

Effects of filtering of harmonics from biosonar echoes on delay acuity by big brown bats (*Eptesicus fuscus*)

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Big brown bats emit FM biosonar sounds containing two principal harmonics (FM1 ~ 55–22 kHz; FM2 ~ 105–45 kHz). To examine the role of harmonics, they were selectively filtered from stimuli in electronic-echo delay discrimination experiments. Positive stimuli were delayed by 3.16 ms (55 cm simulated target range); negative stimuli were by delayed by 3.96 ms (68 cm). This large 800- μ s delay difference (nearly 14 cm) was easily discriminated for echoes containing equal-strength FM1 and FM2. Performance gradually decreased as highpass filters removed progressively larger segments from FM1. For echoes with FM2 alone, performance collapsed to chance, but performance remained good for lowpass echoes containing FM1 alone. Attenuation of FM2 by 3 dB relative to FM1 also decreased performance, but shortening electronic delay of the attenuated FM2 by 48 μ s counteracted amplitude-latency trading and restored performance. Bats require the auditory representations of FM1 and FM2 to be in temporal register for high delay acuity. Misalignment of neuronal responses degrades acuity, but outright removal of FM2, leaving only FM1, causes little loss of acuity. Functional asymmetry of harmonics reflects lowpass effects from beaming and atmospheric propagation, which leave FM1 intact. It may cooperate with latency shifts to aid in suppression of clutter. © 2010 Acoustical Society of America. [DOI: 10.1121/1.3459823]

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I. INTRODUCTION

Big brown bats (*Eptesicus fuscus*) emit trains of wide-band FM biosonar signals at frequencies of about 22–105 kHz that contain multiple harmonics (Saillant *et al.*, 2007; Surlykke and Moss, 2000). They use echoes of these sounds to detect and intercept prey, avoid obstacles, and navigate through spatially complex surroundings such as vegetation (Griffin, 1958; Neuweiler, 2000). The two most prominent harmonics in the broadcasts are the first (FM1), which typically sweeps downward from 55 to 22 kHz, and the second (FM2), which sweeps downward from 105 to 45 kHz. Although big brown bats often capture flying insect prey, they also are observed to forage near clutter, such as dense vegetation, and to glean insects from the ground or other surfaces (Simmons, 2005; Simmons *et al.*, 2001). Flying near vegetation or the ground exposes the bat to clutter that could obscure the presence of objects of interest, such as insects to be pursued or obstacles to be avoided. Bats would encounter difficulty in detecting echoes from such objects if these are masked by the more intense echoes from background clutter (Schnitzler *et al.*, 2003). Several FM bat species nevertheless are able to detect and capture prey located close to clutter (Jensen *et al.*, 2001; Moss *et al.*, 2006; Siemers and Schnitzler, 2000). Furthermore, laboratory tests reveal that bats can fly along narrow, turning paths surrounded by dense, deeply

distributed clutter without colliding into obstacles (Petrites, *et al.*, 2009). When flying in the densest clutter conditions, the bats alter the pattern of their broadcasts to shorten the intervals between successive sounds, often so much so that the stream of echoes returning from one sound is not finished before the next sound is broadcast and its stream of echoes begins to arrive (Petrites *et al.*, 2009).

Overlap of echo streams for successive broadcasts results in ambiguity about which broadcast is responsible for which echoes. *Pulse-echo ambiguity* is a kind of self-generated clutter interference that places a premium on recognizing successive broadcasts as sufficiently different from one another that their echoes can be recognized as different, too. Using a miniature radio microphone carried by the bat to record subtle changes in biosonar broadcasts without artifacts related to Doppler shifts and directional beaming, big brown bats were observed to adapt to ambiguity-related clutter by shifting the frequencies of adjacent FM broadcasts away from each other by several kilohertz (Hiryu *et al.*, 2010). Crucially, these frequency shifts only occurred when echo streams overlapped to create pulse-echo ambiguity. Although ambiguity-induced frequency shifts amount to only a few percent of the total bandwidth in broadcast spectra, in spectrograms of the sounds, up to about half of the time-frequency surface occupied by the harmonic sweeps is redistributed, making the sounds easily distinguishable. This finding suggests that bats may be very sensitive to small changes in the relative positions of different frequencies in the FM sweeps of echoes on the time-frequency plane. In effect, bats

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might use auditory “fingerprints” for recognizing echoes and sorting them to their corresponding broadcasts.

To assess this possibility, an experimental technique has been developed that segregates the two principal harmonics in the sonar sounds of big brown bats (FM1 and FM2) into different channels of an electronic target simulator so that the effects of misaligning the harmonics in time could be measured. When FM2 is delayed 300 μs relative to FM1 in such a “split-harmonic” echo-delay discrimination task, the echo-delay acuity of about 50 μs normally obtained in 2-choice discrimination tests deteriorates extraordinarily to about 1000 μs (Stamper *et al.*, 2009). For all practical purposes, the 300- μs offset of harmonics caused the bat’s delay acuity to collapse completely.

The experiments described here were carried out to determine whether selective removal of frequencies in FM1 or FM2 affects bats’ delay acuity as drastically as the 300- μs delay offset of the harmonics. For example, does slight attenuation or complete removal of FM2 cause the bat’s delay acuity to become as poor as when FM2 is delayed by 300 μs more than FM1? What happens when the spectrum of FM1 is truncated or entirely removed? The split-harmonic target simulator is used to create differential changes in the amplitude or spectrum of FM1 and FM2 in echoes, allowing us to measure the effects of these acoustic manipulations on the bat’s delay discrimination performance. Bats were trained to choose echoes arriving at a delay of 3.16 ms and not choose echoes arriving at a delay of 3.96 ms. In ordinary conditions, bats easily perform this 800- μs difference task with only about 5% errors. In the 300- μs split-harmonic experiment, the bat’s acuity deteriorates so much that performance fell to about 16% errors, a very significant loss even though the difference is more than twice the bat’s 350- μs integration-time for echo detection (Simmons, 1989).

The 300- μs offset of FM2 in the split-harmonic experiment is manifested as misalignment of the harmonics on the spectrogram’s time-frequency plane, not as a change in the amplitude spectrum as such. Through amplitude-latency trading (the dependence of neuronal response latencies on stimulus amplitude; Bodenhamer and Pollak, 1981; Burkard and Moss, 1994; Ma and Suga, 2008; Simmons *et al.*, 1990), changes in the amplitude of harmonics are transposed into changes in the timing of the auditory representation of the harmonics. Amplitude-latency trading thus creates time shifts between harmonics internal to the bat. The possibility that bats recognize echoes strictly from the timing of the harmonics is explicitly tested by exploiting amplitude-latency trading—inducing a latency shift by reducing the amplitude of FM2 and then compensating for this shift by changing the delay of FM2.

In the present experiments, the bats’ performance on the normally easily-discriminated 800- μs delay difference was used as an index for the effects of manipulating the harmonics in echoes. These new experiments are presented here in the order of their design and conduct (i.e., Experiments 1, 2, 3, and 4) because several of the experiments were based on results obtained from earlier conditions. Together, the results

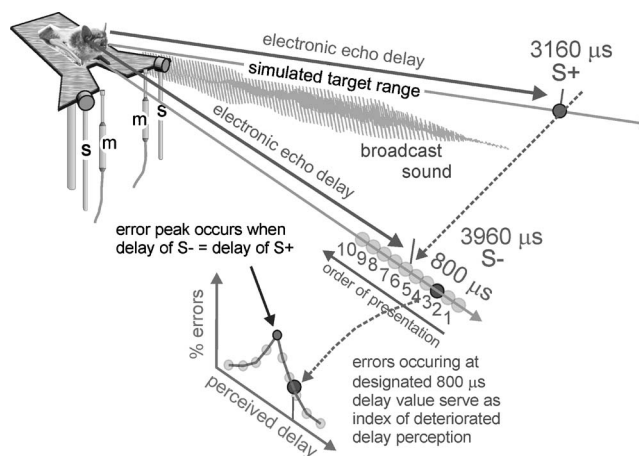


FIG. 1. Diagram of 2-choice electronic-echo delay discrimination set-up with bat on Y-shaped platform: Bat’s broadcast sounds are picked up by microphones (m), delayed and filtered electronically, and returned as echoes of virtual targets from loudspeakers (s). Delay of S+ is fixed at 3160 μs , which simulates a target range of 54.5 cm. Delay of S- is fixed 800 μs later, at 3960 μs , which simulates a target range of 68.3 cm. The 800- μs difference between S- and S+ corresponds to the index point described in Fig. 2. For the present experiments, S+ and S- undergo various filtering conditions to assess effects on performance at 800- μs index point. Idealized percent-error performance curve illustrates relation between peak in error curve when S- matches delay of S+ and the still-elevated performance occurring at 800 μs .

of these experiments indicate that harmonics interact with beamforming and atmospheric effects to contribute to perception of echo delay.

II. GENERAL METHODS

A. Subjects

Four adult big brown bats (Chris, Buddy, Vlad and Marina; three males and one female) were trained to discriminate between electronically produced echoes that differed in delay by 800 μs . The bats were housed individually 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 14.5 and 15.5 g. 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.

B. Psychophysical test

Figure 1 illustrates the two-alternative forced-choice task on which the bats were trained. The experiment was run in a 4 m \times 3 m \times 2.5 m room with panels of sound-absorbent foam (Sonex, Illbrook, Inc.) lining the floor and walls. Light levels were kept dim for training and experimental trials. The equipment for producing the electronic echo stimuli was located in an adjacent room.

The bat’s task was to discriminate between the positive stimulus (rewarded echoes; S+) at a delay of 3160 μs and the negative stimulus (unrewarded echoes; S-) at a delay of 3960 μs . Each bat was trained to sit at the base of an elevated Y-platform and broadcast its echolocation sounds to

TABLE I. Electronic filter settings and attenuation of stimuli for four experiments.

Experiment	Stimulus condition	S+ attenuation		S- attenuation	
		S+ filter settings	(dB)	S- filter settings	(dB)
1	FM1 and FM2 (baseline)	20 kHz HP	-15	20 kHz HP	-20
		90 kHz LP		90 kHz LP	
1	FM1 only	20 kHz HP	-15	20 kHz HP	-20
		44 kHz LP		44 kHz LP	
1	28 kHz HP	28 kHz HP	-15	28 kHz HP	-20
		90 kHz LP		90 kHz LP	
1	32 kHz HP	32 kHz HP	-15	32 kHz HP	-20
		90 kHz LP		90 kHz LP	
1	FM2 only	66 kHz HP	-15	66 kHz HP	-20
		90 kHz LP		90 kHz LP	
	FM1, 0 μ s	20 kHz HP	-15	20 kHz HP	-20
		44 kHz LP		44 kHz LP	
	FM2, 0 μ s	66 kHz HP	-15	66 kHz HP	-20
		90 kHz LP		90 kHz LP	
2	FM1, 0 μ s	20 kHz HP	-15	20 kHz HP	-20
		44 kHz LP		44 kHz LP	
	FM2, 300 μ s	66 kHz HP	-15	66 kHz HP	-20
		90 kHz LP		90 kHz LP	
3	FM2 only (S+)	66 kHz HP	-15	20 kHz HP	-20
		90 kHz LP		90 kHz LP	
4	FM2 -3dB (S+)	20 kHz HP	FM1: -15	20 kHz HP	-20
		90 kHz LP	FM2: -12	90 kHz LP	
4	FM2 -3dB -48 μ s (S+)	20 kHz HP	FM1: -15	20 kHz HP	-20
		90 kHz LP	FM2: -12	90 kHz LP	

ward two ultrasonic microphones (Bruel & Kjaer Model 4138 “1/8-inch” condenser microphones), one located on each end of the platform. As shown in Fig. 1, microphones were mounted 20 cm away and separated by 40°. Echolocation sounds emitted by the bat were picked up by the microphones, filtered and delayed electronically and then delivered back to the bat from small electrostatic loudspeakers 15 mm in diameter (RCA, Model 112343). Speakers were mounted next to the microphones at the ends of both arms of the platform, 20 cm away from the bat and 50° apart (Fig. 1). The bat was rewarded with a piece of mealworm for walking down the arm of the Y-platform corresponding to the loudspeaker that delivered the positive stimulus, which was presented on either the left or right side in a pseudorandomized Gellerman sequence (Gellerman, 1933). If the bat made an incorrect response, a broadband sound was made to signal to the bat that it made an error. All trials were run using a double-blind procedure. Two experimenters were present while bats were run, a trainer who handled the bat and was blind to the position of the correct choice and a recorder who controlled which loudspeakers generated the stimuli and recorded the bat’s response. The recorder observed the bat using a black and white CCD video camera (Supercircuits, Inc., Type 15-CB22-1) mounted on the ceiling above the Y-platform. Illumination for the camera was provided by two infrared LED panels (Supercircuits, Inc.) located on either side of the video camera. The recorder was able to monitor the bat’s performance on a Sony digital 8-mm video walkman recorder located behind the trainer and the Y-platform.

Once the bat was able to perform the task for normal echoes (baseline, full-band echo condition) at better than

90% correct responses, sets of 50 experimental trials were conducted each day for three days for every condition. Each bat completed 150 trials over three days for each stimulus condition, for which the percentage of correct responses was accumulated.

C. Electronic stimuli

The 2-channel electronic target-simulator system has been described fully elsewhere; no changes were made for the new experiments described here (see Fig. 4, Stamper *et al.*, 2009). From bat sound to echo, the total gain of this system was approximately -35 dB for S+ and -40 dB for S-. The 5 dB attenuation of S- relative to S+ approximately compensates for the 5-dB increased sensitivity of the bat for echoes at the longer delay of 3960 μ s compared to the shorter delay of 3160 μ s (Kick and Simmons, 1984). All echoes were highpass (HP) filtered at 20 kHz and lowpass (LP) filtered at 90 kHz to set the boundaries of the echo band and remove background noise. Additional highpass or lowpass filtering used to restrict the frequency band for echoes serving as S+ or S- was introduced using filters already present in the simulator system. All values of filter settings and attenuations relative to a system gain of -35 dB are given in Table I.

A series of four different experiments were conducted using specific values of echo delay and filter settings as described below. However, the experiments were not carried out independently of each other; stimulus settings used in later experiments were chosen to explore the significance of results found in earlier experiments. Consequently, it is nec-

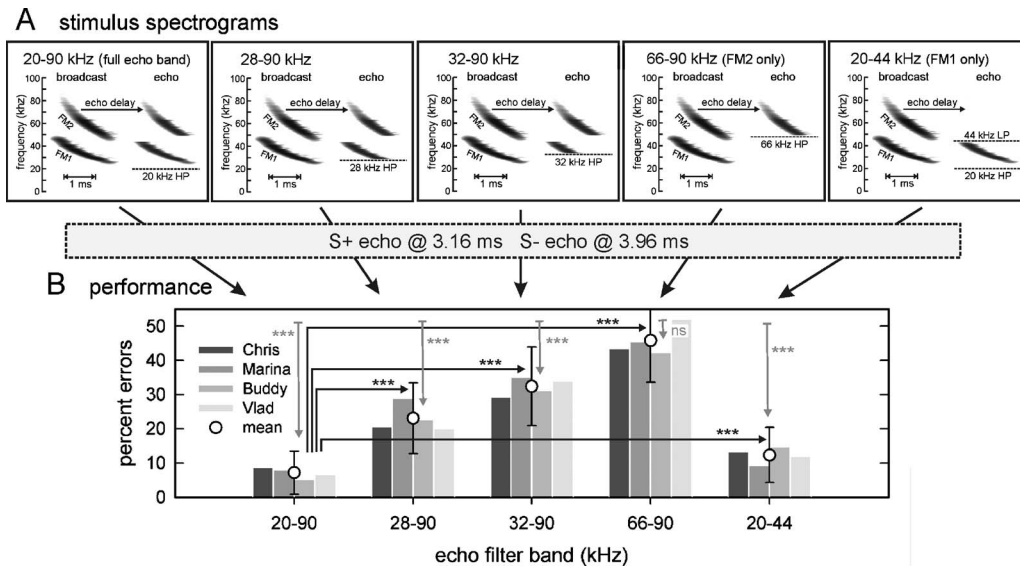


FIG. 2. Experiment 1. Effects of removing harmonics on delay acuity: (a) Spectrograms for stimuli used as echoes of a representative bat broadcast containing FM1 and FM2. Highpass filtering restricts the echo band to 20–90, 28–90, 32–90, or 66–90 kHz, which removes progressively larger segments from the low-frequency end of FM1. Lowpass filtering to 20–44 kHz completely removes FM2, leaving FM1 mostly intact. Filters have roll-off of 115 dB/octave to sharply cut out the unwanted part of the echo spectrum. Both S+ and S– are filtered as indicated and then delivered with the index delay difference of 800 μ s (Fig. 3). (b) Bar-graph showing performance on delay-discrimination tasks (percent errors) for four bats (150 trials/bat), with mean performance \pm 1 SD (circles). Removal of FM1 in small stages causes progressive, significant loss of delay acuity (more errors) for 800- μ s difference between S+ and S– (***) ($p < 0.001$), culminating in chance performance ($ns = p > 0.05$) for echoes containing only FM2. Performance recovers but still is not completely normal when echoes contain only FM1.

essary to describe the stimuli in the order they were used and the results in the order they were obtained. For each experiment, spectrograms are used to illustrate the stimuli, accompanied by graphs showing the bats' performance (percent errors in 2-choice task) on these stimuli. As a complication, S+ and S– were the same in some experiments but different

in others. To facilitate presentation of the experiments, spectrograms and results are combined into one figure for each experiment. All four bats completed the entire series of experiments. Their performances are plotted in Figs. 2(b), 3(b), 4(b), and 5(b) as percent errors (with 0% being perfect performance and 50% being chance performance).

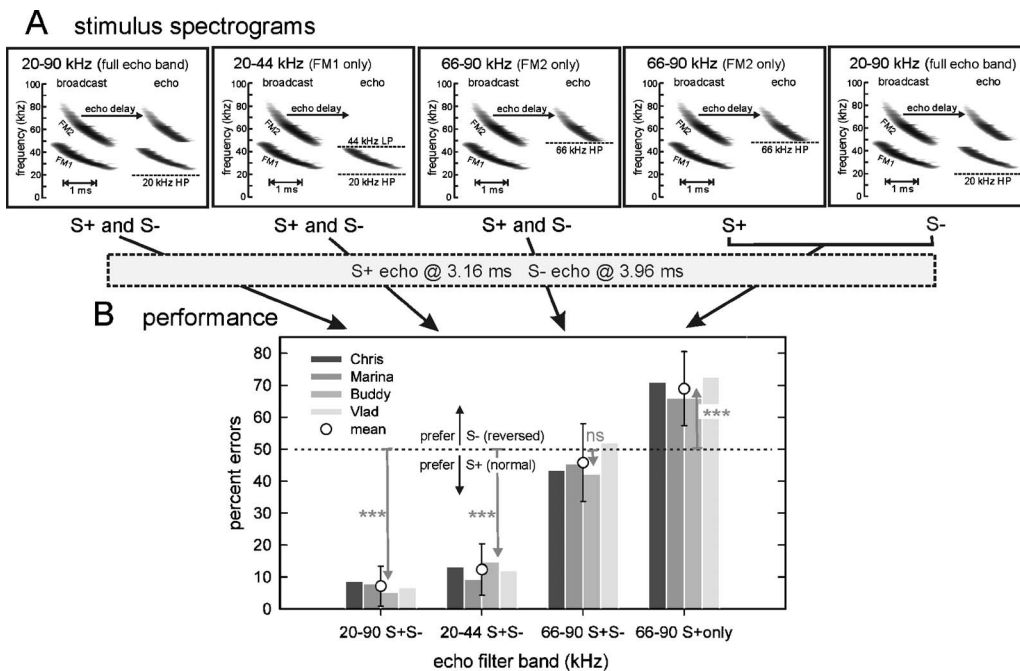


FIG. 3. Experiment 2. Relative salience of harmonics: (a) Spectrograms for representative stimuli containing only FM1 or only FM2 for S+ and S–. Full-band, normal echoes are shown at left. At right, S+ contains only FM2 while S– contains FM1 and FM2 (full band). (b) Bar graph showing performance on delay-discrimination tasks (percent errors) for four bats with mean performance \pm 1 SD. As already shown in Fig. 2, performance on 800- μ s delay difference is good (***) ($p < 0.001$) if echoes contain only FM1 but chance ($ns = p > 0.05$) if echoes contain only FM2. When offered a choice between S– containing FM1 and FM2 versus S+ containing FM2 alone, bats prefer S– even though it is delivered 800 μ s later than S+ (***) ($p < 0.001$).

III. EXPERIMENT 1—EFFECTS OF REMOVING HARMONICS ON DELAY ACUITY

A. Procedure

Figure 2(a) shows spectrograms and electronic filter settings for the five stimulus conditions used for Experiment 1. The first condition illustrated by the spectrograms is the baseline, with full-band echoes (20–90 kHz), in which S+ is presented at 3160 μ s and S– is presented at 3960 μ s, with both FM1 and FM2 intact and arriving simultaneously. The next three spectrograms for S+ and S– (28–90 kHz; 32–90 kHz; 66–90 kHz) illustrate a progression of three stimulus conditions in which progressively larger segments of the lower-frequency end of FM1 are removed. At the end of this series, FM1 is removed entirely and the stimuli contain only FM2. The last spectrogram in Fig. 2(a) shows the FM1 only condition (20–44 kHz), in which the sound was lowpass filtered to selectively remove FM2, leaving only FM1. For all of the conditions illustrated in Fig. 2(a), the same filtering was applied to both S+ and S–. Thus, the bat would receive echoes filtered in the same manner from both arms of the platform. For all of these conditions in Experiment 1, S+ and S– differed only in delay.

B. Results

The bar-graph in Fig. 2(b) shows the performance of the four bats on the stimulus conditions of Experiment 1 (Fig. 2(a)). Mean performance ± 1 SD is plotted over the vertical bars for the individual bats (white circles with vertical error lines). The bats' performance was uniformly good (few errors) for the baseline, full-band condition (indicated as 20–90 on horizontal kHz axis). On average, the bats made only 6% errors, which was significantly better than chance (4 bats \times 150 trials/bat; N=600, $p < 0.001$). (This and all subsequent statistics report probabilities from exact binomial two-tailed tests.)

Highpass filtering that removed increasingly larger portions from the low-frequency end of FM1 caused progressive losses in delay acuity (more errors) relative to the baseline, full-band condition. In the 28–90 kHz filter condition (Fig. 2(b)), mean percent errors was 20.9%. This was significantly different from both the baseline condition ($p < 0.001$), and from chance (50%) performance ($p < 0.001$). Mean percent errors in the 32–90 kHz filter condition was 30%, which differed significantly from both the baseline, full-band condition ($p < 0.001$) and from chance performance ($p < 0.001$). For echoes containing only FM2 in the 66–90 kHz filter condition, performance fell to an average of 45.8% errors. This was significantly worse than baseline performance ($p < 0.001$), but it was not significantly different than chance ($p = 0.121$).

Finally, in the 20–44 kHz filter condition, which delivered FM1 alone, the bats made an average of 12.3% errors, which differed significantly from both baseline, full-band performance ($p < 0.001$), and from chance performance ($p < 0.001$).

IV. EXPERIMENT 2—RELATIVE SALIENCE OF HARMONICS

A. Procedure

The results from Experiment 1 reveal effectively chance performance (45.8% errors) for discrimination of the index 800- μ s difference in echo delay if echoes contain only FM2 (66–90 kHz filtering), but good performance for echoes containing only FM1 (20–44 kHz filtering). Experiment 2 was conducted to determine whether the chance performance for FM2 reflects poor delay acuity as such, or whether big brown bats do not treat stimuli containing just FM2 as “echoes” at all. Echoes containing FM1 alone would occur naturally for off-axis or far-away targets, but echoes containing just FM2 are not normally experienced by bats. Experiment 2 presented bats with echoes containing only FM2 as S+ (66–90 kHz filter condition), and baseline, full-band echoes (20–90 kHz filter condition) as S–. Figure 3(a) shows the spectrograms for these stimuli. By giving the bat a choice between FM2 alone for S+ at a shorter, normally easily-discriminated delay of 3160 μ s and full-band echoes containing both FM1 and FM2 for S– at a much longer delay of 3960 μ s, the possibility that the bats might reject FM2 can be assessed. Because the intent of Experiment 2, in conjunction with several of the conditions from Experiment 1, is to identify the relative roles of the harmonics in echoes, Fig. 3(a) shows spectrograms for full-band echoes (20–90 kHz) containing both FM1 and FM2, along with echoes containing only FM1 (20–44 kHz) or only FM2 (66–90 kHz).

B. Results

Figure 3(b) plots the individual performance of the four bats, along with the mean ± 1 SD, on the several conditions with FM1 or FM2 side-by-side for comparison. The horizontal dotted line at 50% errors indicates performance at chance levels. Performance below this line, toward 0% errors, indicates that the bats prefer S+ (rewarded choice); performance above this line, toward 100% errors, indicates that the bats prefer S– over S+ (reversed preference). As previously shown in Fig. 2(b), the bats' performance discriminating the 800- μ s index delay difference is significantly better than chance for the baseline full-band (20–90 kHz) condition ($p < 0.001$), and for the FM1 only (20–44 kHz) condition ($p < 0.001$). Performance is at chance for the FM2 only (66–90 kHz) condition ($p > 0.05$). The new condition for Experiment 2 examines whether this inability to select S+ reveals poor delay acuity for FM2 by itself, so that the 800- μ s difference is not perceptible, or whether FM2 is simply not considered to be an echo by the bat. When given echoes containing only FM2 as S+ and full-band echoes as S–, the bats' performance *reverses* to become better than chance, but for S–, not S+ ($p < 0.001$). This reversal of performance when bats are presented with echoes containing only FM2 at a much earlier delay than echoes containing FM1 and FM2 suggests that sounds containing only FM2 are not accepted as echoes, so the bats choose instead the normal, full-band echoes.

V. EXPERIMENT 3—EFFECTS OF HARMONIC-SPLIT FILTERING ON DELAY ACUITY

A. Rationale

Responses evoked in individual neurons of the big brown bat's inferior colliculus and auditory cortex by short-duration FM sounds such as the signal illustrated in the spectrograms of Figs. 2(a) and 3(a) consist, on average, of a single action-potential at a well-defined latency for each presentation of the stimulus (Sanderson and Simmons, 2000, 2002, 2005; Simmons *et al.*, 1998). These neurons are tuned to a well-defined best frequency in the bat's 15–100 kHz echolocation band, but they respond equally well over a wide range of stimulus amplitudes. That is, they exhibit poor tuning to specific stimulus amplitudes. However, response latencies to FM stimuli are exquisitely sensitive to amplitude changes, shifting later by about 16 μs for each decibel of decrease in amplitude (Bodenhamer and Pollak, 1981; Burkard and Moss, 1994; Ma and Suga, 2008; Simmons *et al.*, 1990). Changing the amplitude of FM1 relative to FM2 thus affects the latencies of responses evoked by individual frequencies in the FM sweep with far greater precision than it affects the probability of a response actually occurring. From Experiment 1, bats discriminate the 800- μs index delay difference progressively worse for echoes that have increasingly large segments of FM1 removed by filters (Fig. 2(b)). Does the change in FM1 amplitude, which leads to lengthening of the latencies of responses to FM1, disrupt the normal simultaneity, or temporal coherence, of neural responses to FM1 and FM2? Does this loss of temporal coherence within the bat's auditory representation then cause the poor performance in the 800- μs delay discrimination tests (Fig. 2(b))?

The previous split-harmonic experiment, in which echoes were delivered with FM2 at a 300- μs later delay than FM1, revealed a surprising collapse in the sharpness of the big brown bat's delay image, which provided the rationale for using a large delay difference of 800 μs for the present experiments. Although this first split-harmonic experiment separated FM2 from FM1 by fully 300 μs , the split-harmonic procedure itself provides a means for adjusting the delays of FM1 and FM2 independently in much smaller steps, too. If amplitude-latency trading disrupts the temporal coherence of the harmonic representations inside the bat's auditory system when the strength of one harmonic is changed relative to the other (trading ratio is $-16 \mu\text{s}/\text{dB}$), thus causing delay acuity to collapse, then shifting the *delay* of the changed harmonic by an equal but opposite amount in time should restore coherence and remove the poor performance in the 800- μs delay discrimination task. Because this test involves measuring whether the bats make more errors or less errors in different stimulus conditions, it is important to know whether the split-harmonic filtering arrangement itself can cause some loss in delay acuity.

B. Procedure

Experiment 3 was designed to determine whether introducing the split-harmonic filter settings (20–44 kHz to isolate FM1; 66–90 kHz to isolate FM2) worsens the perfor-

mance of the bats on the 800- μs delay discrimination task by such a large amount that it would obscure any further worsening caused by changing the amplitude of one harmonic relative to the other, or by adjusting the delay of the harmonics to compensate for amplitude-latency trading. Figure 4(a) shows spectrograms for three stimulus conditions—on left, baseline, full-band echoes for S+ and S- (from Fig. 2(a)), in middle, split-harmonic conditions (20–44 kHz for FM1; 66–90 kHz for FM2) with the same delay for FM1 and FM2 (given as 0 μs relative to the total delay of 3160 μs for S+ and 3960 μs for S-) or with the previously-tested 300- μs offset of FM2 relative to FM1. On right, S- consists of split-harmonic echoes with the same delay for FM1 and FM2.

C. Results

Figure 4(b) shows the performance of the four bats, and the mean performance ± 1 SD, on the baseline, full-band stimulus condition of Experiment 1 (Fig. 2(b)) along with performance on the two split-harmonic conditions. When the split-harmonic filters were introduced with no delay offset of FM2 relative to FM1 (both at 0 μs), performance declined from a mean of 7.2% errors to a mean of 9.3% errors, which was a slight but statistically significant increase in errors ($p < 0.05$). When FM2 is additionally delayed by 300 μs relative to FM1, performance declined further to 17.0%, which is significantly different than for the split-harmonic filters alone ($p < 0.001$). Thus, while introduction of the split-harmonic filters to segregate FM1 and FM2 produces a small decrease in delay acuity at 800 μs , it is not enough to obscure the much larger effects of disrupting the timing of the harmonics.

VI. EXPERIMENT 4—AMPLITUDE-LATENCY TRADING AND COMPENSATORY TIME SHIFT

A. Procedure

The results from Experiment 3 (Fig. 4(b)) reveal that it is feasible to use the split-harmonic technique to assess, first, the loss in acuity caused by changing the amplitude of one harmonic relative to the other, and second, the potential restoration of acuity caused by adding a countervailing change in the delay of one harmonic relative to the other. Two stimulus conditions were run in order to demonstrate the amplitude-latency trading effect, in which decreasing the amplitude of FM2 in echoes retards their perceived delay by 16 $\mu\text{s}/\text{dB}$, and its removal by advancing the delay of FM2 by an equal amount. The spectrograms in Fig. 5(a) illustrate conditions for Experiment 4 along with two conditions from Experiment 3 for comparison. The first spectrogram on the left of Fig. 5(a) shows the baseline, full-band echo from experiment 1 used as S+. The second spectrogram shows the split-harmonic echo with 0 μs delay difference between FM1 and FM2 used as S+. The third spectrogram shows a split-harmonic echo with FM2 attenuated by 3 dB relative to FM1 used as S+ (first of two new conditions for Experiment 4). Based on the amplitude-latency trading ratio of $-16 \mu\text{s}/\text{dB}$, an attenuation of 3 dB should retard neural re-

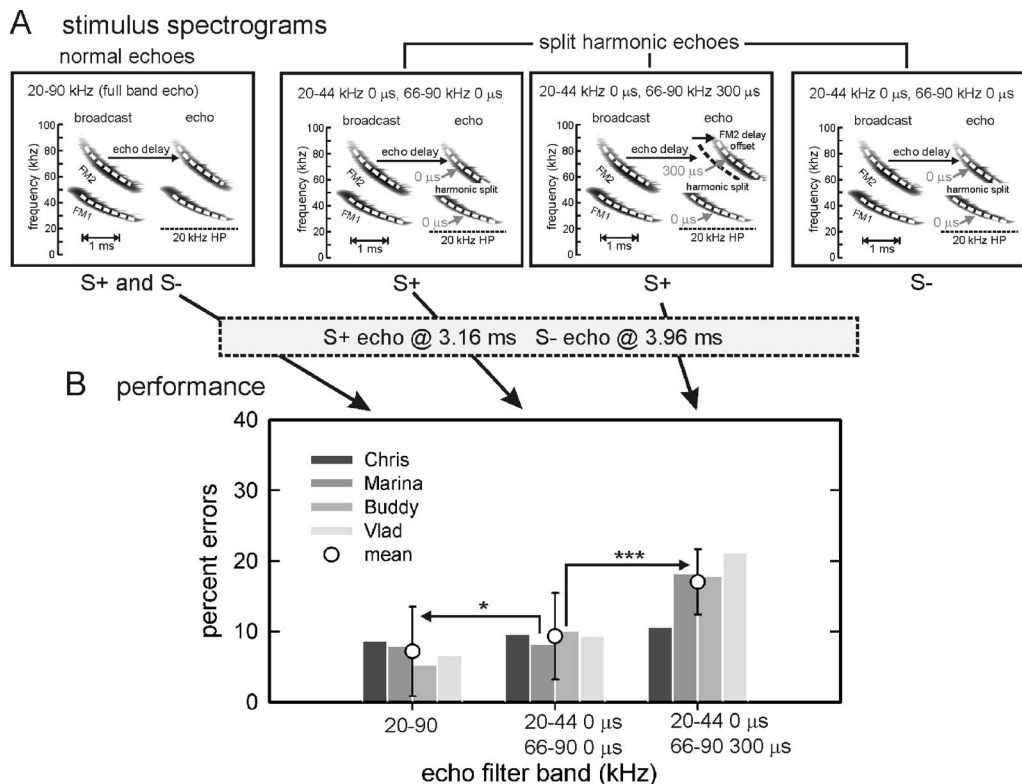


FIG. 4. Experiment 3. Effects of harmonic-split filtering on delay acuity: (a) Spectrograms for representative stimuli testing the effect of introducing the harmonic-split filters on the 800- μ s index delay discrimination task. Full-band, normal echoes with no harmonic split for S+ and S- are shown at left (note slight overlap of harmonics at 50–55 kHz). Next, to split the harmonics into two parallel electronic channels, echoes for both S+ and S- are filtered at 20–44 kHz to remove FM2 and 66–90 kHz to remove FM1. The isolated harmonics are delayed and amplified differently, then recombined (added) to create split-harmonic echoes that now have a narrow spectral gap eliminating frequencies around 55 kHz where FM1 and FM2 overlap. S+ echoes have either the harmonic split alone (FM1 and FM2 both at 0 μ s) or the harmonic split plus 300- μ s offset of FM2 relative to FM1 (FM1 at 0 μ s, FM2 at 300 μ s). S- echoes have the harmonic split alone (FM1 and FM2 at 0 μ s). (b) Bar graph showing performance on delay-discrimination tasks (percent errors) for four bats (150 trials/bat, with mean performance \pm 1 SD shown by circles). Introduction of harmonic-split filters with no other change causes small, significant decrease in acuity (more errors) compared to full-band echoes (* = $p < 0.05$). Addition of 300- μ s offset to FM2 relative to FM1 causes large decline in acuity beyond what occurs for split-harmonic condition with no delay difference (*** = $p < 0.001$).

sponses evoked by FM2 by about 48 μ s relative to responses evoked by FM1. The fourth spectrogram in Fig. 5(a) shows the split-harmonic echo with FM2 reduced by 3 dB and advanced in time by 48 μ s used as S+, to compensate for amplitude-latency trading. The spectrogram on the right shows the baseline, full-band echo with both FM1 and FM2 used as S- for all of the illustrated conditions.

B. Results

Figure 5(b) shows the results for the two new conditions in Experiment 4, along with two previous results for comparison. As shown earlier, performance with split harmonic echoes with 0 μ s harmonic shift (Fig. 4(b)) was only slightly, albeit significantly, worse than performance with baseline, full-band echoes. When bats were presented with split-harmonic S+ echoes in which FM2 was attenuated by 3 dB relative to FM1, performance declined drastically to 29% errors due just to the 3-dB change in amplitude ($p < 0.001$). However, shortening the delay of FM2 by 48 μ s, while it is attenuated by 3 dB, counteracted the amplitude-latency trading effect and improved performance to 10.3%. Critically, the improved performance restores acuity to what occurs for split-harmonic filtering without any additional amplitude or time manipulation ($ns = p > 0.05$). It thus appears that big

brown bats use the timing of neural responses to represent the harmonic sweeps, at least to achieve acuity for perception of echo delay.

VII. DISCUSSION

Taken together, the results of Experiments 1–4 confirm the expectation that big brown bats are sensitive to small perturbations of the FM harmonics in echoes (Hiryu *et al.*, 2010). What is interesting here is that their sensitivity is manifested as a *loss in acuity* for perception of echo delay. Experiments 1–4 were not designed to determine whether bats can discriminate between echoes containing FM1 or FM2 in various combinations, but that these various combinations have effects on a fundamental perceptual dimension of echolocation—the delay of echoes.

Previous echo-delay discrimination experiments have used different types of echoes as stimuli, including electronically-returned faithful replicas of each broadcast (as in the experiments described here) or “model” echoes, essentially a fixed, synthetic echo waveform triggered by the bat’s sounds and presented at a controlled delay. Individual bat sounds will change from one broadcast to the next, but the model echo stays the same. Triggering of the model echo sound by each bat sound introduces significant timing jitter

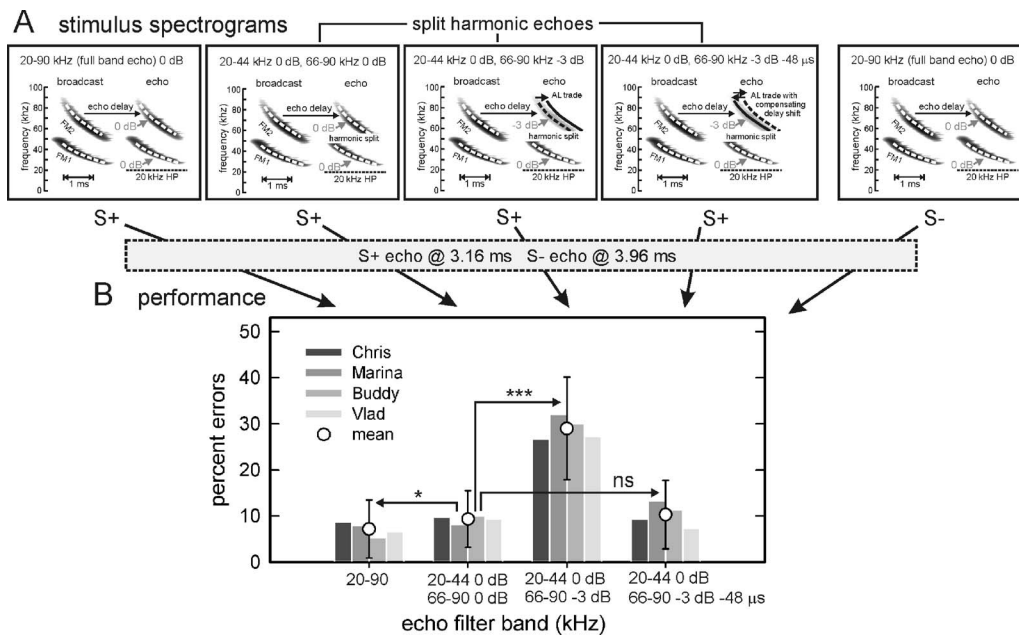


FIG. 5. Experiment 4. Amplitude-latency trading and compensatory time shift: (a) Spectrograms for representative stimuli used to assess the loss in delay acuity if FM2 is decreased by 3 dB relative to FM1, and for testing the role of amplitude-latency trading by advancing FM2 in time by a compensatory 48 μ s. (Amplitude-latency trading ratio for bats is -16μ s/dB.) The two spectrograms at left show full-band, normal echoes with *no* harmonic split for S+ and *with* harmonic split for S+ (from Fig. 4). Next two spectrograms show FM2 decreased in strength by 3 dB relative to FM1, or decreased by 3 dB and moved earlier in time by 48 μ s. All S- are full-band echoes with no harmonic split (at right). (b) Bar graph showing performance on delay-discrimination tasks (percent errors) for four bats (150 trials/bat, with mean performance \pm 1 SD shown by circles). Introduction of harmonic-split filters with no other change causes small, significant decrease in acuity (more errors) compared to full-band echoes ($*=p<0.05$). Decreasing FM2 by 3 dB causes further, large decline in performance ($***=p<0.001$), but advancing FM2 in time by 48 μ s compensates for amplitude-latency trading and restores performance ($ns=p>0.05$). Results show no evidence for perceptual effect from 3 dB loss of FM2 except for the associated latency shift.

of 50 μ s or more from one broadcast to the next, which limits the utility of model echo experiments to observing deterioration in performance beyond the 50- μ s limit inherent in all 2-choice delay discrimination procedures. Given this limited accuracy of the 2-choice method, bats have no more difficulty in discriminating the delay of model echoes (Masters and Jacobs, 1989) than the delay of real echoes from physical targets (Simmons 1971, 1973; Surlykke and Miller, 1985; Roverud and Grinnell, 1985) or from true electronic echoes that are delayed and attenuated versions of each of the bat's vocalizations (Denzinger and Schnitzler, 1994; Simmons, 1979, 1989). When certain parameters of model echoes are changed enough to exceed the 50- μ s limit of the 2-choice method, bats do exhibit greater difficulty in discriminating their delays. For example, big brown bats can successfully *detect* model echoes presented either forward or reversed in time, but their delay discrimination threshold is normal (50–100 μ s) only for echoes presented in their correct, forward direction; thresholds worsen substantially for time-reversed model echoes (Masters and Jacobs, 1989). Other studies have reported decrements in delay acuity only when the time-frequency structure of model echoes had been altered enough to matter (Surlykke, 1992; Masters and Raver, 2000). For example, when model echo duration, amplitude of FM2 relative to FM1, frequency sweep range, and curvature of frequency sweeps are systematically altered, the bats' performance was only affected by changing sweep shape (Masters and Raver, 2000). These experiments establish the plausibility of results that involve manipulations to

deliberately make performance worse than the expected 50- μ s limit of the 2-choice method.

In Experiments 1–4 described above, the harmonics (FM1, FM2) in echoes that big brown bats received in two-choice delay discrimination tests were electronically manipulated to assess their significance for perception of echo delay. A relatively large delay difference of 800 μ s (3160 μ s for S+ versus 3960 μ s for S-) was used to ensure that any effects obtained by manipulating harmonics would not be a consequence simply of reducing echo bandwidth or changing echo center frequency. (In experiments using identical apparatus and stimulus levels, effects related to bandwidth and center frequency do occur, but on a much finer time scale of delay hyperacuity in fractions of a microsecond; Simmons *et al.*, 2004). The 800- μ s difference was used here to ensure that any changes in performance actually obtained would constitute a disruptive effect strong enough to spread over a span of time nearly a millisecond wide. It thus would represent a significant loss of acuity to the bat. From Experiments 1–4, several manipulations, including truncation or removal of FM1 and separation of FM2 from FM1 in time, yielded large decreases in the bats' performance (more errors) on the nominally easy 800- μ s task, indicating that the loss in delay acuity associated with these manipulations was severe. Normal acuity in 2-choice discrimination results is roughly 50 μ s (Simmons, 1973; see Moss and Schnitzler, 1995; Simmons *et al.*, 1995), but here the bat's acuity must have deteriorated to roughly 800–1000 μ s, judging from the performance decrements obtained in the results described

above. In spatial terms, this is equivalent to degrading the bat's normal, biologically quite useful distance acuity of about 1cm to a nearly-useless distance acuity of 16–20 cm. Several specific conclusions are warranted from these findings.

A. Asymmetry in the role of harmonics

The most obvious conclusion is that the two harmonics are asymmetric in their contributions to delay acuity. The results of Experiment 1 (Fig. 2(b)) show that big brown bats are sensitive in a graded manner to partial removal of FM1, and that performance falls to chance when FM1 is removed entirely. In contrast, complete removal of FM2 had only a slight effect on performance. Clearly, bats require the presence of FM1 to accurately perceive the delay of echoes, but the presence of FM2 is not required. Highpass filtering that removed small portions of the low-frequency end of FM1 disproportionately affected delay acuity (Fig. 2). Performance worsened when larger segments of low-end frequencies were removed. These results emphasize the importance of the low frequencies at the terminal end of FM1, which previous experiments have shown to be especially important for target detection (Bates *et al.*, 2008). Results from Experiments 1–2 are consistent with a previous finding that big brown bats can detect echo-delay jitter as small as 4 μ s equally well with FM1 and FM2 present together as with FM1 alone, but that the bats fail to perform the jitter task at all for echoes with FM2 alone (Moss and Schnitzler, 1989). As indicated by that earlier result and now also by the results of Experiment 2, big brown bats seem not to treat sounds containing only FM2 as being echoes at all. In Experiment 2, they prefer FM1 and FM2 together over FM2 alone, even when sounds containing just FM2 arrives full 800 μ s earlier—a delay difference so large that the bats do not appear to judge FM2 by itself as even *having* a well-defined delay.

The auditory mechanisms underlying the behaviorally-observed asymmetry in harmonic function must be far more complicated than just having responses to FM1 required for the determination of delay, with responses to FM2 adding only a little more information if FM2 is present. From Experiments 3 and 4, retarding the timing of FM2 relative to FM1 causes a significantly larger loss in acuity (17% errors for 300- μ s offset introduced directly as in Fig. 4; 29% errors for 48- μ s offset induced indirectly by amplitude-latency trading as in Fig. 5) than does total removal of FM2 (12.3% errors as in Fig. 2). The seemingly paradoxical result that misaligning responses to FM2 in time relative to responses to FM1 has a larger impact on performance than the complete absence of any responses at all to FM2 leads to a further conclusion. The bat's greater sensitivity to misalignment suggests that neuronal inhibition must be evoked by responses to frequencies in FM1, but must be applied to responses evoked by the higher frequencies in FM2. The proposed inhibition must be initiated by FM1 and must then persist over a short span of time following FM1. This inhibition normally would trail behind simultaneously-occurring excitatory responses to both FM2 and FM1, so that excitatory responses to FM2

would be finished before the inhibition caused by FM1 has started. However, retarding responses evoked by FM2 (either directly by shifting FM2 to a later time or indirectly by amplitude-latency trading when FM2 is attenuated) causes these responses to intrude into the inhibitory time window excited by FM1, which then leads to disruption of delay acuity.

The observed asymmetry of harmonic function seems to favor contributions from FM1 over contributions from FM2. To be clear, FM2 is not without function, it is just that its role is manifested here as causing a precipitous deterioration in delay acuity when retarded relative to FM1. The 2-choice echo-delay acuity observed in normal conditions appears to be due almost entirely to FM1 because graded removal of FM1 has corresponding effects on performance, while, when FM2 is totally absent, its contribution seems slight. The direction of the asymmetry revealed by Experiments 1–4 conforms to acoustic and auditory asymmetries normally experienced by echolocating bats, which leads to consideration of the purpose that is served by the asymmetry. (In a different type of experiment that probes the big brown bat's perception of delay on much finer time scale, graded removal of frequencies from either FM2 or from FM1 leads to a graded decrease in delay hyperacuity; Simmons *et al.*, 2004. In those experiments, no abrupt deterioration occurs when FM1 is truncated. Both FM1 and FM2 are capable by themselves of supporting delay hyperacuity, which nevertheless is better when both harmonics are present).

B. Harmonic misalignment as a mechanism for rejection of clutter

Retarding of auditory responses to FM2 so they follow responses to FM1 causes the bats' delay acuity to decline so severely as to constitute a collapse of the bat's image along the delay axis. So extreme a consequence of merely shifting the auditory representation of FM2 by a small fraction of a millisecond, compared to the slight effect of complete removal of FM2, signifies that some important characteristic of echoes is bound up in the temporal relation between FM2 and FM1. Moreover, this characteristic must be important enough that the bat benefits from the resulting substantial loss of delay acuity for those sources. How might the bat gain advantage from deliberately creating a *loss* of acuity? Although true temporal lagging of FM2 after FM1 does not occur acoustically during sound propagation or reflection in air because sound velocities are the same for frequencies in both harmonics, *attenuation* of FM2 relative to FM1 due to lowpass filtering during propagation or from broadcast beaming *does* occur. In contrast, attenuation of FM1 relative to FM2 through highpass filtering is unlikely to occur because echoes from insect-sized targets have, on average, flat spectra over the frequencies used by big brown bats (Moss and Zagaeski, 1994; Simmons and Chen, 1989). When FM2 is weakened relative to FM1, amplitude-latency trading at a ratio of approximately -16μ s/dB (Bodenhamer and Pollak, 1981; Burkard and Moss, 1994; Ma and Suga, 2008; Simmons *et al.*, 1990) shifts responses evoked by FM2 into a time window that follows responses to FM1. The results of Experiment 4 (Fig. 5) establish unambiguously that a small

(3 dB) reduction in the amplitude of FM2 causes retardation of responses through amplitude-latency trading, a retardation that can be offset by advancing the timing of FM2 itself. For these reasons, amplitude-latency trading is the only practical origin of temporal misalignment between harmonics experienced by bats. It is the only realistic path for causing the bat's delay acuity to decrease by mechanisms identified from the results of Experiments 1–4.

What are the common features of objects whose echoes undergo lowpass filtering? The bat emits a broadcast containing FM1 and FM2 at approximately equal strength. The sounds that impinge on targets located directly in front of the bat and not too far away contain both of these harmonics at equal strength, too. But bats' broadcasts are emitted with a directivity that is dependent on frequency (Hartley and Suthers, 1989). The broadcast beam is very wide for frequencies of 20–30 kHz, present in the terminal end of FM1, but the beam grows narrower at higher frequencies, so that the frequencies of 55–90 kHz in FM2 are localized in a narrower zone in the center of the beam than the frequencies of 22–55 in FM1. As off-axis direction increases, the higher frequencies (e.g., FM2) are attenuated. Atmospheric attenuation also is stronger at higher ultrasonic frequencies. As target distance increases, FM2 gets progressively weakened relative to FM1 (e.g., Lawrence and Simmons, 1982). Thus, echolocation sounds impinging on targets located off to the sides or far away always undergo lowpass filtering, and echoes thus always return from objects in these locations with attenuation of FM2 relative to FM1. Due to amplitude-latency trading, the auditory representation of these echoes will include temporal misalignment of responses for FM2 relative to FM1, and correspondingly degraded acuity for perception of delay. In contrast, targets located immediately to the bat's front will be ensonified with both harmonics, and echoes will return with FM2 and FM1 at about the same strengths because the total distance of propagation is short. The practical significance of this distinction is that clutter—objects off to the sides or in the background—virtually always return lowpass echoes that, due to relative attenuation of FM2, will be perceived with poor delay acuity. Echoes from any objects located in the frontal zone of immediate concern to the bat will be perceived as having well-defined delays. If this distinction is correct, then bats may have evolved low delay acuity as a means of preventing interference from clutter. It thus appears that FM2 may serve a specific perceptual purpose in the echolocation by big brown bats, and not a purpose encompassed just by the added bandwidth it represents.

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