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RESEARCH ARTICLE

Adaptive frequency shifts of echolocation sounds in *Miniopterus fuliginosus* according to the frequency-modulated pattern of jamming sounds

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ABSTRACT

When flying in a group, echolocating bats have to separate their own echoes from pulses and echoes belonging to other individuals to extract only the information necessary for their own navigation. Previous studies have demonstrated that frequency-modulated (FM) bats change the terminal frequencies (TFs) of downward FM pulses under acoustic interference. However, it is not yet clear which acoustic characteristics of the jamming signals induce the TF shift according to the degree of acoustic interference. In this study, we examined changes in the acoustic characteristics of pulses emitted by *Miniopterus fuliginosus* while presenting jamming stimuli with different FM patterns to the bat flying alone. Bats significantly altered their TFs when responding to downward (dExp) and upward (uExp) exponential FM sounds as well as to a constant-frequency (CF) stimulus, by approximately 1–2 kHz (dExp: 2.1±0.9 kHz; uExp: 1.7 ±0.3 kHz; CF: 1.3±0.4 kHz) but not for linear FM sounds. The feature common to the spectra of these three jamming stimuli is a spectrum peak near the TF frequency, demonstrating that the bats shift the TF to avoid masking of jamming sounds on the TF frequency range. These results suggest that direct frequency masking near the TF frequency range induces the TF shift, which simultaneously decreases the similarity between their own echolocation sounds and jamming signals.

KEY WORDS: Bats, Jamming avoidance response, Terminal frequency

INTRODUCTION

The frequency-modulated (FM) pattern of echolocation pulses emitted by bats is generally similar among conspecific individuals. However, even in situations involving acoustic interference, the sensing mechanism of the bat appears to work very accurately. For example, even though many bats are flying at the same time, they never collide with each other while capturing small insect prey using echolocation. Therefore, bats probably possess a mechanism for listening to the echoes of pulses that they themselves emit within a complex auditory scene created by the pulses emitted by every conspecific individual flying together.

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Because a bat emits a signal intermittently for echolocation, information obtained from echoes is fragmentary. Therefore, bats increase the pulse emission rate to increase the number of acquisitions of target information, but this strategy exacerbates any interference. From the instant of pulse emission, bats are thought to have a time window of several tens of milliseconds during which to processes returning echoes (Simmons et al., 1979). However, separating echo information using only this time window tactic can become difficult in the following cases: (1) during self-jamming conditions when their own echoes from the surroundings overlap temporally with the target echo within the time window and (2) under conspecific-jamming conditions when a pulse or echo belonging to other conspecific bats overlaps with their own pulse or echo within the time window. For jamming due to a cluttered environment, *Eptesicus fuscus* shifts the terminal frequency (TF) of its downward FM sounds by a few kilohertz, only when echo streams of consecutive emitted pulses ('strobe groups') temporally overlap and create ambiguity about matching echoes with emission (Hiryu et al., 2010). This strategy represents one type of jamming-avoidance response (JAR) to assign echoes to their own emissions by shifting the TF during echolocation. For jamming environments caused by conspecifics, some field experiments have reported that bats avoid interference by changing the frequency of the emitted pulses during foraging flights with conspecifics (Habersetzer, 1981; Ibáñez et al., 2004; Moss and Surlykke, 2001; Necknig and Zahn, 2011). In addition to studies of free-flying bats under natural conspecific jamming conditions, playback experiments also found that some FM bats alter their TFs in response to playback of bat-like FM sounds (Gillam et al., 2007; Hase et al., 2016; Luo and Moss, 2017; Takahashi et al., 2014) and to artificially generated constant-frequency (CF) or noise stimuli (Bates et al., 2008; Tressler and Smotherman, 2009). The reported responses to FM sounds were the same as those to CF sounds or noise stimuli (i.e. increasing frequency, duration or sound pressure level). Recently, Gillam and Montero (2016) evaluated the effects of CF and FM sounds followed by CF components of various durations on freely flying *Tadarida brasiliensis* in the field, and reported that the bandwidths of the jamming signals affected the strength of the JAR. However, to our knowledge, no other studies have investigated whether and how FM echolocating bats respond differently to naturalistic stimuli like pulse, tone burst or noise stimuli.

The majority of previous studies have reported TF shifts under acoustic interference conditions during echolocation. However, it is not yet clear which acoustic characteristics of jamming signals cause the TF shift. In this study, we examined the following two hypotheses: (1) bats shift the TF in response to a jamming signal with an FM pattern very similar to their own echolocation signals, or (2) bats shift their TF any time the TF of the returning echoes is masked acoustically because the TF is important for echolocation in FM bat species. We conducted playback experiments using

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loudspeakers in a laboratory flight chamber; five jamming stimuli with different FM patterns were presented to free-flying bats so that we could investigate whether the sounds that mimic the entire echolocation pulse have a greater effect than sounds that merely mask the loudest (terminal) portion of the call. Changes in the acoustic characteristics of the pulses under acoustic interference were investigated using a telemetry microphone system (Hase et al., 2016). We created four FM sounds as jamming stimuli (downward or upward and exponential or linear) and one CF sound. If the first hypothesis about the cause of the TF shift were supported, bats would be expected to respond only to the downward exponential FM sound, as it most closely matches their own echolocation sound. In contrast, if the second hypothesis were supported, a TF shift would be expected to occur for the downward and upward exponential FM sounds as well as a CF sound at the TF.

MATERIALS AND METHODS
Subjects
Eight *Miniopterus fuliginosus* Hodgson 1835 (body mass, 10.8–13.4 g; five males and three females) were used in this experiment. The bats were caught in the wild from large colonies roosting in natural caves in Fukui Prefecture, Japan, under license and in compliance with current Japanese laws. Animals were kept in a temperature- and humidity-controlled room (4.0×3.0×2.35 m; L×W×H) at Doshisha University (Kyoto, Japan). Bats were fed mealworms *ad libitum* and had free access to vitamin-enriched water. The day–night cycle of the room was set to 12 h light and 12 h dark. *Miniopterus fuliginosus* emit downward FM pulses with maximum energy at the fundamental component.

All experiments complied with the Principles of Animal Care, publication no. 86-23, revised 1985, of the National Institutes of Health and with current Japanese laws. All experiments were approved by the Animal Experiment Committee at Doshisha University.

Experimental procedure
We conducted the experiments in a flight chamber (9.0×4.5×2.35 m; L×W×H) at Doshisha University. The chamber was constructed of steel plates to lower the risk of interference from external electromagnetic noise and commercial FM radio stations. During our experiments, long-wavelength lighting with filters (filtering out wavelengths below 650 nm) was used to prevent the bat from using visual information. The bats flew in a flight space that was delimited by a net suspended from the ceiling and walls (3.0×4.5×2.35 m; L×W×H). We set four loudspeakers (Pioneer Corp., PT-R7 III, Kanagawa, Japan, frequency range: 20–80 kHz) at each corner of the flight space in the experimental chamber. The height of the four loudspeakers was 1 m above the floor, and the direction of each loudspeaker was set to face the center of the flight chamber. The experimental procedure was similar to that used in a previous study (Hase et al., 2016). First, an individual bat was flown in the absence of jamming sounds (jamming off). Then, the same bat was flown in the presence of jamming sounds simultaneously presented from the four loudspeakers (jamming on). In this experiment, we recorded for about 20–30 s while flying the bat under the jamming-off and -on conditions (note that the jamming sounds were presented to the bats approximately 10–15 s after the bat had started to fly). Then, pulses emitted during a 10 s period under either the jamming-off or the jamming-on condition were analyzed. All bats flew in a circular orbit within the chamber. We tested whether flying bats modified the acoustic characteristics of their vocalizations according to the FM patterns of the presented jamming sounds.

Sound stimuli
We generated sound stimuli using Matlab 2014a. We created five types of jamming sounds with different FM patterns using the following formula (Parsons and Jones, 2000):

$$f(t) = \frac{f_0}{f_0 - af_1} \left\{ (f_0 - f_1)\left(\frac{af_1}{f_0}\right)^t + (1-a)f_1 \right\}, \qquad (1)$$

where f_0 and f_1 indicate the start and terminal frequencies, respectively, and a is a constant that determines the shape of the sweep. By changing the value of a, jamming sounds with different frequency sweeps (including CF sounds) were created (Fig. 1): one CF sound of 45 kHz, which is slightly lower than the average TF (approximately 48 kHz) of this bat species (Hase et al., 2018); and four different types of FM sound with a minimum frequency of 45 kHz, a maximum frequency of 85 kHz and a bandwidth of 40 kHz: (1) downward exponential (dExp), (2) upward exponential (uExp), (3) downward linear (dLin) and (4) upward linear (uLin) FM sounds. The signal length of all sounds was 3 ms. In the dExp jamming sound, the FM pattern falls exponentially in the way of an echolocation FM pulse of *M. fuliginosus*. The interpulse interval between sounds was set at 50 ms. The sound pressure level of the jamming FM sounds ranged from 110 to 120 dB sound pressure level peak-to-peak at 10 cm from the loudspeaker.

Telemike recordings
Echolocation pulses emitted by flying bats were recorded using a custom-made telemetry microphone (Telemike) mounted on the back of the bat (Hase et al., 2016). The Telemike consisted of a 1/8 inch omni-directional condenser microphone (Knowles, Model FG-3329, Itasca, IL, USA), a miniature custom-designed FM transmitter unit, a 1.5 V hearing-aid battery (Sony, Type SR521SW, Tokyo, Japan) and a transmitting antenna; it weighed ~0.6 g, including the battery. The Telemike was attached to the back of the bat using double-sided adhesive tape, with the microphone pointing forward, between the bat's ears and 1 cm above the bat's mouth. The transmitter of the Telemike generated FM radio signals with a carrier frequency between 76 and 104 MHz, which was received by an FM radio antenna (Terk Technologies Corporation, FM+, Commack, NY, USA) suspended from the ceiling of the flight chamber. The received signals were demodulated using a custom-made FM receiver (ArumoTech Corporation, Kyoto, Japan) and digitized using a high-speed data-acquisition card (National Instruments, Model NI PXI-6358, Tokyo, Japan; 16 bit, sampling frequency=500 kHz). The total frequency response of the Telemike system was flat within ±3 dB between 20 and 100 kHz.

Sound analysis
The sound analysis was performed as described previously (Hase et al., 2016). The acoustic characteristics of emitted pulses from flying bats were analyzed from spectrograms from the Telemike recordings using custom-written Matlab 2014a scripts on a personal computer. In this study, we defined the initial frequency and TF of each sound as the highest and lowest frequencies in the spectrogram, respectively, that were −25 dB from the maximum energy portion of the spectrogram. The interpulse interval and duration of each sound were also determined from the spectrogram at −25 dB relative to the maximum energy portion. The bandwidth of each sound was calculated by subtracting the TF from the initial frequency. The sound pressure level was calculated from the peak-to-peak amplitude voltage of each pulse in the time domain. We compared the sound pressure level between jamming-off and
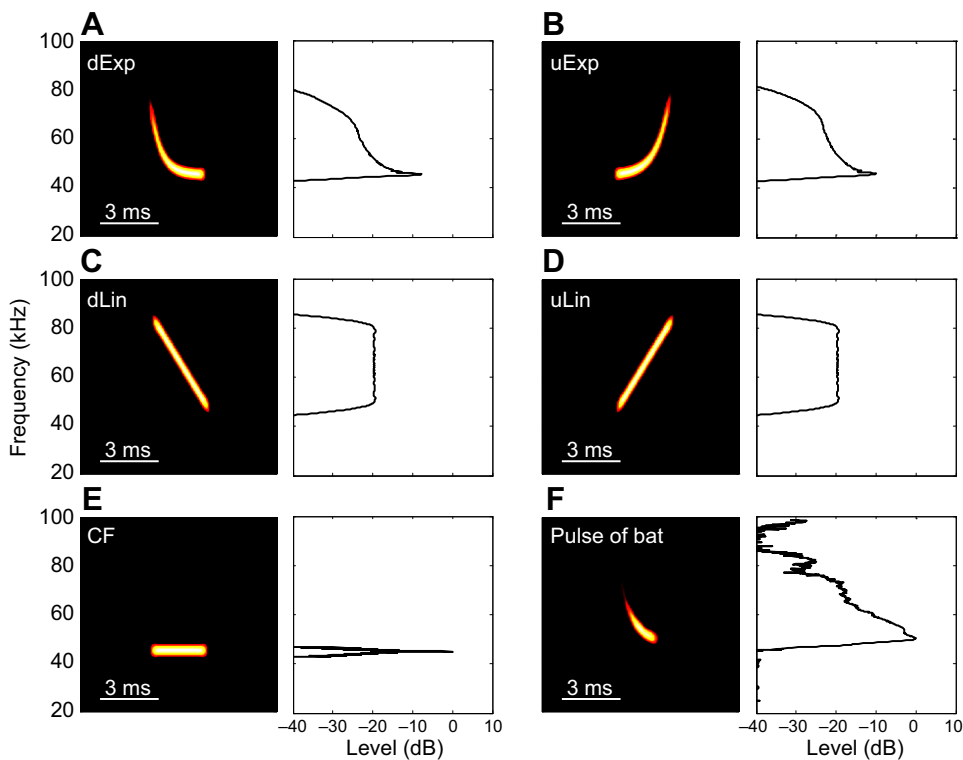
Fig. 1. Spectrogram (left) and spectrum (right) of five types of jamming stimuli used in this experiment. (A) Downward exponential jamming sound (dExp) with a sweep similar to the echolocation pulse of *Miniopterus fuliginosus*. (B) Upward exponential jamming stimulus (uExp). (C) Downward linear jamming stimulus (dLin). (D) Upward linear jamming stimulus (uLin). (E) Constant-frequency sound (CF) at 45 kHz. (F) Example of a typical pulse of *M. fuliginosus*. The powers in the spectra of five jamming stimuli were normalized to the peak power of CF sounds.

jamming-on conditions for each bat without removing the Telemike so that we could accurately evaluate changes in sound pressure level in response to the jamming sounds.

We performed Kruskal–Wallis tests to investigate whether a representative bat changed the TFs of its echolocation pulses in response to jamming sounds. If significant, we then used Mann–Whitney U-tests with Holm's correction to compare the TFs of pulses emitted under jamming-off and jamming-on conditions in response to the presentation of each stimulus. We also tested whether the mean changes in the acoustic characteristics of all bats under the jamming-on condition differed from 0 in response to each jamming stimulus using a one-sample t-test with Holm's correction. We used SPSS version 25.0 (IBM, Armonk, NY, USA) for all statistical analyses. Results are presented as means±s.d.
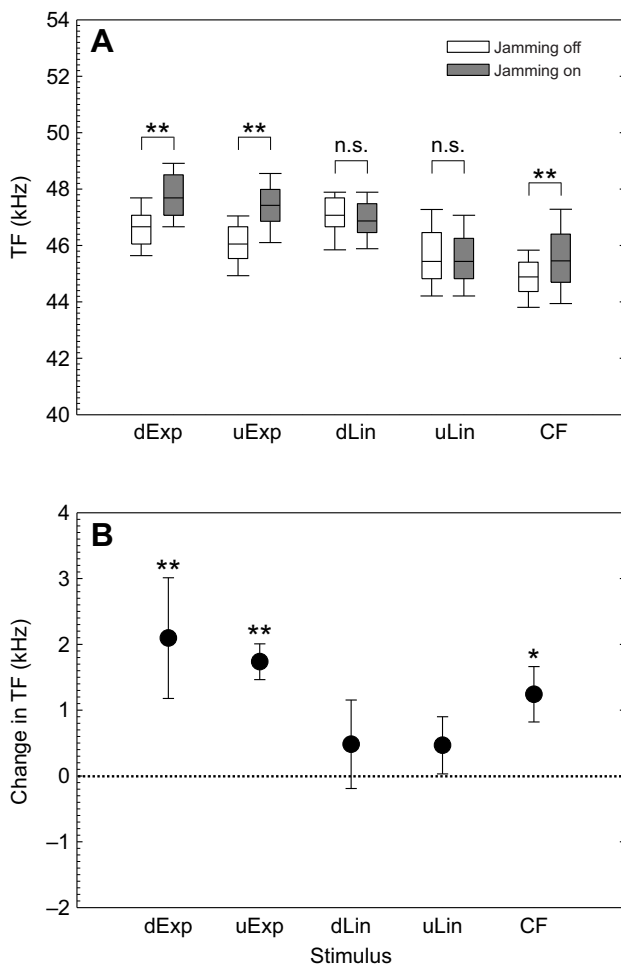
RESULTS
Changes in acoustic characteristics for each stimulus

The bat was exposed to the jamming sounds while flying in circles in the flight space; the state of the flight did not change regardless of the presence or absence of jamming sounds, similar to the findings of our previous study (Hase et al., 2016). The telemetry microphone recorded not only the pulses emitted by bats during flight but also the jamming sounds reaching the bats from the loudspeakers (Fig. 2). Fig. 2 shows that after receiving the dExp jamming sounds, the bat shifted the TF of the first emitted pulse (see yellow bars).

Fig. 3A shows a representative result from one individual. This bat significantly increased TF in response to dExp, uExp and CF (mean±s.d., dExp: from 46.7±0.8 to 47.8±0.9 kHz; uExp: from 45.9±1.0 to 47.5±0.9 kHz; CF: from 44.8±0.7 to 45.6±1.2 kHz, Mann–Whitney U-test, $Z<-5.269$, $P<0.01$). In contrast, the bat did
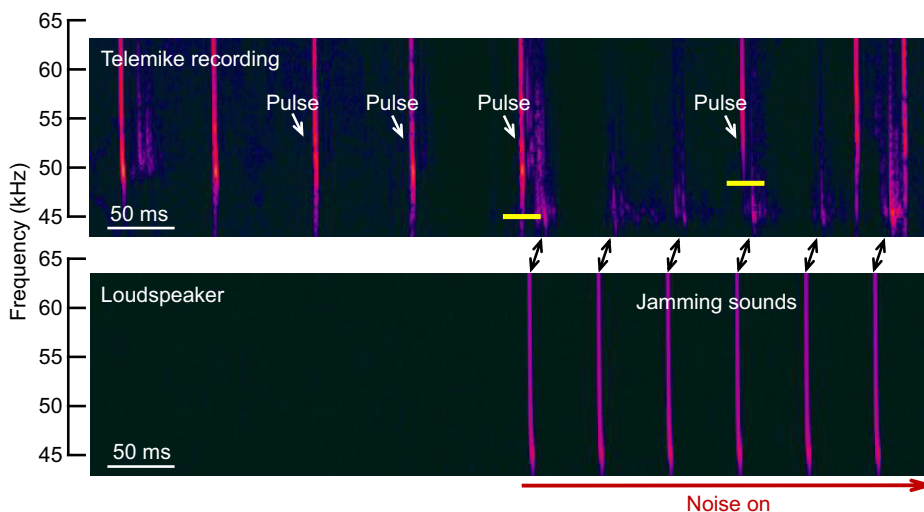
Fig. 2. Representative sound sequence recorded by the telemetry microphone during flight when dExp was presented at 50 ms intervals. At the moment of the jamming sound, the bat stopped emitting pulses, then increased the terminal frequency (TF, see yellow bars) of the emitted FM pulse.

Fig. 3. Comparison of changes in TF among five patterns of jamming stimuli in bat A. (A) Each boxplot shows the results of pulses emitted during a 10 s period under either the jamming-off or the jamming-on condition. Bat A significantly changed its TF in response to dExp, uExp and CF (Mann–Whitney U-test with Holm's correction, **$P<0.01$), whereas linear FM sounds (dLin and uLin) did not induce a TF shift (Mann–Whitney U-test with Holm's correction, $P>0.218$; n.s., not significant). (B) Comparison of changes in TF among five patterns of jamming stimuli for all bats. Significant changes in TFs were observed for dExp, uExp and CF (one-sample t-test with Holm's correction, **$P<0.01$, *$P<0.05$), whereas no significant changes in TFs occurred for dLin and uLin (one-sample t-test with Holm's correction, $P>0.134$). Results are presented as means ±s.d. Number of pulses analyzed in this study: dExp, 1889 pulses; uExp, 1512 pulses; dLin, 1662 pulses; uLin, 1532 pulses; CF; 1027 pulses.

not significantly change TF in response to dLin or uLin (dLin: from 46.9±1.0 to 46.9±0.9 kHz; uLin: from 45.6±1.1 to 45.6±1.1 kHz, Mann–Whitney U-test, $P>0.218$). Fig. 3B shows the changes in TF for all individuals. We subtracted the mean TF of each animal under the jamming-off condition from the TF of each pulse when presenting jamming sounds and then obtained individual means of the TF shift for all pulses of all individuals. Significant changes in TF were observed for dExp, uExp and CF (dExp: 2.1±0.9 kHz, $n=8$ bats, $t=6.068$, $P<0.01$; uExp: 1.7±0.3 kHz, $n=5$, $t=12.270$, $P<0.01$; CF: 1.3±0.4 kHz, $n=4$, $t=5.191$, $P<0.05$), whereas no significant changes in TF occurred for dLin and uLin (dLin: 0.5±0.7 kHz, $n=7$, $t=1.732$, $P=0.197$; uLin: 0.5±0.4 kHz, $n=5$, $t=2.145$, $P>0.134$).

Fig. 4 presents changes in the sound pressure level, duration, bandwidth and interpulse interval of all individuals. Regardless of the pattern of jamming sounds, the change in sound pressure level was not

significant (dExp: 1.2±1.7 dB; uExp: −0.8±1.4 dB; dLin: 0.5±2.3 dB; uLin: 0±0.9 dB; CF: −0.6±0.8 dB; one-sample t-test, $P>0.696$; Fig. 4A). Similarly, no significant changes were observed in the duration of the emitted pulse (dExp: 0.1±0.2 ms; uExp: 0±0.3 ms; dLin: 0±0.2 ms; uLin: 0.2±0.1 ms; CF: 0±0.3 ms; one-sample t-test, $P>0.262$; Fig. 4B). Although bandwidth slightly expanded in response to the jamming sounds, none of the changes was significant (dExp: 2.8±2.7 kHz; uExp: 1.9±3.7 kHz; dLin: 1.9±6.5 kHz; uLin: 1.5± 3.2 kHz; CF: 0.3±3.1 kHz, one-sample t-test, $P>0.220$; Fig. 4C). Similarly, no significant changes in the interpulse interval were observed in response to the different jamming sounds (dExp: 4.4± 6.6 ms; uExp: −5.1±5.0 ms; dLin: 1.9±7.3 ms; uLin: 7.1±6.8 ms; CF: 10.9±4.8 ms; one-sample t-test, $P>0.151$; Fig. 4D).

Rapid TF shift of bats responding to jamming stimuli
Fig. 5A,B shows the mean shifts in TF of emitted pulses of all bats in successive 50 ms time bins when presenting dExp and dLin. For dExp, an obvious shift of the mean TF occurred, whereas no such TF shift occurred in the presence of dLin. To determine how rapidly the bats changed TF in response to the jamming sounds, the size of the shift in TF for all bats was normalized as a frequency difference from the mean TF of each individual measured during the jamming-off condition. For the responses to jamming sounds other than dLin and uLin (which did not cause obvious TF shifts), we calculated the on-response time, which was defined as the time it took the mean TF of the bats to reach 63% of the mean TF during the jamming-on condition (Hase et al., 2016). By fitting a curve to the data for the temporal change in TF for all individuals (e.g. Fig. 5A), the on-response time was 140 ms for dExp, 50 ms for μExp and 320 ms for CF.

DISCUSSION
Acoustic characteristics of jamming signals that impact the TF shift
Previous studies have reported TF shifts by FM-echolocating bats under acoustic interference, e.g. when flying with other conspecifics in the field (Habersetzer, 1981; Ibáñez et al., 2004; Moss and Surlykke, 2001; Necknig and Zahn, 2011) or under artificial clutter conditions created by playback experiments using jamming sounds (Bates et al., 2008; Gillam and Montero, 2016; Gillam et al., 2007; Hase et al., 2016; Luo and Moss, 2017; Takahashi et al., 2014). However, few studies have addressed how the pattern of the FM of jamming signals impacts the degree of the TF shift (Gillam and Montero, 2016; Jones et al., 2018). Therefore, in the present study, we created five jamming sounds with different FM patterns to compare the behavioral response, i.e. the TF shift, as an index to determine which types of acoustic features of jamming sounds directly induce the TF shift in *M. fuliginosus* during free flight. For all bats used in the experiment, our results indicated significant TF shifts in response to only dExp, uExp and CF and not to dLin and uLin. Because the bats exhibited a TF shift in response to the uExp jamming sound, our findings did not support our first hypothesis, which predicted that bats shift the TF because the jamming signal is similar to the FM pattern of their own echolocation signals.

Fig. 1 shows that the spectral pattern of uExp is the same as that of dExp, which mimics the FM-echolocating sounds of *M. fuliginosus*. Although the response was slightly weaker compared with that to dExp and uExp, a significant change in the TF was also observed with CF jamming sounds. The common feature among the spectra of these three jamming stimuli is a spectrum peak near the TF. Our results may support the second hypothesis that bats shift their TF to avoid the masking of jamming sounds when the TF of the returning echoes is masked acoustically.
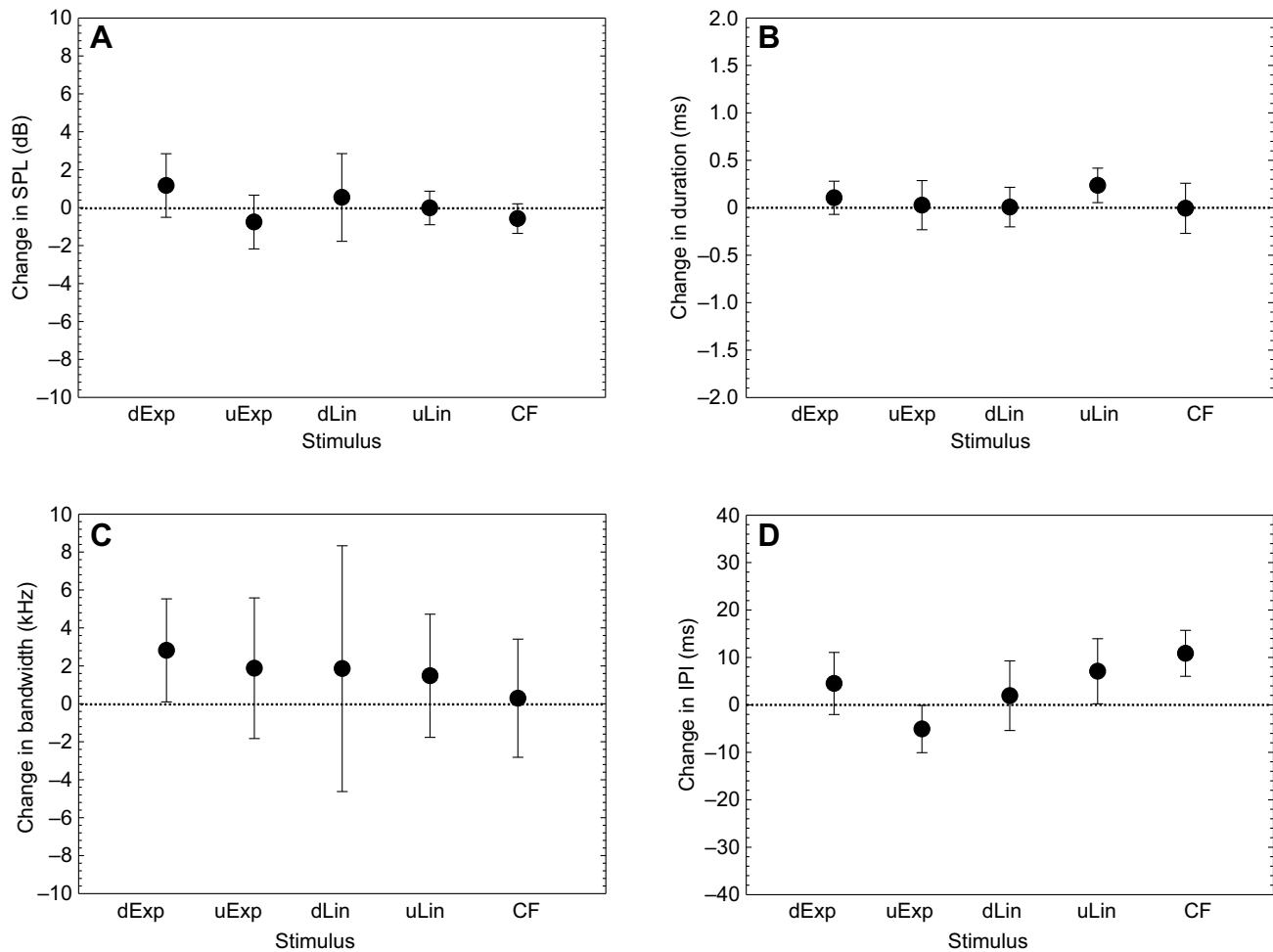
Fig. 4. Comparison of changes in the acoustic parameters of an emitted pulse among five patterns of jamming stimuli for all bats. (A) Sound pressure level (SPL). (B) Duration. (C) Bandwidth. (D) Interpulse interval (IPI). No significant changes were observed for sound pressure level (one-sample *t*-test with Holm's correction, *P*>0.696), duration (one-sample *t*-test with Holm's correction, *P*>0.262), bandwidth (one-sample *t*-test with Holm's correction, *P*>0.220) or interpulse interval (one-sample *t*-test with Holm's correction, *P*>0.151) in response to any of the stimuli.

Response time of the TF shift

In the present study, the on-response time was 140 ms for dExp and 50 ms for uExp. A recent study documented that *Eptesicus fuscus* rapidly shifted the TF of the first vocalization in response to jamming stimuli (FM sounds with three harmonics mimicking echolocation calls of *E. fuscus*) in the range 66–94 ms (Luo and Moss, 2017). Bats also reportedly change their frequency within 200 ms after FM-jamming sounds are presented in the field (Gillam et al., 2007). Gillam and Montero (2016) also demonstrated that the bandwidth of the jamming signal impacted
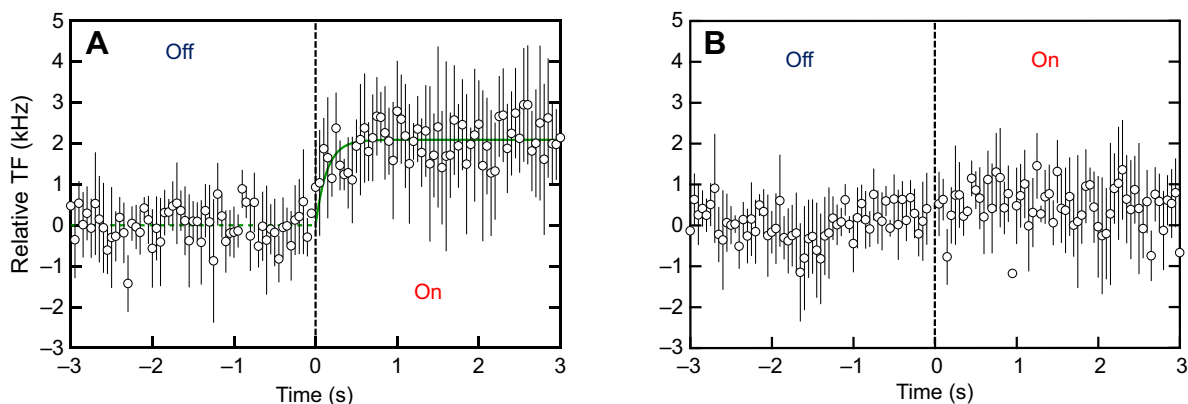
Fig. 5. Temporal changes in TF for dExp and dLin. The plots show the mean value of the TF for all individuals in each 50 ms time bin for (A) dExp and (B) dLin. The green solid line in A is the curve fitted to the data.

the response of the observed JAR, and the CF playback did not induce a significant TF shift. In the present study, the response to CF jamming sounds was significant but slightly weaker than the responses to dExp and uExp (the on-response time of the CF jamming sounds was estimated to be 320 ms). These findings suggest that the type of jamming stimulus affects the response time and the degree of the TF shift.

Improving the signal-to-noise ratio by raising their own sound pressure level is termed the Lombard effect. The response latency of the Lombard effect has been estimated to be about 150–175 ms for humans (Bauer et al., 2006; Heinks-Maldonado and Houde, 2005) and 150 ms for birds (Osmanski and Dooling, 2009). Bats reportedly increase both the amplitude and frequency of the first call emitted after jamming sounds are presented, indicating that the Lombard effect occurs on a rapid time scale (Hage et al., 2013; Luo et al., 2017). The range of the response latency due to the Lombard effect was similar to the observed on-reaction time in the present study. However, no significant changes in the sound pressure level or duration were observed in the presence of jamming sounds in the present study (Fig. 4), suggesting that the observed TF shift was not a reaction to the Lombard effect. Furthermore, a previous study documented that bats were able to exhibit independent shifts between frequency and amplitude under ambient noise (Hage et al., 2013). Based on these observations, we suggest that bats can avoid spectral masking of the near-TF frequency range by shifting the TF without directly improving the signal-to-noise ratio of the echoes by raising the sound pressure level or lengthening the duration of emitted pulses.

Solutions to acoustic interference in FM-echolocating bats

Amichai et al. (2015) conducted an experiment in which various jamming sounds from loudspeakers were presented to *Pipistrellus kuhlii* during a landing flight task. Even against a time-reversed echolocation sound where the spectral content was unaffected, longer and louder calls were perceived to be identical to other jamming sounds, which appeared to increase the signal-to-noise ratio of echoes received for echolocation. In contrast, in *E. fuscus*, no changes in the target detection capability were observed for a time-reversed playback echo, but the capacity of range discrimination decreased compared with a normal echo (Masters and Jacobs, 1989). These previous findings confirm that similarities in the FM pattern between sounds, and not the simple spectral pattern, cause jamming of echolocation at a higher order, such as target ranging, which utilizes the template of their own echolocation sounds (Masters and Raver, 1996, 2000). In fact, during group flight, *M. fuliginosus* reportedly extend the frequency difference in individual TFs while increasing the intensity of emitted pulses and lengthening the pulse duration (Hase et al., 2018). Furthermore, Hase et al. (2018) also demonstrated that the slight TF shift decreases the similarity between the dExp signals. Taken together, echolocating bats could employ various strategies to avoid acoustic interference; they could improve the signal-to-noise ratio of their echoes by emitting louder and longer pulses, which is referred to as the Lombard effect. In addition, they presumably shift the TF to avoid spectral masking, which simultaneously results in decreases in the similarity between signals, which is necessary for 'higher-order' echolocation – this may require comparison of the returning echo with a neural template of their own emitted echolocation sounds at higher-order stages of auditory processing. Our findings will help researchers to understand how bats recognize and interpret their own echoes by adaptively changing the acoustic parameters of echolocation sounds.

Conclusions

We presented five types of jamming sounds with different FM patterns for *M. fuliginosus* flying alone. For the stimuli that were similar in spectrum to the pulse emitted by the bats and for the CF stimulus, *M. fuliginosus* shifted their TFs. However, no changes were observed for linear FM stimuli. We also measured several other parameters, such as sound pressure level, duration, bandwidth and interpulse interval, but the bats did not significantly change these parameters in response to the experimental stimuli. Our findings indicate that direct frequency masking near the TF range induces the TF shift in *M. fuliginosus*, which simultaneously results in a reduced similarity between the signals produced by their own echolocation sounds and the jamming sounds.

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