

Storage of Doppler-Shift Information in the Echolocation System of the “CF-FM”-Bat, *Rhinolophus ferrumequinum**

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Summary. The greater horseshoe bat (*Rhinolophus ferrumequinum*) emits echolocation sounds consisting of a long constant-frequency (CF) component preceded and followed by a short frequency-modulated (FM) component. When an echo returns with an upward Doppler-shift, the bat compensates for the frequency-shift by lowering the emitted frequency in the subsequent orientation sounds and stabilizes the echo image. The bat can accurately store frequency-shift information during silent periods of at least several minutes. The stored frequency-shift information is not affected by tone bursts delivered during silent periods without an overlap with an emitted orientation sound. The system for storage of Doppler-shift information has properties similar to a sample and hold circuit with sampling at vocalization time and with a rather flat slewing rate for the stored frequency information.

Introduction

The orientation sound of the greater horseshoe bat (*Rhinolophus ferrumequinum*) always consists of a long constant-frequency (CF) component preceded and followed by short frequency-modulated (FM) components. The bat shows an acoustic behavior called “Doppler-shift compensation” (Schnitzler, 1968): when a stationary bat is regularly emitting orientation sounds and receiving echoes which are not Doppler-shifted, the bat accurately keeps the frequency of the CF component at a certain frequency, the *resting frequency*. The resting frequency for this species is commonly between 82 and 85 kHz. When the bat receives positively Doppler-shifted echoes, however, it lowers the frequency of the subsequent orientation sounds in order to stabilize the frequency of the CF component in the Doppler-shifted echo at a certain frequency, the

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reference frequency (Schuller *et al.*, 1974). The frequency of the CF component during Doppler-shift compensation is hereafter called the *compensation frequency*. The duration of the CF component ranges between 10 and 65 msec, and the Doppler-shifted echo always returns during emission of the latter part of the orientation sound. The bat, however, does not change the frequency of the CF component in that sound, but changes the frequency of subsequent orientation sounds. The Doppler-shift compensation system consists of the auditory and vocalization system apparently coupled into a regulating network with a long feedback time. This means that the Doppler-shift compensation system analyzes the frequency of the echo returning during emission of the orientation sound and stores the frequency-shift information until the next orientation sound is vocalized, at which time compensation occurs. This paper describes how long and how accurately *Rhinolophus ferrumequinum* stores frequency information about echoes.

Methods

Five *Rhinolophus ferrumequinum* were selected which intermittently emitted orientation sounds with variable silent periods but compensated properly for Doppler-shifts. Each of these bats was put in a plastic holder and was placed in a partially anechoic chamber in which artificial echoes with or without Doppler-shifts were delivered to the bat with an electronic Doppler-shift simulator triggered by each echolocation sound (Schuller *et al.*, 1974). Since the condenser loudspeaker was placed 68 cm in front of the bat, these echoes were always delayed by about 4 msec from the orientation sounds, the same delay natural echoes from that distance would have. The frequency of the CF component of the emitted orientation sounds was continuously recorded on a strip chart recorder (Helcoscriptor He-1) for further evaluation. The record yielded the interpulse intervals and the emitted frequency of the first sound after such silent periods.

Theoretically the heterodyning system of the Doppler-shift simulator gives an output only if the bat is vocalizing. In reality noise and a weak 90 kHz signal (heterodyning frequency) are present during the silent periods at intensities 60 dB and 30 dB respectively below the signal intensity. The frequency components during vocalization are not present during silent periods. To be sure that the bat was not disturbed in its performance by any acoustical input during silent periods, the loudspeaker was turned off during the silent periods in one of five series of experiments. The detection threshold for the bat's orientation sounds was adjusted to the most sensitive level just above the noise level of the apparatus, in order not to miss any vocalization which would have refreshed the Doppler-shift information without being detected.

Results

In each animal the resting and the compensation frequencies were first measured when it was emitting orientation sounds at a rate of about 4/sec. The resting frequencies of the bats ranged between 82 and 85 kHz. Fig. 1B shows an example of the change in the frequency of the CF component when a +3 kHz artificial Doppler-shift was suddenly introduced and then removed as shown in Fig. 1A. Frequency histograms and standard deviations from the mean frequency characterize the animals accuracy in keeping its resting and compensation frequencies (Fig. 1C). The accuracy of the control system is extraordinary and either frequency is maintained within a few tens of Hz. When a bat that has been emitting regularly its resting frequency falls silent for some time, however,

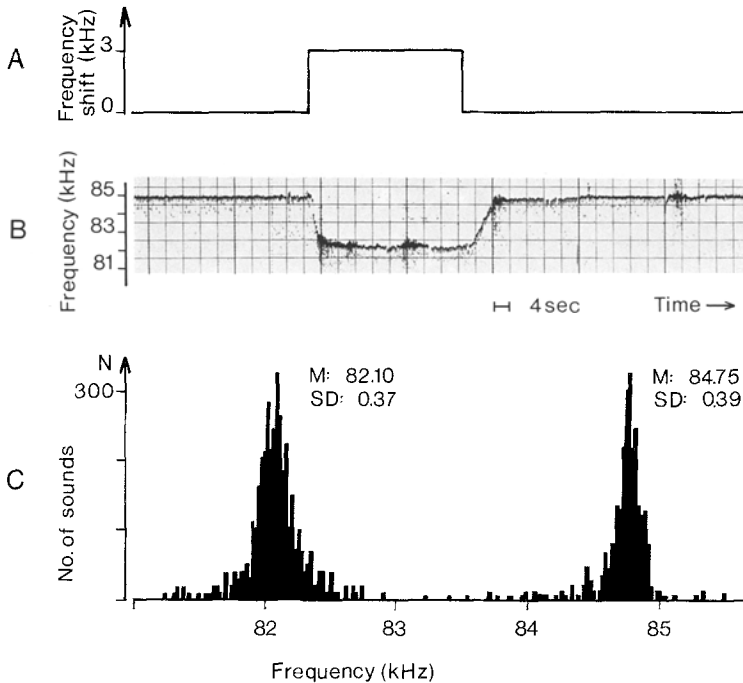


Fig. 1A-C. Compensation for a Doppler-shift in a bat emitting orientation sounds at a rate of about 4/sec. (A) Time course of a +3 kHz Doppler-shift introduced in artificial echoes. (B) Change in the frequency of the CF component in the orientation sound with the introduction of the +3 kHz Doppler-shift shown in (A). Each dash represents the CF component of the sound. In (A) and (B), the ordinates represent frequency in kHz and abscissae represent time in sec. (C) Distributions of the resting and compensation frequencies are shown by the right and left histograms, respectively. *M* mean value, *SD* standard deviation. The ordinate and abscissa represent the number of orientation sounds emitted and the frequencies of the CF components of these sounds

the first sound emitted after the silent period tends to be slightly lower in frequency than that maintained during regular emission. The longer the silent period, the lower was the frequency, at least up to intervals of several minutes, the mean deviation from the resting frequency for such delays may be as much as 400 to 500 Hz. The resting frequency is rapidly restored when repetitive emission resumes. Fig. 2A and 2B show a sample record in which silent periods occurred with and without frequency-shifted echoes. The frequency of the CF component of the first orientation sound after each silent period was measured as a function of the duration of the silent period during a zero and +3 kHz Doppler-shift of the echo. The filled circles in Fig. 2C show the relationship between the duration of the silent period and the frequency of the first sound emitted after it when the bat emits its resting frequency. When time is plotted logarithmically, the relationship is almost straight. The slope of the regression line was about -0.3 kHz per log time unit.

If the last echo a bat heard before a silent period was shifted by +3 kHz, it retained this information and emitted its next sound with compensation still present, however, with a gradual loss of compensation as a function of the

duration of the silent period. The relationship between compensation frequency and the length of the silent period is represented by the open circles in Fig. 2C. The change in mean compensation frequency was less than 400 Hz for silent periods of up to 5 min. In one bat out of five it was nearly zero for silent periods as long as 3 min. No bat fully returned to its resting (uncompensated) frequency even after 16 min of silence. The tendency of the regression lines showing the relationship between the silent period and the frequency after shifted and unshifted echoes to converge at very long silent periods suggests that they might reach an intermediate level if the silent period were sufficiently long. It is clear also that regular auditory feedback increases the precision of the control system, for the distributions of frequencies from intermittently vocalizing bats (Fig. 2C) have much larger deviations from the mean than the corresponding distributions of the continuously emitting bats. The bat that showed no change in mean compensation frequency even after 3 min of silence nevertheless showed about twice as broad a distribution of frequencies around the mean that it did during regular vocalization. It should be emphasized that this slow change in emitted frequency in the absence of auditory feedback is not a necessary limitation on the speed of change in emitted frequency. When the frequency shift introduced in the echo was turned off during the silent period, the next pulse showed continued compensation, but subsequent sounds had returned to the uncompensated resting frequencies.

To examine for the possibility that the bat was obtaining cues for controlling the frequency of the orientation sounds from the low level sound leaking out from the loudspeaker during silent periods, a series of experiments was made with the loudspeaker turned off when the bat was not emitting sounds and turned back on again after the onset of each orientation sound. The results of these measurements (e.g. open circles in Fig. 2D) indicate that the bat retained its "memory" of compensation frequency as well as it had in the other experiments (e.g. open circles in Fig. 2C). The slopes of the regression lines for these two types of measurements were not significantly different from each other: 0.11 in Fig. 2C and 0.19 in Fig. 2D (kHz per log time unit).

As a further control and a demonstration of the lack of importance of sounds heard during the silent period, a tone which was 1 kHz higher than the resting frequency was delivered during the silent periods between orientation sounds, without overlapping artificial echoes which were shifted by +3 kHz. It was found that the bat's ability to store the 3 kHz-shift information was not affected by such a tone. As long as the 1 kHz-shifted tone did not overlap with the emitted sound, it had no influence on the bat's compensation.

It could also be demonstrated that continuous exposure to a shifted echo frequency had no effect on a bat's ability to maintain its normal uncompensated resting frequency. Fig. 2D (filled circles) shows the frequency in the first orientation sound after silent periods of different durations in the bat that had first been exposed to 3 kHz Doppler-shifted echoes for 6 hours and then tested after the artificial echoes had been turned off. It was noticed that the resting frequency was held equally well even after long term compensation as before (Fig. 2C, filled circles). The slopes of the regression lines in the two cases were -0.27 and -0.35 (kHz per log time unit).

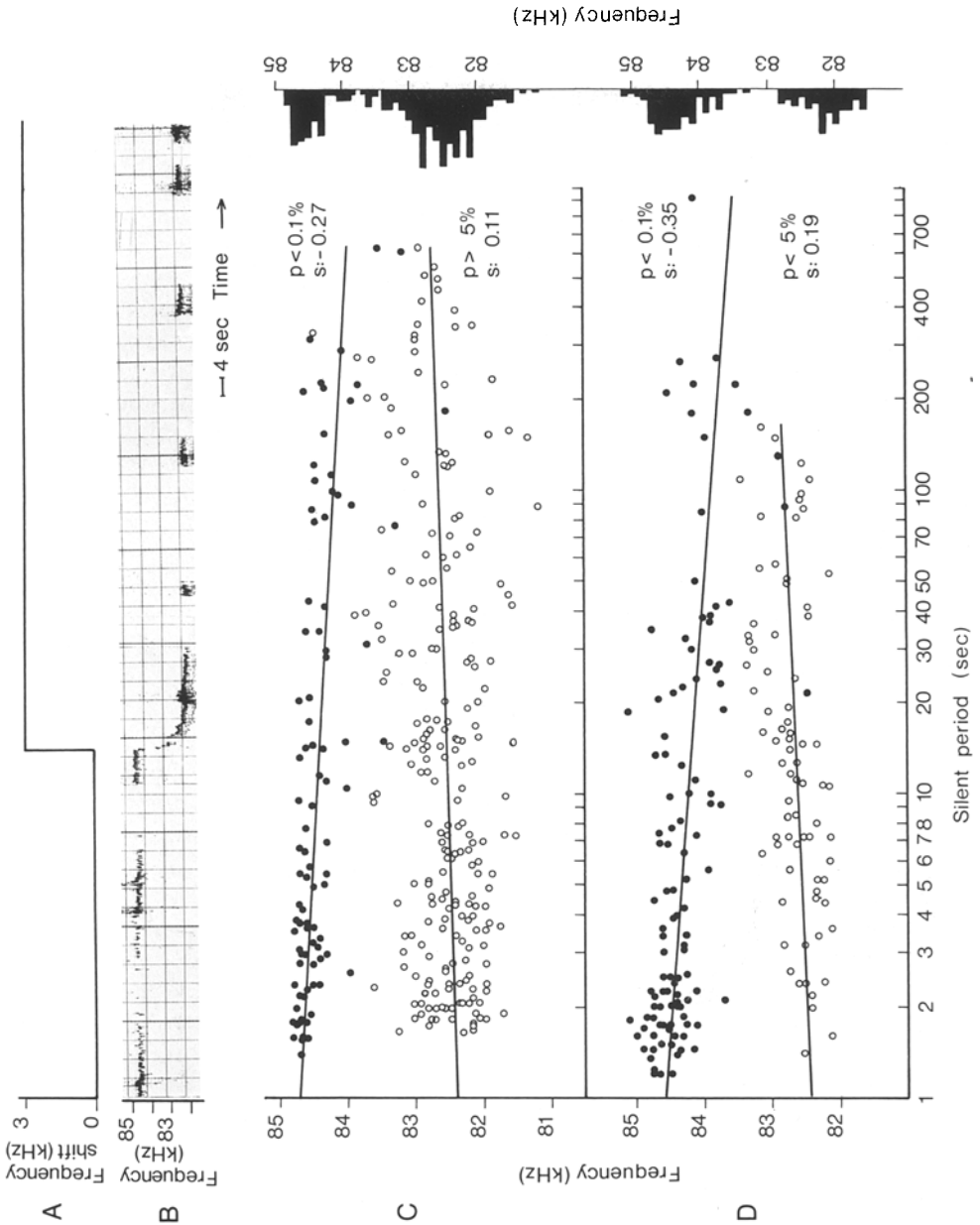


Fig. 2A-D. Resting frequency and compensation frequency for a +3 kHz Doppler-shift in an intermittently vocalizing bat. (A) Time course of the Doppler-shift introduced in the echoes. (B) Change in the frequency of the CF component in the orientation sound with the introduction of the Doppler-shift. Note the long silent periods between emitted sounds. The coordinates and symbols in (A) and (B) are the same as those in Fig. 1 (A and B). (C) Frequency of the CF component of the first sound (ordinate) after each silent period as a function of its duration (abscissa). Filled circles: resting frequencies. Open circles: compensation frequencies. The data were obtained from one and the same bat. The solid lines represent the regression lines calculated for the time in logarithmic scale. p error probability, s slope in kHz per log time unit. The histograms to the right represent the distributions of the frequencies of the CF components in the orientation sounds shown in the graph. (D) Frequency of the CF component of the first sound (ordinate) after each silent period as a function of its duration (abscissa). Filled circles: resting frequencies after a six hour exposure to a +3 kHz Doppler-shift. Open circles: compensation frequencies. The loudspeaker was turned off during silent periods. The data were obtained from a single bat. Solid lines, symbols, and histograms are the same as those in (C)

Discussion

In bats frequently emitting orientation sounds the complete adjustment of the emitted frequency following a sudden Doppler-shift of 4 kHz in the echo can be accomplished in less than 4 sec. Lowering the frequency away from the resting frequency was faster than raising it towards the resting frequency (Schuller *et al.*, 1975). That these lowered frequencies can be kept for long periods at about the same level in intermittent vocalization therefore cannot be explained as slow responding of the Doppler compensation or the frequency tuning systems. Since no change or refreshing of the frequency-shift information occurs during the silent periods, the system seems to store the information until it is changed by a new input during vocalization. The slope of the regression lines indicates that the system has a rather low decay, which gives a 13% frequency deviation in terms of the frequency-shift or a 0.5% frequency deviation in the absolute frequencies after a 5 min long non-vocal period.

Whether information on the frequency-shift or on the absolute frequency is stored in the compensation system cannot be answered from our data. The resting frequency on the other hand decreases with increasing silent periods during intermittent vocalization. This result fits with the observation described by Schuller *et al.* (1974) that the frequency of the first sound in bursts lies a few hundred Hz below the resting frequency.

Artificial signals with different frequency-shifts inserted during silent periods proved to be ineffective for changing information in the system on frequency-shifts. This again shows that overlap of the frequency-shifted echo with the outgoing sound is essential for the activation of the compensation system (Schuller, 1974). The experiments in which the frequency-shift was altered between sounds show also that the frequency-shift information in the last sound heard is conserved through a silent period and changed to the new value of frequency-shift only after the first sound is emitted. The system can be compared with a sample and hold circuit taking up new information only when triggered for sampling by emission of an echolocation sound and with a storage decay rate shown by the regression line in the frequency versus silent-period plot (Fig. 2).

Under natural conditions the storage of frequency-shift information for long periods of time is probably not important, as moving targets producing Doppler-shifts stay only a few seconds in the range of the echolocating bat. Therefore the present data describe only an important aspect of the Doppler-shift compensation system seen as a biological control system. The site of storage for the frequency-shift information within the control system remains an unanswered question.

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