Babbling in a vocal learning bat resembles human infant babbling

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Babbling is a production milestone in infant speech development. Evidence for babbling in nonhuman mammals is scarce, which has prevented cross-species comparisons. In this study, we investigated the conspicuous babbling behavior of Saccopteryx bilineata, a bat capable of vocal production learning. We analyzed the babbling of 20 bat pups in the field during their 3-month ontogeny and compared its features to those that characterize babbling in human infants. Our findings demonstrate that babbling in bat pups is characterized by the same eight features as babbling in human infants, including the conspicuous features reduplication and rhythmicity. These parallels in vocal ontogeny between two mammalian species offer future possibilities for comparison of cognitive and neuromolecular mechanisms and adaptive functions of babbling in bats and humans.

Key components of spoken language include the ability to modify a signal on the basis of auditory input (called vocal production learning (7)), syntactical composition, and semantic reference (2). Speech, the vocal motor output of language, requires precise control over the articulators of the vocal apparatus. The first utterances resembling speech sounds occur during babbling, a distinctive vocal behavior of human infants (3, 4). The ability to produce canonical syllables, such as “da’da’,” during babbling is required for successful language acquisition, and age-appropriate babbling is an indication of typical child development (4). Babbling enables infants to practice speech sounds by gaining control over the speech articulators and probably by reinforcing neuromotor connections (4). This behavior is characterized by universal features (Table 1).

Evidence for babbling exists in very few nonhuman taxa (table S1), one of which is the greater sac-winged bat (Saccopteryx bilineata). This neotropical bat exhibits vocal production learning (5) in addition to a conspicuous vocal practice behavior during ontogeny (figs. S1 and S2). This vocal practice has been described as resembling human infant babbling (6), but formal analyses have been lacking. The auditory input of S. bilineata pups consists of various conspecific vocalizations, the most notable being multisyllabic songs that adult males produce daily to defend their territories and attract females (figs. S3 and S4) (7). During babbling, pups acquire territorial songs by imitating adult tutors (5, 6). In this Report, we provide the first formal comparison of babbling features across mammals capable of vocal production learning and show that babbling behavior in S. bilineata pups is characterized by features similar to those of babbling in human infants.

We investigated the undisturbed, unmanipulated babbling behavior of 20 pups from two wild populations in Costa Rica and Panama throughout the pups’ vocal ontogeny and analyzed 55,056 syllables from 216 babbling bouts (Fig. 1) (8). We defined a syllable as a sound surrounded by silence; the term is thus not synonymous to the speechlike syllables produced by human infants (Table 1). For 7 to 10 weeks, pups spent almost 30% of their diurnal activity with vocal practice (fig. S2B). Babbling bouts were composed of several multisyllable trains (fig. S5) and had an average duration of 7 min; a single bout could last up to 43 min (adult vocalizations have a duration of several seconds to less than 1 min (7)).

Pup babbling started within the first 3 weeks after birth, at approximately one-third of the way through their 10-week vocal ontogeny (Fig. 2A). The adult vocal repertoire of S. bilineata consists of 25 different syllable types that are combined in various ways into 10 distinct vocalization types (7, 9). Producing the different syllable types during a pronounced babbling phase might be necessary to gain precise control over the vocal apparatus by means of sensorimotor learning. Pup babbling occurs during a circumscribed early developmental period and likely reflects a sensitive period for vocal production learning, as has been documented in humans and songbirds (20).

Pup babbling bouts consisted of undifferentiated protosyllables and adultlike syllable types (Fig. 2B). Undifferentiated protosyllables

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Table 1. Features of human infant babbling used for comparison to bat pup babbling. Speech precursors (protophones) encompass all precanonical sounds (e.g., “raspberries,” “goong”) and speechlike canonical syllables (e.g., “ba”). A canonical syllable consists of a consonant-like element transitioning rapidly into a mature vowel-like element. Protophones are present from birth onward and subsequently expand in quantity and type. Vegetative sounds (e.g., coughing, burping) and fixed vocal signals (e.g., crying, laughing) are not included (3). Canonical babbling contains well-formed, canonical syllables (“ga”), sometimes in reduplicated sequences (“da’da’”), as well as other protophones. It is preceded by marginal babbling (syllables with slow, slurred consonant-vowel transitions) and succeeded by variegated babbling (syllables with non-reduplicated consonants (“ba’ba’”) (3).

| Feature                              | Description                                      |
|--------------------------------------|-------------------------------------------------|
| Early babbling onset                 | Marginal babbling occurs from ~3 months onward; canonical babbling occurs from ~6 to 7 months onward; variegated babbling normally begins later than canonical babbling (3) |
| Babbling bout composition            | Combination of precanonical sounds and canonical syllables in long sequences (3) |
| Syllable subset acquisition          | Production of a small, universal subset of all syllable types that occur in natural languages (4) |
| Syllable type emergence              | Emergence of syllable type categories is variable across infants and ontogenetic speech stages, peaking at the expansion stage (i.e., sudden emergence of many syllable type categories) (4) |
| Reduplication                        | Repetition of canonical syllables (4) |
| Rhythmicity                          | Auditory impression of rhythmic phonation caused by cyclic alternation of rhythmic opening and closing of the supraglottal vocal tract (4) |
| Nonmandatory social context and function | Social context not required; lack of semantic information (3) |
| Universality                         | Produced by all typically developing infants irrespective of sex, culture, and language (3) |
were exclusively present during the entire babbling phase, clearly distinguishable from the adultlike syllable types (table S2), and not part of the adult vocal repertoire. These protosyllables were the most frequent syllable type in babbling bouts (39% of syllables; data S1) and were highly variable (table S3). This high variability may reflect vocal exploration and may help pups to shape their vocal output toward adult vocalizations in an apparently playful manner. Furthermore, undifferentiated protosyllables might facilitate the production switch between two distinct adultlike syllable types, because undifferentiated protosyllables were mainly located between them (fig. S6).

Fig. 1. Babbling in the bat Saccopteryx bilineata. (A) Babbling bout excerpt. Babbling bouts are composed of syllable trains (i.e., sequences of syllables) interspaced with silent intervals. Average and maximum durations of syllables (level 1), syllable trains (level 2), and babbling bouts (level 3) are indicated. Our analyses were conducted on these three levels. Labels depict different adultlike syllable types (fig. S3) and undifferentiated protosyllables (UPS), which were highly variable (fig. S6 and table S3) and exclusively produced by babbling pups. See the supplementary materials for a detailed description of each syllable type. For additional information on pup vocal development and time dedicated to babbling, see fig. S2. (B) Similarity of syllable types from the adult vocal repertoire and adultlike syllables produced by pups. (Top) Selection of syllable types produced by pups. (Bottom) Corresponding syllable types from the adult vocal repertoire. (C) Overview of social behaviors associated with babbling. Dark fur, pup; light fur, mother. At present, we can neither confirm nor discard the influence of maternal responses on babbling characteristics. [Drawings: C. Mumm]
Undifferentiated protosyllables may be comparable to speech precursors in human infants [i.e., sounds not commonly used in mature speech (3)], whereas adultlike syllable types may be comparable to the canonical syllables produced by babbling human infants [i.e., acoustic structure clearly reminiscent of fully developed adult syllable types (3)].

Not a single pup acquired the entire adult repertoire of 25 syllable types at weaning age (3 months; Fig. 2C). Final pup repertoire sizes ranged from 12 to 20 adult syllable types and had universal characteristics as regards the presence or absence of particular syllable types (data S2): First, all pups acquired the same

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**Fig. 2. Pup babbling is characterized by many key features similar to those of babbling in human infants.**

(A) Babbling starts early in vocal ontogeny and (B) is composed of adultlike syllable types and highly variable undifferentiated protosyllables, which are exclusively produced by pups. (C) Only a subset of the adult syllable-type repertoire is acquired during babbling. (D) Acquisition of syllable types during ontogeny is not linear. Day 0 indicates the point in time at which pups commence babbling (mean: 18 days after birth). The acquisition spurt denotes the highest rate of syllable acquisition. (E) Correlation matrix showing the proportion of reduplicated syllables (percentage) for all 21 syllable types found in babbling bouts. The observed repetition rate was significantly higher than the predicted repetition rate based on the number of produced syllables (data S1). Syllable types, except undifferentiated protosyllables, are ordered according to their function in the adult vocal repertoire [aggressive, neutral, isolation (I), affiliative]. Darker squares, mainly found in the main diagonal of the matrix, indicate higher reduplication percentages. (F) Regular beat (red bars) in syllable trains of babbling bouts was analyzed by measuring syllable inter-onset intervals (IOIs; black arrows), and rhythmicity was assessed with a normalized pairwise variability index (nPVI). Syllable trains were placed into five categories based on the function of their most prominent syllable. CV, coefficient of variation. (G) Babbling does not require a social context but does not necessarily have a social function. [Drawings: C. Mumm] (H) Babbling characteristics are comparable irrespective of regional origin or sex.

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**Table 1. Babbling characteristics**

| Syllable type | Population | Female | Male |
|--------------|------------|--------|------|
| Panama       | 17.5 (1.0) | 16.0 (0.8) | 18.0 (2.0) |
| Costa Rica   | 16.5 (2.5) | 10.0 (0.6) | 17.0 (2.0) |
| Total Female | 16.0 (0.8) |        |      |
| Total Male   | 18.0 (2.0) |        |      |

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10 syllable types, including the syllable types belonging to the later adult territorial song. Second, at weaning the same five adult syllable types had not yet emerged in any pup. The emergence of pups’ adultlike syllable types was not linear but characterized by a sudden expansion of syllable types comparable to the expansion stage in infant speech development (3), followed by a period during which previously unused syllable types emerged only infrequently and unequally across pups (Fig. 2D).

Babbling bouts were dominated by the reduplication of syllable types (Fig. 2E): 77% of syllables were succeeded by those belonging to the same syllable type, and the observed reduplication rate was significantly higher than the predicted reduplication rate based on the number of produced syllables (data S1). Similar to vocal learning behaviors in human infants, the benefit of syllable reduplication in bat pups may be to support vocal practice by repetition (“rehearsing”), likely by facilitating neural sensorimotor integration (11). In humans, one proximate mechanism of repetitive syllable production in babbling might result from underlying oscillations of the neural motor system (22), which may also be one of the mechanisms underlying reduplication in bat pup babbling. Additionally, the repetition of syllables by bat pups might reflect the fact that several adult vocalization types (fig. S4) contain repetitions of the same syllable types (7). Furthermore, the syllabic composition of pup babbling was mostly characterized by rhythmicity. Four of the five different syllable train categories (fig. S5) found in babbling bouts had a regular beat (Fig. 2F and table S4). Rhythmicity is also a salient characteristic of babbling in human infants (3).

Babbling bouts did not require a social context for production, even though pups often babbled during interactions with their mothers (see supplementary materials). Moreover, adultlike syllables generated in babbling bouts did not elicit the same reactions that they would evoke when produced by adult bats (Fig. 2G). The absence of adult responses may be explained by the fact that the sender was a pup or by the different sequence of syllable types. Furthermore, the social context did not correspond to adult vocalization types. Syllables in human infant babbling also lack semantic information but can transmit affect to a caregiver (3). Furthermore, human infant babbling could serve as a fitness signal for caregivers (13–15) because babbling is a sign of typical child development. It is unclear whether babbling in S. bilineata pups may also signal fitness to mothers.

Irrespective of sex or regional origin, all pups babbled during ontogeny and produced undifferentiated protosyllables. We found no differences in age at babbling onset, duration of the babbling phase, and size of the pups’ final syllable-type repertoire (Fig. 2H and table S5). However, future investigations of more than two populations will be necessary to corroborate the universal occurrence of babbling in S. bilineata. Notably, both sexes acquired the syllable types constituting the adult male territorial song and produced them in the correct sequential order, even though only males sing as adults (5). Females’ own experience of producing song syllables might facilitate their assessment of male song, thus influencing future mating decisions.

Our study provides the first formal analysis of bat pup babbling and reveals substantial parallels in multiple dimensions to babbling in human infants. The similarities in babbling features between two species with common traits such as laryngeal sound production, similar brain architecture, and vocal production learning offer future possibilities for understanding shared cognitive skills and neuro-molecular foundations.

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SUPPLEMENTAL MATERIALS

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Material and Methods
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