positions and directionality of the speakers to minimize the recorded intensity of the stimuli while maximizing the recorded intensity of the bat pulses, which facilitated the digital extraction of echolocation pulses from the background noise. Incoming

signals were digitized with a National Instruments DA-Qmx, NI PCI-6251 (200 kHz, 16-bit sample rate), and viewed with Avisoft Recorder v3.0.

Echolocation pulse extraction and analysis

Recordings were analyzed using SASLab Pro v4.39. As the bat approached the microphone, only the last 10–15 pulses before the bat passed the vertical plane of the microphone were selected for analysis, ensuring that all analyzed pulses were emitted within approximately 1-m depth of the microphone, and thus that pulses from the same relative time-period within the flight path were compared across all experimental conditions. Additionally, only pulses that were at least 15-dB louder than the recorded noise stimuli were included in the analysis to ensure accurate measurements of all acoustic parameters. We used the methods of Penna et al. (2005) to subtract the contributions of stimulus amplitude on the measurements of pulse amplitude. Doppler effects on the frequency of the echolocation pulses were accounted for in the post hoc analysis.

In the flight tunnel, free-tailed bats emitted short (4–7 ms), downward frequency-modulated pulses that typically began around 45 kHz and ended around 25 kHz. The spectral parameters of the pulses were summarized by three measurements at three different time points within the pulse (Gillam and McCracken 2007; Schwartz et al. 2007; Ulanovsky and Moss 2007), including the frequency at the start of the pulse (F_{start}), the frequency of the end of the pulse (F_{end}), and the frequency of maximum pulse intensity (F_{peak}). F_{peak} was taken from the power spectrum, and F_{start} and F_{end} were defined as the frequencies at the lower and upper end, respectively, of the spectrum –15 dB relative to the intensity of the peak frequency (Schwartz et al. 2007; Surlykke and Moss 2000). The slope of the pulse was calculated by subtracting the F_{start} from F_{end} and dividing by the duration of the pulse, providing a simple estimate of the overall rate of frequency change. One hundred echo-location pulses from each bat in each treatment were selected at random for analysis. For temporal analyses, we used 256-point fast Fourier transforms (FFTs) with 93.75% overlap, providing 976-Hz spectral and 0.064-ms temporal resolutions. For spectral analysis 1024-point FFTs provided 244-Hz spectral and 0.256-ms temporal resolutions.

Experimental procedure

Twenty bats were chosen at random from the captive colony and randomly assigned to two groups of 10 bats each. Group 1 was used only for trials utilizing broadband noise, group 2 only band-limited noise. The same individuals were not exposed to both stimuli to prevent a confounding effect from stimulus order and undue stress due to excessively long experimental trials. All experiments were conducted during the time of day when the bats were normally most active within the vivarium (10 a.m.–2 p.m.). All individuals had previous experience flying in the chamber and had been habituated to the experimental procedures and daily handling. Bats were acclimatized to the experimental chamber before beginning each trial, and they were “warmed up” by letting them fly freely in the room before beginning experiments. For each trial, individuals were recorded flying back and forth multiple times between two perches located at opposite ends of the flight tunnel. Approximately 12–15 flights across the room were needed for each trial to collect the minimum number of pulses satisfying all the threshold criteria defined above. Baseline recordings of bats flying back and forth between the perches in the absence of acoustic stimuli were recorded before beginning each experimental trial, and the various acoustic stimuli were presented in a pseudo-random fashion and were alternated with silent trials to track any potential changes in pulse parameters associated with time spent in flight.

Statistical analysis

All statistical procedures were performed utilizing SAS v9.2 and SAS-JMP v7.0.7. A MANOVA analysis was performed to determine if there was a significant effect of noise on echolocation pulse structure. If the effect of interference was shown to be significant by MANOVA ($P \leq 0.05$, $\alpha = 0.05$), the results of ANOVA analysis to determine significant effect within parameters was reported. Student's t test pair-wise multiple comparison procedure ($\alpha = 0.05$) was used to determine significant differences between different treatments within a parameter if a significant effect of noise was found. Both MANOVA and ANOVA analysis were conducted as a mixed model design with individual bat as a random variable. Results are given as means $\pm$ SE unless stated otherwise.

Results

Effects on broadband noise on pulse structure

The presence and intensity of the broadband noise had an effect on all pulse parameters (Fig. 1). As the intensity of the white noise increased, F_{start} and F_{end} increased and decreased, respectively. F_{end} decreased significantly from baseline when the broadband noise was within 10 dB of maximum. F_{start} increased significantly for all stimulus intensity levels. Duration, bandwidth and pulse amplitude all increased with increased broadband noise amplitude. All levels of stimulus amplitude significantly increased both the duration and the bandwidth from baseline levels. Pulse amplitude was not significantly affected by noise that was -30 dB of the maximum. Stimulus intensity had a significant effect on all pulse parameters except F_{peak} . Although F_{peak} appeared to be slightly elevated in the presence of noise, the change was not significantly different from baseline at any intensity (see Table 1 for numerical comparisons and P values).

The distribution of F_{peak} was bimodal in both the presence and the absence of broadband noise (Fig. 2); the two peaks in the histogram corresponded to two different pulse structures used by the bats while flying in cluttered spaces, one being a typical FM pulse with an F_{peak} near the center of the pulse, and the other being a quasi-CF-FM pulse wherein the bats include a short-intense CF at the start of the pulse resulting in a higher F_{peak} . Broadband noise caused a slight change in the distribution of F_{peaks} that corresponded with an increase in the number of CF-FM pulses containing F_{peaks} between 40 and 45 kHz; however, there was no statistically significant change in the mean F_{peak} . Since any observed changes in the mean F_{peak} could have been accounted for by either shifts in pulse frequency or switches in the relative numbers of pulse types emitted (FM vs. CF-FM), the upper and lower modes were analyzed both separately and as a single population; however for broadband noises, the statistical results were the same for F_{peak} in either case (i.e., no significant change in F_{peak}). These results were further confirmed by comparison of the distributions of F_{peak} between treatments. For all subsequent analyses of noise stimuli on F_{peak} the relative contributions of changes in calling mode versus shifts in the median frequencies of each mode were taken into account and are presented where significant differences were observed.

Effects of band-limited noise on pulse structure

Inference had a significant effect on the F_{start} ($P < 0.0001$) and F_{end} ($P < 0.0001$). The effect of center frequency on the average F_{start} and F_{end} of the echolocation pulse can be seen in Fig. 3a, b. The response of F_{start} and F_{end} to band-limited noise stimuli differed from that observed for broadband noise. First, F_{start} significantly decreases from a mean baseline frequency of 45.3 ± 4.4 kHz to 43.2 ± 8.7 kHz at the band-limited noise of 22.5 kHz. The F_{start} remained at this lower frequency without significant change for the 27.5- and 32.5-kHz band-limited noise. For the 17.5-kHz band-limited noise and for all stimulus frequencies greater than 32.5 kHz,

there was no significant change in F_{start} from the baseline. As seen in broadband noise, F_{end} initially decreased significantly from a baseline of 26.9 ± 3.3 to 25.7 ± 4.1 kHz at the 22.5 kHz band-limited noise. At the 32.5-, 37.5-, and 42.5-kHz band-limited noise; however, the F_{end} increased significantly above baseline to 28.6 ± 3.9 , 28.8 ± 4.5 , and 27.8 ± 4.7 kHz, respectively. At the 47.5-kHz band-limited noise the F_{end} decreases significantly from the 32.5-kHz band-limited noise, but remained significantly greater than baseline frequency at 27.7 ± 4.1 kHz. The F_{end} at the 17.5, 52.5, and 57.5 kHz, band-limited noise were not significantly different from the baseline frequency.

The combined effect of the change in F_{start} and F_{end} resulted in a significant decrease in the bandwidth (Fig. 3d; $P < 0.0001$). In the presence of band-limited noise at 17.5 and 22.5 kHz, we observed what appeared to be a decrease in echolocation bandwidth to 18.0 ± 6.7 and 17.4 ± 8.2 kHz but the change was not statistically significant. The 27.5-kHz band-limited noise did cause a significant decrease in bandwidth down to 16.2 ± 8.0 kHz. The maximum change in bandwidth was evoked by the 32.5-kHz band-limited noise, with a significant decrease to 14.3 ± 8.3 kHz, which is opposite to the response observed when bats echolocated in the presence of broadband noise. As the noise center frequency was raised above the 32.5-kHz frequency, the bandwidth of the echolocation pulse increased to 16.0 ± 7.8 kHz at 37.5-kHz band-limited noise and the bandwidth returned to a value not significantly different from baseline (17.2 ± 6.7 kHz) at the 42.5-kHz band-limited noise.

A significant effect on duration in response to the band-limited noise was also observed (Fig. 3c; $P = 0.0012$). As observed in response to broadband noise, we also observed an increase in duration for several band-limited noises. A significant increase from the 5.8 ± 1.2 -ms baseline pulse length to 6.3 ± 1.4 ms occurred at the 22.5-kHz band-limited noise. Pulse duration was also significantly elevated by the 27.5- and 32.5-kHz band-limited noise. Pulse duration returned to within one standard deviation of the baseline duration for the 37.5-kHz band-limited noise and all stimuli at higher frequencies. Unlike the response to white noise, however, the increases in pulse duration evoked by the band-limited noise were not accompanied by increased pulse amplitude. There was no significant effect of band-limited noise frequency on pulse amplitude (Fig. 3f; $P = 0.3568$).

The decreasing bandwidth combined with the increasing pulse length resulted in a significant decrease in pulse slope (Fig. 3e; $P < 0.0001$). In the absence of noise, the average echolocation pulse had a slope of -3.5 ± 1.7 kHz/ms. In the presence of the band-limited noise, the slope of the pulse decreased because the bandwidth decreased while the duration increased. The slope decreased linearly as the center frequency of the band-limited noise was increased from 22.5 kHz (-3.1 ± 1.8 kHz/ms) up to 32.5 kHz (-2.6 ± 2.0 kHz/ms). Slope of the pulse then increased with increasing band-limited noise frequency until it returned to baseline levels at the 42.5-kHz band-limited noise and above.

Characterizing the effect of band-limited noise frequency range on F_{peak}

In contrast to the response to broadband noise, the F_{peak} changed significantly in response to the band-limited noise ($P = 0.0016$) and the response pattern appeared slightly dependent on the stimulus frequency (Fig. 4). The average baseline F_{peak} was 37.8 ± 5.6 kHz. At each band-limited noise frequency below the 37.5-kHz stimulus the baseline F_{peak} was well above and did not overlap with the band-width of the stimulus, and yet all the stimuli caused a significant elevation in F_{peak} . The F_{peak} significantly increased from baseline to 39.1 ± 5.2 kHz in the presence of the 17.5 kHz band-limited noise, which did not overlap in frequency with any portion of the baseline pulse. The F_{peak} at the 22.5-, 27.5-, and 32.5-kHz band-limited noise were also significantly elevated but did not significantly differ from the response to the 17.5-kHz band-limited noise. At the 37.5-kHz band-limited noise (the bandwidth containing the

baseline F_{peak} frequency), F_{peak} increased to its maximum level of 39.9 ± 5.2 kHz; at this stimulus frequency roughly half the F_{peak} values would have been raised above the band-limited bandwidth. For band-limited noise frequencies that were greater than 37.5 kHz, the F_{peak} dropped to a mean value not significantly different from baseline, at which point essentially all F_{peak} values would have fallen below the bandwidth of the band-limited noise.

As mentioned previously the distribution of F_{peak} is bimodal (Fig. 4b) with a peak falling on average between 30 and 35 kHz, and a second peak at 45 kHz. Very few pulses exhibited an F_{peak} near 40 kHz, accounting for the deep trough separating the two peaks. In general the effect of band-limited noise was similar to that of broadband noise, which was to cause a slight increase in the relative number of CF-FM type pulses emitted. For both the 32.5 and the 47.5 band-limited noises the number of pulses with an F_{peak} between 30 and 35 kHz decreased with corresponding increases in the number of pulses with an F_{peak} at 45 kHz. Unlike the observed effect of white noise, the upper bound of the lower peak did not increase in the presence of noise. The 32.5-kHz band-limited noise caused an increase in the upper bound of the upper peak, suggesting that not only did the bats increase the number of CF-FM type pulses being emitted, but also that those pulses often had a slightly higher peak frequency than normal. The increase in mean F_{peak} was therefore, as in white noise, primarily due to an increase in the number of pulses utilizing an F_{peak} that fell within the 45-kHz peak, and only slightly accounted for by an increase in the mean frequency of the upper peak. The greater change in F_{peak} observed in the 32.5-kHz band-limited can be explained by the increase in the mean of the upper peak that is not present in the 47.5-kHz band-limited.

Examination of the mean response across bats revealed that a general pattern of response existed, yet upon closer inspection we observed that there was a large amount of variability within that general pattern between bats, especially in the way they regulated F_{peak} and pulse duration.

Figure 4c shows the individual response of one bat to the nine different band-limited noises whose behavior was not completely represented by the pooled data. Stimulus bandwidths that either included or were below the bats baseline F_{peak} resulted in an increase in F_{peak} up to a maximum frequency of 40.256 ± 5.092 kHz at the 27.5-kHz band-limited noise. A drastic decrease in F_{peak} from its maximum value was observed at the 42.5-kHz band-limited noise. This band-limited noise represents the first interference bandwidth that is higher in frequency than the bats baseline F_{peak} , 35.106 ± 5.587 kHz. The mean F_{peak} significantly increased at the 47.5-kHz band-limited (but did not overlap with the stimulus bandwidth), and then declined again back toward baseline levels. Examination of the distribution of pulse F_{peak} for this bat showed that the underlying cause of the change in mean F_{peak} was caused by a combination of two factors. Figure 4c shows that band-limited noise center at 32.5 kHz caused an increase in the number of pulses in the upper mode as expected, but unlike the results from the pooled data, there was also an upward shift of the peak in both the lower and the upper modes, meaning that the increase in mean F_{peak} was due to both a change in mode peak size and an increase in the mean of each mode. The 42.5-kHz band-limited noise also caused an increase in the number of pulses utilizing the upper mode, but at this stimulus frequency the peak of both the upper and the lower mode was the same as baseline. Additionally, there was an increase in the number of pulses with an F_{peak} less than 25 kHz. Thus, even though the mean F_{peak} of bats flying in 42.5-kHz interference was not significantly different from baseline, the noise still had an effect on the distribution of pulse F_{peak} . We did not observe these specific shifts in frequency in enough bats to conclude that this is a standard response for this species; however, the fact that we saw in some bats indicates that this mechanism of vocal control is possible in this species, and may be more important under other different or more natural conditions.

Another example of how the bats differed in their individual responses is shown in Fig. 5, which shows the mean pulse durations of three separate individuals across all noise center frequencies. In each case, duration increased in response to an intermediate range of different band-limited noise. However, the extent of duration increase was different for each individual and appeared to vary with baseline durations. Bat 29 (Fig. 5a), which had initial mean pulse duration of 6.041 ± 0.784 ms, increased maximally at the 32.5-kHz band-limited noise by 0.916 kHz. Bat 33 (Fig. 5b) used pulses that were notably longer than average (7.413 ± 1.046 ms) and Bat 34 (Fig. 5c) used pulses that were shorter than average (5.211 ± 0.839 ms). Both Bats 33 and 34 increased their mean pulse duration, but the bat that started out using the longer pulses only increased duration by 0.356 ms, whereas the bat using the shortest pulses (Bat 34) increased its pulse durations by 1.979 ms. This may indicate that bats with shorter initial pulse durations displayed a greater magnitude of change than those with longer initial pulse durations. There was a non-significant ($P = 0.0830$) correlation of -0.6070 between the initial pulse duration and the maximum change in duration for nine bats. The magnitude of change for the 10th individual was abnormally large and was excluded by jackknife outlier analysis. The inclusion of more individuals would likely result in a significant correlation, as the variation in duration between individuals was high.

Discussion

Previous studies have shown that many species of bats alter their echolocation pulses in response to noise (Habersetzer 1981; Surlykke and Moss 2000; Ibanez et al. 2004; Ratcliffe et al. 2004; Ulanovsky et al. 2004; Gillam and McCracken 2007; Gillam et al. 2007; Bates et al. 2008). In these cases, the bats' vocal response to noise was categorized as a specialized adaptation for echolocation; however, many other vertebrates that do not possess an active sensory system also alter their vocalizations in the presence of noise. It is therefore possible that some of the ways bats respond to noise are reflective of a more generalized vertebrate response to noise. We sought to determine if the JAR observed in *Tadarida brasiliensis* was indeed a separate response from the general vertebrate response to noise. In order to do so, we detailed the response of several parameters to both band-limited and broadband noise. In broadband noise, echolocation pulse amplitude, duration, and bandwidth increased; and the nature and magnitude of these changes were similar to what has been reported for a variety of other vertebrates. The bats responses to band-limited noise, however, were collectively different from the responses to broadband noise in important ways. Duration increased similar to the response to broadband noise, but otherwise pulse parameters changed differently; F_{peak} increased, bandwidth decreased, and amplitude remained unchanged from initial levels. The changes of F_{peak} and bandwidth in band-limited noise appear to be specific to echolocation behavior.

We compared the response of our bats in the lab using short broadband FM pulses to report similar studies conducted on free-tailed bats in the field where they used long narrow-bandwidth search pulses to determine if the response to noise was dependent on the characteristics of the pulse being emitted. We found that the frequencies of noise that best evoked a vocal change in the laboratory differed from that previously observed in the field. The F_{peak} increased in response to band-limited noise frequencies that overlapped with the initial F_{peak} emitted in the laboratory, which is 10–20 kHz higher than the F_{peak} of search pulses emitted in the field.

Vocal response to broadband noise

In the presence of broadband noise, pulse amplitude, duration, and bandwidth increased significantly from initial levels. The change in pulse bandwidth was due to both an increase in

F_{start} and a decrease in F_{end} . For all these parameters the magnitude of change was dependent on the intensity of broadband noise presented. Broadband noise did not have a significant effect on the F_{peak} or slope of the pulse.

An increase in call amplitude in response to noise, analogous to the human Lombard response (Lombard 1911), has been consistently observed in many other taxa. In frogs (Penna et al. 2005), birds (Brumm and Todt 2002; Leonard and Horn 2005), whales (Foote et al. 2004; Scheifele et al. 2005), primates (Brumm et al. 2004; Egnor and Hauser, 2006; Sinnott et al. 1975), and bats (Simmons et al. 1978) the increase in amplitude is accompanied with an increase in call duration. The increase in amplitude is presumed to increase the signal-to-noise ratio when calling in noisy environments. For echolocating bats this might also increase the maximum distance from which an object could be detected or distinguished. Less consistent is the effect of broadband noise on the frequency of vocalization across taxa. Swallow begging calls in the presence of noise displayed a change in bandwidth, duration, and amplitude similar to that observed for free-tailed bat's echolocation pulses (Leonard and Horn 2005). The fundamental frequency of human speech was significantly increased by the presence of white noise (Loren et al. 1986). In contrast, despite an increase in both call duration and amplitude, white noise had no significant effect on the fundamental frequency of cotton-top tamarin's combination long calls (Egnor and Hauser 2006). The effect of noise on call amplitude and duration appears to be highly conserved across taxa, with more variation seen in the control of spectral call parameters. The free-tailed bat's vocal response to broadband noise seems to correspond well with the general vertebrate response to noise, and we interpret the changes in duration and bandwidth to be by-products of an increase in amplitude.

Vocal response to band-limited noise

Echolocation pulse duration but not amplitude increased significantly in the presence of band-limited noise. The 22.5-, 27.5- and 32.5-kHz band-limited noise produced a statistically significant increase that did not significantly differ from the other stimuli that overlapped with the initial echolocation pulse bandwidth. Similar to observations in macaques (Sinnott et al. 1975), band-limited noise frequencies that did not include echolocation pulse frequencies did not cause a significant change in pulse duration. Mean call duration did not increase more than 8 ms in any of the bats tested; probably because, for bats, pulse-echo delay times are also highly salient cues for regulating pulse duration and in the lab echo delay times are always short. As pulses get longer outgoing pulses may overlap in time with quickly returning echoes and thus interfere with echo perception. The magnitude of duration increases also appeared to be dependent on an individual's relative pulse duration. Individuals exhibiting longer baseline pulses tended to lengthen their pulses less in response to band-limited noise than those with shorter initial durations.

Context dependency of the vocal response to noise

In the field, free-tailed bats use a high proportion of long (12–16 ms) pulses for their navigation and foraging tasks (Schwartz et al. 2007), but in the lab bats used pulses of roughly 4–6 ms. In the field, free-tailed bats responded to the sounds of chorusing insects by increasing all frequency parameters including bandwidth and decreasing duration (Gillam and McCracken 2007). More generally an inverse relationship between pulse duration and frequency was observed in the field (Gillam and McCracken 2007), suggesting that these two parameters are tightly coupled. Those authors concluded that free-tailed bats do not directly adjust pulse duration, but changes in duration occurred indirectly as a result of frequency adjustments. In the current study we observed that band-limited noises caused increases in F_{peak} and F_{end} similar in magnitude and spectral sensitivity to the field results, and likewise we observed no consistent changes in amplitude. However unlike the field measurements, we observed a

decrease in F_{start} (F_{max} in Gillam and McCracken 2007), an increase in duration, and a decrease in bandwidth. These differences seem to be related to differences in the types of pulses being used, but they show that key frequency parameters (F_{peak} and F_{end}) can be elevated even while pulse durations are increasing. These results also showed that starting and ending frequencies can be manipulated independently and do not always increase and decrease in unison. It seems likely that the bats' responses to band-limited noises are more complex than what would be predicted by the graded response to broadband noise. How echolocation pulse duration, frequency, and bandwidth is altered in response to noise depends on what type of echolocation pulse is being used and other current acoustic conditions such as the array of pulse-echo delays that comprise the bats' acoustic scene. Generally, if the frequency of noise and the frequency of any portion of a bats echolocation pulse coincide, a change in pulse duration would be expected. The magnitude of the response will be dependent on the intensity and frequency-content of the noise. Interestingly, whether pulse duration will increase or decrease is dependent on pulse type, or at least what the duration of the pulse would have been if emitted in silence.

Band-limited noise caused a significant increase in the F_{peak} for some but not all stimulus frequencies. Unlike other pulse parameters, the distribution of F_{peak} was bimodal. Changes in the mean F_{peak} were the result of a small upward shift in the mean of both modes, and an increase in the number of pulses whose F_{peak} fell in the upper mode. None of the stimuli tested caused the F_{peak} to decrease below initial levels. The stimulus frequencies that cause the greatest change in F_{peak} were typically in the range of 30–35 kHz, which is different from the best stimulus frequencies reported for evoking JAR in the field (Ulanovsky et al. 2004; Gillam et al. 2007) but consistent with the elevated range of mean F_{peak} values for bats echolocating in the lab. The F_{peak} of the pulses used in the lab, 35.7 ± 5.9 kHz, was significantly higher the mean F_{peak} of search pulses recorded in the field, 26.4 ± 1.6 kHz (Schwartz et al. 2007). The best frequency for eliciting changes in F_{peak} in the lab does not appear to correspond well with the region of greatest sensitivity in the auditory system (Pollak et al. 1978), which instead appears to be more closely related to peak frequencies of pulses used in open spaces. Nor could similar changes in F_{peak} be evoked by varying the intensity of broadband noise. The response of F_{peak} to band-limited noise is consistent with what has been described as a JAR in the field for *Tadarida brasiliensis* (Gillam et al. 2007; Ratcliffe et al. 2004). The magnitude of the change in F_{peak} was not closely correlated with how closely the stimulus frequency matched the initial pulse F_{peak} , but similar to the report for big brown bats (Bates et al. 2008) the upper range of stimulus frequencies at which the bats stopped elevating their F_{peak} did seem to correlate well with the stimulus passing above the baseline F_{peak} values. Presumably the change in F_{peak} allows the free-tailed bat to maximize the signal-to-noise ratio for an important pulse component without increasing pulse amplitude. Collectively these data suggest that the best frequency for eliciting the JAR in free-tailed bats appears to change that depend on the shape of the pulse being used. Thus, the frequency component of the vocal response to noise of *Tadarida brasiliensis* is context dependent, with both the type of pulse being emitted and the nature of the noise present affecting the response.

An important question not directly addressed in these experiments was whether the bats made adjustments in their pulse acoustics due to distortions in their perception of the outgoing pulse or the returning echo. The acoustic structure of the echo will differ from the pulse because of greater atmospheric attenuation at higher frequencies and also because of Doppler effects. The effects of greater attenuation at higher (start) frequencies of the echo but not the pulse might have caused bats to be more sensitive to noises at higher frequencies since those noises would have had a greater impact on the signal-to-noise ratio at that bandwidth, but such a hypothesis was not supported by the data. Similarly, Doppler effects, though small, shift the echo frequencies 350–650 Hz higher than the frequencies of the outgoing pulse. If the bats were trying to minimize overlap between the band-limited noise stimuli and the F_{Peak} of the echo,

then the most effective stimulus band-width would have been 350–650 Hz higher than the recorded pulse F_{peak} . Since we used stimulus bandwidths of 5 kHz, it was not possible from these results to discriminate such a difference. Thus, while it is possible that the bats' behavior was focused on improved echo resolution, we cannot say specifically whether the bats were cueing to the relationship between stimulus bandwidth and either pulse or echo frequencies.

Implications for the neurobiology of vocal control

Mammalian vocalizations are produced by brainstem pattern generators (Jürgens 2002; Jürgens and Hage 2007). Humans alter syllable acoustics via direct projections from speech motor cortex onto respiratory and laryngeal spinal motor neurons, but the functional significance of similar pathways is unknown in other mammals (Jürgens 2009). The change in F_{peak} exhibited by free-tailed bats appears to be a fine-tuned context-dependent vocal response that might be better explained by forebrain mechanism rather than midbrain circuitry (Smotherman 2007). Importantly, changes in F_{peak} would appear to be inherently respiratory rather than laryngeal in mechanism. By definition, F_{peak} is the frequency of the pulse at which the maximum energy is reached. Examination of the mean pulse envelope shows that the increase in F_{peak} seen in free-tailed bats occurred due to maximum energy being applied to the pulse earlier in the time course (Fig. 6). This change can only be accomplished by changing the time course of expiratory force during pulse emission. Thus, changes in F_{peak} describe a respiratory modification rather than a laryngeal modification of the vocal motor pattern. Normal respiratory rhythm is controlled by brainstem regions which can be temporarily subverted by forebrain mechanisms to exert volitional control (Corne and Bshouty 2005; Schulz et al. 2005). Fine volitional control of respiration has been shown to be critical in the evolution of human speech (MacLarnon and Hewitt 1999). The free-tailed bat's F_{peak} response to band-limited noise is an insightful example of an animal utilizing a respiratory mechanism to alter the spectral components of its vocalizations, and provides an opportunity to study a mechanism for context-dependent vocal control.

In conclusion, broadband and band-limited noise had different effects on the pulses of *Tadarida brasiliensis*. The response to broadband noise was generally consistent with vocal adaptations for calling in noise exhibited by many vertebrates, i.e., a Lombard response, and in this case increases in amplitude and duration, and possibly frequency are likely to be biomechanically linked. Alternatively, some components of the response to band-limited noises were in many instances the opposite of their counterpart responses to broadband noise. The frequency of band-limited noise that best evoked a JAR response in the laboratory was different from values determined in field experiments. We conclude that the JAR displayed by the free-tailed bat is maintained in the lab and dependent on the spectral characteristics of the emitted pulse, especially the F_{peak} . In this way, free-tailed bats appear to differ from big brown bats, since the JAR in those bats was most sensitive to ending frequency in echolocation pulses both in the field and in the lab (Bates et al. 2008). These results show that the complex vocal responses of *Tadarida brasiliensis* are context dependent, with both frequency range of stimulus and the acoustic characteristics of emitted pulses affecting the nature and magnitude of response.

Acknowledgments

We thank Mr. Clint Netherland and the Texas A&M University Athletic Department for access to the bats of Kyle Field. We thank the Texas Parks and Wildlife Department for the collection permits. We thank Kristin Denton for her most excellent animal care and help with running the experiments, Dr. Kirsten Bohn for help with statistics, and Christine Schwartz, Jenna Jarvis, Dr. Bohn, and Dr. George Pollak for many informative discussions. All husbandry and experimental procedures were in accordance with NIH guidelines for experiments involving vertebrate animals and were approved by the local IACUC. The research was supported by Texas A&M University and NIH Grant DC007962 to M.S. Smotherman

Abbreviations

JAR	Jamming avoidance response
FM	Frequency-modulated
CF	Constant-frequency
F_{start}	Start frequency of the pulse
F_{end}	End frequency of the pulse
F_{peak}	Frequency of the part of the pulse with greatest amplitude

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Fig. 1.

The effects of broadband noises of varying intensity on echolocation pulse parameters. Each bar represents the mean of 10 bats flying in silence (baseline) or broadband noise. Zero decibel represents the loudest broadband noise (85-dB SPL), with magnitude decreased by 10, 20, and 30 dB from maximum. Error bars denote one standard error from the mean, *asterisks* designate results significantly different from baseline ($\alpha = 0.05$)

Fig. 2.

Bimodal distribution of F_{peak} and representative echolocation pulse types. **a** The distribution of F_{peak} in the absence (*gray line*) and presence (*black line*) of broadband noise. Both curves represent the number of pulses (n) exhibiting an F_{peak} at the given frequency. The change in distribution did not result in a significant difference between silence and broadband trials. Spectrogram in **(b)** is a representative of the FM-type pulse, while the spectrogram in **(c)** is representative of the CF-FM-type pulse

Fig. 3.

Effect of the frequency of band-limited noise on echolocation pulse parameters. Baseline measurements were made in the absence of any noise stimulus. Each point represents the mean of 10 individuals, 100 pulses per individual. Error bars denote one standard error from the mean. There was no significant overall effect of band-limited noise on the amplitude of echolocation pulses (ANOVA P value = 0.3568). Band-limited noise had a significant effect on all other parameters

Fig. 4.

Effect of the frequency of band-limited noise on the mean F_{peak} of 10 bats (**a, b**) and a single individual's responses (**c, d**). Asterisks denote significant difference from baseline. **a** Top left the effect of band-limited noise on the mean F_{peak} is shown. The open circle represents the highest band-limited noise that overlapped with the mean initial F_{peak} . **b** Top right the mean distribution for all 10 individuals initially (baseline, gray line), and in the presence of a 32.5-kHz band-limited noise (solid black line) and a 47.5-kHz band-limited noise (dashed black line). **c** Bottom left the effect of band-limited noise on the F_{peak} of a single individual is shown; each point represents the mean of 100 pulses. **d** Bottom right the distribution of the same bat's echolocation F_{peak} initially (baseline, gray line), and in the presence of 32.5-kHz band-limited noise (solid black line) and 42.5 band-limited noise (dashed black line)

Fig. 5.

Inter-individual variations on the effect of band-limited noise stimuli on duration. Each point signifies the mean duration of 100 pulses, *asterisks* denote significant difference from baseline ($\alpha = 0.05$). **a** Bat 29 represents the response of an individual whose initial pulse duration was close the population mean. Bats 33 (**b**) and 34 (**c**) represent the response of individuals whose initial pulse duration was longer or shorter than the mean, respectively. Note that the shorter the initial pulse duration, the greater the maximum response to band-limited noise

Fig. 6.

The mean pulse envelope of an individual flying in the presence and absence of noise. Pulse envelopes show the change in pulse energy, measured in mV, over the time course of the pulse, measured in ms from pulse onset. Each point represents the mean for 10 pulses initially (baseline, *closed circles*) and in presence of band-limited noise at the 32.5-kHz band-limited noise for one individual. The point when the maximum energy is reached defines the F_{peak} of the pulse

Table 1

The effect of broadband noise and band-limited noise centered at 32.5 kHz on the echolocation pulse parameters (mean $\pm$ SD) of two groups of *Tadarida brasiliensis*

	Broadband noise				32.5-kHz band-limited noise			
	Off	On	Δ	<i>P</i> value	Off	On	Δ	<i>P</i> value
Duration (ms)	4.76 $\pm$ 1.19	5.34 $\pm$ 1.31	0.58	<0.001	5.85 $\pm$ 1.38	6.33 $\pm$ 1.55	0.48	0.001
F_{start} (kHz)	43.50 $\pm$ 4.93	45.95 $\pm$ 4.36	2.45	<0.001	45.31 $\pm$ 4.47	42.71 $\pm$ 7.24	-2.60	<0.001
F_{end} (kHz)	27.33 $\pm$ 2.94	26.33 $\pm$ 2.94	-1.00	0.017	26.90 $\pm$ 3.42	28.58 $\pm$ 3.92	1.69	<0.001
F_{peak} (kHz)	35.74 $\pm$ 5.88	36.24 $\pm$ 6.01	0.49	0.965	37.85 $\pm$ 5.63	39.56 $\pm$ 5.52	1.71	0.002
Amplitude (V)	0.27 $\pm$ 0.21	0.71 $\pm$ 0.63	0.43	<0.001	0.45 $\pm$ 0.27	0.59 $\pm$ 0.42	0.13	0.357
Bandwidth (kHz)	16.17 $\pm$ 4.97	19.62 $\pm$ 4.81	3.45	<0.001	18.41 $\pm$ 5.63	14.13 $\pm$ 8.40	-4.29	<0.001
Slope (kHz/ms)	3.62 $\pm$ 1.44	3.88 $\pm$ 1.24	0.28	0.061	3.49 $\pm$ 1.71	2.61 $\pm$ 2.61	-0.88	<0.001

Column Δ gives the difference between noises off and on for each treatment. Values were obtained from 100 pulses per individual, 10 individuals per noise type. *P* values are reported for ANOVA test of significance for noise on pulse parameter