

ONTOGENY OF VOCAL SIGNALS IN THE BIG BROWN BAT, *EPTESICUS FUSCUS*

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INTRODUCTION

The production of vocal signals by infant bats is important for communication and may play a role in the development of sonar signals used for echolocation. Recordings of infant vocalizations from a variety of species show many similarities, even across different families of bats (e.g. Brown, 1976; Gould, 1971, 1975a, 1979; Matsumura, 1979; Brown and Grinnell, 1980; Brown, Brown and Grinnell, 1983). Young infant bats often emit multiple-harmonic sounds that are lower in frequency than the sounds of conspecific adults. In many species, the infant vocal repertoire includes sounds with relatively constant frequency components which are typically identified as isolation sounds. These sounds often promote approach and retrieval of an infant by its mother (e.g. Davis, Barbour and Hassell, 1968; Gould, 1971, 1975a; Brown, 1976; Thomson, Fenton, and Barclay, 1985).

A detailed study of vocal ontogeny in bats permits careful assessment of the relation between communication and echolocation sounds and can also provide information concerning vocal production, and how it changes over the course of development. It may be particularly valuable to study vocal ontogeny in a species for which sonar capacity has been carefully examined. The big brown bat (*Eptesicus fuscus*) has been the subject of extensive psychophysical studies on hearing and echolocation (e.g. Simmons and Vernon, 1971; Simmons, 1973; Kick, 1982; Kick and Simmons, 1984). Infant vocalizations have also been described (Gould, 1971); however, the published work on vocal ontogeny in *Eptesicus fuscus* omits a developmental series of spectrograms, thus precluding close examination of the structure of communication and echolocation sounds and how they change with age. With the goal of evaluating these factors, this study attempts a detailed, comprehensive spectrographic analysis of vocal development in *Eptesicus fuscus*.

METHODS

Pregnant female *Eptesicus fuscus* were collected from maternity colonies in Rhode Island and Massachusetts during the late spring of 1986. They gave birth in the laboratory between June 11 and July 4, 1986 and nursed their young until 4 weeks postnatal.

All recordings of vocalizations were made in a foam-padded sound-attenuating chamber. The sounds of 7 infant bats were recorded longitudinally during the first 6 weeks of life. Sounds were recorded from the infants while in contact with the mother, while temporarily separated from her, and then again when reunited with her. The mother's vocalizations were also recorded. In addition, vocalizations were recorded from females that did not give birth this year, from those whose infants did not survive this year, and from males. All vocalizations were recorded with a Racal tape recorder, located outside the chamber. During recording, the speed of the tape recorder was set at 60 inches per second. Sounds were later played back at 1/64 the original recording speed and analyzed using a Nicolet Spectrum Analyzer (VA-500A).

RESULTS

At 6 hours postnatal, *Eptesicus fuscus* emit a variety of sounds that differ in frequency content and duration. Spectrograms show that newborns emit both relatively constant frequency (CF) and frequency modulated (FM) calls, a finding which contrasts with Gould's report (1971; 1975a) that *Eptesicus* infants only emit CF sounds until 3-5 days. The frequency components are lower than those of adult echolocation calls: CF calls are often about 15 kHz and FM calls typically sweep from about 20-25 kHz down to 10 kHz, whereas the adult echolocation call of *Eptesicus* sweeps from about 60 to 25 kHz. Sound duration is also longer in infant calls than the 2 ms sonar sounds of adults. The duration of infant CF calls is highly variable (20-125 ms) and often exceeds that observed for infant FM calls (20-30 ms).

Infants at one day of age show the same pattern of vocalizations; however, calls are occasionally shorter than those recorded from newborns. Between 5 and 7 days postnatal, bats produce sounds that are similar to those of newborns, although they now also emit sounds of shorter duration. These shorter sounds are less than 10 ms and contain multiple harmonics. The fundamental frequency is somewhat lower than the longer duration sounds (8-15 kHz) and shows shallow FM.

Figure 1 summarizes the vocal patterns observed in bats from 6 hours to 7 days postnatal. Presented on the left are spectrograms of sounds emitted by infants in contact with their mothers and on the right, those emitted by infants separated from their mothers. This figure illustrates that, in general, infants in close proximity of their mothers tend to produce longer duration sounds with less FM than those completely isolated from their mothers. It also shows a tendency for sound duration to decrease with age. There is, however, a great deal of individual variability in the spectral and temporal structure of infant sounds, and those recorded in different contexts cannot be unambiguously categorized. In spite of the individual variability, mothers apparently use infant calls (along with olfactory cues) to identify their own young (Gould, 1971). Mothers leave their young behind in the roost when they forage. Upon return, they retrieve and selectively nurse their own infants (Davis et al., 1968).

Spectrograms of vocalizations by bats from 7 days to adult are presented in Figure 2. Between 7 and 14 days postnatal, the starting frequency of some FM calls rises and the duration of these calls shows a marked decrease (Fig 2A). Bats at this age also appear less distressed when separated from their mothers and often do not vocalize when isolated from

or reunited with them. It is interesting to note that in the wild, mothers begin leaving the roost for longer periods of time when their infants are older (Davis et al., 1968). By 14 days, FM calls closely resembling the adult sonar signals are present; these calls are 2-5 ms in duration and sweep from approximately 40 to 20 kHz.

At 21 days, young *Eptesicus* are capable of flight (Davis et al., 1968; Gould, 1971; present study), and their sonar signals are similar to those of adults, although somewhat lower in frequency (sweeping from 45-20 kHz) and longer in duration (up to 5 ms). Between 21 and 28 days, the sonar signals become higher in frequency and shorter in duration.

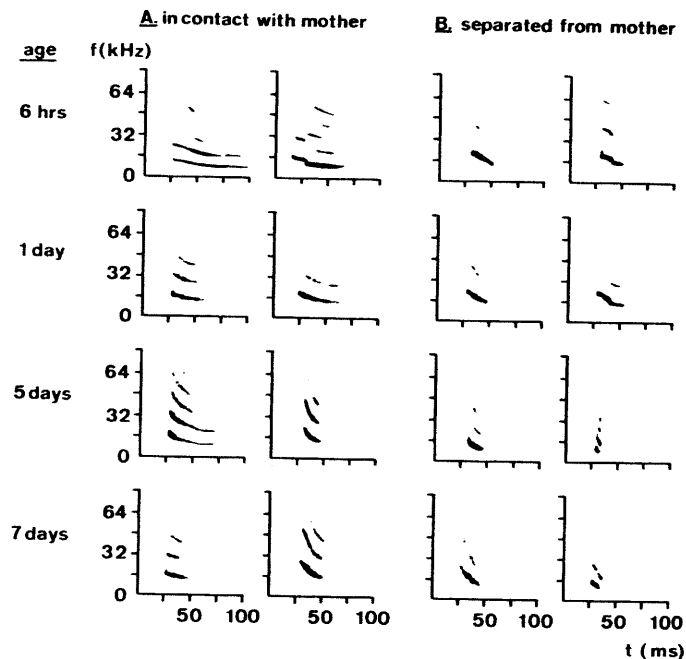


Figure 1. Spectrograms of sounds emitted by infants between 6 hours and 7 days postnatal; in contact with mother (left) and separated from mother (right).

Twenty-eight-day-old bats are capable of foraging on their own (Gould, 1971), and their sonar sounds are virtually indistinguishable from those of adults (Fig 2A).

Figure 2B shows that infant and juvenile bats, as well as adults, emit the short, low frequency pulses first recorded from 5-day-old bats. The short duration and shallow FM of these sounds in younger bats first suggested that they may be precursors of adult sonar signals; however, the fact that these pulses show little change with age indicates that they do not evolve into adult sonar sounds.

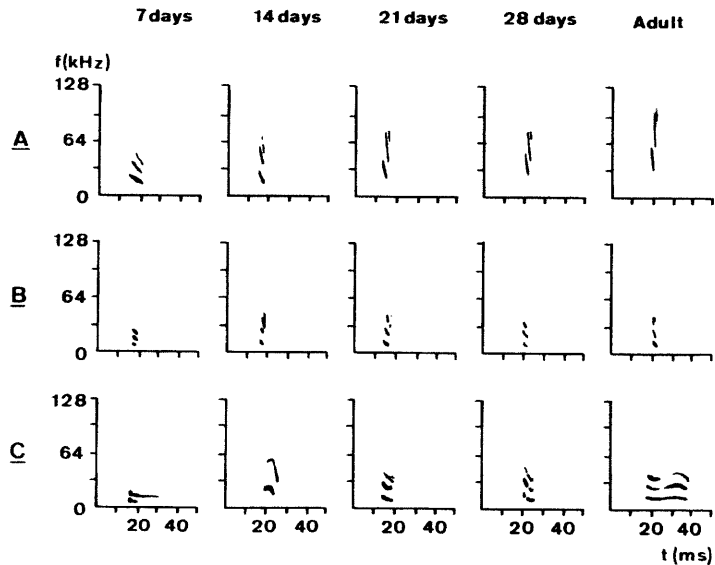


Figure 2. Spectrograms of sounds emitted by bats from 7 days to adult. A. FM sounds. B. Short low frequency pulses C. Communication sounds.

In Figure 2C, spectrograms of various other calls emitted by *Eptesicus* are presented. CF calls are not only recorded from infant bats but also from adults. The adult CF sound shown in this figure was emitted by a mother separated from her infant. A variety of other distress calls are also emitted by adults (not shown), many closely resembling the long, shallow FM and CF sounds produced by infants. Such adult distress calls are not unique to a mother separated from her infant. Similar vocalizations were also recorded from other adult *Eptesicus*, including females that did not give birth this year, those whose offspring did not survive this year, and males.

At intermediate ages (14-28 days), a variety of sounds were also recorded that could not be readily classified as FM sonar sounds or short, low frequency pulses. Shown for a 14-day-old bat is what appears to be an anomalous adult sonar sound, with an almost CF portion followed by a downward FM sweep. The structure of this sound may reflect lack of vocal control, or it may represent a communication signal. The spectrograms presented for 21- and 28-day-old bats are relatively low in frequency and resemble calls of younger infants. Perhaps they also serve a communicative function.

DISCUSSION

The major developmental trend in vocalizations by *Eptesicus* is a rise in sound frequency, accompanied by a reduction in sound duration. Although general patterns of vocalization do change with age, virtually all sound types emitted by infant *Eptesicus* are also emitted by adults. Adult calls differing from the typical echolocation sound are often produced by

distressed or agitated animals and thus probably function as communication signals.

The observation that adult *Eptesicus* emit calls resembling those more typical of infants has two important implications: First, there may be some overlap of sounds used for communication and those used for echolocation. This implies that sounds emitted by young *Eptesicus* may serve a dual function. Indeed, the infant bat may inadvertently begin using echoes of its own signals while engaged in social communication. Second, the calls of a young infant *Eptesicus* do not disappear from its repertoire as it matures, suggesting that no single infant sound evolves into the adult echolocation call. Rather, production of a group of sounds may stimulate the maturation of the vocal apparatus which then permits production of a brief FM sweep characteristic of adult sonar calls.

The results of this study may be useful to further evaluate the mechanisms of vocal production and their development. In *Eptesicus* the frequency of brief ultrasonic pulses is controlled by contraction and relaxation of the cricothyroid muscle surrounding the larynx. When the cricothyroid muscle contracts, it increases tension on the laryngeal membranes. Relaxation occurs during phonation. It appears that the magnitude of muscle contraction determines the frequency at which the laryngeal membranes vibrate, and gradual relaxation produces the downward FM sweep. The cricothyroid muscle is innervated by the motor branch of the superior laryngeal nerve (SLN), and section of this nerve results in a dramatic drop in the fundamental frequency of vocalizations and elimination of frequency modulation (Novick and Griffin, 1961; Suthers and Fattu, 1973, 1982).

Since infant bats emit sounds that are lower in frequency and show less depth of frequency modulation than adults, it is interesting to speculate that this may reflect immaturity of the larynx, its muscles and perhaps also its innervation. Gould (1975b) reports that the motor branch of the SLN is unmyelinated in premature *Eptesicus* and thickly myelinated in subadults. Data for intermediate ages are not reported, but it may be that postnatal myelination of the SLN permits greater contraction of the cricothyroid muscle and hence higher frequency phonation and deeper frequency modulation. Clearly, further data on developmental changes in the vocal apparatus of bats are needed to determine the mechanisms involved in vocal ontogeny.

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