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# Vocal production learning in bats

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Echolocating bats exhibit excellent control over their acoustic signals emitted and skillfully interpret the returning echoes, allowing orientation and foraging in complete darkness. Echolocation may be a preadaptation for sophisticated vocal communication with conspecifics and, ultimately, vocal learning processes. In humans, the importance of auditory input for correct speech acquisition is obvious, whereas vocal production learning is rare and patchily distributed among non-human mammals. Bats comprise one of the few mammalian taxa capable of vocal production learning, with current behavioral evidence for three species belonging to two families; more evidence will probably forthcoming. The taxon's speciose nature makes bats well suited for phylogenetically controlled, comparative studies on proximate and ultimate mechanisms of mammalian vocal production learning.

### Addresses

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### Introduction

While many taxa show the ability to learn the usage and comprehension of acoustic signals, only a select few are capable of vocal production learning (reviewed in [1–3]). Vocal production learning requires both excellent control over the sound production apparatus and a neural interface that coordinates precise adjustments in signal production according to the auditory input received. Two general types of vocal production learning exist, namely social modification and learned acquisition (*sensu* [3]). Social modification refers to gradual changes of already existing signals, whereas learned acquisition denotes the acquirement of new signals. Both learning types rely on vocal influences from conspecifics; however, each type

may be subjected to different selective pressures and require different behavioral and neural mechanisms.

Bats are a promising taxon to study vocal production learning because their highly flexible echolocation behavior requires remarkable control during signal production and rapid, precise auditory perception when interpreting the returning echoes (reviewed in e.g. [4–7]). Moreover, many bat species are both very gregarious and long-lived [8,9], providing ample opportunities to learn from conspecifics [10,11]. Despite these widespread prerequisites, current evidence for vocal production learning in bats remains scarce. This discrepancy is most likely caused by the difficulty of studying these nocturnal, highly mobile animals. The following section provides a short overview of current knowledge on vocal production learning in bats. Afterwards, I discuss proximate and ultimate mechanisms and highlight promising avenues of future research.

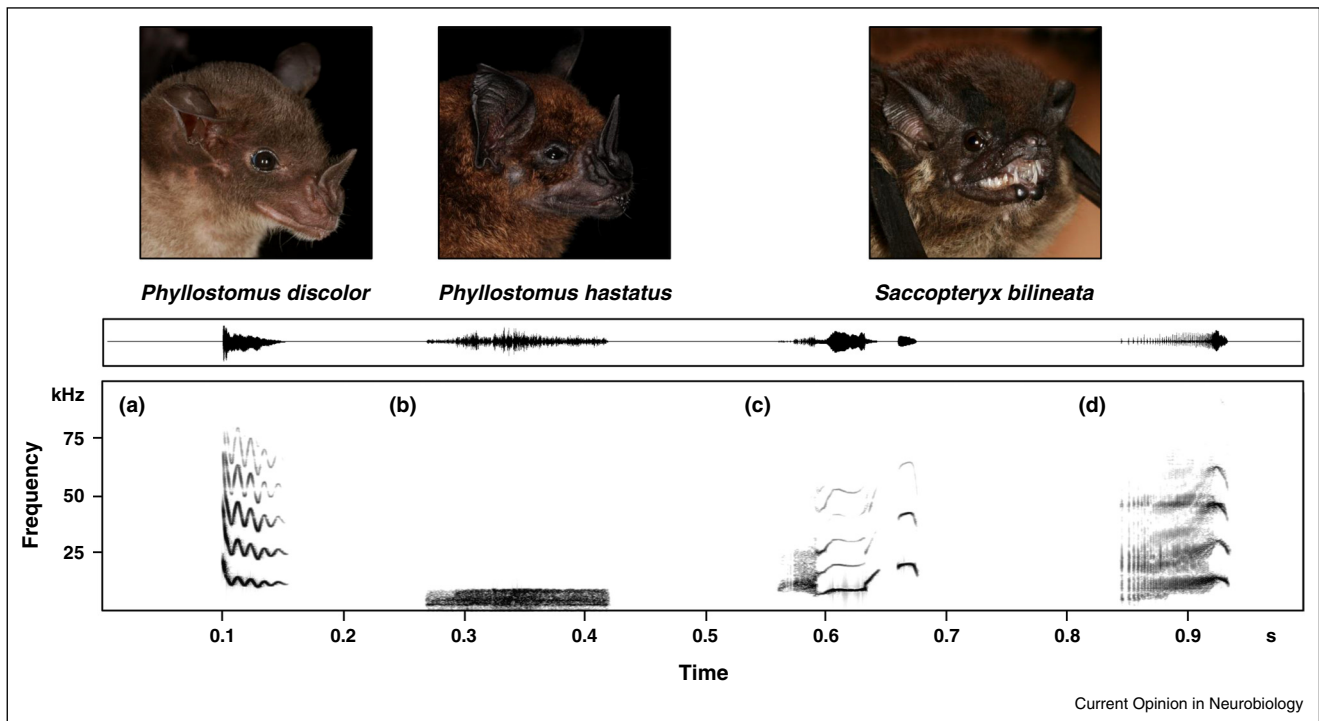
### Case studies

To date, three bat species from two families are known to be capable of vocal production learning. However, it is likely that more vocal learning bat species exist, because only a fraction of the speciose taxon has been investigated so far. Vocal production learning can shape social vocalizations of both sexes [12<sup>••</sup>,13<sup>••</sup>,14<sup>••</sup>,15<sup>••</sup>], while evidence for its influence on echolocation calls is feasible but less certain (see [16<sup>•</sup>,17]). Learned bat vocalizations may be shaped by natural selection pressures [12<sup>••</sup>,13<sup>••</sup>], sexual selection pressures [14<sup>••</sup>] or both [15<sup>••</sup>].

### Pale spear-nosed bats, *Phyllostomus discolor* (Phyllostomidae)

Both observational and experimental studies on captive pale spear-nosed bats, a tropical New World species, demonstrate convincingly that pups progressively adapt their isolation calls to maternal directive calls ([18<sup>•</sup>; Figure 1a) or to an invariable computer-generated directive call which was broadcast to pups that were hand-reared in isolation [12<sup>••</sup>]. Pup isolation calls and maternal directive calls are sinusoidally frequency-modulated signals which are produced antiphonally during mother-pup reunions [18<sup>•</sup>]. An individual signature is encoded in the frequency modulation pattern of maternal directive calls [18<sup>•</sup>] and several psychoacoustic studies indicate that the auditory system of *Phyllostomus discolor* is well adapted to resolve the respective differences in frequency modulation (reviewed in [19]). The basic structure of isolation calls is innate, as they are produced shortly after birth [18<sup>•</sup>]. Thus, the observed gradual changes are caused by social modification, namely maternal influences during

Figure 1



Examples of social vocalizations from three different bat species illustrating the structural diversity of learned vocalization types. In each species, the documented learning processes acted upon the respiratory and phonatory systems of the vocal production apparatus. The spectrogram depicts frequency as a function of time and was generated using a 1024-point fast Fourier transform, a frame size of 100% and a Hamming window with 93.75% overlap (files with 300-kHz sampling frequency and 16-bit depth). **(a)** Pup isolation call of *Phyllostomus discolor* (courtesy of K.-H. Esser). **(b)** Screech call of adult female *Phyllostomus hastatus* (courtesy of K. Bohn). **(c)** Pup isolation call excerpt of *Saccopteryx bilineata* (only one composite end syllable is shown). **(d)** Territorial song excerpt of adult male *Saccopteryx bilineata* (only one composite buzz syllable is shown). Photos courtesy of M. Tschapka (*P. discolor* and *P. hastatus*) and S. Yanoviak (*S. bilineata*).

antiphonal calling bouts. However, ontogenetic maturation effects certainly influence pups' isolation call adaptation as well. Maternal directive calls from captive groups with different geographic origin show distinct 'dialectal' acoustic differences [20] but the respective contribution of genetic differences and learning processes is not yet resolved. Thus, the indication for learned dialects remains tentative.

### Greater spear-nosed bats, *Phyllostomus hastatus* (Phyllostomidae)

An experimental study on captive greater spear-nosed bats, another tropical New World species, provided unequivocal evidence that a vocalization type facilitating group foraging encodes a group signature that is maintained by vocal production learning [13<sup>\*\*</sup>]. *Phyllostomus hastatus* forms stable groups of unrelated females which communicate via noisy screech calls during joint foraging bouts [21]. Screech calls of different individuals are statistically indistinguishable, whereas considerable differences exist between social groups [22], thus enabling bats to discriminate between group and non-group members [23]. When adult females join an already

existing social group, screech calls of all group members converge over time to maintain a group-specific vocal signature ([13<sup>\*\*</sup>]; Figure 1b). An experiment mimicking naturally occurring dispersal in captive groups demonstrated that screech calls are socially modified based on vocal influences of group mates [13<sup>\*\*</sup>]. Moreover, there is evidence for geographic variation in screech calls of free-living bats. However, it is unclear whether vocal production learning, genetic isolation or both contribute to the observed geographic variation in screech calls [23]. Thus, evidence for learned dialects is tentative, albeit very plausible.

### Greater sac-winged bats, *Saccopteryx bilineata* (Emballonuridae)

Several observational studies demonstrate conclusively that both social modification and learned acquisition exist in the tropical New World bat *Saccopteryx bilineata*. Pup isolation calls are innate signals encoding an individual signature that is used by mothers to discriminate between their own and alien pups [24]. These isolation calls also encode a group signature that is modified over time based on vocal influences of other pups belonging to the same

social group ([15<sup>••</sup>]; Figure 1c). Unlike isolation calls, territorial songs are not innate but must be learned during ontogeny through the imitation of adult tutor males ([14<sup>••</sup>]; Figure 1d). Territorial songs are regularly produced by adult males defending their roosting territory [25]; they encode both an individual and a group signature [26]. At two weeks of age, pups start to produce territorial song precursors that gradually develop into full adult territorial songs at 10 weeks of age [14<sup>••</sup>]. This development cannot be coherently explained by maturation effects alone since pup territorial songs converge towards the tutor's songs and not towards a species mean. Moreover, the observed convergence is not influenced by the relatedness between pups and tutors, demonstrating the crucial role of auditory input in song acquisition [14<sup>••</sup>]. Territorial song precursors are first produced during conspicuous babbling bouts [27<sup>•</sup>] in which pups utter long sequences of various syllables in a repetitive and juxtaposed fashion reminiscent of human canonical babbling or avian plastic song [28–30]. Precursors of all adult vocalization types known to date are found in babbling bouts of pups, making it highly probable that babbling plays a crucial role in the species' vocal repertoire acquisition [27<sup>•</sup>].

### Proximate mechanisms

The vocal production apparatus consists of different components, namely respiratory, phonatory and filter systems (reviewed in [31]), all of which could be influenced by learning processes. Changing frequency characteristics is considered to be more difficult than changing temporal characteristics [2–3]. In bats, there is evidence for respiratory and phonatory learning (Figure 1a–d), but no evidence for vocal tract filter learning so far. Chiropteran filter learning constitutes an interesting area of future research, since formants are observed in both noisy, low-frequency social vocalizations and broadband echolocation calls. Formant-related features that encode individual signatures enable bats to discriminate between conspecifics based on echolocation calls [32<sup>•</sup>], indicating that bats are capable of processing formant information.

Social modification can occur at any developmental stage but learned acquisition is often age-dependent (reviewed in [1,3,29]) and occurs more frequently during ontogeny than during adulthood. In bats, there is evidence for social modification in both juveniles [12<sup>••</sup>,15<sup>••</sup>] and adults [13<sup>••</sup>] and for learned acquisition in juveniles [14<sup>••</sup>]. To date, it is unclear whether bats are capable of learning completely new acoustic signals as adults (comparable to avian open-ended learners, e.g. starlings; [33]).

Virtually nothing is known about the precise neural substrates governing vocal production learning in bats, particularly the mechanisms of dynamic sensory feedback and sensorimotor integration crucial for vocal production learning, and very little information is available on the

behavioral mechanisms involved. As in songbirds (reviewed in [29]), bats may have to create or reinforce an acoustic template and match their vocal output accordingly but how this is achieved in detail is unknown. While adult *P. hastatus* need considerable time to modify a given vocalization type (150 days; [13<sup>••</sup>]), juvenile *P. discolor* and *S. bilineata* are notably faster (50 days; [12<sup>••</sup>]; 70 days; [15<sup>••</sup>]). Young *S. bilineata* are even capable of learning a new vocalization type in this time span [14<sup>••</sup>] and show an extraordinary vocal 'babbling' behavior while doing so: pups produce long sequences with a repetitive and juxtaposed syllable order [27<sup>•</sup>] that strongly resemble human canonical babbling and/or avian plastic song [28–30]. Prior to weaning, pups of both sexes produce the complete adult repertoire in their babbling bouts [27<sup>•</sup>], suggesting that babbling facilitates vocal production learning and the species' repertoire acquisition through some type of synaptic pruning process.

The transcription factor FoxP2, a gene relevant for vocal learning in humans and birds [34–36], shows comparatively high levels of sequence diversity in echolocating bats [37]. This accelerated evolution of FoxP2 in bats is intriguing, but the role of diverse FoxP2 sequences in Chiropteran vocal learning is currently unknown. Correspondingly, there is no evidence of specific FoxP2 sequence variations associated with vocal learning abilities in birds or mammals [38–40]. Nevertheless, the emerging potential for molecular manipulation of FoxP2 in bats [41] opens exciting avenues for future research aiming to understand the precise role of FoxP2 in Chiropteran vocal learning.

### Ultimate mechanisms

Assuming that it is beneficial for the signaler to be recognized, vocal production learning is adaptive when signal similarity is essential for signal function and cannot be encoded genetically, e.g. when signals indicate group membership among unrelated individuals (as in the bat *P. hastatus*; [13<sup>••</sup>]), or when signal similarity enhances signal function in addition to a genetic encoding, e.g. when pup isolation calls converge towards their mothers' calls (as in the bat *P. discolor*; [12<sup>••</sup>]). The same logic may apply to signals whose function is enhanced by the degree of *dissimilarity* between group members, partners or territorial neighbors, etc., whether they are related or not. In bats, signals shaped by vocal learning mechanisms are used to recognize individuals [12<sup>••</sup>,14<sup>••</sup>,15<sup>••</sup>], group members [13<sup>••</sup>,14<sup>••</sup>] and maybe even populations (i.e. tentative evidence for dialects; see [20,23]).

In several avian and mammalian taxa, social complexity is correlated with vocal complexity [42–45] and this complexity may require advanced learning capacities. When the vocal repertoire of a species is large or when complex signals are sexually selected and thus advantageous, vocal production learning may be adaptive. This argument

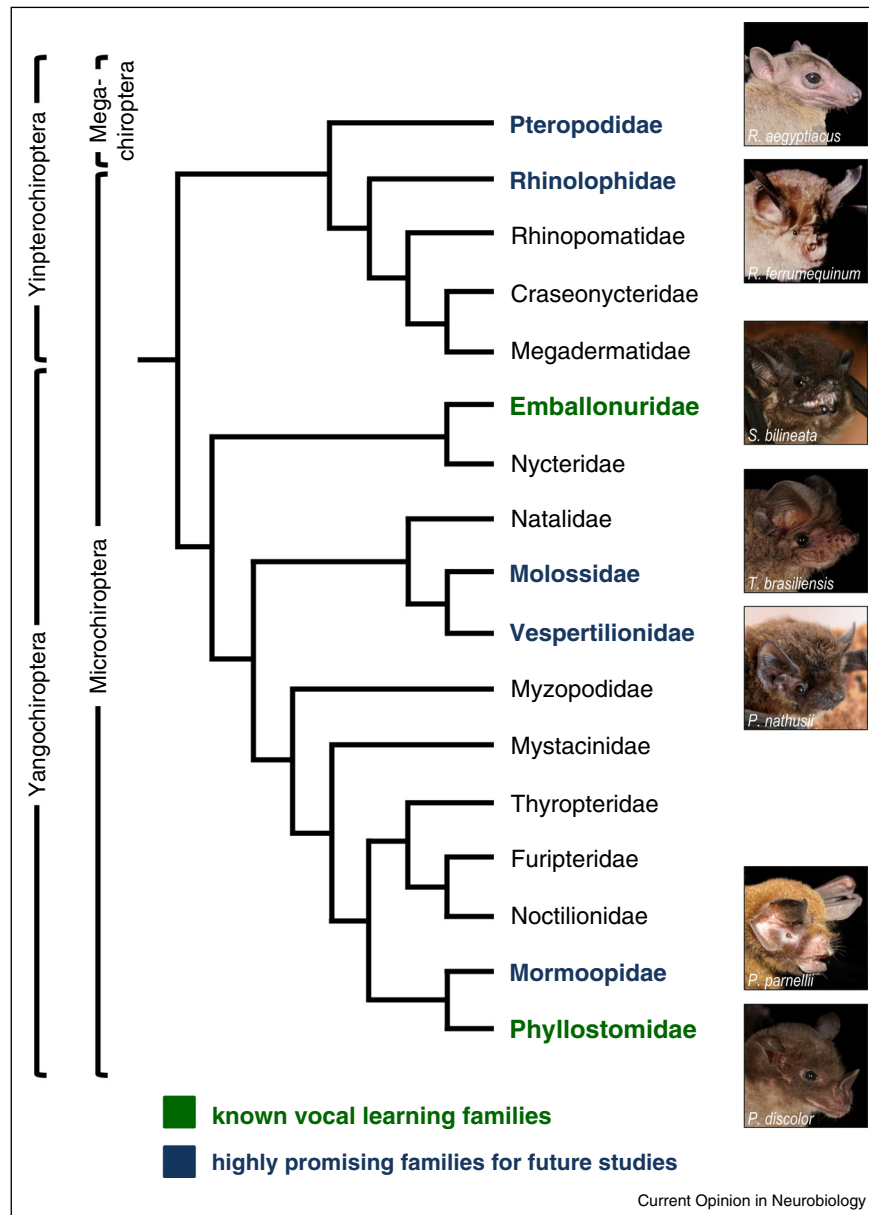
applies to the bat *S. bilineata*, a species with a comparatively large vocal repertoire [25] and learned territorial songs [14\*\*] that are used in aggressive male-male interactions.

## Conclusions

Bats are highly promising candidates for in-depth studies on mammalian vocal production learning. The speciose nature of this taxon (more than 1100 extant species; [46])

allows for comparative studies on selective pressures shaping the occurrence of vocal production learning while controlling for phylogenetic effects. In addition to the two families already known to contain vocal learning species (Phyllostomidae, Emballonuridae), four other families are of special interest for future studies, namely Rhinolophidae, Molossidae, Vespertilionidae, and Mormoopidae (Figure 2). This is suggested by the fact that certain

Figure 2



Molecular phylogenetic tree depicting the inferred evolutionary relationships of chiropteran taxa (adapted from Teeling *et al.* [46]. Reprinted with permission from AAAS and modified with permission from E.C. Teeling). For clarity, the proposed suborders from two controversial phylogenetic hypotheses are plotted, namely Yinpterochiroptera and Yangochiroptera (supported by molecular data) and Megachiroptera and Microchiroptera (supported by morphological data). Known vocal learning families (Emballonuridae, Phyllostomidae) and highly promising families for future studies on vocal production learning of social vocalizations (Pteropodidae, Rhinolophidae, Molossidae, Vespertilionidae, Mormoopidae) are highlighted. Photos courtesy of A.V. Vogeler (*R. aegyptiacus*), H. Schneider (*R. ferrumequinum*), S. Yanoviak (*S. bilineata*), P. Wagneur (*P. nathusii*), M. Knörnschild (*P. parnellii*) and M. Tschapka (*T. brasiliensis*, *P. discolor* and *P. hastatus*).



members from each family have structurally complex vocalization types and sufficient opportunities to learn from conspecifics (Molossidae: e.g. *Tadarida brasiliensis* [47,48]; Vespertilionidae: e.g. *Pipistrellus nathusii* [49,50]; Mormoopidae: e.g. *Pteronotus parnellii* [51]; Rhinolophidae: e.g. *Rhinolophus ferrumequinum* [52]). Pteropodidae, the flying foxes of the Old World, may also be suitable to study vocal production learning since they are highly social and vocally active (e.g. [53]). The genus *Rousettus*, with its basic capacity for echolocation [54], would be particularly auspicious.

Several bat species, including the vocal learning *P. discolor* [55], are currently used as model organisms in neurophysiological studies on auditory production and perception (reviewed in [56]), and are promising species to explore the mechanistic basis for vocal learning. It is crucial that future research efforts on bat vocal production learning include more established neurophysiological model organisms, such as *T. brasiliensis*, *Eptesicus fuscus*, *P. parnellii*, *R. ferrumequinum* or *Carollia perspicillata* [57–61], all of which belong to the bat families mentioned above. Ultimately, these efforts could establish bats as a mammalian model system for comparative neurophysiological studies aiming to improve our understanding of neural mechanisms governing speech processing and acquisition in humans.

## Conflict of interest

Nothing declared.

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