

RESEARCH ARTICLE

Active acoustic interference elicits echolocation changes in heterospecific bats

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ABSTRACT

Echolocating bats often forage in the presence of both conspecific and heterospecific individuals, which have the potential to produce acoustic interference. Recent studies have shown that at least one bat species, the Brazilian free-tailed bat (*Tadarida brasiliensis*), produces specialized social signals that disrupt the sonar of conspecific competitors. We herein discuss the differences between passive and active jamming signals and test whether heterospecific jamming occurs in species overlapping spatiotemporally, as well as whether such interference elicits a jamming avoidance response. We compare the capture rates of tethered moths and the echolocation parameters of big brown bats (*Eptesicus fuscus*) challenged with the playback of the jamming signal normally produced by Brazilian free-tailed bats and playback of deconstructed versions of this signal. There were no differences in the capture rates of targets with and without the jamming signal, although significant changes in both spectral and temporal features of the bats' echolocation were observed. These changes are consistent with improvements of the signal-to-noise ratio in the presence of acoustic interference. Accordingly, we propose to expand the traditional definition of the jamming avoidance response, stating that echolocation changes in response to interference should decrease similarity between the two signals, to include any change that increases the ability to separate returning echoes from active jamming stimuli originating from conspecific and heterospecific organisms. Flexibility in echolocation is an important characteristic for overcoming various forms of acoustic interference and may serve a purpose in interspecific interactions as well as intraspecific ones.

KEY WORDS: JAR, *Tadarida brasiliensis*, *Eptesicus fuscus*, Jamming avoidance response

INTRODUCTION

In many species of echolocating bats, sonar signals are composed of frequency modulated (FM) sound pulses separated by varying lengths of silence during which the bat listens to the returning echoes. This method of active sensing using self-generated acoustic signals yields information crucial in navigating complex environments as well as detecting and pursuing prey in conditions with little or no light (Fenton, 2003; Griffin, 1958). However, echolocation is susceptible to acoustic interference, including sonar jamming, which can potentially disrupt foraging. Interference can come from ambient sources of noise in the environment such as

running water, rustling leaves, anthropogenic noise and the high-frequency calls of insects. The solution of avoiding jamming under these circumstances is relatively effortless as the bats can choose to forage elsewhere. Yet, interference can also originate from the calls of other bats (Dusenbery, 1992). In these scenarios, the solution for avoiding interference is less straightforward.

Foraging bats often 'eavesdrop' on others to find food (Cvikel et al., 2015a) by listening for the terminal (feeding) buzzes of conspecifics, meaning that the sounds of feeding will always have the potential to attract additional individuals, even should that bat change foraging sites. When bats feed in mixed-species groups, heterospecific individuals may also cue in on feeding calls (Barclay, 1982). Although bats are capable of distinguishing heterospecific calls from the calls of conspecifics (Dorado-Correa et al., 2013), species that share certain ecological dimensions, such as diet, may converge upon the same resources (Li et al., 2014). With multiple bats foraging in the same area, the acoustic background unavoidably becomes more problematic as the potential for passive jamming rises. Adding to this complexity, Brazilian free-tailed bats (*Tadarida brasiliensis*) produce distinct social signals that actively jam the sonar of conspecific competitors, causing them to miss their targets (Corcoran and Conner, 2014). Bats have been observed employing a number of tactics to avoid sonar jamming, including remaining silent while using passive sensing (Chiu et al., 2008) and altering various parameters of echolocation calls in real time (Gillam et al., 2007). Collectively, these dynamic vocal adjustments can be utilized to avoid both spectral overlap (Surlykke and Moss, 2000) and temporal coincidences (Obrist, 1995) in the form of a jamming avoidance response (JAR), similar to the behavior found in weakly electric fishes (Bullock et al., 1972). But investigators study numerous species and there is little consistency in the types of signals presented and the behavioral tasks being performed. This makes it difficult to interpret results. Measurement of potential JARs is further complicated by the fact that bats adjust their vocalizations in response to the presence of other individuals, others' vocalizations or both (Amichai et al., 2015). In addition to controlling for the complication of multiple bats, we herein differentiate the difference between passive and active jamming. Passive jamming may be elicited by any interfering sound in the environment, including the echolocation of other bats foraging nearby, whereas active jamming refers to those signals either generated by heterospecific and conspecific bats as an adaptation to decrease food competition or produced by sonar jamming moths (Corcoran et al., 2009).

We tested whether active jamming signals of bats can elicit similar behavioral changes in heterospecific individuals. Only a few studies have documented effects in heterospecifics (Bartonička et al., 2007; Fawcett et al., 2015; Necknig and Zahn, 2011), all of which document changes in free-flying bats performing no specific task, and to date, only two other studies have presented active jamming signals to bats and documented the resulting changes in

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echolocation (Corcoran and Conner, 2014; Corcoran et al., 2011). This experiment will be the first to present active interference stimuli of heterospecifics to bats performing a behavioral task. We chose to use sinusoidal FM (sinFM) signals of *T. brasiliensis* as our potential jamming signal, as its effectiveness on conspecifics has been documented (Corcoran and Conner, 2014). The big brown bat [*Eptesicus fuscus* (Palisot de Beauvois 1796)] was chosen as the target species because of its ecological overlap with *T. brasiliensis*. Both species share similar geographic and dietary components and have been observed foraging in the same areas (A. J. Corcoran, personal communication) and both have well documented JAR behaviors (Bates et al., 2008; Gillam et al., 2007).

We predicted that sinFM calls of *T. brasiliensis* would jam a foraging *E. fuscus*, causing failed capture attempts, eliciting a JAR or both. To test this hypothesis, we used playback experiments presenting sinFM signals to free-flying *E. fuscus* as they attempted to capture tethered prey items. Our results illustrate that active sonar jamming signals can affect the echolocation calls emitted by heterospecific bats.

MATERIALS AND METHODS

Animals

The Wake Forest University Animal Care and Use Committee approved all procedures described herein (A16-127). We used three wild-caught, adult male big brown bats (*E. fuscus*) captured near Wake Forest University (Forsyth County, NC, USA) under NC state collecting permit 16-SC01070. The bats were housed together in cages in a temperature-controlled room (~25°C) on a 12 h:12 h light:dark cycle. Bats had continuous access to water and were fed mealworms (*Tenebrio molitor* larvae) and adult female greater wax moths (*Galleria mellonella*) nightly. Moths were acquired as larvae from King's Wholesale Bait (Liberty, IN, USA) and reared to adulthood. Individual bats were trained to remove food from a tether (described below) prior to starting playback experiments.

Experimental setup

Trials took place in an outdoor flight cage (18 m long, 5.5 m wide, 3 m tall) adjacent to Winston Hall on the Wake Forest University

campus (Fig. 1). *Galleria mellonella* were deafened by ablating their tympanic membranes. They were tethered by the abdomen to the ceiling of the flight cage with a single monofilament line (1 m long, 0.38 mm diameter) that allowed them a limited flight radius. The flight cage was illuminated with three Raytec Raymax 200 platinum infrared illuminators (Ashington, UK).

Bat stimuli and playback

SinFM calls previously recorded from *T. brasiliensis* (sample rate=300 kHz) were deconstructed to include only their downsweep ($n=27$) or upsweep ($n=30$) components (Fig. 2). We included these deconstructed signals as a way of determining whether directionality of a FM signal influences its effectiveness, as measured by successful captures and/or alterations in echolocation parameters. Given that bats possess neurons that respond selectively to sweep direction (Andoni et al., 2007; Razak and Fuzessery, 2006; Suga, 1968; Voytenko and Galazyuk, 2007), we were interested whether the presentation of these different stimuli would result in observable behavioral changes. These signals, along with the full sinFM signal ($n=57$) were played back to three bats individually during capture attempts via an AT100 ultrasonic transmitter (Binary Acoustics Technology, Tucson, AZ, USA). The transmitter was placed 1 m above the moth and sinFM signals were produced at 95 dB SPL, measured at the position of the moth (RMS) with a Brüel and Kjær (B&K, Nærum, Denmark) ¼ inch microphone connected to a B&K 2610 amplifier. Playback was triggered manually as the bat approached the target and playback of the signal occurred continuously until the bat made contact with the target. The timing (during the search or approach phase of the echolocation sequence) was determined post-recording. The control condition was silence ($n=129$).

Video and audio recording

Each trial was recorded with three calibrated high-speed, infrared-sensitive cameras (Basler Ace acA-2000-50gmNIR; Ahrensburg, Germany). Video recordings were acquired with StreamPix6 software (Norpix, Inc., Montreal, Canada) at 80 frames s^{-1} with 1280×720 pixel resolution. The echolocation calls were recorded

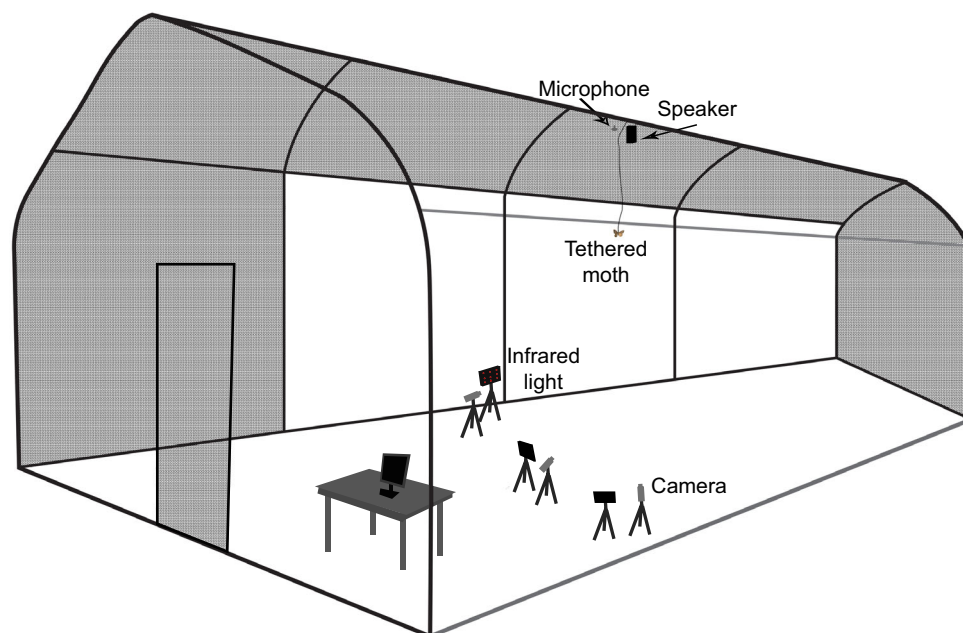


Fig. 1. Diagram of recording setup in the mesh-covered flight cage.

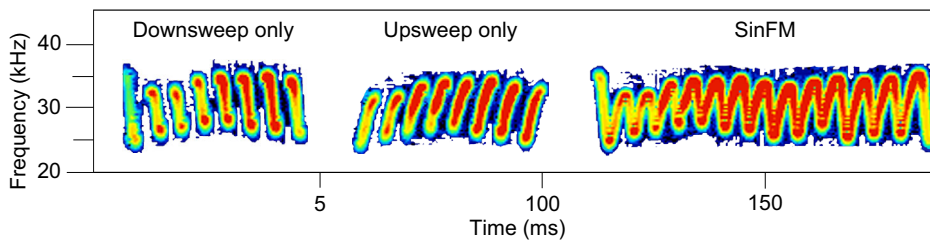


Fig. 2. Sinusoidal frequency modulated (sinFM) signal deconstructed to only the downsweep or upsweep components compared with the full sinFM. The relative amplitude of frequency content is indicated by color variations; warmer colors indicate higher amplitude.

for each trial with a small (3 mm diameter) ultrasonic microphone placed 1 m above the moth and connected to an Avisoft USGH recording unit (Avisoft Bioacoustics, Glienicke, Germany), sampling at 250 kHz. Cameras and microphones recorded in synchrony, triggered via a TTL pulse generated with custom hardware (Innovation Systems, Columbiaville, MI, USA).

Video recordings were reviewed and categorized as (1) successful capture ($n=184$; Movie 1); (2) attempted capture, unsuccessful ($n=59$; Movie 2); or (3) no attempted capture or aborted attack ($n=42$; Movie 3). Aborted attacks were differentiated from attempted captures by the physical behavior of the bat. In an attempted capture, bats would curl the tail or wing membranes to capture the moth, regardless of whether they made contact with the moth. Those that made no attempted capture would fly by the moth without appearing to slow or displaying any changes in body conformation that would indicate capture. In aborted attacks, bats would reduce their speed and/or change directions completely, avoiding all contact with moths. Trials in which bats simply flew past the tether were not scored. Often, bats would make multiple attempts following a failed initial attempt and be successful; however, only the first attempt was evaluated in every trial. Only trials that were scored as a 1 ($n=184$) or 2 ($n=59$) were included in the analyses.

Audio recordings were reviewed, and only those in which the sinFM signal was triggered prior to, and played throughout the duration of, the terminal buzz were included. These audio files were then edited in Adobe Audition v. 5.0.2 (Adobe Systems, Inc., San Jose, CA, USA) to isolate the echolocation calls of the first capture attempt, verified with the timing of the synchronized video recordings, by manually removing the echoes of individual calls, the second and third harmonics, and the stimuli. Post-processing, parameter values were taken from the automatic parameter measurement tool in Avisoft. Files were high- and low-pass filtered at 15 and 200 kHz, respectively. The duration threshold was set to be

approximately 1 ms and frequency thresholds were set to be -38 dB. We also chose to only analyze the primary, or first, harmonic. For the purpose of this study, bat attack phases were determined based on the inter-pulse interval (IPI) of the echolocation calls and are defined as: <5 –12 ms (buzz), 12–49 ms (approach) and ≥ 50 ms (search). A list of all measured parameters along with their abbreviations and definitions can be found in Table 1.

Statistical analysis

We first analyzed the video trials to determine whether the playback of sinFM signals resulted in more failed capture attempts than in silent conditions using a generalized linear mixed model (GLMM) with a binomial error distribution. We next examined the echolocation calls emitted by each bat during their capture attempts in order to determine whether the signal playback would result in the spectral or temporal changes associated with JAR behaviors. From each audio recording, we extracted the following parameters for bat calls in the approach and buzz phases: maximum frequency (F_{\max}), minimum frequency (F_{\min}), bandwidth (F_{bw}), peak frequency (F_{peak}), IPI, pulse duration (D_{call}) and sweep rate (SR) (Table 1). Measurements for F_{\max} , F_{\min} , F_{bw} , F_{peak} and SR were taken from the spectrogram (FFT length=512, Hamming window) using SASLab Pro (Avisoft Bioacoustics). Measurements for IPI and D_{call} were taken from the oscillogram using MATLAB (The MathWorks, Natick, MA, USA). Data for each parameter were placed into a different linear mixed model (LMM). To compensate for multiple comparisons, the resulting P -values were adjusted using the Benjamini–Hochberg method.

All data analysis was conducted in R v. 3.3.2 (<https://www.r-project.org/>) using the lme4 package (Bates et al., 2015). For all statistical models, individual bat identification was used as a random effect to account for the lack of independence in using individuals for multiple trials over the course of several nights. For the LMMs, the individual file containing the series of bat calls for one trial and the day on which trials were conducted were also used as separate random effects. *Post hoc* analyses were conducted with the lsmeans package (Lenth, 2016) and multiple comparisons were corrected with the Bonferroni-based false discovery rate method ($\alpha=0.05$).

Table 1. Parameters measured from each audio recording along with the abbreviations used throughout this paper and its definition

Acoustic parameter	Abbreviation	Definition
Pulse duration	D_{call}	Duration of individual sonar emissions
Maximum frequency	F_{\max}	Highest frequency (kHz) of a sonar emission
Minimum frequency	F_{\min}	Lowest frequency (kHz) of a sonar emission
Peak frequency	F_{peak}	Frequency (kHz) with the most energy in a sonar beam
Bandwidth	F_{bw}	Range of frequencies covered in a sonar emission
Inter-pulse interval	IPI	Time (ms) between successive sonar emissions
Sweep rate	SR	Quotient of bandwidth÷pulse duration; describes the slope of a frequency modulated call

RESULTS

We found no significant difference in the proportion of successful captures between each stimulus condition ($F_{3,236.08}=0.73$, $P=0.53$). Regardless of stimuli, the bats had a high rate of successful captures, always surpassing 60% (Table 2). For the echolocation parameters

Table 2. The percentage of successful captures under each playback condition across all nights

Stimulus	Successful captures (%)
Silent	78
Downsweep only	67
Upsweep only	70
SinFM	77

analyzed, we present only those that were found to be statistically significant; all other data can be found in Fig. S1.

There was a significant increase between D_{call} in silent conditions and the playback stimuli in both the approach ($F_{3,229.15}=6.94$, $P<0.001$) and the buzz phase ($F_{3,234.94}=3.78$, $P=0.026$). There was a significant decrease in F_{bw} during the buzz phase ($F_{3,238.18}=5.42$, $P=0.0035$), and the buzz phase also showed a significant increase in F_{peak} ($F_{3,229.71}=5.68$, $P=0.0031$).

We also determined that SR of both phases was significantly decreased in playback conditions (approach: $F_{3,226.89}=10.10$, $P<0.001$; buzz: $F_{3,230.06}=8.24$, $P=0.0022$). *Post hoc* analyses reveal that the full sinFM signals consistently elicited longer D_{call} (Fig. 3A), lower F_{bw} (Fig. 3B) and lower SR (Fig. 3C) than other conditions. F_{peak} was significantly increased compared with the silent condition for all jamming stimuli (Fig. 3D).

DISCUSSION

We predicted that *E. fuscus* would fail to capture prey items and/or exhibit echolocation changes to counteract the effects of our jamming stimuli. The bats were able to catch the prey item under all of our test conditions; thus, we did not find evidence to support heterospecific jamming capabilities. We would like to acknowledge that this could potentially be attributed to the setup of our

experiment, in which the prey items were tethered and restricted in their ability to fly away, possibly minimizing the overall effectiveness of the stimuli. We did, however, show that four parameters – D_{call} (approach and buzz), F_{bw} (buzz), F_{peak} (buzz) and SR (approach and buzz) – were significantly altered between silent conditions and the different playback stimuli.

Under the strictest definition of JARs, spectrotemporal changes should increase the differences between the bats' emitted signal and the jamming stimulus (Ulanovsky et al., 2004). We suggest expanding the definition of a JAR to include all changes that may increase the signal-to-noise ratio, as well as those that maximize spectral or temporal differences between the bats' own calls and active jamming stimuli originating from conspecific and heterospecific organisms. The term was first applied to the behaviors of weakly electric fishes and it included only the reflexive shifting of frequency, or change in timing, of electric pulses to increase disparity between two individuals (Bullock et al., 1972). This definition most likely encompassed such a limited range of changes because the only natural scenario in which these animals face interference is in the presence of other electrogenic fish. Because bats can encounter interference in their dominant sensing modality from numerous sources and can alter many more parameters of their signal, the traditional usage is far too constrained to account for the all of the possible responses to these sources.

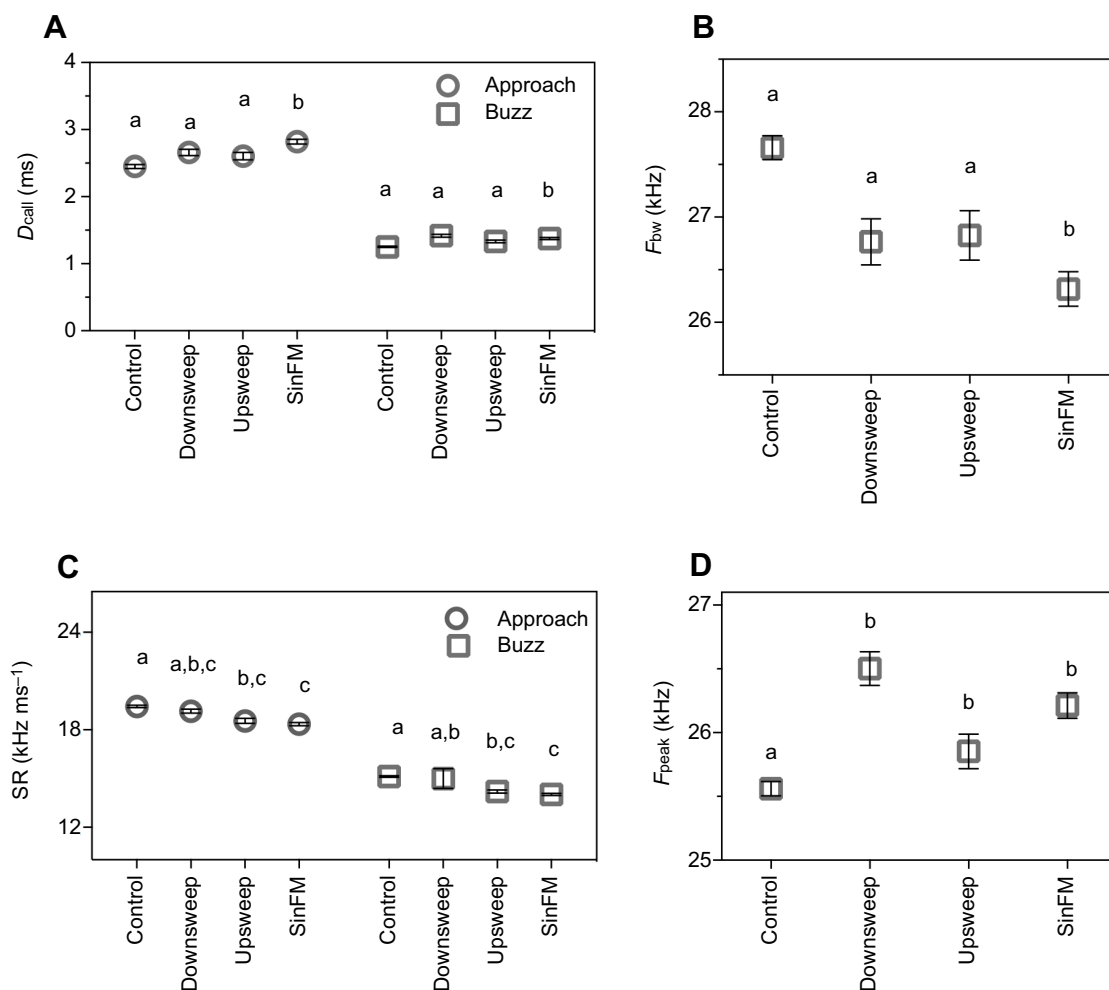


Fig. 3. Echolocation parameters that were significantly altered in response to playback. (A) Differences in pulse duration (D_{call}) among stimuli for both the approach and buzz phases. (B) Effects of stimulus type on bandwidth (F_{bw}) of the buzz phase. (C) Differences in sweep rate (SR) by stimulus type for both the approach and buzz phases. (D) Effects of stimulus type on peak frequency (F_{peak}) of the buzz phase. Groups sharing a letter are not significantly different (false discovery rate *post hoc* test, $P<0.05$). All data are means \pm s.e.m.

Additionally, it is unclear whether the myriad of changes observed in bat echolocation can be attributed solely to reflexive shifts in response to stimuli, as we do not see evidence of stereotyped responses to even the same type of stimulus across studies. The traditional definition would also require the presence of another bat, but we already acknowledge that jamming signals can have alternate origins, such as sonar-jamming moths (Corcoran et al., 2011; Miller, 1991). Ultimately, this would mean that all changes in signal design in response to the presentation of active jamming stimuli generated from conspecifics and heterospecifics that have the potential to improve echo reception would be considered a JAR in bat species.

The nature of echolocation is to derive meaningful information from subtle shifts in spectrotemporal characteristics, and it is likely that these fine-scale adjustments in call design can significantly impact the perception of echoes and influence task performance. The absolute changes we observed in the bats' pulse duration and sweep rates were modest, varying by approximately 1 ms or less. Other studies utilizing *E. fuscus* have shown that they are capable of changing many other echolocation parameters depending on the task being performed. These include altering start and end frequencies and bandwidth (Chiu et al., 2009), as well as increasing call duration and shortening the duration of the buzz phase (Corcoran et al., 2011) and ceasing echolocating altogether (Chiu et al., 2008). Many of these changes were also small scale, on the order of a few kilohertz and or milliseconds, just like our observations.

Bats responded differently to each of the stimuli presented. Playback of the full sinFM resulted in the most changes in echolocation parameters and we consider it to be the most effective at eliciting changes. Upsweep-only and downsweep-only signals elicited similar responses. These results are somewhat counterintuitive, as it was expected that signals most similar to the bats' own calls, the downsweep-only signals, would be most effective.

Evidence to the contrary could possibly be due to bats utilizing templates of their own calls for echo recognition. It has been proposed that bats compare the time–frequency structure of their call emissions with that of the returning echoes (reviewed in Corcoran and Moss, 2017). *Eptesicus fuscus* presented with upward-sweeping FM calls (Masters and Jacobs, 1989) or stimuli otherwise altered in time or frequency (Masters and Raver, 1996, 2000) displayed reduced abilities in range discrimination tasks.

These studies suggest that bats are most capable of extracting information from calls that are most similar to their own templates.

Although this provides a feasible argument as to why downward-sweeping FM calls require the least compensation, it is still difficult to determine how all of these stimuli provoked changes in echolocation. However, we can evaluate the potential advantages these changes provide. FM calls are best for determining target range and structure as the increased bandwidth increases the resolving power of the call (Holderied, 2006). Though we observe an approximately 1 kHz downshift in bandwidth in the buzz phase, we argue that bats could afford this potential sacrifice in resolution because of the high information redundancy of an increased pulse rate typical of shifting from approach to buzz (Ratcliffe et al., 2013). Bats may also decrease bandwidth to concentrate more energy into fewer frequencies in order to increase the signal-to-noise ratio. The changes in peak frequency are most often attributed to increasing the differences between an individual bat and surrounding bats (Bates et al., 2008; Ibáñez et al., 2004; Necknig and Zahn, 2011; Ratcliffe et al., 2004), or in this case, the simulated bat emitting the sinFM. However, we observed an increase in peak frequency towards that of the stimulus, and believe this to be another compromise to increase signal-to-noise ratio (Tressler and Smotherman, 2009). Increasing pulse durations increases signal energy, and this is thought to be a way for bats to increase the signal-to-noise ratio by increasing echo detectability (Amichai et al., 2015). The resulting combination of bandwidth and pulse duration, i.e. sweep rate, can thus be optimized for the echolocation task being performed.

Boonman and Ostwald (2007) used a computer model to simulate the bat cochlea responding to returning echoes and found that an optimal sweep rate is critical to the temporal resolution of multiple echoes. Sweep rate generally becomes faster as the bat closes on its target (Inoue et al., 2002), and this is likely to allow the bat to receive the clearest acoustic image of the target as the acuity of each echo is improved and bats are able to better determine the timing of each echo. However, faster sweep rates decrease the chances of channel activation in computer simulations, which correspond to the inner hair cells of the bat cochlea (Boonman and Ostwald, 2007). Thus, decreasing sweep rates (our observation) are more likely to increase the number of individually detected echoes. This further emphasizes the sensory trade-offs bats face (Schnitzler et al., 2003;

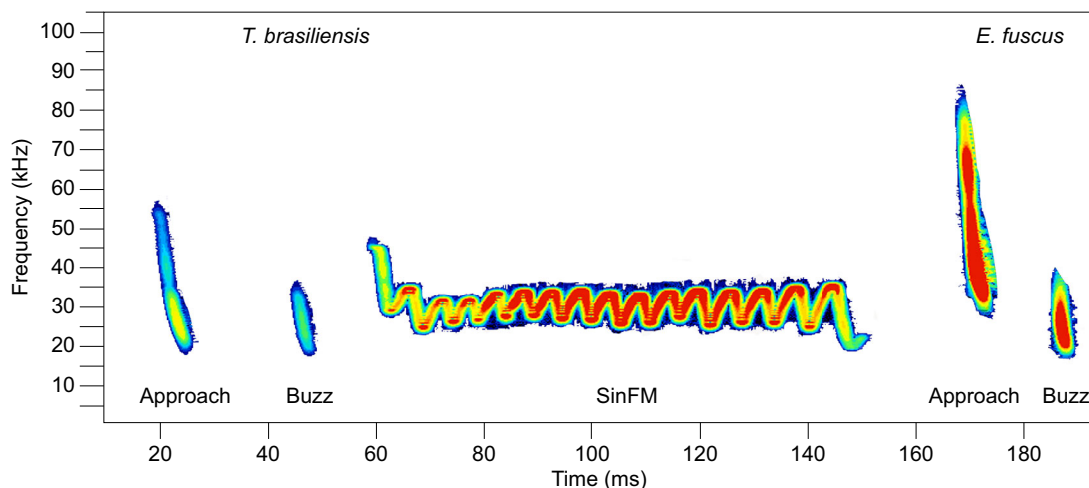


Fig. 4. Examples of first harmonic approach and buzz calls for *Tadarida brasiliensis* and *Eptesicus fuscus* compared with the sinFM signal used in playback. There is considerably more overlap in the *E. fuscus* buzz call, and this may be why we see greater flexibility demonstrated in this portion of the signal.

Ulanovsky and Moss, 2008) and that these trade-offs are necessary to optimize target detection and localization.

It is important to note that not all of these parameters in which we observe changes may necessarily provide perceptible changes in returning echoes, especially given their small scale. Some changes may simply be by-products of others, but all of these changes in various combinations may contribute something to increasing the ability to resolve returning echoes. Additionally, there are some changes we fail to see that have been documented in other studies, such as significant changes to minimum or maximum frequency. The approach calls of *E. fuscus* overlap fewer frequencies with the sinFM signal than do those of *T. brasiliensis* (Fig. 4), and the increased bandwidth possibly eliminates the need for any changes to further maximize differences. This could also explain why the sinFM signal did not have a negative effect on the capture success rates of *E. fuscus*. In *T. brasiliensis*, Corcoran and Conner (2014) demonstrated that playback of the sinFM resulted in a decreased number of successful captures. In response, the jammed bats only significantly increased their maximum and minimum frequencies and this did not significantly alter the overall bandwidth of the calls. Other parameters, such as call duration and IPI, were unaffected as well. This upward shift in call frequency is consistent with other studies on *T. brasiliensis* in the presence of acoustic interference. The normal echolocation calls of *T. brasiliensis* have more spectral overlap with the sinFM signal, and this shift may be an example of a traditional spectral JAR.

However, there are two alternatives that could explain the changes observed. The first is that bats were exhibiting the Lombard effect – a physiological change in the larynx resulting in changes in intensity, often accompanied by frequency and call duration changes. This response has been documented in *E. fuscus* and results in louder calls (Luo et al., 2017). We were unable to record intensity values for the bats during their capture attempts, owing to equipment limitations, and thus, we cannot confirm or deny that they were perhaps exhibiting the Lombard effect. Because this phenomenon is generally accompanied by calls of increased duration (Luo et al., 2015; Takahashi et al., 2014) and frequency (Hage et al., 2013) and because our bats lengthened the duration of their calls and increased the minimum and maximum frequencies in the approach phase (though not significantly so), this is a possibility. The second explanation is the attention hypothesis that states that bats will differentially alter their echolocation based on objects in their acoustic environment drawing their attention. These objects may be various prey items, other bats, or obstacles such as buildings or trees. Bats may shorten their pulse duration to avoid pulse–echo overlap, just as they would if they were approaching clutter (Kalko and Schnitzler, 1993; Melcón et al., 2007; Schnitzler et al., 2003). This would suggest our bats were responding to the jamming stimulus as if it were an object entering their acoustic field of view, despite its purpose to reduce capture success, and this possibility has been implicated in other studies (Cvikel et al., 2015b; Götze et al., 2016). For our experiment, this is the less likely scenario, as it might be assumed that a bat shifting its attention from its current task, in this case, prey capture, would result in more failures.

Much work has been done on the subject of echolocating bats and whether they exhibit some type of response to jamming signals, though there is currently no consensus on the matter. To date, evidence for spectral or temporal JAR is somewhat conflicting as variation in echolocation is highly context dependent and experimental designs are structured with major differences. We found that in the presence of the active jamming sinFM signal of *T. brasiliensis*, *E. fuscus* significantly alters its echolocation. This is

the first documentation of bat active jamming signals affecting heterospecifics and is also one of the first presentations of evidence that bats alter the structure of the terminal buzz in response to acoustic interference. Bats increased their pulse duration to increase echo detectability and decreased sweep rates to generate more accurate echo timing in both the approach and buzz phases. In the buzz phase, bats decrease their bandwidth to concentrate energy over a reduced range of frequencies and increase the peak frequency to help differentiate their calls from the stimuli. Many of these changes reflect similarities found in other JAR studies while others are novel findings. All of our observations support the hypothesis that bats are altering their echolocation to increase the signal-to-noise ratio of perceived echoes, a JAR under our expanded definition. Though our understanding of how particular features of jamming stimuli elicit changes is still developing, it is clear that the echolocation flexibility of bats allows them to remain successful dominators of the night sky in the presence of passive and active jamming signals.

Acknowledgements

We would like to thank Nicholas J. Dowdy and Yohami Fernandez-Delgado for their assistance in experimental design and data collection.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: T.K.J., W.E.C.; Methodology: T.K.J., W.E.C.; Software: M.J.W.; Formal analysis: T.K.J.; Resources: W.E.C.; Writing - original draft: T.K.J.; Writing - review & editing: T.K.J., W.E.C.; Visualization: T.K.J.; Supervision: W.E.C.; Project administration: W.E.C.; Funding acquisition: W.E.C.

Funding

This material is based upon work supported by the National Science Foundation Graduate Research Fellowship Program under grant no. 1452598.

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.176511.supplemental>

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