

## Jamming avoidance response of big brown bats in target detection

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### SUMMARY

**When searching for prey, big brown bats (*Eptesicus fuscus*) enhance the range of their sonar by concentrating more energy in the nearly constant-frequency (CF) tail portion of their frequency-modulated (FM) sweeps. We hypothesize that this portion of their signals may be vulnerable to interference from conspecifics using the same frequencies in their own emissions. To determine how bats modify their signals when confronted with an interfering stimulus, we compared the echolocation calls of bats when a CF jamming tone was on and off. The bats performed a two-alternative forced-choice detection task in the laboratory that required the use of echolocation. All three bats shifted the tail-end CF component of their emitted frequency bidirectionally away from the CF jamming stimulus only when the jamming frequency was within 2–3 kHz of the preferred baseline frequency of the bat. The duration of their emissions did not differ between the jamming and no-jamming trials. The jamming avoidance response of bats may serve to avoid masking or interference in a narrow range of frequencies important for target detection.**

Key words: echolocating bat, biosonar, jamming avoidance, echo processing.

### INTRODUCTION

Many echolocating bats are highly social and can live in roosts that house from dozens to millions of individuals (Kunz and Lumsden, 2003). In the presence of so many echolocating conspecifics, they face the potential problem of acoustical interference from neighbors utilizing the same range of frequencies in their echolocation signals. Yet videos of swarming bats indicate that they have little problem orienting and capturing prey in the presence of many other echolocating bats (Simmons et al., 2001). Animals that emit their own orienting signals could adapt by changing the frequencies of their signals in the presence of interference in order to avoid masking or ‘jamming’. The best known example of this is the behavioral jamming avoidance response (JAR) in weakly electric fish such as *Eigenmannia* that use another active sensory system, electrolocation (Bullock et al., 1972; Heiligenberg, 1991; Watanabe and Takeda, 1963). These single-frequency wave-type electric fish alter the frequency of their emitted electric organ discharge (EOD) when it overlaps with the EODs of nearby conspecific fish.

The effects of acoustical interference from conspecifics on bats utilizing broadband frequency-modulated (FM) biosonar are less well understood. In an early test of jamming in echolocating bats, high intensity white noise only moderately affected the performance of long-eared bats (*Plecotus*) in obstacle-avoidance tests (Griffin et al., 1963). The bats continued to avoid the wires but altered the approach direction of their flights to create differences in reception of echoes compared to the noise at the two ears. However, these experiments did not address whether the bats shifted their own calls to different frequencies in the presence of the noise in a manner analogous to the electric fish JAR. More recent research on avoidance of mutual interference by echolocating bats has consisted mainly of field observations, often of groups of bats flying together. Some investigators have reported greater differences in emitted frequency between two bats of the same species flying in close proximity than between two randomly selected single bats of the same species (Habersetzer, 1981; Miller

and Degn, 1981; Surlykke and Moss, 2000; Ratcliffe et al., 2004; Ulanovsky et al., 2004). Bats flying in groups have been observed to change the duration of their pulses or their inter-pulse intervals (Obrist, 1995; Surlykke and Moss, 2000) as well as the frequencies of their broadcasts. Interestingly, the observed shifts in emitted frequency sometimes only appear to be upward (Gillam et al., 2007; Ibáñez et al., 2004). In a playback experiment in the field (Gillam et al., 2007), bats made only these upward frequency shifts even when their initial call frequency was below that of the playback sounds. Other observations from the field suggest that bats may actively avoid hunting in areas that contain high levels of ultrasonic background noise (e.g. near turbulent water in streams) because this noise interferes with their echolocation (von Frenckell and Barclay, 1987). Moreover, there are other factors in the acoustic environment that influence bats to change their calls, such as foraging environment (Aldridge and Rautenbach, 1987; Simmons et al., 1979; Simmons and Stein, 1980) and changes in the composition of the colony (Hiryu et al., 2006). Taken together, the existing observations of changes in broadcast frequency by bats flying in groups or responding to playback in the field do not provide conclusive evidence for a JAR in bats. In studies such as these, one cannot identify individual bats among several bats flying together to observe how they might alter their emissions in differing conditions. It is also difficult to determine the extent to which changes in emitted frequency might be due to the Doppler shift in frequencies when recordings of flying bats are made from stationary microphones located on the ground. Finally, under these conditions, unlike those of a detection task in a laboratory, one cannot be certain of what the bats are attending to.

Our study was conducted to determine whether a frequency-specific JAR occurs in the big brown bat *Eptesicus fuscus*. This species was chosen because, although they emit harmonically structured FM sounds that cover a wide band of ultrasonic frequencies from 20 to 100 kHz, there is a narrow range of frequencies from about 22 to 28 kHz within this broader band that

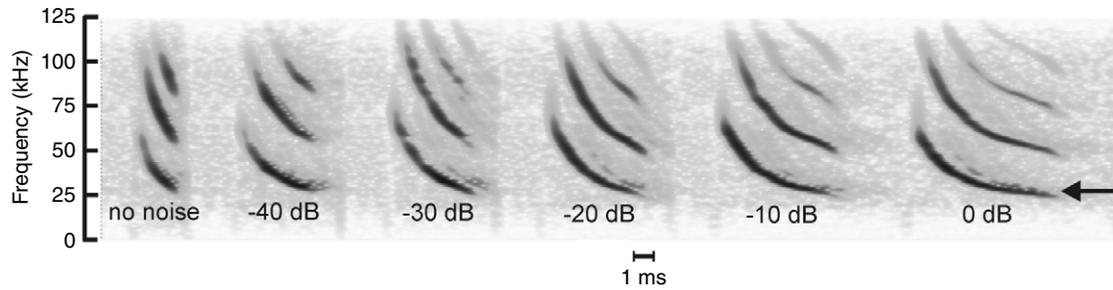


Fig. 1. Spectrograms of sonar sounds emitted by a big brown bat in target-detection tasks while wideband random noise of different amplitudes was delivered from a loudspeaker (Simmons et al., 1974). In response to the noise, the bat lengthens its FM sweeps, which have a curvilinear shape and tail down to a shallow sweep around 22–28 kHz (arrow). Its detection performance remains approximately constant in ambient conditions and in –40 to –10 dB noise, but it declines to chance in 0 dB noise.

is emphasized for long-range target detection. For insect-sized targets, the operating range of echolocation in this species is at least 5 m (Kick, 1982). When searching for insects in open spaces at long range, big brown bats greatly lengthen the shallow-sweeping part of the first-harmonic from 28 down to 22 kHz, which boosts the energy in this band (Simmons et al., 1979; Surlykke and Moss, 2000). Fig. 1 (Simmons et al., 1974) shows the FM sweeps produced by a big brown bat in conditions of varying wideband noise during a target detection task. In response to the noise, the bat lengthens its FM sweeps. The arrow indicates the frequency of the first-harmonic as it terminates at a nearly constant frequency, the component of the sound used for long-range detection. By changing the duration to extend the terminal portion of the sweep disproportionately, the bat emphasizes energy in the 22–28 kHz band. Similar changes occur for the bat's sounds in the field as operating range lengthens (Surlykke and Moss, 2000). The bat's emphasis on the low frequencies in the sound is important: atmospheric absorption of sound is least at these low frequencies, so they can penetrate farther through the air and still return as

echoes that would be audible to the bat (Lawrence and Simmons, 1982).

We designed the present experiment around a laboratory psychophysical method to avoid the issues inherent in field studies, such as the identification of individual bats and the consequences of Doppler shifts. This design allowed us to have stricter control of experimental parameters and of the acoustic environment of the bats. We compared the echolocation calls of bats trained to perform a target-detection task in the laboratory when a constant frequency (CF) jamming tone (at individual frequencies in the range of 18–32 kHz) was turned on and when it was off. Free-flying bats may encounter such continuous interfering noises in natural situations; *Tadarida brasiliensis* have been found to adjust the frequencies of their echolocation emissions in the presence of high frequency sounds produced by chorusing insects, but only when the frequency of such choruses is within the range of the bats' own emissions (Gillam and McCracken, 2007). In the present experiment, frequency analysis of the tail-end of the first-harmonic FM sweeps in sounds emitted during jamming revealed that all bats shifted the frequencies of their own signals up or down to move the ending frequencies away from the CF jamming frequency, but only when the jamming was within 2–3 kHz of their baseline frequency. Outside this narrow window of frequencies, the bats did not alter the frequency of their echolocation calls.

## MATERIALS AND METHODS

### Subjects

Animal care procedures were consistent with guidelines established by the National Institute of Health and were approved by Brown University Animal Care and Use Committee. The subjects, Marina, Snuffles and Vlad, were three adult big brown bats, *Eptesicus fuscus* (one female and two males), which were wild-caught in Rhode Island. [For notes on the biology of this species, see Kurta and Baker (Kurta and Baker, 1990).] The bats were housed in individual cages in a temperature and humidity controlled room on a 12:12 reverse light:dark cycle. They were given vitamin-enriched (Poly-Vi-Sol) water *ad libitum* and fed mealworms (*Tenebrio molitor* larvae) daily. All subjects weighed between 14 and 15 g.

### Procedure

Fig. 2 shows the behavioral set-up for the experiment and the arrangement for the CF jamming sound delivery system. Each bat was placed on an elevated Y-shaped platform and trained on a two-alternative forced choice task to detect a target (plastic cylinder, 3 cm high, 2.5 cm in diameter) located on the bat's right or left side. The bat was trained to sit in the middle of the base of the platform,

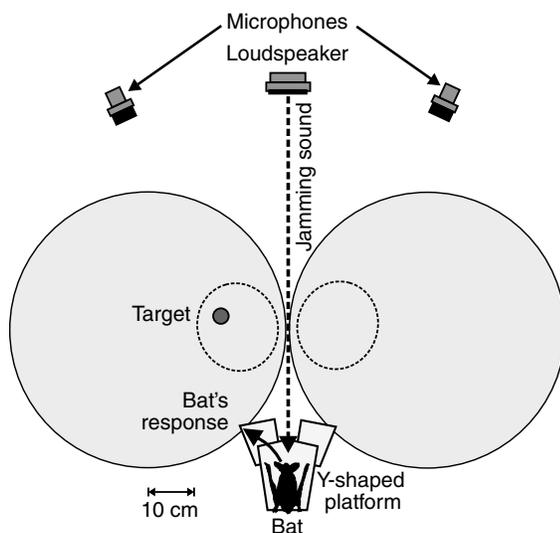


Fig. 2. Diagram of experimental set-up. Bats were trained to sit on the Y-shaped platform and search for the target located 30 cm away, responding by moving forward onto the corresponding platform arm for food reward. CF jamming sounds were presented from the loudspeaker located 1.5 m away, and the bat's sonar sounds were recorded by microphones located 1.5 m away and separated by 30°.

direct its sonar signals to detect the target (located approximately 30 cm away on either side), and then walk towards the target on the corresponding arm of the Y-platform. Correct responses were rewarded with a piece of a mealworm offered in plastic forceps, while incorrect responses were followed by a broadband high frequency sound that signaled that the bat had made an error. After each trial, the bat was picked up and returned to the base of the platform, which it crawled up to from the trainer's hand. Trials were run in the dark using a double-blind procedure. The trainer handling the bat was unaware of the location of the target and a second experimenter moved the target and recorded the responses of the bats. Target location on the left or right was alternated according to a pseudorandom Gellerman sequence (Gellerman, 1933). Bats were trained to perform the detection task, in the absence of any interference, for 1 week with 50 trials per day. At the end of this period, all bats were above 90% correct. For testing, 20 trials were run for each jamming frequency (12 sessions) – 10 trials with no jamming sound, followed by 10 trials with the jamming sound turned on. In addition, 20 trials were conducted as baseline recordings for each bat in a separate session before testing trials were initiated. The bats were well trained and motivated, and a typical trial lasted less than 5 s.

The jamming stimulus was a continuous CF tone that was turned on and remained on for all 10 jamming trials. Presenting tone-bursts instead of a continuous tone introduces spectral 'splatter' at the onset and offset of each burst, and this widens the spectrum enough that it might disrupt the sharpness of the jamming frequency to the bat. Without knowing how specific any potential jamming effect might be to each frequency, it is better to keep the interfering stimulus restricted to one frequency at a time. For each session a different fixed frequency in the frequency range from 18 to 32 kHz was used as the CF jamming stimulus. Each bat completed one session (day) of testing for each jamming condition with the CF jamming stimulus at 18, 20, 22, 23, 24, 25, 26, 27, 28, 29, 30 and 32 kHz. These sessions were presented in a pseudorandom order on separate days. The CF jamming sounds were generated by a Model 27A Audio Generator (Leader, Inc., Yokohama, Japan), and delivered from an electrostatic loudspeaker Model EST-2 (LTV, Corp., Los Angeles, CA, USA) after being amplified by a Model 7500 power amplifier (Krohn-Hite, Inc., Avon, MA). As shown in Fig. 2, the loudspeaker was located 1.5 m from the bat and was oriented to produce a uniform sound field around the bat's location on the Y-shaped platform. The frequency of the jamming sound was adjusted by the recorder using a Model LDC-831 Frequency Counter (Leader, Inc., Japan). Fig. 3 shows the frequencies and sound pressures of the CF jamming stimuli in relation to the hearing sensitivity (audiogram) of the big brown bat (Dalland, 1965; Koay et al., 1997). Sound pressures were measured at the center of the Y-platform, at the starting point for the bats. The hearing sensitivity of the bats varies by only a few decibels around 10 dB SPL at frequencies from 18 to 32 kHz, and the jamming sounds were adjusted in amplitude to be at a fixed sensation level of 65 dB for all these frequencies. This level is approximately that of the echoes that the bat was receiving from the experimental target. The bats' own emissions were much more intense (100–110 dB SPL) and were clearly discernable from the jamming stimulus on waveforms and spectrograms of the trials.

During experimental trials, the bat's FM sounds and the CF jamming stimulus (if present) were picked up with two ultrasonic microphones (Titley Electronics, Ltd, Ballina, NSW, Australia) positioned 1.5 m away from the bat and separated by 30° (see Fig. 2). The two channels of ultrasonic signals from these

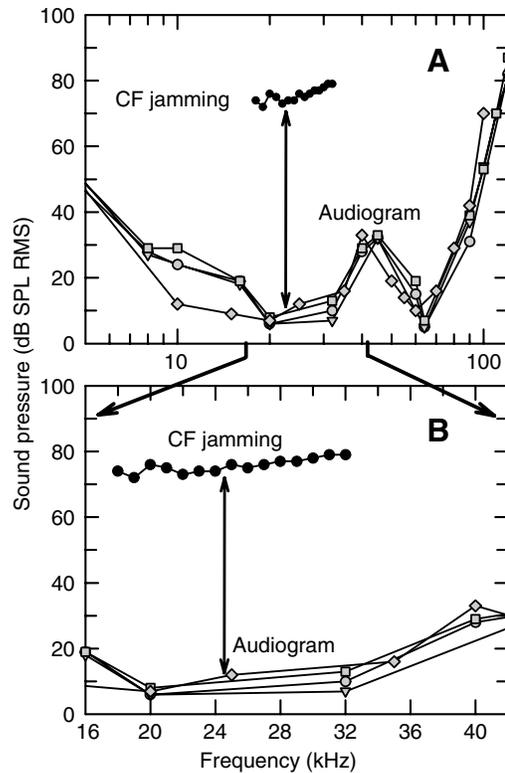


Fig. 3. Frequencies and sound pressures of constant-frequency (CF) jamming sounds in relation to the audiogram of big brown bats. (A) Full frequency range. (B) Expanded frequency range used for jamming experiments. At frequencies of 18–32 kHz, the jamming stimuli have a constant sensation level of about 65 dB. Filled symbols indicate CF jamming stimuli; other symbols indicate individual animals. [Replotted from Dalland (Dalland, 1965) and Koay et al. (Koay et al., 1997).]

microphones were amplified 10× and filtered to a passband of 15–100 kHz with two Model 442 analog variable bandpass filters (Wavetek Rockland, San Diego, CA). The amplified bat signals were recorded on two channels of a Sony SIR-1000W digital instrumentation recorder (Sony Precision Technology America Corp., Lake Forest, CA, USA) using a sampling rate of 384 kHz on each channel. A Model 15-CB22-1 black and white video camera and IR14 infrared illuminator (Supercircuits, Inc., Austin, TX, USA) were mounted on the ceiling of the test room pointing down on the bat, the Y-shaped platform, and the target. A video record of each trial – with or without the jamming sound – was made using the video channel of the Sony recorder. The video record, which contained a video track and two ultrasonic sound tracks, was used to locate the brief period of time, up to about 4 s in duration, when the bat scanned the area to locate the target.

#### Data analysis

For each trial in the experiment, the recorded data were windowed to a 4 sec segment that contained all the echolocation emissions of the bat during the detection task on a given trial. Each was then transferred from the Sony recorder as a digital file in a PC-type Pentium-III computer (Gateway, Inc.) using programs that are part of the Sony recorder system (Sony PC-Scan Real-Time software package). The video of each trial was used to select the period of time when the bat was scanning the two arms of the platform. All sounds emitted during this time (1–3 s) were exported as stereo 'wav' files (Sony PC-Scan Streamer software package) for

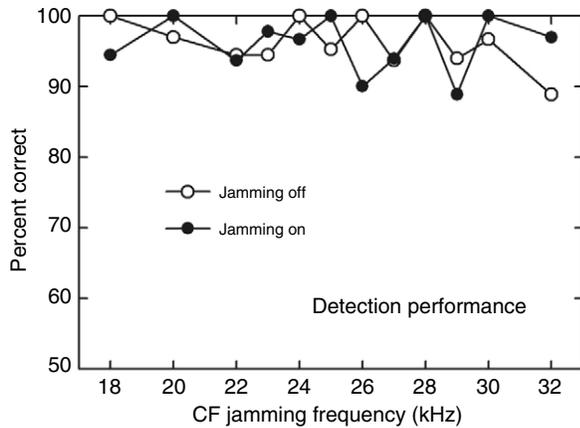


Fig. 4. Plot showing percentage of correct trials averaged across the three bats ( $F_{11,22}=1.691$ ,  $P=0.142$ ).  $N=30$  trials per data point (10 per bat).

analysis using Adobe Audition v. 1.0 (Adobe Systems, Inc.). Only sounds emitted by the bat on correct trials were analyzed to determine their tail-end frequency and duration (~90% of trials; see Fig. 4). The files for each condition (CF frequency, jamming off or on) were opened in Adobe Audition 1.0, and successive sounds were displayed as spectrograms. The cursor was then expanded to encompass each sound in succession to determine its low-end sweep frequency and duration. For frequency, the Adobe Audition 'Analyze Frequency' function was opened, and a fast Fourier transform (FFT) was run with a 1024 sample size and Blackman envelope windowing. To determine the low frequency in the sweep, the cursor was moved to a point half-way from the peak of the first-harmonic energy (typically 35 kHz) on the low-frequency skirt and the frequency value saved as a text file. A separate text file was prepared for each CF jamming condition. These frequency values serve as estimates for the nearly CF tail-end of the first-harmonic FM sweep. The mean and 99% confidence intervals of the tail-end frequency values for all sounds in a condition were determined for each bat for each jamming frequency with the CF jamming tone on versus off. The duration of each sound was measured from the spectrogram display using the cursor because its color-coded levels made the starting and ending points unambiguous.

In Table 1, the number of echolocation emissions analyzed for all bats in each condition is listed. All sounds within the 1–3 s time window in which the bat was producing emissions and walking down the arm of the platform were analyzed. Because the bats differed in the length of time they spent on the platform (even between trials within a single session), we could not compare the number of sounds they emitted in different conditions. There appear to also be individual differences between the three bats in their number of emissions, but these differences were not associated with differences in target detection performance.

## RESULTS

We compared the echolocation calls of bats performing a target detection task in the laboratory when a CF jamming stimulus was on and off. In Fig. 4, the performance of the bats (percentage correct trials) for the jamming on and jamming off conditions is plotted. A repeated measures ANOVA revealed no significant difference between the bats' performances when the jamming stimulus was on compared to when it was off ( $F_{11,22}=1.691$ ,  $P=0.142$ ). Mean performance ranged between 91% and 100% for individual bats: Marina jamming on,  $92\pm0.067\%$  (mean  $\pm$  s.d.);

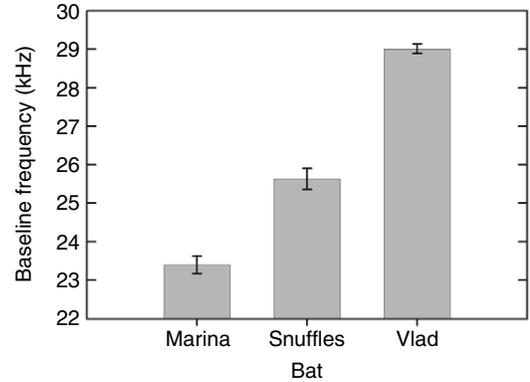


Fig. 5. Individual bats' mean baseline terminal frequencies for first-harmonic FM sweeps with 99% confidence intervals (Marina,  $N=130$ ; Snuffles,  $N=249$ ; Vlad,  $N=457$ ).

Marina jamming off,  $91\pm0.069\%$ ; Snuffles jamming on,  $100\pm0.000\%$ ; Snuffles jamming off,  $100\pm0.000\%$ ; Vlad jamming on,  $96\pm0.062\%$ ; Vlad jamming off,  $97\pm0.056\%$ .

Fig. 5 shows the mean baseline tail-end first-harmonic sweep frequencies (recorded in the absence of the jamming stimulus) measured from 20 trials for each bat, with 99% confidence intervals. This baseline frequency was measured, in the absence of any interference, on a day prior to the initiation of trials with the CF jamming sound on. Although the preferred baseline frequencies differed among bats, the plot in Fig. 6 illustrates that the end-sweep frequencies recorded during the pre-testing baseline session did not reliably differ from those measured during the testing trials when the CF jamming stimulus was off. The mean tail-end sweep frequencies recorded when the CF jamming stimulus was off, averaged across the three bats, are shown for all 12 testing sessions. Also plotted is the mean tail-end sweep frequency from the baseline recording. The mean emitted frequencies of the bats in the absence of any jamming stimulus do not appear to have changed over the course of the experiment.

Fig. 7 shows the mean tail-end sweep frequencies for each bat from 10 trials with no jamming, followed by 10 trials with jamming at each of the CF jamming frequencies from 18 to 32 kHz. An

Table 1. Number of echolocation sounds in 10 trials with CF jamming off, 10 trials with CF jamming on, and 20 trials for baseline for each bat

Jamming frequency	Marina		Snuffles		Vlad	
	CF off	CF on	CF off	CF on	CF off	CF on
18 kHz	63	76	136	104	121	116
20 kHz	94	72	126	148	109	115
22 kHz	67	61	166	111	102	93
23 kHz	66	56	173	139	186	159
24 kHz	91	83	134	95	124	96
25 kHz	72	75	124	98	170	136
26 kHz	97	96	144	114	170	131
27 kHz	72	65	136	180	107	84
28 kHz	66	62	100	121	80	56
29 kHz	69	61	131	124	101	62
30 kHz	64	73	130	124	115	73
32 kHz	70	74	151	132	92	70
Total	891	854	1651	1490	1324	1191
Baseline	130		249		457	

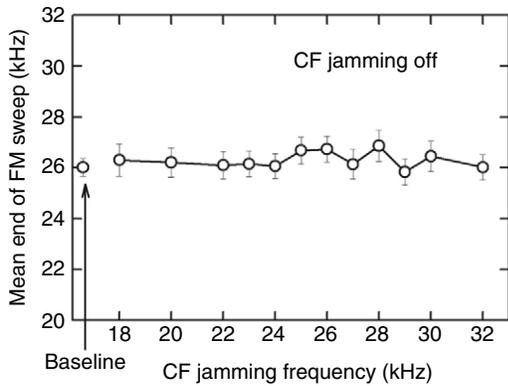


Fig. 6 Mean tail-end frequency averaged across bats for CF jamming off trials and initial pre-testing baseline. Bars indicate 99% confidence intervals.

arrow labeled  $f_{\text{base}}$  indicates the baseline reference frequency for a given bat. For each bat, a comparison between the curves for no jamming and for jamming, in Fig. 7A, reveals a consistent pattern of changes in the emitted tail-end frequency as a function of the jamming frequency. Relative to the frequencies emitted with no jamming, there is an upward shift in emitted frequencies for low jamming frequencies, with a crossover to a downward frequency shift at higher jamming frequencies. Fig. 7B shows the frequency

shifts between jamming on and jamming off conditions in Fig. 7A by plotting the frequency shift when the CF jamming stimulus is on relative to the CF off frequencies. These plots illustrate the consistency of the frequency shift as a function of jamming frequency. The crossover point between upward frequency shifts for low jamming frequencies and downward frequency shifts for high jamming frequencies occurs when the jamming frequency becomes higher than each bat's baseline frequency.

For each bat, the JAR is restricted to a narrow frequency region that extends about 2–3 kHz above and below each bat's baseline frequency. Note that the JAR is bidirectional – with an increase in emitted frequency if the jamming sound is below the baseline frequency, and a decrease in emitted frequency if the jamming sound is above the baseline frequency. The bats shifted their own emitted frequencies upward until the stimulus tone corresponded to their own baseline frequency. When this frequency was reached, the bats shifted their echolocation frequencies downward, ensuring that the tail-end sweep frequency would diverge from the CF tone during target detection trials. Although the frequency at which this change occurred differed among the bats, they all demonstrated the same pattern of an upward frequency shift followed by a downward shift when the jamming sound passed each bat's baseline frequency.

Because the sonar sounds of big brown bats are frequency modulated, the terminal frequency in the first-harmonic sweeps can be adjusted either by raising the frequencies themselves, or they

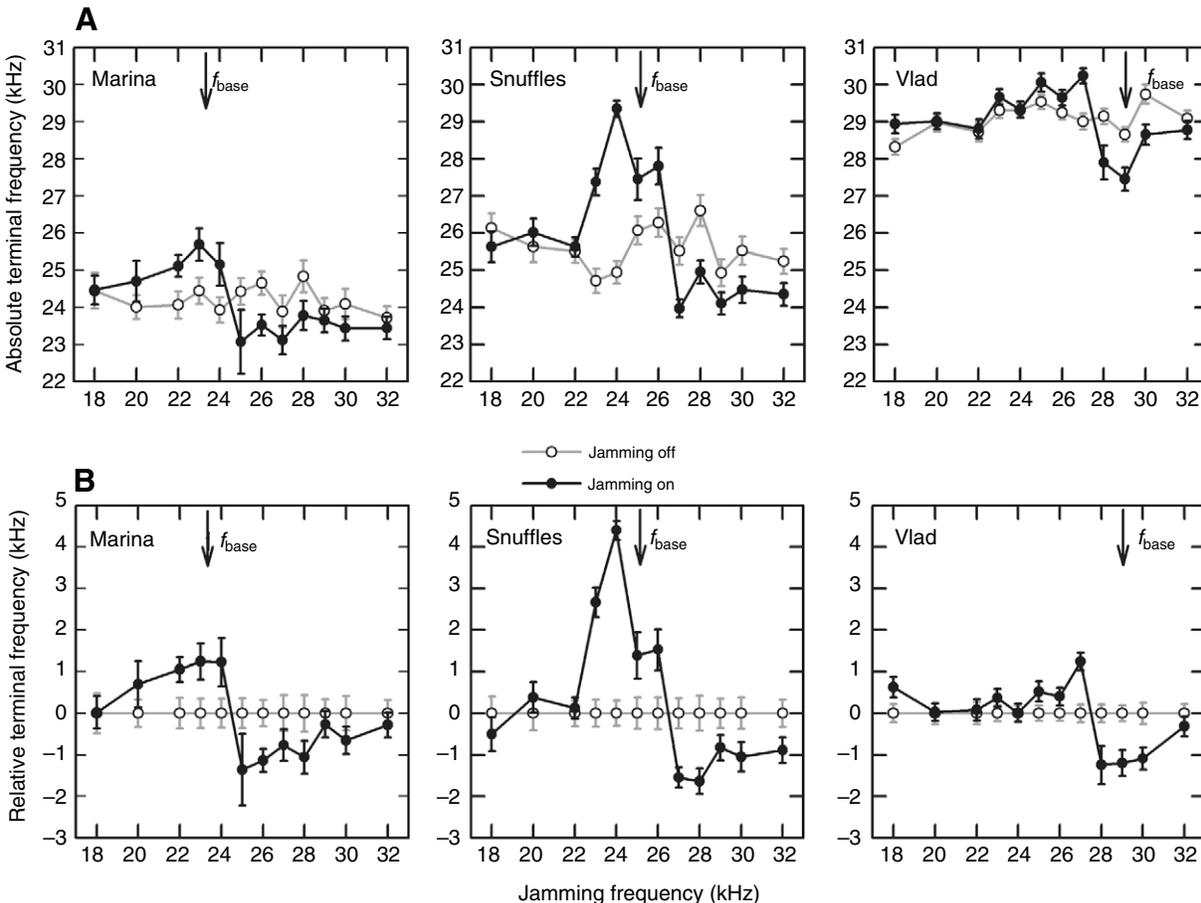


Fig. 7. Plots showing jamming avoidance response (terminal first-harmonic frequencies). (A) Size of frequency change in raw frequency coordinates with 99% confidence intervals. Black points, CF jamming stimulus on; white points, CF jamming stimulus off. Arrows ( $f_{\text{base}}$ ) indicate the mean pre-testing baseline frequency of each bat (see Fig. 5). (B) Plots showing change in frequency relative to CF off frequencies.

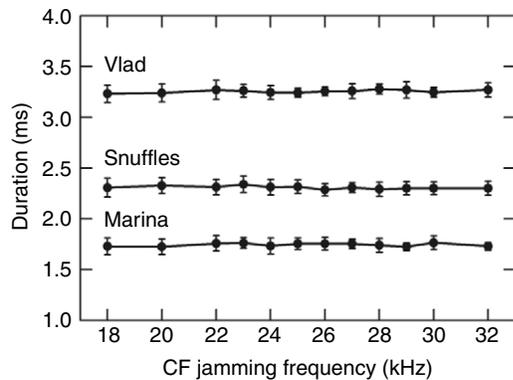


Fig. 8. Plot of durations of broadcasts during trials at each CF jamming frequency with 99% confidence intervals. Only the duration of the sounds emitted during the trials in which the CF jamming stimulus was present (10 trials per bat per frequency) are plotted.

might be adjusted by altering the duration of the sounds. If the sounds are shortened in duration, the sweep as a whole could be truncated at a slightly higher frequency, whereas if the sounds are lengthened in duration, the sweep could finish at a lower frequency. To determine whether frequency shifts occurred directly or as a secondary effect of changes in duration, the durations of each bat's echolocation emissions were measured across the twelve jamming frequencies. Fig. 8 shows the mean durations for each bat. Although the three bats used sounds of different durations, just as they used sounds with different baseline frequencies, they used sounds with the same durations across the different jamming frequencies. Thus the shifts in frequency observed when the CF jamming frequency approached each bat's baseline frequency (the JAR; Fig. 7) were not caused by a shortening or lengthening of the echolocation emissions. They are a consequence of the bat changing the frequencies of the tail-end of its sweeps in response to the jamming.

## DISCUSSION

In a laboratory target detection task, three big brown bats demonstrated a JAR to continuous interfering CF tones. All the bats showed a clear bidirectional shift in the frequency of the tail-end portion of their emitted FM sweeps, and this was not due to a change in the duration of their emissions. The range over which the JAR occurred was very narrow, and although the width varied slightly between the three bats it was consistently centered on each bat's baseline frequency. The response also was bidirectional around this center. This result is to be expected if big brown bats dedicate a specific frequency region around the end of the 1st-harmonic FM sweep to target detection at long range.

Our experiment demonstrates the occurrence of JAR in big brown bats by embedding the jamming procedure within a psychophysical target detection task. Other studies rely on field observations of freely moving bats; however, data gathered in this manner may be difficult to analyze due to Doppler effects and the difficulty of identifying individual subjects within a group. In field observations in which two *Tadarida teniotis* were flying together, the bat emitting the higher frequency call would shift its frequency upward by more than 1 kHz, whereas the bat emitting at lower frequency shifted its call downward by the same amount (Ulanovsky et al., 2004). These symmetric shifts in frequency were apparent in pairs of bats for several seconds of recording. In this same study, bats also demonstrated a dynamic JAR in which high-

frequency-call bats shifted upwards when approached by a lower-frequency-call bat, whose frequency did not change. Unlike the symmetric frequency shifts, these shifts were only brief frequency fluctuations, much shorter in duration. In a field experiment that attempted to jam the echolocation of the bat *Tadarida brasiliensis* (Gillam et al., 2007) recordings of echolocation calls at six different frequencies were broadcast to groups of foraging bats. The frequencies that the bats emitted, presumably, but not definitely, in response to the playbacks, fell into a bimodal distribution, with a notch in the distribution at the callback frequency. When these emissions were compared to those produced in the absence of any playback, it appeared that the bats shifted their frequencies upwards in the presence of lower frequency playback calls. In a second experiment, the frequency of the playback stimulus was abruptly switched as an echolocating bat approached. All bats shifted their emitted frequencies up above the playback, even when they were already above it. By contrast, we found that big brown bats would either raise or lower their emitted frequency depending on the frequency of the interfering signal.

Schmidt and Joermann suggest that bats that primarily depend upon CF signals are more susceptible to jamming because a CF emission lacks the bandwidth of an FM signal that might distinguish it from the calls of other bats (Schmidt and Joermann, 1986). However, it has been more challenging to jam the echolocation of CF bats than to jam that of bats using primarily FM sounds. No frequency shift for the multiharmonic CF bat *Rhinopoma microphyllum* in group flight was reported (Schmidt and Joermann, 1986). When several *Craseonycteris thonglongyai*, which employ a multiharmonic CF signal, were recorded flying together, they all emitted signals centered closely around 73 kHz with no evidence of frequency shifting (Surlykke et al., 1993). In two studies with bats in the family *Hipposideridae*, no evidence was found for a shift in CF frequency during group flight (Jones et al., 1993) or in response to playback of calls from conspecifics (Jones et al., 1994). A study of the use of echolocation sounds by the mouse-tailed bat *Rhinopoma hardwickei* (Habersetzer, 1981) raises questions about the context in which bats employ CF and FM signals. They were observed to use FM emissions when leaving the roost in clusters, but bats leaving singly emitted CF sounds. At the hunting grounds, bats flying in groups produced CF sounds at three different frequency bands, whereas bats flying alone used only the middle frequency band. This suggests that the CF component of echolocation calls is treated differently by the bat, and it either shifts the frequency of this component in the presence of other bats, or switches to the use of broadband calls. In another study, Miller and Degn (Miller and Degn, 1981) reported that when flying in groups, *Pipistrellus pipistrellus* separated the CF portions of their calls by as much as 14 kHz. Again, this CF component appears to be the portion of the call that is most actively protected from interference by the bat.

Although the three bats we tested demonstrated the same response pattern, the point at which they shifted their frequencies, and the degree to which they did so, differed among individuals. In other species of bat, researchers have found variations in auditory cortex tonotopic representation that correspond to individual differences in emitted frequency (Suga et al., 1987). In the mustached bat, *Pteronotus parnellii*, the resting frequency of the CF component of the second harmonic (CF2) of the biosonar signal can vary several kHz between individuals. The functional organization of the Doppler-shifted CF processing (DSCF) area of the auditory cortex varies in a similar manner, with the distribution of best frequencies of neurons matching the properties of the bat's

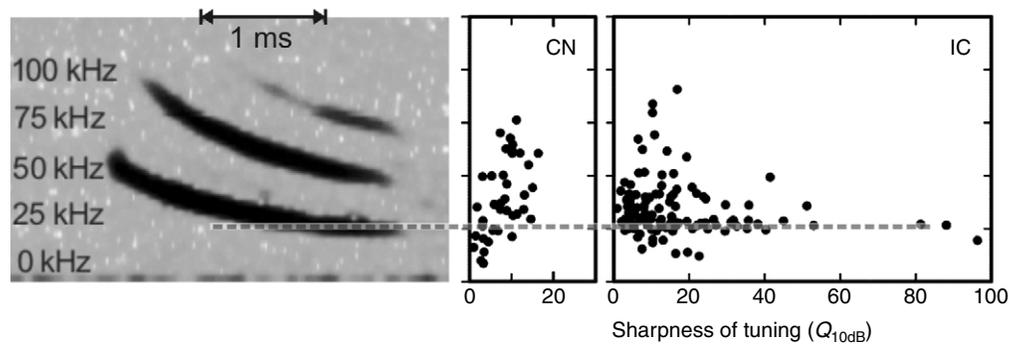


Fig. 9. A typical big brown bat echolocation sound (left) with sharpness of frequency tuning for neurons in the bat's cochlear nucleus (CN) and inferior colliculus (IC) [replotted from Haplea et al. (Haplea et al., 1994)]. The horizontal broken line indicates where the sweep tails off in the first harmonic at approximately 23 kHz. With no other constraints, frequencies within this range are used for target detection. In this example, IC tuning is much sharper at frequencies around 23–25 kHz, with  $Q_{10\text{dB}}$  values ranging from 2 to 40, and some as high as 90.

own CF2 resting frequency. In this way, both the orientation sound and the auditory cortex of individual bats are 'personalized' for echolocation. It is possible that such personalized modifications of the auditory cortex exist in species such as the big brown bat, as well. Their sonar signals are known to differ enough between bats for individuals to recognize each other (Masters et al., 1995). The bats in the present experiment may have been shifting their tail-end CF frequencies out of the range of interference in order to keep them within a window of sensitive frequencies determined by their own baseline frequency and corresponding sharply-tuned neurons.

To effectively hunt their flying insect prey, echolocating bats must perform two different tasks: detect the presence of a possible prey item, and accurately determine their distance from it. Information from the returning echoes is conveyed to two separate neuronal pathways that are specialized for these purposes. Big brown bats estimate the distance to targets using the time delay between their FM broadcasts and the returning echoes (Moss and Schnitzler, 1995; Simmons et al., 1995). The bat's auditory system registers the timing of each frequency in echoes and combines information across frequencies to achieve very high delay accuracy of fractions of a microsecond (Simmons et al., 1996). The frequency tuning of neurons used in echo delay perception is only moderately sharp, which is necessary to maintain accuracy of timing registration (Menne, 1988). The graphs in Fig. 9 plot the sharpness of frequency tuning (given as values of  $Q_{10\text{dB}}$ ) as a function of frequency in the big brown bat's cochlear nucleus and inferior colliculus (see Haplea et al., 1994). Neurons in the cochlear nucleus are tuned approximately optimally for registering the timing of the frequencies, with  $Q_{10\text{dB}}$  values mostly in the range of about five to 15 from 20 to 75 kHz (Menne, 1988). A different subpopulation of neurons in the inferior colliculus is more sharply tuned, with  $Q_{10\text{dB}}$  values ranging from two to as high as 90 for frequencies ranging from 22 to 28 kHz. These sharply-tuned neurons constitute a separate neuronal pathway, parallel to the less sharply tuned pathway for processing echo delay, which is used for target detection. Big brown bats lose echo-delay accuracy in proportion to reduced relative echo bandwidth, including for small frequency segments of 20–25 kHz (Simmons et al., 2004). Thus, the presence of a different population of neurons that have 'normal', moderate tuning indicates that these bats have two parallel sonar receivers at frequencies of approximately 22–28 kHz – one for detection and the other for delay estimation.

The jamming of echolocation by conspecifics may be a major problem for free-flying bats, many of which live in large social

groups and forage together. It is likely that bats possess several mechanisms for dealing with this type of potential interference. Suga et al. (Suga et al., 1983) listed several such possibilities, based on knowledge of bat neurophysiology, including: (1) the directionality of the bat's emissions, (2) the directional sensitivity of the bat's ear, (3) binaural processing, (4) sequential processing of echoes and (5) an auditory time gate for echo processing. Behavioral studies have also revealed strategies that echolocating bats may use to reduce jamming in the presence of conspecifics. A commonly observed mechanism is to alter the duration of pulses or the inter-pulse interval to avoid overlapping the sounds produced by nearby bats (Obrist, 1995; Surlykke and Moss, 2000). This change in the timing of emissions is also seen in 'pulse'-type electric fish (Heiligenberg, 1991). Finally, bats that travel the same route from roost site to foraging grounds night after night (Rydell, 1990) may be relying on spatial memory and not on the echoes of their surroundings to navigate in familiar areas (Griffin, 1958; Höller, 1995). Altering the frequency of their emissions may be only one of several mechanisms that bats may use to solve the problem of interference from other bats.

#### LIST OF SYMBOLS AND ABBREVIATIONS

CF	constant frequency
CN	cochlear nucleus
DSCF	Doppler-shifted constant frequency
EOD	electric organ discharge
FM	frequency-modulated
IC	inferior colliculus
JAR	jamming avoidance response
$Q_{10\text{dB}}$	sharpness of tuning (best frequency/tuning width 10 dB above tuning-curve threshold)

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