Vocal control of acoustic information for sonar discriminations by the echolocating bat, *Eptesicus fuscus*

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This study aimed to determine whether bats using frequency modulated (FM) echolocation signals adapt the features of their vocalizations to the perceptual demands of a particular sonar task. Quantitative measures were obtained from the vocal signals produced by echolocating bats (*Eptesicus fuscus*) that were trained to perform in two distinct perceptual tasks, echo delay and Doppler-shift discriminations. In both perceptual tasks, the bats learned to discriminate electronically manipulated playback signals of their own echolocation sounds, which simulated echoes from sonar targets. Both tasks utilized a single-channel electronic target simulator and tested the bat's in a two-alternative forced choice procedure. The results of this study demonstrate changes in the features of the FM bats' sonar sounds with echolocation task demands, lending support to the notion that this animal actively controls the echo information that guides its behavior. © *2000 Acoustical Society of America.* [S0001-4966(00)06103-3]

INTRODUCTION

An echolocating bat's vocal behavior directly influences the acoustic information carried by sonar echoes. In particular, changes in the bandwidth, duration, and timing of the bat's sonar transmissions determine the signal parameters available to its acoustic imaging system. Sonar/radar theory and its application demonstrate that broadband signals are best suited for target ranging, because each frequency in the returning echo provides a marker for arrival time, the parameter used to measure the distance of a sonar target (Woodward, 1964; Simmons and Stein, 1980; Skolnik, 1980). Narrow-band signals are well suited for target detection, because signal energy concentrated in a limited frequency band maximizes the signal-to-noise ratio in the returning echo (Woodward, 1964; Simmons and Stein, 1980; Møhl, 1988). Narrow-band signals are also well suited to carry velocity information through Doppler shifts in the returning echoes (e.g., Simmons and Stein, 1980; Skolnik, 1980; Altes, 1984).

Studies of echolocation behavior in the field provide indirect evidence that bats exercise active control over the echo information for changing sonar tasks (e.g., Griffin, 1958; Kalko and Schnitzler, 1998; Schnitzler and Kalko, 1998). Bats that typically hunt insects in open space use frequency modulated (FM) signals for echolocation, and these signals show distinct patterns of change at different phases of foraging (Griffin, 1953; Webster *et al.*, 1965; Simmons and Kick, 1984; Kalko and Schnitzler, 1998). During the search phase of insect pursuit, the big brown bat, *Eptesicus fuscus*, produces shallow FM signals, with the first harmonic sweeping from 25–22 kHz in 15–20 msec (Griffin, 1953, 1958). These sounds are well suited for target detection (Møhl, 1988),

maximizing the signal-to-noise ratio in a narrow frequency band. Once the bat begins to approach a prey item, its sonar sounds shorten in duration, increase in bandwidth, and increase in repetition rate. The first harmonic sweeps from approximately 60 to 25 kHz in 2–5 msec during the approach phase of insect pursuit. Finally, at the end of the terminal phase of insect pursuit, the first harmonic of *Eptesicus*'s sonar sounds sweeps from approximately 25 to 12 kHz in less than a msec (Griffin, 1953; Simmons *et al.*, 1979; Schnitzler and Henson, 1980). The brief, broadband signals that are used in the approach and terminal phases are well suited to provide sharp registration of echo arrival time (Woodward, 1964; Simmons and Stein, 1980; Skolnik, 1980), the bat's measure of target distance (Hartridge, 1945; Simmons, 1973).

Reports from laboratory studies suggest that some bat species adapt the features of their sounds to influence the information available for specific sonar discriminations. For example, von der Emde and Menne (1989) report that the CF-FM bat, *Rhinolophus ferrumequinum*, increased the duty cycle of its sounds from about 40% at baseline to 70% when discriminating echoes from insect prey that differed in flutter rate. The increase in duty cycle provided the bat with more information about the fluttering insect's wingbeats over time.

Laboratory studies of bats using frequency modulated (FM) signals offer little data in support of the idea that bats show task-dependent vocal behavior. For example, negative evidence for active vocal control by FM bats was reported by Habersetzer and Vogler (1983), who trained *Myotis myotis* to discriminate targets with differing surface structure. They observed no changes in the parameters of the sonar signals used by bats performing in the task compared with those emitted by bats during free flight. It is possible that changes in sound features were present (and even perceptually salient

to the bats) but too small for the experimenters to identify using standard signal analysis techniques.

Most changes in vocal behavior reported in the literature are qualitative descriptions. For example, Simmons *et al.* (1975) noted that the FM bat, *Eptesicus fuscus*, modified its sounds in a range discrimination task when tested under noisy conditions. They describe the bat's addition of a short constant frequency (CF) component at around 23 kHz to the end of the FM sweep, which serves to improve the signal-to-noise-ratio. Kick (1982) reported that sounds produced by *Eptesicus fuscus* in a detection task were 4–8 msec in duration, longer than those recorded from bats performing in a ranging task (Simmons, 1973). Kick described a quasi-CF component at the end of the bat's FM sweep, similar to that reported by Simmons *et al.* (1975). The sounds described by Simmons *et al.* (1975) and Kick (1982) are suggestive of adaptive vocal control by FM bats under changing task conditions, but no quantitative measures were reported that directly compare sounds produced by the same bats under different task conditions.

One study of FM bat vocal behavior included extensive quantitative comparisons of signal features produced by bats performing in two distinct perceptual tasks; however, the results do not argue strongly for adaptive vocal behavior. Masters *et al.* (1991) measured small differences in the features of sonar signals produced by *Eptesicus fuscus* performing in echo detection and echo ranging tasks; however, they found larger differences between the sound features of individual bats performing in the same task than within a bat performing different tasks.

While sonar/radar theory demonstrates the utility of changing signal parameters with task demands, data on the FM bat's active role in echolocation performance is presently incomplete. In particular, laboratory studies of FM bats have not yet provided compelling data demonstrating active vocal control in bats that is specific to changing task demands. Given data from field recordings that suggest adaptive vocal behavior in FM bats (Griffin *et al.*, 1958; Kalko and Schnitzler, 1998; Schnitzler and Kalko, 1998), we propose that the appropriate task comparisons should yield corresponding vocal control data from the laboratory.

In the present study, we made quantitative comparisons of echolocation sounds produced by the FM bat, *Eptesicus fuscus*, in two distinct perceptual tasks: Target range discrimination and Doppler shift discrimination. These tasks were selected to maximize possible differences in vocal production patterns. Range discrimination requires signals that permit accurate measurement of echo arrival time, while Doppler discrimination requires signals that permit accurate measurement of echo frequency shifts. The results of our study provide clear evidence for task-dependent vocal behavior in the FM bat, *Eptesicus fuscus*.

I. METHODS

A. Animals

Three female FM bats of the species *Eptesicus fuscus* served as subjects in two different perceptual tasks. The animals were collected from private homes in Maryland during the summer of 1996 and housed in a colony room at the University of Maryland in College Park, Maryland. The temperature in the colony room was maintained at approximately 27 °C and the day/light cycle was reversed, with lights out between 7:00 a.m. and 7:00 p.m. Bats were given free access to water and maintained at about 85% of *ad lib* body weight. Food was available only as a reward during behavioral experiments, which were carried out 6–7 days/ week over a period of 21 months.

B. Apparatus and target simulation

Behavioral experiments took place in a large (6.2×6.7 ×2.5 m) carpeted room, whose walls and ceiling were lined with acoustic foam (Sonex) that reduced the amplitude of ultrasonic reverberation by a minimum of 20–30 dB below what would be present if the room surfaces were hard and smooth.

Each bat was trained to rest at the base of an elevated Y-shaped platform (1.2 m above the floor) and to produce sonar sounds. The bat's sonar sounds were picked up by a vertically oriented 1/8″ Bruel and Kjaer condenser microphone (model 4138) that was centered between the arms of the platform at a distance of 17 cm from the bat. The bat's echolocation sounds were amplified, bandpass filtered at 20–99 kHz (Stewart filter, model VBF7), digitized with 12-bit accuracy at a rate of 496 kHz (see below), electronically delayed (custom DSP board, SPB2-Signal Data, installed in a '486 computer), attenuated (PA-4, Tucker-Davis Technologies), low-pass filtered (Krone-Hite), and broadcast back to the bat through a custom electrostatic loudspeaker (designed by Lee Miller, University of Odense, Denmark). The loudspeaker, positioned in front of the microphone (0.5 cm lower than the microphone grid) and 15 cm from the bat, was powered by a direct current (dc) amplifier (Ultrasound Advice) and had a frequency response that was flat within 3 dB between 25 and 95 kHz (see Fig. 1). Placement of the microphone behind the speaker eliminated feedback in the system, and the signals recorded were not distorted by the presence of the speaker.

A programmable function generator (Stanford Research Systems, model DS345) was connected to the DSP board in the '486 computer via an RS232 interface, allowing for Doppler shifts of the returning echoes by external control of the digital/analog (D/A) sample rate. For conditions in which no Doppler shift was introduced, the D/A sample rate was fixed at 496 kHz. Doppler shifts were introduced by adjusting the D/A sample rate, generating a percentage frequency shift in the playback echoes that was specified by the experimenter.

The total gain of the system feeding into the DSP board was approximately 60 dB, to bring the peak–peak amplitude of most bat sonar sounds to a level just below the 12-bit limit of the processor and for maximum signal-to-noise ratio. Digital attenuators (PA-4, Tucker-Davis Technologies) permitted adjustment of the playback level of the sounds returning to the bat's ears, which was set at approximately 80 dB SPL for all experiments.

Each sound produced by the bat resulted in a single sonar signal playback that simulated an echo from a target positioned directly in front of the bat, whose distance was
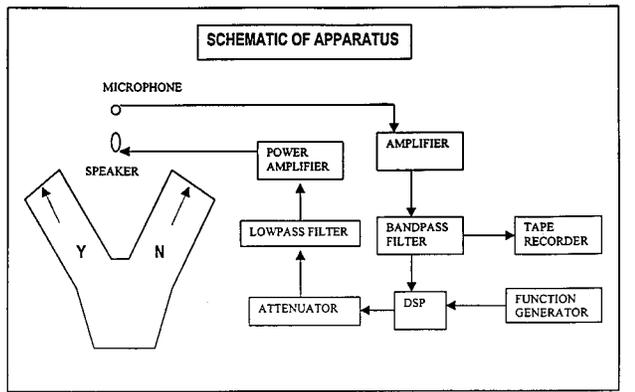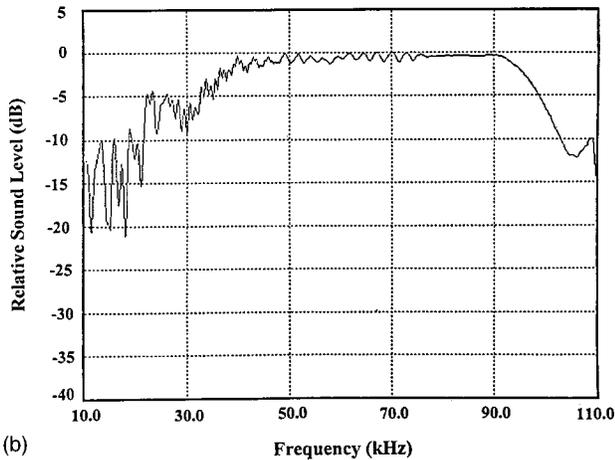
FIG. 1. (a) Schematic of sonar signal playback apparatus and response platform. The bat rested at the base of the Y-shaped platform, emitting echolocation sounds that were picked up by an 1/8″ Bruel and Kjaer microphone, filtered, amplified, digitized, electronically delayed, Doppler shifted (in some trials), and played back through an electrostatic loudspeaker. The bat received a food reward for crawling down the left arm of the platform when presented with stimulus Y (yes) and for crawling down the right arm of the platform when presented with stimulus N (no). For a description of stimulus Y and N, see text. (b) Standard calibration curve displays the frequency response of all equipment in the apparatus, except the 1/8″ Bruel and Kjaer microphone, which was tested separately.

C. Echolocation sound recordings

For each experimental session, the bats' echolocation sounds were recorded on tape at 30 in. per sec with a Racal Store-4 high-speed recorder. The sounds were later played back at 1/16 the recording speed, low-pass filtered and digitized (effective sample rate 240 kHz), analyzed and displayed spectrographically (Sona-PC, Waldmann©). Spectrograms were calculated using 256-point fast Fourier transforms (FFT's). Signal measurements included the duration, interpulse interval, duty cycle, and spectral characteristics of the bats' signals recorded under different task conditions.

D. Behavioral tasks

1. Experiment I: Range difference discrimination

Each of the bats was trained in a two-alternative forced-choice procedure to discriminate the echo delay difference of electronically simulated sonar targets. The bat learned to report whether the perceived target distance was at a shorter, standard delay by crawling down the left arm of the platform to indicate a ''yes'' (close target) response or at a longer delay by crawling down the right arm of the platform to indicate a ''no'' (far target) response. The echo delay of the standard target was set at 4.3 msec, simulating a target at 74.0 cm. The echo delay of the more distant target was variable, at values that ranged from 4.4 msec, simulating a target at 75.7 cm, to 5.1 msec, simulating a target at 87.7 cm. The echo delay values used in this experiment were all above discrimination threshold reported in other studies (see Moss and Schnitzler, 1995). The presentation of ''close'' (standard) and ''far'' targets followed a pseudorandom schedule (Gellerman, 1933), and the bat's response (yes/left or no/right) was recorded. For each correct response, the bat received a food reward (a piece of mealworm), and for each incorrect response, the bat experienced a 10–30-sec time out. No correction trials were introduced.

2. Experiment II: Doppler-shift discrimination

Each of the bats was trained in a two-alternative forced-choice procedure to discriminate the Doppler shift of electronically simulated sonar targets. On all trials, the echo delay was fixed at 4.3 msec (74.0 cm). For a given trial, the bat learned to report whether it perceived a Doppler shift in the echo, by crawling to the left to indicate ''yes'' and to the right to indicate ''no.'' The presentation of Doppler shifts in the playback echoes followed a pseudorandom schedule (Gellerman, 1933), and the bat's response (yes/left or no/right) was recorded. For each correct response, the bat received a food reward (a piece of mealworm), and for each incorrect response, the bat experienced a 10–30-sec time out. We tested both positive and negative Doppler shifts between 1% and 16%. No correction trials were introduced.

II. RESULTS

Behavioral data are reported here for the Doppler discrimination task, as performance in this task has not been previously described for bats using frequency modulated

determined by an electronic delay controlled by the experimenter. The shortest echo delay used was 4.3 msec, corresponding to a target distance of 74.0 cm. At this echo delay, the bat's sonar transmissions shorter than 3.3 msec did not overlap the simulated echoes.

Before each experiment, a calibration routine was run, to test each of the components of the target simulator. The electrostatic loudspeaker broadcast a linear 1-msec 10–100-kHz frequency modulated sweep that was picked up by a condenser microphone (QMC) positioned on the test platform. The signal received by the microphone was amplified, filtered (10–99 kHz), and delivered to the DSP board. The arrival time and power spectrum of the FM sound picked up by the microphone were measured and compared against standard values. Experimental data were collected only when the delay and power spectrum of the calibration signal matched the standard values, a 0.29-msec delay when the microphone was positioned 10 cm from the speaker (one-way travel delay, 2.9 ms/m) and a relatively flat spectrum [±3 dB at 25–95 kHz; see Fig. 1(b)].
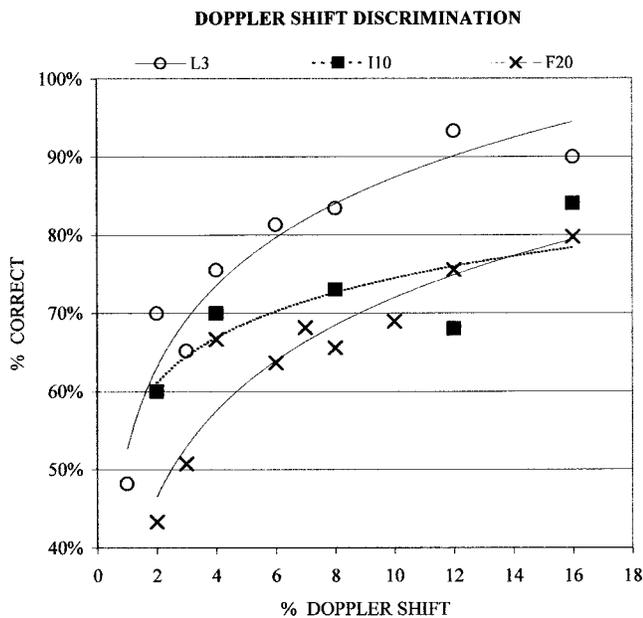
FIG. 2. Psychometric functions plotting percent correct performance for each of the three bats (L-3, I-10, F-20) tested across a range of Doppler shifts. Each data point represents the mean performance measure taken over an average of 60 trials.
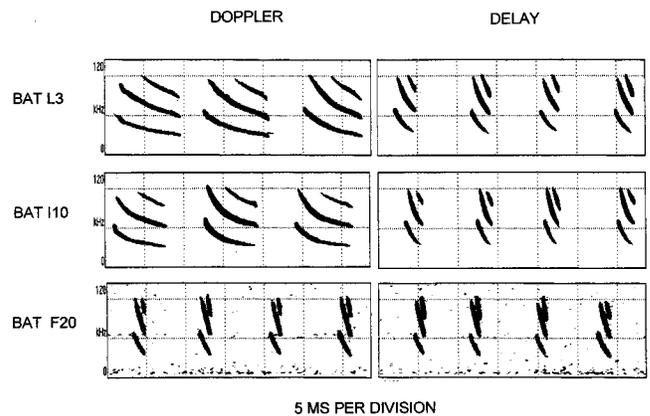

FIG. 3. Spectrograms of representative echolocation sounds produced by each of the three bats (L-3, I-10, F-20) under different task conditions. The left panel for each bat shows sounds recorded during a Doppler discrimination trial and the right panel shows sounds recorded during a delay discrimination trial. The figure does not represent actual sonar signal sequences. Sweeps are presented on the time axis at intervals convenient for display. The vertical axis divisions occur at 50-kHz intervals and the horizontal axis divisions occur at 5-msec intervals.

echolocation sounds. For all three bats studied, discrimination performance systematically increased with the magnitude of the Doppler shift; however, there were large individual differences. The data are plotted in Fig. 2, and each point summarizes mean performance over an average of 60 trials. One bat (L-3) performed at about 50% correct with a 1% Doppler shift, and showed a steady rise in performance for larger Doppler shifts, reaching about 90% correct for Doppler shifts at or above 12%. The other two bats (F-20 and I-10) also showed an increase in performance with Doppler shift, but overall discrimination levels were lower. While data were collected using both positive and negative Doppler shifts, all three bats died before complete psychometric functions with the positive Doppler shifts could be obtained. Therefore, the data reported here come from negative Doppler conditions, which the bat would experience, for example, when an insect wing moved away from it. Using 70% correct performance as an arbitrary criterion for threshold estimation, Doppler discrimination thresholds for L-3, I-10, and F-20 were 3.2%, 5.8%, and 8.8%, respectively.

For each of the bats, we analyzed the sonar vocalizations for Doppler-shift conditions that yielded behavioral discrimination performance at about 70% correct, our criterion for threshold in this study. We compared these sounds with those recorded from the same individual bat performing in the echo delay discrimination task. When the Doppler shift was close to the bat's threshold, we observed consistent changes in the features of the sounds produced by two of the three bats (L-3 and I-10). Interestingly, F-20 produced a different pattern of vocalizations in the two tasks and also showed the highest Doppler discrimination threshold of the three bats tested.

Representative examples of sounds produced by each of the three bats are displayed spectrographically in Fig. 3. The left panel for each bat shows sounds recorded during a Dop-

pler discrimination trial, and the right panel shows sounds recorded during a delay discrimination trial. Though the order in which the sounds in each panel occurred has been preserved, the intervals between sounds were created for display purposes only. All bats produced FM sonar sounds; however, the time-frequency structure of the sounds depended on the task condition. In the delay discrimination task, the FM sounds of all three bats swept from approximately 60 kHz down to 28 kHz in approximately 1.7–3 msec. In the Doppler discrimination task, bat F-20's sounds showed a small decrease in sound duration and an increase in the end frequency of the sweep. By contrast, the two bats that showed the highest performance in the Doppler discrimination task showed the opposite trend, with an increase in signal duration (over 4 msec) and a drop in the end frequency of the sweep (25 kHz).

Duration data from individual Doppler and delay discrimination trials are summarized in Fig. 4. Data are presented in panels for each of the three bats, with the Doppler discrimination trial shown on the left and the echo delay discrimination trial shown on the right. Each of these panels displays data taken from sounds recorded sequentially during a single trial in which the bat made a correct response.

Figure 5 presents quantitative comparisons of several measures taken from signals produced by the bats in the delay and Doppler discrimination tasks. These measures are signal duration, duty cycle, interpulse interval, beginning frequency of the fundamental, ending frequency of the fundamental, and the total spectral bandwidth of the fundamental. This figure includes analysis of 720 sounds recorded from three bats. Data from 240 sounds are presented for each bat, half recorded in delay discrimination trials and half recorded during Doppler discrimination trials, yielding 120 sounds analyzed for each bat from the two task conditions. Histograms display the mean and standard deviations separately for each of the three bats, with the Doppler discrimination measures shown in solid bars and delay discrimination mea-

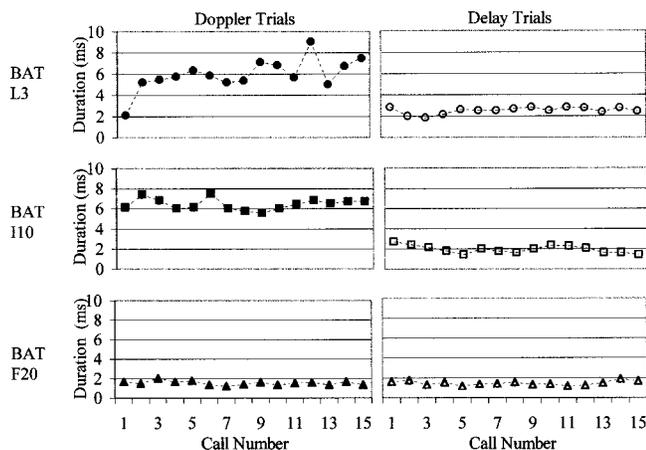## Complete Call Sequences From Representative Trials

FIG. 4. Sound duration data taken from individual Doppler discrimination (left) and delay discrimination (right) trials for each of the three bats tested (L-3, I-10, F-20). Each panel displays duration measures taken from the first 15 sounds produced by the bat in the trial.

sures shown in open bars. All of the data summarized here come from the first 15 sounds produced by the bat in any given trial. Although some trials contained many more than 15 sounds, limiting the analysis to the first 15 sounds ensured that the data summaries did not include sounds produced by the bat as it crawled down the platform for its food reward
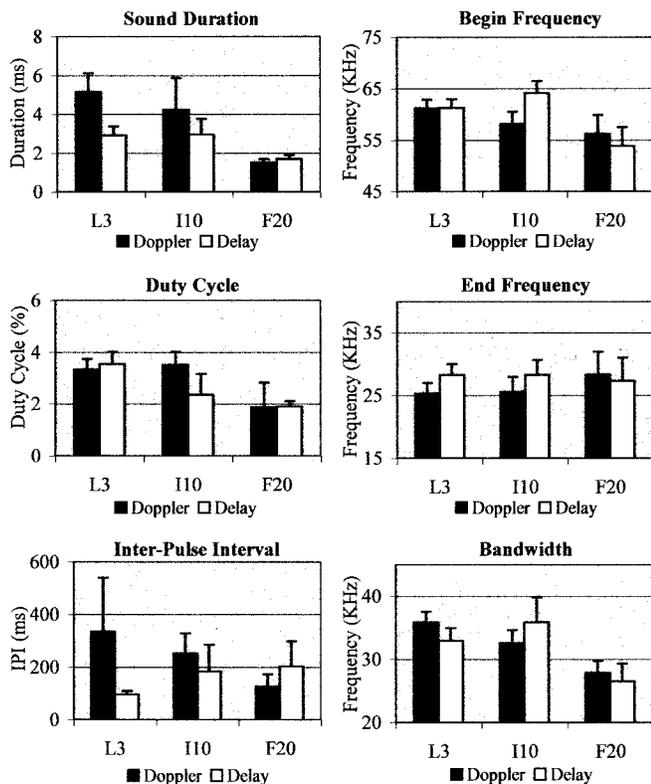

FIG. 5. Signal parameter measurements taken for each of the three bats (L-3, I-10, F-20) tested in an echo Doppler-shift discrimination task (filled bars) and in an echo delay difference discrimination task (open bars). Parameters summarized are signal duration, duty cycle, interpulse interval, beginning and end frequencies of the fundamental, and the bandwidth of the fundamental. Each histogram summarizes mean and standard deviation for 120 echolocation calls.

TABLE I. Results of the analysis of variance (ANOVA) on signal measures (duration, beginning and end frequencies of the fundamental, bandwidth of the fundamental, interpulse interval, and duty cycle) taken from sonar vocalizations produced in Doppler and delay discrimination test conditions. The degrees of freedom (df) for the ANOVA are shown in the table. Asterisks indicate statistically significant differences in signal measures in the two conditions, across subjects, and subject by condition interactions, with the corresponding p values.

	Condition df=1,714		Subject df=2,714		Interaction df=2,714	
	F	P-Value	F	P-Value	F	P-Value
Duration	206.21	<0.001*	368.62	<0.001*	83.27	<0.001*
Begin fund	10.29	0.001*	116.15	<0.001*	42.42	<0.001*
End fund	91.66	<0.001*	16.27	<0.001*	61.73	<0.001*
Bandwidth	0.65	0.419	127.36	<0.001*	19.67	<0.001*
IPI	2.99	0.001*	2.23	0.109	15.02	<0.001*
Duty cycle	10.78	0.084	32.12	<0.001*	6.24	0.002*

after making a decision. Data are reported only for trials in which the bat responded correctly.

An analysis of variance (ANOVA) performed on this data set shows that many of the parameters measured from the bats' sounds recorded under the two test conditions differed significantly. Signal duration, beginning and end frequencies of the fundamental sweep, and interpulse interval all differed significantly between the Doppler and delay discrimination trials. Statistically reliable differences between subjects appeared in all measures except IPI. Stimulus condition by subject interactions were statistically significant for all signal parameters (see Table I).

While individual differences account for the statistically significant subject and subject by condition interactions (consistent with data reported by Masters *et al.*, 1991), we wish to highlight the task-dependent differences in sonar signals and to relate these differences to the bats' Doppler discrimination performance. Bats L-3 and I-10 showed higher Doppler discrimination performance than bat F-20, and these two bats produced sonar signals in this task that were longer in duration, swept to a lower end frequency, and exhibited an increase in the interpulse interval, compared with sounds produced in the delay discrimination task. Bat F-20 showed the opposite pattern in its vocalizations, with shorter mean sound duration, shorter interpulse interval and higher end frequency in the Doppler discrimination task than in the delay discrimination task. Interestingly, this bat also showed the poorest performance in the Doppler discrimination task.

For bats L-3 and I-10, an increase in sonar signal duration accompanied a drop in the end frequency, as illustrated in Fig. 6 (left). Each panel shows data from each of the individual bats tested under the Doppler (crosses) and delay (open symbols) discrimination tasks. The data plotted in Fig. 6 are the same as those summarized in Fig. 4, with 240 signals measured for each bat (half in the Doppler and half in the delay discrimination tasks). In general, there is a tendency for the longest signals to also contain the lowest end frequencies, a trend that appears most clearly in the data from bat L-3, the bat with the lowest Doppler discrimination threshold. For bat F-20, sound duration and end frequency under the two behavioral test conditions cluster more closely.

Figure 6 (right) plots the relation between signal band-

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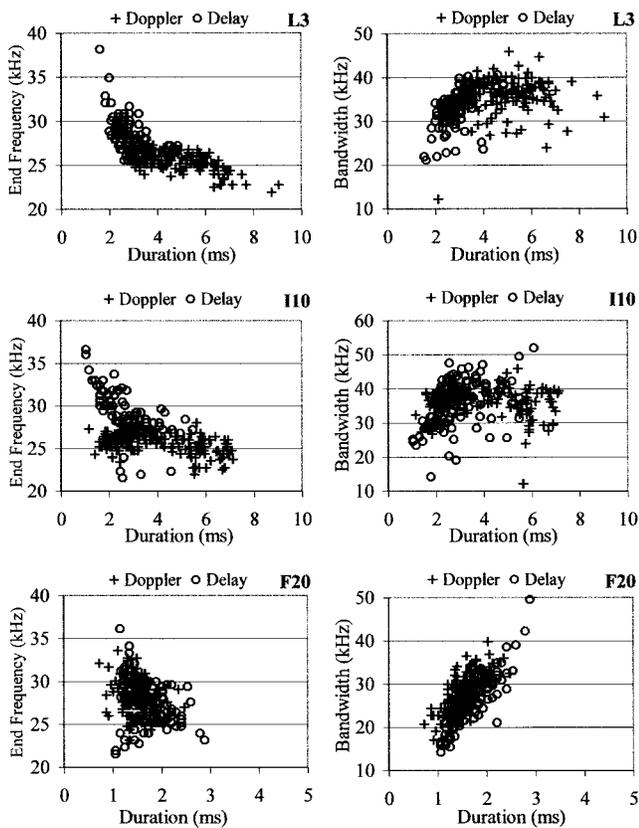J. Wadsworth and C. F. Moss: Vocal control of echoes by bats   2269

FIG. 6. Left panels: Signal end frequency (kHz) versus signal duration (msec). Right panels: Bandwidth of the fundamental (kHz) versus signal duration (msec). Both figures plot data separately for the three bats tested in the Doppler (crosses) and delay (open circles) discrimination tasks. Each bat's plot includes 240 data points, 120 measures taken from signals produced in each of the two task conditions.

width (fundamental frequency) and duration in the Doppler and delay discrimination tasks. Sounds produced by bats L-3 and I-10 show no correlation between bandwidth and duration. Bat F-20's signals show an overall increase in bandwidth with signal duration, and the sounds recorded in delay discrimination trials tend to contain the largest bandwidths.

III. DISCUSSION

The results of this study demonstrate adaptive vocal behavior in the FM-bat, *Eptesicus fuscus*, for shaping the acoustic information available in two distinct perceptual tasks. The sounds produced by bats in the echo delay discrimination task were brief and swept continuously from high to low frequencies. By contrast, the longer signals used by the bats for Doppler discrimination included a shallow FM tail from approximately 28–25 kHz, similar to the signal type described by Simmons *et al.* (1975) and Kick (1982). The differences in these sound characteristics produced by the bat under different task conditions correspond to those predicted by sonar/radar theory (Woodward, 1964; Simmons and Stein, 1980; Skolnik, 1980; Møhl, 1988).

An echo delay discrimination task requires that the bat register the echo arrival time with high accuracy, and sonar theory asserts that brief, broadband signals are best suited for this task. Each frequency in the FM sweep provides a marker for its time of arrival, and the broad bandwidth sharpens its

time-domain representation (Woodward, 1964; Simmons and Stein, 1980; Skolnik, 1980; Menne and Hackbarth, 1986). Doppler discrimination requires that the bat detect frequency changes in the echo, and a signal that remains at a comparatively stable frequency over time is best suited for this task (Simmons and Stein, 1980; Skolnik, 1980; Altes, 1984). Thus the longer signals with the shallow FM tail, used by *Eptesicus fuscus* for Doppler discriminations, are better suited for frequency discrimination than the shorter FM sweeps used for echo delay discrimination.

The sounds produced by *Eptesicus fuscus* in this Doppler discrimination study are not typically observed in the laboratory. To our knowledge, the only other reports of similar sonar signals recorded from this species in the laboratory are those of Simmons *et al.* (1975) and Kick (1982). Both reports include qualitative descriptions of a shallow FM at the end of the sweep, noting that the bat's signals differed from those typically observed in the laboratory. However, these reports make no direct comparisons of signals produced by the same individual animals performing in different tasks.

In this study, the two bats showing better overall performance and lower thresholds in the Doppler discrimination task showed similar patterns in vocal production that differed in some respects from the third bat tested with the highest Doppler discrimination threshold. The two bats with the lower Doppler discrimination thresholds added the shallow FM tail to their signals in the Doppler task, and this tail resulted in a lower end frequency and longer duration signals. Bat L-3, the animal with the lowest Doppler discrimination threshold in this study, showed the strongest effect of task on signal duration and end frequency. While L-3 and I-10 showed similar, task-dependent patterns in signal duration and end frequency, they showed different patterns of change in total first harmonic bandwidth with task. L-3 produced sonar signals with higher bandwidth in the Doppler condition and I-10 produced signals with higher bandwidth in the delay discrimination condition, because the start frequencies of the FM sweeps used by these two bats in the different tasks changed in opposite directions. The individual differences in signal parameters used by the three bats in the two tasks is consistent with the report of individual vocal patterns presented by Masters *et al.* (1991).

Extensive field data from *Eptesicus fuscus* have not been published, but we speculate here that the longer sonar signals, with a shallow FM tail, produced by *Eptesicus* during the late search phase and early approach phase of insect pursuit (Griffin, 1958), may draw the same potential advantages as signals used by CF-FM bats, namely fluttering prey detection and discrimination (e.g., Schnitzler *et al.*, 1983; von der Emde and Menne, 1989; Kober and Schnitzler, 1990). In this context, it is worth noting that FM bats can discriminate between artificial wing beat stimuli that flutter at different rates (Grossetête and Moss, 1998; Roverud *et al.*, 1991; Sum and Menne, 1988). Sum and Menne (1988) first postulated that FM bats may perform this task by listening for a delay difference between echoes from the stationary and moving parts of the apparatus used to study flutter rate discrimination. The moving target produces a Doppler-induced echo

delay shift, whose magnitude varies with the target's velocity. The stationary parts of the apparatus return echoes at a fixed delay, and thus, the echo delay difference between moving and stationary target echoes increases with target velocity. Grossetête and Moss (1998) conducted acoustic studies of FM sonar echoes from an artificial wingbeat simulator and demonstrated that the magnitude of the Doppler-induced delay difference between the moving and stationary target echoes is influenced by the characteristics of the bat's sonar signals, in particular signal duration. Given the influence of signal duration on Doppler information, it is not surprising that the bat in this study that performed the best in the Doppler discrimination task also produced the longest sonar signals.

In summary, we present here quantitative comparisons of sonar signals produced by the same individual bats performing in distinct perceptual tasks. The data show task-dependent differences in sound duration and frequency structure of the bat's echolocation sounds, and the changes reported here for two bats are consistent with those predicted by sonar/radar theory. These results suggest that the sounds produced by echolocating bats may provide a window to understanding the information processing requirements of a given sonar task. Since we are limited by signal processing techniques that do not tap into the perceptual salience of signal changes to the bat, we can only speculate that more subtle changes in sonar sounds may also occur which reflect the bat's active enhancement of sonar images.

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