

Auditory-Feedback Control of Temporal Call Patterns in Echolocating Horseshoe Bats

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Smotherman, Michael and Walter Metzner. Auditory-feedback control of temporal call patterns in echolocating horseshoe bats. *J Neurophysiol* 93: 1295–1303, 2005. First published October 20, 2004; doi:10.1152/jn.00653.2004. During flight, auditory feedback causes horseshoe bats to adjust the duration and repetition rate of their vocalizations in a context-dependent manner. As these bats approach a target, they make finely graded adjustments in call duration and interpulse interval (IPI), but their echolocation behavior is also characterized by abrupt transitions in overall temporal calling patterns. We investigated the relative contributions of two prominent acoustic cues, echo frequency and delay, toward the control of both graded and transitional changes in call duration and IPI. Echoes returning at frequencies above the emitted call frequency caused bats to switch from long single calls to pairs of short calls (doublets). Alternatively, increasing echo delay caused progressive increases in IPI but caused no accompanying changes in call duration. When frequency shifts were combined with changing echo delays, echo delay altered the IPIs occurring between doublets but not the IPI within a doublet. When the echo mimic was replaced by presentation of either an artificial constant-frequency (CF) stimulus or a frequency-modulated (FM) stimulus, each designed to mimic major components of the echo acoustic structure, we found that CF stimuli could trigger the switch to doublets, but changing CF delay had no influence on IPI, whereas the timing of an FM-sweep presentation had a strong effect on IPI. Because CF and FM sounds are known to be processed separately in the bat auditory system, the results indicate that at least two distinct neural feedback pathways may be used to control the temporal patterns of vocalization in echolocating horseshoe bats.

INTRODUCTION

Human speech is generated by stringing together sequences of short sounds known as formants, each of which represent unique combinations of constant frequencies and transient frequency modulations (Fitch et al. 1997). Because speakers vary widely in the fundamental pitch of their speech, it is the temporal pattern of constant- and frequency-modulated sounds that is recognized as speech by listeners (Fitch et al. 1997). Producing natural-sounding human speech requires that the speaker accurately hear their own vocalizations (Doupe and Kuhl 1999). In particular, the fluid emission of formant sequences is tightly regulated by auditory feedback, the disruption of which can lead to speech dysfluencies such as stuttering and dysarthria (Bloodstein 1995; Van Riper 1982). Analogous to humans, echolocating bats also require persistent auditory feedback for the ongoing control of vocal emissions, and like the human formant, bat echolocation calls possess flexible combinations of constant- and frequency-modulated compo-

nents (Kalko and Schnitzler 1993; Kanwal et al. 1994; Suga 1992), the temporal patterns of which bats rely on for their very survival (Griffin 1958; Neuweiler 2000; Schnitzler and Kalko 2001; Simmons et al. 1979). In this study, we present evidence collected from echolocating horseshoe bats that sheds light on the mechanisms of auditory feedback control over the temporal patterns of mammalian vocalizations.

Different echolocation tasks benefit from the use of different call structures and emission patterns (Neuweiler 2000; Schnitzler and Kalko 2001; Schnitzler et al. 2003). Broadband frequency-modulated sounds (FM sweeps) appear to be utilized by all echolocating bats for target range discrimination, whereas comparatively long, constant-frequency (CF) sounds can provide valuable cues for prey detection and identification (Neuweiler 2000; Schnitzler and Kalko 2001; Simmons 1973; Simmons and Grinnell 1988; Simmons and Stein 1980). Many bats use flexible combinations of CF and FM signals to meet the varied perceptual demands associated with different echolocation tasks (Neuweiler 2000; Schnitzler and Kalko 2001; Simmons and Stein 1980). Horseshoe bat echolocation calls are characterized by their exceptionally long CF component, which they use to discriminate wing-beating insects from dense foliage (Neuweiler et al. 1987; Schnitzler and Kalko 2001), but their call also includes FM components, which they, like other bats, rely on for range discrimination (Simmons 1973; Simmons and Chen 1989; Simmons and Stein 1980). Therefore the horseshoe bat uses information contained in the CF and FM components of the returning echo separately in support of different sensory tasks during echolocation (Neuweiler 2000; Schnitzler and Kalko 2001; Simmons and Stein 1980).

Horseshoe bats make coordinated yet independent changes in the CF and FM components of their calls during target approach (Tian and Schnitzler 1997). During the final few meters of target approach, returning echoes follow call emission with progressively shorter delays, echo intensities increase rapidly, and Doppler-effects cause positive shifts in echo frequency, all of which cause horseshoe bats to rapidly alter call structure and timing (Griffin 1958; Neuweiler 2000; Simmons and Stein 1980). Like other echolocating bats, horseshoe bats shorten their call durations and increase their call emission rate during target approach (Schnitzler and Kalko 2001; Tian and Schnitzler 1997). Because the time delay of the echo FM component is the principal source of target range information, we presume that the arrival time of the echo's FM component must strongly influence the time course of subsequent call emissions.

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Alternatively, the information contained in the CF component of the echo is used to control the frequency of subsequent calls. Horseshoe bats exhibit a Doppler-shift compensation behavior (DSC) for moving targets: they adjust their call frequency in response to flight-induced shifts in the frequency of the CF component of the returning echo (Schnitzler 1968; Schuller et al. 1974; Simmons 1974). The acoustic parameters that cause call-frequency changes during DSC have been thoroughly characterized (Metzner et al. 2002; Schuller et al. 1974, 1975; Smotherman and Metzner 2003); however, concurrent adjustments in the temporal patterns of call emissions during DSC have not previously been discussed, even though call rate has been clearly identified as a critical determinant of DSC performance (Schuller 1986; Smotherman and Metzner 2003). DSC behavior benefits from higher call rates because this allows for more rapid and finely tuned adjustments in call frequency during target approach (Schuller 1986; Smotherman and Metzner 2003). Therefore echo-frequency information might be expected to directly influence call rate either separately or in coordination with ranging information extracted from the echo FM component.

In the present study, we quantified the relative contributions of echo frequency and delay on call temporal patterns. Results presented here show that in horseshoe bats, echo frequencies raised above the bat's resting call frequency (RF, i.e., the call frequency emitted when not flying and not compensating for Doppler-shifts) can trigger a sudden change in the timing of subsequent call emissions that is characterized as a switch from emitting solitary to pairs of calls (doublets). Alternatively, gradual adjustments in call rate, such as those exhibited by all echolocating bats during target approach, appear to be controlled exclusively by the time delay of the returning echo's terminal FM component (Griffin 1958; Neuweiler 2000; Schnitzler and Kalko 2001; Simmons 1971, 1973, 1993; Simmons et al. 1998). Thus it appears that for horseshoe bats both the frequency and time course of auditory feedback are capable of influencing the temporal patterns of vocalization. The results indicate the presence of at least two different auditory feedback mechanisms that contribute to the temporal control of vocal behavior: one mediating an abrupt behavioral transition and another mediating more precisely graded changes in vocal timing.

METHODS

A total of 15 Greater Horseshoe Bats, *Rhinolophus ferrumequinum*, 6 males and 9 females collected in the People's Republic of China, were examined as part of this study; however, none of the 15 contributed to all of the experiments reported here: 7 female and 3 male bats were used to quantify the effects of echo frequency on call temporal parameters, 5 other bats (3 males and 2 females) were used to investigate the comparative effects of echo frequency and delay, and 3 of the latter group (1 male and 2 females) also contributed to an investigation on the effects of artificial stimuli on calling behavior. Procedures were in accordance with National Institutes of Health guidelines for the care and use of animals and were approved by UCLA's Animal Research Committee.

Echo playbacks, which served as echo mimics, and artificial stimuli were generated as described previously (Metzner et al. 2002; Schuller et al. 1974). Briefly, vocalizations were captured by a 1/4-in Brüel and Kjaer (type 4135) microphone placed 15 cm ahead of the bat's nostrils. These calls were then electronically delayed (custom-built delay line) and played back to the bat under free-field conditions via

a power amplifier (Krohn-Hite, Model No. 7500, Avon, MA) and an ultrasonic condenser-type loudspeaker (Panasonic; Secaucus, NJ) positioned 15 cm in front of the bat, off-center but within an angle of 20° lateral, left or right. The playback system allowed delivering pure tone pulses of ≤ 122 dB SPL, measured at the position of the bats' pinnae, over the complete range of vocalization frequencies that might typically be uttered by these bats during normal echolocation behavior (60–85 kHz). Within the frequency range of 71–85 kHz, the playback system (including loudspeaker) had a frequency response of ± 3 dB and a harmonic distortion for pure tone signals of < 60 dB SPL. Calibration of the playback system was performed with a 1/4-in ultrasonic microphone and power amplifier (Brüel and Kjaer) using commercial signal analysis software (Signal; Engineering Design, Belmont, MA).

To simulate Doppler shifts in the echo frequency, the frequency of the echo mimic was slowly increased (from 0 to 3 kHz maximum) above the bat's RF and then decreased in a sinusoidal manner. The rate at which the playback frequency was raised and lowered was defined as the modulation frequency (Schuller et al. 1975) and was held constant at 0.1 Hz (10 s/cycle). Call frequencies were shifted by a double-heterodyning technique (custom design modified after Schuller et al. 1974), with parameters of the imposed frequency shift (modulation frequency, polarity, and peak magnitude) controlled manually by a function generator (Stanford Research Systems, Palo Alto, CA; Model No. DS335). Artificial stimuli were generated using custom software and the TDT System II hardware modules (Tucker Davis Technologies, Gainesville, FL). Artificial stimuli were either a 30- to 40-ms CF stimulus customized to mimic the CF portion of each bat's echolocation call at rest by matching its duration to the previously determined mean call duration of the bat or a 3-ms downward frequency-modulated (FM) sweep (from each bat's RF to 15 kHz below RF) customized to mimic the terminal FM component of each bat's echolocation call. The rise/fall times of the stimuli were 1 ms, and the intensity was 85dB SPL, which corresponds to intensities that reach the bat's ear when emitting calls (Pietsch and Schuller 1987).

We also elicited DSC behavior from bats swung on a pendulum facing a large reflective surface (Gaioni et al. 1990), during which the bat was exposed to natural Doppler-shifts in the returning echoes. Pendulum experiments have been used previously to explore basic aspects of echolocation behavior (Gaioni et al. 1990; Smotherman and Metzner 2003) and were used here to verify the extent to which these bats' response to artificial playback mimicked their response to natural Doppler-shifted echoes. The bats were placed in a body mold made from soft foam and attached to the base of the pendulum. The pendulum was suspended from the ceiling and had a length of 2.0 m. It swung through an arc of 80° (~2.6 m). The minimum distance between bat and floor was 20 cm, which was reached at the mid-point of the swing. Pendulum position was recorded electronically. A large plywood target (225 × 125 cm) was placed 10–15 cm beyond the most forward point of the pendulum's swing. The ceiling as well as either side of the path along which the pendulum swung was lined with sound-absorbing material to reduce echoes returning from the sides. The bat's calls were monitored by an ultrasonic microphone (1/4-in Brüel and Kjaer) that was attached to the pendulum 7 cm above the bat's head and pointed toward it.

Call intensities varied from ~90 to 115 dB SPL between experiments and were recorded on analog videotape after being transformed by a custom-built AC/DC converter. At 0 dB attenuation, the playback system was calibrated to produce a playback signal from the speaker equal in intensity (at the bat) to the recorded call intensity at the microphone placed 15 cm directly ahead of the bat. The remaining 15-cm traveling distance contributed ~6 dB of added attenuation, thus our un-attenuated playback was approximately –6 dB relative to the emitted call at the bat. Cross-talk between the speaker and microphone was minimized by a piece of sound-insulating foam placed between the microphone and loudspeaker and projecting 5 cm toward the bat. All sound levels are given relative to the intensity of the preceding

call. All experiments were performed in an anechoic chamber. Some minor natural echoes emanating from the experimental apparatus were present during the experiments, the potential significance of which has been addressed previously (Smotherman and Metzner 2003).

The time delay that occurs between call emission and return of the echo is related to target distance by the speed of sound, ~ 346 m/s in air at 25°C . In our experiments, the minimum delay allowed by our hardware was 4 ms between recorded call onset and playback initiation, which corresponds to a target distance of ~ 0.69 m. The additional 15-cm travel distance from the bat to the microphone, and from the speaker to the bat, would have introduced an extra delay of < 1 ms, which was not incorporated into the final results. We presented bats with playback delayed by ≤ 20 ms, corresponding to a target distance of 3.5 m. Previous behavioral studies have demonstrated that the transition from search to approach phase occurs when target distance falls below ~ 2 m. The frequency-compensation behavior may be initiated when delays fall < 25 ms, which corresponds to a target range of ~ 4.2 m (Schuller 1977; Tian and Schnitzler 1997). Taking the above factors into consideration, a range of 4- to 20-ms playback delays was accepted as adequate for testing the effect of echo delay on horseshoe bat echolocation behavior. Playback timing was controlled by customized software on a PC and could be set relative to either the onset or offset of the prior call.

Echolocation calls were digitized and stored on VHS tape (model 3000A, A.R. Vetter, Rebersberg, PA) after transforming the dominant second harmonic of the CF component via a custom-made frequency-to-voltage converter, and analyzed off-line using the software suite Datapak 2K2 (Run Technologies, Mission Viejo, CA) and commercially available statistical software (SigmaStat and SigmaPlot, Jandel, San Rafael, CA). Frequency measurements after digitization were accurate to within ± 48 Hz or $\pm 0.06\%$. Call frequencies reported here are based on measurements of the maximum frequency achieved within the CF component as determined in **Signal (Engineering Design)**. Call durations and corresponding IPIs were obtained digitally via automated measurements of the length of each call after transformation of the entire call by the frequency-to-voltage converter and include the time duration over which the converted voltage measurement was $> 90\%$ of the maximum obtained value. IPI was measured as the time between the offset of one call and the onset of the next. For statistical comparisons, either a Student's *t*-test or a nonparametric ANOVA (Mann Whitney rank sum test) was used to establish significant differences in call parameters between data sets. Each bat's RF was determined experimentally by recording ≥ 60 s of calls both at the beginning and at the end of each recording session. Data are presented as means \pm SD unless indicated otherwise.

RESULTS

Figure 1 illustrates the acoustic structure of a typical horseshoe bat call. The long (20–50 ms) CF portion of a single call is bracketed by a brief (< 3 ms) upward sweep in frequency known as the initial FM component and an equally brief downward frequency sweep, called the terminal FM component (Neuweiler et al. 1987; Tian and Schnitzler 1997). Among the bats used in this study, the frequency of the CF call-components uttered at rest varied from 76.9 to 78.7 kHz (mean of the means, 77.8 ± 0.6 kHz). During these experiments, stationary bats produced primarily either single calls or doublets (2 calls uttered in rapid succession, see Fig. 1), although other multiplets (≥ 3 calls uttered in rapid succession) were also, but less frequently, observed.

In the following, we will first describe how auditory feedback triggered the switch from single calls to doublets, followed by an analysis of how echo delay influenced call

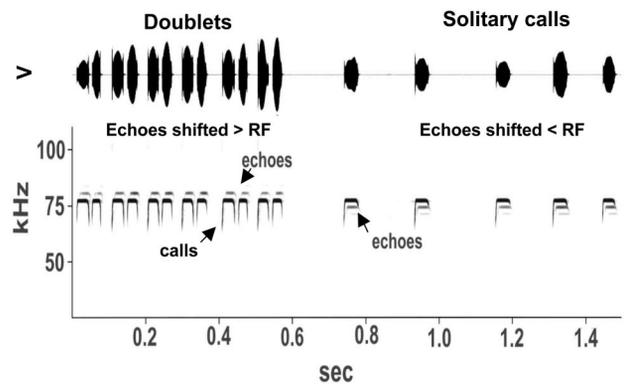


FIG. 1. Spectrogram of horseshoe bat echolocation calls and echoes. Call envelopes (*top*) and corresponding spectrograms (*bottom*) are plotted for a series of echolocation calls emitted by a stationary horseshoe bat while hearing electronically frequency-shifted versions of its own calls played back as echo mimics after 4-ms delays. During the st 0.7 s of the trace, echo mimics were shifted +3 kHz relative to the frequency of the previous call, during which time the bat emitted doublets; at 0.7 s, the playback was switched to a -3 -kHz shift, and the bat transitioned to emitting solitary calls. Echo intensities were -20 dB re: call intensity.

duration and IPI while emitting calls at RF and during DSC. Finally, we mimicked separate components of the bat's call with artificial stimuli and tested their effects on call duration and IPI.

Effect of echo frequency on call duration and IPI

We started with an investigation into the effects of changing echo frequency on subsequent call durations and IPIs. We compared three conditions, which are exemplified by one representative bat in Fig. 2. 1) The bat's spontaneously emitted calls (with frequencies at the bat's RF) were played back to the bat without electronically inducing any frequency shifts. Thus all echo mimics had frequencies at RF that did not elicit DSC behavior (Fig. 2, *A* and *B*). 2) Playback frequencies were electronically shifted in frequency, thus eliciting DSC behavior in the bats (Fig. 2, *C* and *D*). 3) DSC performance was evoked by naturally Doppler-shifted echoes when the bats were swung on a pendulum (Fig. 2, *E* and *F*). By comparing the bats responses to both natural (pendulum) and electronically generated changes in echo frequency, we were able to effectively uncouple the response to echo frequency from the response to echo delay because both frequency and delay change simultaneously on the pendulum but could be controlled independently by the electronic playback. We found that DSC performance was associated with a specific and consistent pattern of change in call durations and IPIs, as illustrated in Fig. 2 for *bat 6*; these patterns were observed in every bat tested, although the absolute numbers for the mean call durations and IPIs varied considerably between the bats. As we will show in the following text, the observed changes in temporal call patterns evoked by a positive shift in echo frequency (i.e., shift above RF) could be summarized as reflecting the switch from emitting single long calls to pairs of short calls.

Under the first condition, i.e., when the bat responded to echo mimics presented at RF and thus was not performing DSC ("at rest," Fig. 2, *A* and *B*), call durations and IPIs exhibited distinct modes centered around 38 ms (Fig. 2*A*; mean duration, 33.44 ± 12.41 ms) and 80 ms (Fig. 2*B*; mean IPI, 123.0 ± 91.3

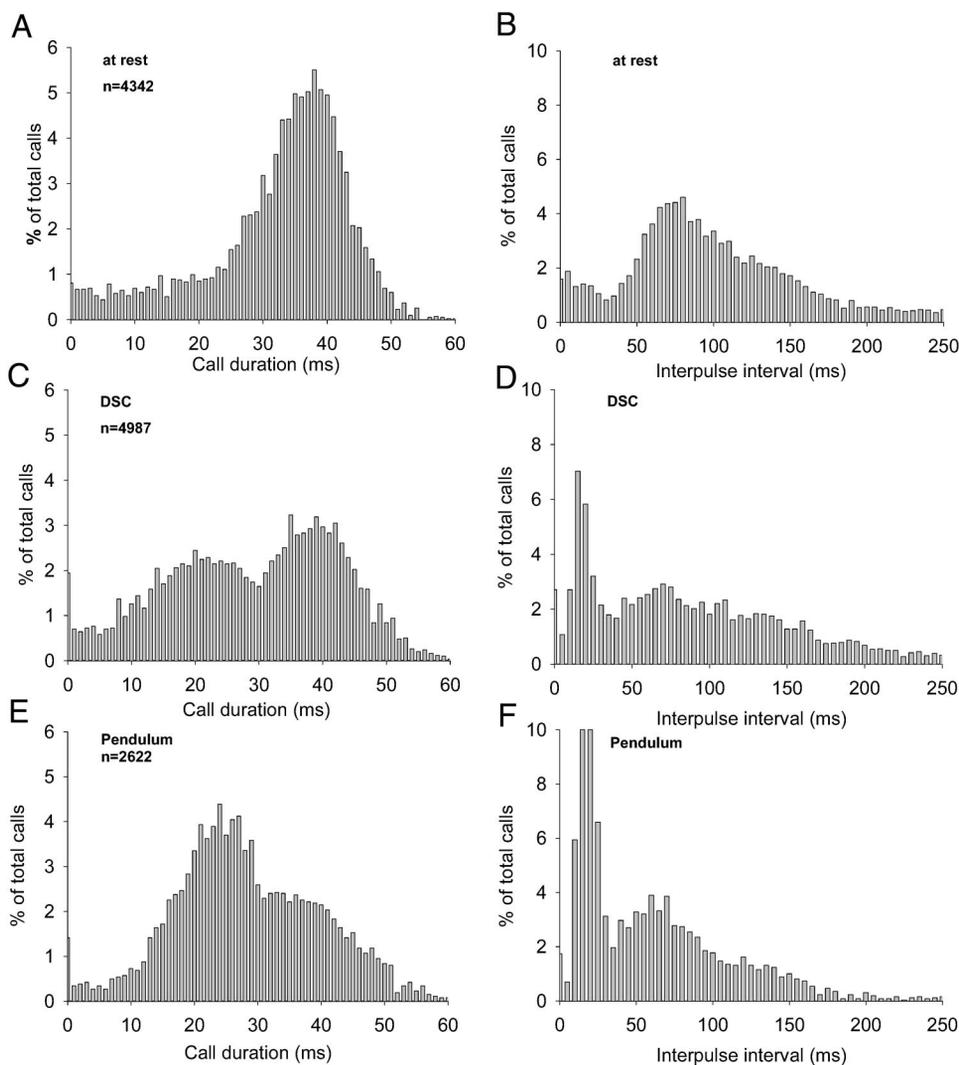


FIG. 2. Distribution of call durations (left: bin width, 1 ms) and interpulse intervals (IPIs; right: bin width, 5 ms) in response to different playback/echo conditions exemplified for 1 individual bat (bat 6 of Table 1). *A* and *B*: bat responding to playback of preceding emitted calls (at rest; delay: 4 ms, intensity: -10 dB rel. bat's own call). *A*: call durations were distributed unimodally (mean: 33.44 ± 12.41 ms; mode: 38.5 ms; kurtosis: 11.06; skewness: 0.34), and *B*: the majority of IPIs varied between 50 and 200 ms (mean \pm SD: 123.0 ± 91.3). *C* and *D*: bat was performing a DSC in response to electronically frequency-shifted playback of the previously emitted calls (see METHODS for details; sinusoidal frequency-shifts between 0 and $+3$ kHz rel. RF at 10 s cycles, presented with a 4-ms delay and at an intensity of -10 dB rel. to emitted call). *C*: the distribution of call durations became distinctly bimodal (mean 29.62 ± 14.10 ms, modes at 22 and 39 ms, kurtosis -0.56 , skewness -0.15), and *D*: a large proportion of calls were now emitted following interpulse intervals (IPIs) of <40 ms (mean \pm SD, 115.1 ± 99.9). *E* and *F*: bat performing Doppler-shift compensation behavior (DSC) in response to naturally Doppler-shifted echoes while swinging on a pendulum (see METHODS for details). Call durations (*E*) and IPIs (*F*) were distributed similar to DSC in response to electronically frequency-shifted echo mimics (see *C*; call durations: mean 30.78 ± 12.57 ms, mode: 24.5 ms, kurtosis: 0.22, skewness: 0.18; IPIs: mean \pm S.D 69.1 ± 64.0). Total numbers of calls recorded for each condition over a 10-min period (*A*–*D*) or 20 pendulum swings (*E* and *F*) is given (left).

ms), respectively. The mean call duration for 10 bats was 36.69 ± 11.47 ms (23,098 calls; Table 1, "at rest") and the associated mean IPI was 136.1 ± 101.0 ms. The mean IPI of calls emitted at RF varied widely between experimental sessions, even for the same bat as indicated by the large overall SD of 101 ms.

When performing a DSC in response to frequency-shifted playback signals, as in the second condition, these temporal call parameters changed (Fig. 2, *C* and *D*). Interestingly, however, the distribution of call durations did not simply shift toward shorter values, as one might have concluded from a statistical comparison of the means (Fig. 2*C*, "DSC": mean

TABLE 1. Standardized measures of temporal call parameters when calling at rest and during DSC behavior for 10 bats

Animal No.	Call Duration, ms		Percentage of IPI ≤ 40 ms	
	At rest	During DSC	At rest	During DSC
1	35.54 ± 11.58 (995)	30.04 ± 11.02 (1077)	13.10	32.37
2	28.18 ± 8.48 (4680)	26.78 ± 10.05 (2860)	25.28	35.81
3	33.05 ± 6.47 (2376)	28.24 ± 11.63 (5047)	19.74	36.73
4	32.23 ± 11.95 (777)	23.36 ± 12.25 (1586)	28.00	45.96
5	40.52 ± 12.10 (4050)	30.96 ± 14.41 (4472)	23.56	26.98
6	32.90 ± 11.26 (4342)	29.53 ± 13.46 (4836)	15.86	32.73
7	35.87 ± 10.19 (1331)	33.81 ± 12.38 (1211)	7.15	36.70
8	45.78 ± 12.28 (1928)	39.18 ± 16.68 (1487)	12.96	20.50
9	43.72 ± 13.91 (2010)	27.51 ± 12.75 (449)	26.60	62.98
10	39.13 ± 16.46 (609)	31.78 ± 15.30 (834)	15.77	39.74
Means	36.69 ± 11.47	30.12 ± 12.99	18.80 ± 6.9	37.05 ± 11.4

Values are means \pm SD. Number of calls given in parentheses. DSC, Doppler-shift compensation behavior. Interpulse intervals (IPIs) < 40 ms indicate calls were emitted as parts of doublets (see text for details).

duration, 26.62 ± 14.10 ms), but instead the distribution pattern changed and a clear second peak located at a mode of ~ 20 ms emerged (Fig. 2C). Coincident with the appearance of this second population of shorter calls was the emergence of a large proportion of calls emitted at much higher repetition rates, i.e., with IPIs < 40 ms (Fig. 2D). Despite the normally high variability of IPIs, this large increase in the proportion of IPIs falling < 40 ms was a consistent feature of temporal call parameters emitted during DSC (see Fig. 2D), which is what led us to choose the percentage of IPIs < 40 ms as a key index of each bat's calling behavior (Table 1); the increase in the number of IPIs < 40 ms indicated an increase in the number of calls emitted as doublets. Similar to the changes in the distribution patterns of call durations during DSC versus those produced when not compensating (at rest; see Fig. 2, A and C), a statistical analysis of the IPI means \pm SD for 10 bats (mean IPIs: 114.6 ± 103.8 ms during DSC vs. 136.1 ± 101.0 ms at rest) would not have revealed the clearly changed distribution pattern of IPIs occurring during DSC.

The specific pattern changes in call durations and IPIs elicited by electronically shifting the frequency of echo mimics in stationary bats was also observed to occur in response to naturally Doppler-shifted echoes. We tested this condition in bats that emitted calls while swinging on a pendulum toward a large stationary background target. We found that the distribution patterns for call durations and IPIs emitted during a series of forward and backward pendulum swings (Fig. 2, E and F) were similar to those observed during DSC in response to electronically frequency-shifted echo mimics (compare with Fig. 2, C and D). Although the overall pattern was similar in both conditions, data collected from horseshoe bats swinging on a pendulum was typically biased toward a higher percentage of shorter calls emitted during the forward stroke of the pendulum, with far fewer, generally longer, calls emitted during the backward stroke. This pattern was reflected in the distribution of call durations shown in Fig. 2E, where the first peak centered at a mode of ~ 23 ms was notably larger than the second peak centered around the original resting mode value of 38 ms. Mean call durations were shorter during the pendulum swings (30.78 ± 12.57 ms) compared with the resting condition (33.44 ± 12.41). Simultaneously there was a substantial increase in the proportion of IPIs < 40 ms (Fig. 2F). The mean IPI for three bats swung on a pendulum was 72.0 ± 80 ms, and the mean ratio of IPIs ≤ 40 ms was 55%. Both values were

significantly different from the at rest condition (1-way ANOVA, $P \leq 0.01$) but not from the condition when bats compensated for electronically frequency-shifted echo mimics. Ratios of IPIs ≤ 40 ms that exceed 50% of all IPIs emitted indicate that the bats produced some calls as parts of triplets or other multiplets.

Finally, we analyzed in five bats if call durations and IPIs during DSC changed independently from one another or whether they themselves were linked. From an analysis of 4836 calls uttered sequentially by one representative bat (*bat 6*) during DSC (call durations and IPIs span a wider range during DSC, thus offering a clearer picture of any potentially underlying relationships), we found that the duration of a call depended to a certain degree on the length of the preceding, but not the subsequent, IPI. A Spearman rank-order correlation test revealed a correlation coefficient of $r_s = 0.246$ ($P \leq 0.001$) when correlating call duration with preceding IPI. In contrast, the correlation coefficient was by more than an order of magnitude lower ($r_s = 0.0237$; $P = 0.465$), when comparing call duration with the length of subsequent IPIs. The relationship between call duration and preceding IPI was far from being linear (see Fig. 3): when considering solely IPIs > 40 ms, the IPI was no longer significantly correlated with succeeding call durations. These results in four other bats were consistent with the findings presented above for *bat 6*. Our interpretation is that shorter call durations were correlated with preceding IPIs < 40 ms because together they represent succeeding calls within a doublet/multiplet and may therefore be mechanically linked.

Effect of echo delay on call duration and IPI

We investigated the specific effects of changing echo delay on call duration and repetition rate in five bats. At rest, the mean call duration for these five bats was 35.8 ± 8.5 ms with an accompanying mean IPI of 127.9 ± 110.0 ms.

As described in the preceding text, mean call durations for these five bats were always reduced during DSC performance. Figure 4 compares duration and IPI data for calls produced in response to echo mimics delivered at RF [playback (PB); ●] versus those calls emitted during DSC ("frequency-shifted PB"; ○) over a range of playback delays that varied from 4 to 20 ms relative to call onset. Results for one representative bat are illustrated in Fig. 4, A and B, and the means of all five bats

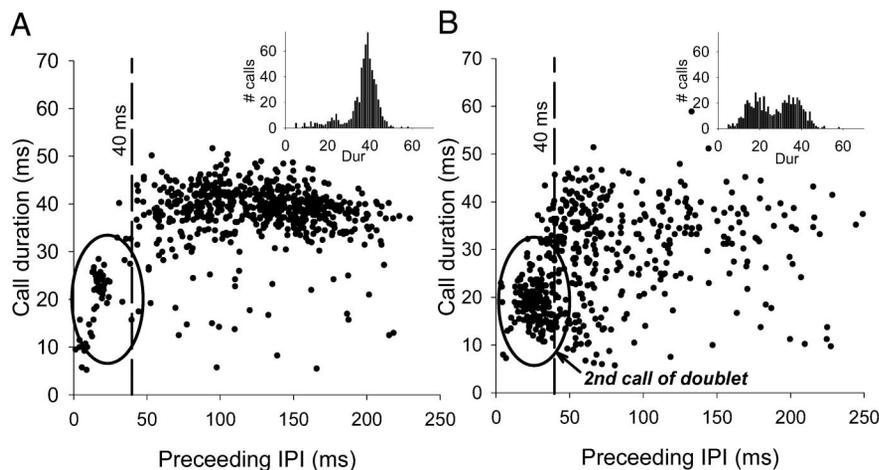


FIG. 3. Relationship between call duration and preceding IPI for a bat calling at resting call frequency (RF; A) and during DSC (B). In A the majority of calls were near the mean (*bat 20* of Table 1) regardless of IPI, and the few short calls followed short IPIs because they were the second calls in a doublet. In B, the appearance of large numbers of short-duration calls evoked by DSC always followed short IPIs, consistent with the conclusion that this subpopulation largely reflects the second calls of doublets. For B, playback frequency was shifted sinusoidally from 0 to 3 kHz at a modulation frequency of 0.1 Hz. A: 659 calls over 60 s; B: 625 calls over 60 s.

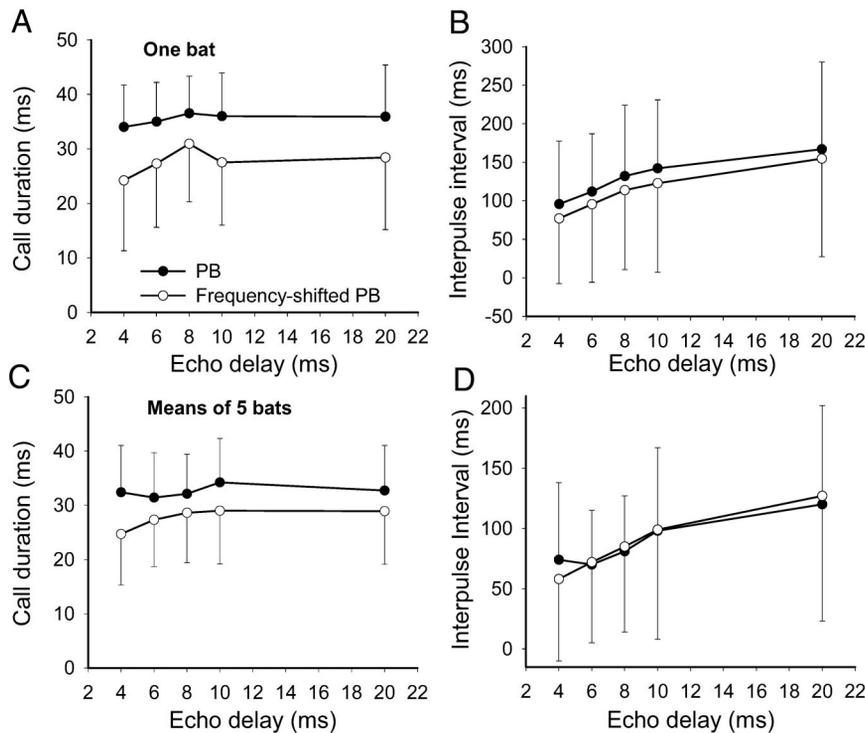


FIG. 4. Effects of changing echo delay on the mean call duration and mean IPI when horseshoe bats were presented with either playback (PB, ●) or frequency-shifted echo mimics (see METHODS) simulating Doppler-effects (frequency-shifted PB, ○). *A* and *B*: 1 representative bat. *C* and *D*: mean of the means of 5 bats, error bars reflect the mean of the SDs. For individual bats, means \pm SD were calculated from 3-min recordings of each bat under each condition during which call rates varied from 5 to 20 calls/s, depending on the bat and the playback condition.

studied are presented in Fig. 4, *C* and *D*. Although call durations varied consistently between the two playback conditions (RF vs. DSC), playback delay was not found to systematically influence call duration under either condition (1-way ANOVA, all pair-wise comparisons, $P > 0.05$; Fig. 4, *A* and *C*) with one exception: on average, call durations were significantly shorter during DSC at 4-ms delays than under any other conditions (1-way ANOVA, $P \leq 0.01$ for 4 ms vs. all other conditions; Fig. 4*C*).

Interestingly, frequency-shifted playback presented at 20-ms delays triggered the same reduction in mean call durations observed at the other, shorter delays, even though none of the bats performed DSC behavior when echoes returned following this delay. The significance of this observation lies in earlier reports that DSC performance is highly sensitive to echo delay, degrading rapidly when echo delays exceed even 10 ms (Schuller 1977). This indicates that in our experiments the frequency-shifted echoes caused the bats to emit doublets, even though the same stimuli were insufficient to provoke a change in call frequency. Overall we observed no correlation between the extent to which any bat performed DSC behavior and the percentage of time they emitted single versus double calls. Although frequency compensation and the transition from single to double calls appeared to be triggered by the same stimulus (i.e., elevated playback frequencies), the two responses appeared to be controlled independently from one another.

Consistent with an increase in the percentage of calls emitted as doublets, frequency-shifted playback caused a concomitant decrease in the mean IPI, and this decrease was observed to be consistent over the entire range of delays in three of the five bats (for example see Fig. 4*B*); in the two other bats there was no significant difference between the mean IPIs at delays of 10 and 20 ms. Overall the effect of echo frequency on mean IPIs

was averaged out by the large variability between bats when data from all five bats were pooled (Fig. 4*D*). In addition to the effects of echo frequency on IPI, we also observed a consistent relationship between playback delay and mean IPIs, and this relationship appeared to be independent of playback frequency (Fig. 4*D*). When responding either to playback at RF or during DSC, the IPI increased on average by 47 or 69 ms, respectively, as delays were increased from 4 to 20 ms. All five bats exhibited shorter mean IPIs at 4-ms delays when performing DSC than at RF; the mean decrease in IPI caused by DSC at 4 ms was 15.5 ± 5.6 ms ($n = 5$), corresponding to a mean reduction of $21.9 \pm 9.2\%$ relative to RF at 4 ms. The lowest mean IPI achieved by any bat under any condition was 40.0 ± 64.5 ms ($n = 3,294$ calls recorded over a 4-min span; 4-ms playback delay, during DSC) during which time the mean call duration was 18.9 ± 8.8 ms; in this record only 12 of 3,294 calls were not uttered as part of a doublet or, in some cases, a triplet or quadruplet.

Isolating the effects of echo CF and FM components on duration and IPI

Optimum DSC performance requires that the returning echo overlaps the outgoing call in time, but it does not require that the echo contain the natural FM components (Schuller 1977). Alternatively, in all echolocating bats, the perception of target distance depends on the processing and recognition of FM sound patterns and, in particular, downward FM sweeps (Griffin 1958; Roverud 1993; Schnitzler and Kalko 2001; Simmons 1973; Simmons and Grinnell 1988). Therefore we investigated separately the effects of changing echo delay on call duration and IPI by simulating either only the CF or the terminal FM component (Fig. 1) with an electronically generated sound pulse and presenting it as a simplified echo mimic.

Effects of the CF component presented alone

We delivered the CF component of the simplified echo mimic following delays of 4, 10, and 20 ms relative to the onset of the outgoing call. The frequency of the CF stimulus was initially set to match the CF portion of the bat's own calls emitted at RF and was later shifted up or down in frequency to test the effects of changing echo CF on call duration and IPI. These experiments were performed in three bats. Only one of the three bats responded actually performed DSC when presented with frequency-shifted CF stimuli in place of frequency-shifted versions of its own calls. Nevertheless, we observed in all three bats that the presentation of CF pulses at frequencies 1 kHz above each bat's RF triggered a significant reduction in their mean IPIs and call durations ($P \leq 0.01$), which we confirmed was due to a switch from emitting single calls to doublets. On average, call durations decreased from 28.1 ± 6.7 to 22.6 ± 8.0 ms, whereas IPIs decreased from 106.0 ± 71.0 to 86.8 ± 67.6 ms (mean of the means, $n = 3$). These changes were similar in magnitude to the changes triggered by the playback of frequency-shifted complete echolocation calls (Figs. 2, 4, and 5). However, call durations and IPIs were not significantly influenced by changing the playback delay of the CF mimic (Fig. 5; ANOVA, $P \geq 0.05$ for all pair-wise

comparisons). Although we did not systematically investigate the effects of different CF frequencies on call temporal parameters, we did confirm that the presentation of CF mimics at frequencies ≥ 1 kHz below the bat's RF did not result in mean call durations or IPIs significantly different from results obtained with CFs presented at the bat's RF. In all cases, however, the presentation of CF mimics caused a significant increase in IPI variability relative to IPIs obtained from bats responding to the playback of their own calls (Fig. 5).

Effects of the FM component presented alone

The terminal FM portion of an echo signal was simulated with acoustic sound pulses that consisted of 3-ms-long signals in which the frequency swept linearly downward for 15 kHz beginning at the bat's mean RF. These FM-sweep echo mimics were delivered at 4-, 10-, or 20-ms delays relative to the end of each emitted call. All three bats exhibited significantly shorter mean IPIs in response to progressively shorter FM-sweep playback delays (Fig. 5). The effects that changing FM delays had on IPIs were very similar in magnitude and range to the effects observed when the bat's own calls were played back at the same delays (PB in Fig. 5). This effect stands in sharp contrast to results obtained with the CF mimic (see preceding text and "CF tones" in Fig. 5). Alternatively, presentation of FM sweeps at differing delays caused no systematic changes in call duration (Fig. 5, *bottom*).

DISCUSSION

During flight horseshoe bats exhibit both abrupt switches in call emission patterns and finely graded changes in the timing of individual calls (Jones and Rayner 1989; Neuweiler et al. 1987; Tian and Schnitzler 1997). These changes occur on 1-ms time scale and appear to be driven almost entirely by auditory feedback. The transition from search to approach phase during echolocation is characterized by a switch from emitting single calls to producing calls in doublets (Griffin 1958; Roverud 1993; Schnitzler and Henson 1980; Schnitzler and Kalko 2001), and it occurs whenever a target comes within a range of ~ 2 m. For flying horseshoe bats, this behavioral transition includes an automatic shortening of call durations, wherein the second call in a doublet, and sometimes the first, become roughly half as long as a typical search phase call, and the two calls are separated by a stereotypically short IPI (Schnitzler and Kalko 2001; Tian and Schnitzler 1997). Our experiments demonstrated that in horseshoe bats the switch from search to approach phase can be triggered in a stationary bat by presenting it with positive shifts in echo frequency, either in response to electronically frequency-shifted echo mimics or when swinging on a pendulum. When swinging on a pendulum, echo delay and frequency always change simultaneously, thus either parameter could account for the observed changes in call emission patterns. However, because echo delay was held constant during the presentation of electronically frequency-shifted echo mimics, yet yielding similar distributions of call durations and IPIs, it appears that changing echo frequencies are sufficient to trigger much of the changes in call emission patterns that we observed on the pendulum.

Horseshoe bats are highly sensitive to any shifts in echo frequency, as evidenced by the remarkable speed and accuracy

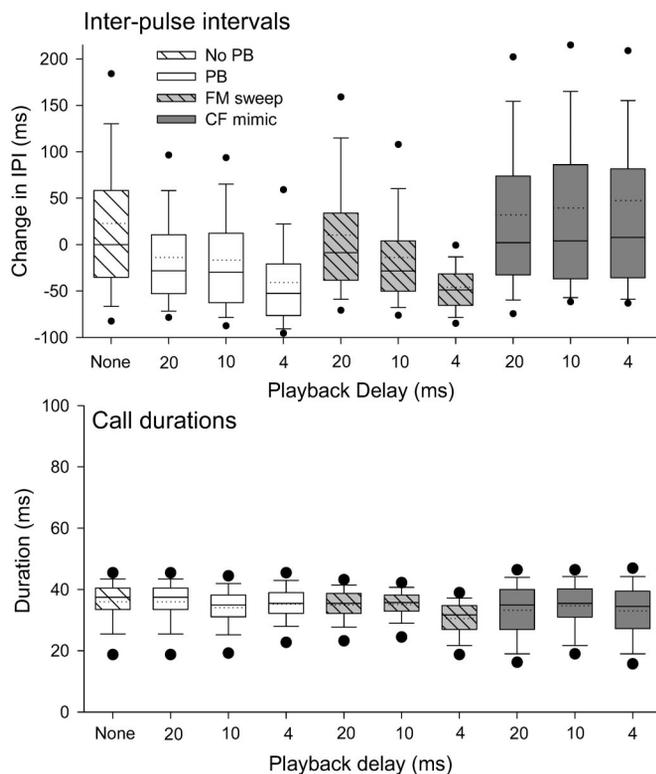


FIG. 5. Effects of changing playback delay on IPI (*top*) and call duration (*bottom*) for 3 different stimulus conditions: playback of the bat's own call (PB), an artificial FM sweep, descending 15 kHz over 3 ms beginning from the median CF value of the bat's own call (FM-sweep), or an artificial constant-frequency tone designed to mimic the CF portion of each bat's own call (CF-mimic). IPI data were normalized relative to median value of the IPIs for each of 3 bats calling at rest prior to being pooled for final comparison. PB and CF-mimics were delayed relative to the onset of the prior emitted call, whereas FM sweeps were delayed relative to call offset. Total number of calls pooled from all 3 bats were: No PB: 4,782; 20-ms PB: 6,393; 10-ms PB: 5,504; 4-ms PB: 7,038; 20-ms FM: 5,229; 10-ms FM: 3,947; 4-ms FM: 6,285; 20-ms CF: 3,560; 10-ms CF: 3,482; 4-ms CF: 3,003.

of their DSC behavior (Grinnell 1989; Schuller et al. 1975; Smotherman and Metzner 2003). Doppler effects are always present during target approach, and for CF bats in particular, positive shifts in echo frequency would be an appropriate and reliable cue for triggering abrupt increases in call rate. Faster calling serves DSC as well as echolocation behavior generally because higher call rates improve DSC performance (Schuller 1986; Smotherman and Metzner 2003). During DSC, horseshoe bats lower their call frequency much faster than they raise it (Metzner et al. 2002; Schuller et al. 1974, 1975), and this appears to be due at least in part to the evidence that the horseshoe bat auditory system is significantly more sensitive to echo frequencies above than below RF (Long and Schnitzler 1975; Metzner et al. 2002). However, the results presented here provide a more salient explanation for why horseshoe bats lower their call frequency faster than they raise: call rate effectively doubles during the response to positive but not negative changes in echo frequency.

Bats determine target range by measuring the time interval between the emitted call and returning echo (Simmons 1973), and bats rely on these measurements to drive precise changes in call rate. We found that in horseshoe bats, increasing the echo delay (in particular that of an FM mimic) from 4 to 20 ms caused a significant and systematic increase in mean IPIs with the greatest increase occurring between 4 and 10 ms. The relationship between echo delay and mean IPI, however, did not depend on whether or not the bat was calling with single calls or doublets (Fig. 4B). This therefore indicates that echo delay affected the time interval occurring between successive doublets but not within doublets.

On the other hand, we found that changing the delay of the echo mimic alone did not appear to have any significant effects on call duration. Call durations were significantly shortened when the delay was shortened to 4 ms but only in the presence of simulated Doppler shifts in playback frequency. Even then, however, the effect of echo delay on call duration was negligible compared with the effect caused by changing echo frequency. The results presented here clearly indicate that echo delay is being used to calculate precise changes in call repetition rate (i.e., IPI), whereas positive shifts in echo frequency are the principle cue for causing the switch from emitting single calls to doublets/multiplets. Thus echo frequency appears to be the primary trigger for the behavioral transition from search to approach phase in horseshoe bats. It is interesting to note, however, that the progressive reduction in IPI that occurs during the approach phase does not require that the bat switch from singles to doublets. Therefore the approach phase of horseshoe bat echolocation is composed of two separate behavioral components.

Target distance measurements depend on the processing and recognition of FM sound patterns (Roverud 1993, 1994; Simmons 1973, 1993; Simmons and Chen 1989; Simmons and Grinnell 1988; Simmons et al. 1998). Our data show that removal or isolation of the FM component in the echo mimic profoundly altered the effects of echo delay on call rate in horseshoe bats. Data shown in Fig. 5 suggest that absence of an FM sweep from the echo mimic led to an increase in the mean and variance of the IPIs regardless of delay value. Conversely, we found that an artificial FM signal that closely resembled the terminal FM sweep of the horseshoe bat's own call affected IPI at least as well as a playback of the bat's actual call. These

results suggest that horseshoe bats use measurements of the delay occurring between the terminal FM sweep of the outgoing call and the terminal FM sweep of the returning echo to control the time course of subsequent call emissions. The horseshoe bat's auditory system, as well as that of other echolocating bats, is known to possess specialized populations of neurons that respond selectively to pairs of FM sweeps separated by specific time delays, so-called FM-FM delay-tuned neurons (Berkowitz and Suga 1989; Feng et al. 1978; O'Neill and Suga 1979, 1982; Portfors and Wenstrup 1999, 2001; Schuller et al. 1991; Suga and Horikawa 1986; Suga and O'Neill 1979; Taniguchi et al. 1986; Wong and Shannon 1988). These neuronal populations could be part of the auditory feedback pathway that controls call repetition rate in echolocating bats. FM-FM delay-tuned neurons are found in the auditory cortex of CF-FM bats (O'Neill and Suga 1979, 1982; Schuller et al. 1991; Suga and Horikawa 1986; Suga and O'Neill 1979; Taniguchi et al. 1986). The evidence presented here indicates that timing cues derived from FM cues are not being used to adjust the shorter time intervals occurring between calls within a doublet but instead are being used to modulate the longer time intervals occurring between solitary calls and between the end of one doublet and the beginning of the next; this may indicate a role for cortical processing of the FM component. However, FM-FM delay-tuned neurons have also been found at earlier stages of auditory processing, such as in the inferior colliculus (Portfors and Wenstrup 1999, 2001); this would imply that cortical processing might not be critical for the normal control of vocal timing. In the horseshoe bat, evidence suggests that the Doppler-shift compensation behavior may be controlled by a midbrain sensory-motor feedback loop (Gaioni et al. 1990; Smotherman et al. 2003). Because the switch from emitting solitary calls to doublets is caused by the same acoustic cue that drives DSC (i.e., elevated echo frequencies), it may be that this too is controlled by an intimate midbrain link between the auditory and vocal motor systems, thus sparing the bat any time constraints that might be associated with more detailed sensory processing.

Under natural conditions call and echo overlap significantly in time, such that the sounds are effectively summed within the cochlea (Henson et al. 1982; Jen and Suga 1976; Pietsch and Schuller 1987). Thus as a horseshoe bat emits calls, it is listening to a persistent stream of alternating constant- and frequency-modulated components fused together to form complex temporal waveforms, the details of which are used to guide the parameters of subsequent vocalizations. In this way, bats are not unlike human speakers. Here we report that echo pitch and delay have distinctly different effects on the ongoing control of vocal timing. In humans, stuttering can be alleviated by presenting the stutterer with either pitch-shifted or delayed auditory feedback (Bloodstein 1995; Fitch et al. 1997; Hargrave et al. 1994; Kalinowski et al. 1993), suggesting that like the bat, humans are using both pitch and delay cues to regulate to flow of speech. In bats, we have the advantage of being able to study the physiology of the neural substrate underlying what appear to be separate but ultimately convergent auditory feedback pathways controlling the temporal patterns of vocal behavior in mammals.

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