American Psychological Association
Behavioral Neuroscience

0735-7044/19/$12.00
2019, Vol. 133, No. 3, 305–319
http://dx.doi.org/10.1037/bne0000308

Auditory Communication Processing in Bats: What We Know and Where to Go

Angeles Salles, Kirsten M. Bohn, and Cynthia F. Moss
Johns Hopkins University

Bats are the second largest mammalian order, with over 1,300 species. These animals show diverse behaviors, diets, and habitats. Most bats produce ultrasonic vocalizations and perceive their environment by processing information carried by returning echoes of their calls. Echolocation is achieved through a sophisticated audio-vocal system that allows bats to emit and detect frequencies that can range from ten to hundreds of kilohertz. In addition, most bat species are gregarious, and produce social communication calls that vary in complexity, form, and function across species. In this article, we (a) highlight the value of bats as model species for research on social communication, (b) review behavioral and neurophysiological studies of bat acoustic communication signal production and processing, and (c) discuss important directions for future research in this field. We propose that comparative studies of bat acoustic communication can provide new insights into sound processing and vocal learning across the animal kingdom.

Keywords: bats, Chiroptera, communication, auditory processing

Understanding how the brain processes communication sounds is a key topic in neuroscience. Researchers have used a variety of animal models to tackle this problem, such as mice, birds, and primates, yet our understanding of vocal communication processing, particularly when it comes to complex, functionally characterized signals, remains rudimentary. Although extensive research has been directed at the production and processing of echolocation signals in bats, comparably fewer studies have investigated social communication signals. Here, we discuss how and why research on bat models can add fundamental insight to a broader understanding of vocal communication in the animal kingdom. Past literature reviews have considered a variety of aspects of bat social communication, such as call diversity, evolution, and ecology (Altringham, McOwat, & Hammond, 2011; Chaverri, Ancillotto, & Russo, 2018; Gillam & Fenton, 2016). Our aim here is to focus on what is known about the production and processing of vocal communication signals and to discuss future steps and challenges to unraveling acoustic communication mechanisms in bats. In particular, we aim to (a) discuss the relevance of bats as model species to broaden our understanding of acoustic communication in mammals, (b) review what is currently known about neural activity evoked by social calls at different levels of the bat auditory pathway, and (c) discuss new questions and techniques that we believe will be fundamental to advancing knowledge of the mechanisms of acoustic communication in bats and other animals.

What We Know

Bats Are Social Animals With Diverse Adaptations

Bats, mammals belonging to the order Chiroptera, are a group of over 1,300 species with the common characteristic that their forelimbs are adapted as wings to support powered flight (Neuweiler & Covey, 2006). Chiroptera is the second largest order of mammals (the largest order being rodents), comprising about 20% of all known mammalian species (Tsang, Cirranello, Bates, & Simmons, 2016). The majority of bat species use echolocation to orient and navigate in the environment, even in complete darkness. Bats are adapted to diverse niches, showing tremendous variety in diet and habitat complexity, which, in turn, coevolves with neural structures that support auditory processing and spatial memory (Safi & Dechmann, 2005). Bats stand out among mammals not only as flying echolocators but also for their gregariousness. By far, the majority of bats live in social groups (Bradbury & Vehrencamp, 1977; Kerth, 2008; McCracken & Wilkinson, 2000), from small tight-knit clusters (e.g., *Phyllostomus hastatus* [McCracken & Bradbury, 1981]) to colonies comprising millions of individuals (e.g., *Tadarida brasiliensis* [Betke et al., 2008; Hristov, Betke, Theriault, Bagchi, & Kunz, 2010; McFarlane, Rentergem, Ruina, Lundberg, & Christenson, 2015; McCracken, 2003]). Their social systems vary greatly from fission–fusion societies to highly stable

This article was published Online First May 2, 2019.
Angeles Salles, Kirsten M. Bohn, and Cynthia F. Moss, Department of Psychological and Brain Sciences, Johns Hopkins University.
We thank the following funding agencies for the resources that allowed us to prepare this review: Human Frontiers Science Program Fellowship awarded to Angeles Salles (LT000220/2018), Brain Initiative (NSF-FO 1734744, Air Force Office of Scientific Research (FA9550-14–1-0398NIFTI), and Office of Naval Research (N00014-17–1-2736). Cynthia F. Moss acknowledges the support of a Sabbatical Award from the James McKeen Cattell Fund.
Correspondence concerning this article should be addressed to Angeles Salles, Department of Psychological and Brain Sciences, Johns Hopkins University, 3400 North Charles Street, Ames Hall, Suite 232, Baltimore, MD 21218. E-mail: angiesalles@gmail.com

social groups that remain cohesive over many years (e.g., Chaverri, 2010; McCracken & Bradbury, 1981; Wilkinson, 1985; see also Wilkinson et al., 2019). Given their sociality, tendency to rely less on vision than hearing, and sophisticated audio-vocal system for echolocation, it is not surprising that bats use a broad array of vocal communication signals (Altringham et al., 2011; Chaverri et al., 2018; Dechmann & Safi, 2005; Gillam & Fenton, 2016). Some species demonstrate vocal learning (Boughman, 1998; Knörnschild, 2014; Knörnschild, Nagy, Metz, Mayer, & von Helversen, 2010; Prat, Azoulay, Dor, & Yovel, 2017; Prat, Taub, & Yovel, 2015, 2016) and highly complex vocalizations (Smotherman, Knörnschild, Smarsh, & Bohn, 2016); however, our understanding of the perception and processing of these signals is yet in its infancy.

Bats Have Specialized Audio-Vocal Systems

Laryngeal echolocators have specialized audio-vocal systems that allow them to adapt echolocation calls in response to acoustic information carried by echoes, which they use to localize objects in the dark with very high accuracy (Busnel, 1980; Fenton & Ratcliffe, 2017; Griffin, 1958; Nachtigall & Moore, 1988; Thomas, Vater, & Moss, 2003); this sophisticated audio-vocal system also supports the production of a wide array of communication calls. Specializations for echolocation include large middle-ear muscles that are activated in coordination with laryngeal signal production to attenuate direct reception of emitted echolocation vocalizations and modulate hearing sensitivity to weak returning echoes (Suga & Jen, 1975). The larynx of echolocating bats has superfast muscles that permit the production of over 100 calls per second (Elemans, Mead, Jakobsen, & Ratcliffe, 2011). This kind of superfast muscle in vertebrates has thus far only been associated with vocal communication, for example, in the songbird syrinx (Elemans, Mead, Rome, & Goller, 2008), though in bats it may be key for echolocation (Elemans et al., 2011).

Superfast laryngeal muscles in bats seem to be necessary for both echolocation and social communication, enabling the production of a wide repertoire of sounds. Laryngeal echolocators can produce sounds that range between 9 and 212 kHz, depending on the species, with lower sound frequencies commonly used for social communication (Bohn, Moss, & Wilkinson, 2006; Ratcliffe, Elemans, Jakobsen, & Surlykke, 2013). Bats use audio-vocal feedback to modulate the frequency content of emitted signals (J. Luo & Moss, 2017; Schuller & Moss, 2003). For example, bats that echolocate using constant frequency (CF) calls adjust the frequency of their CF signals as they fly, which serves to stabilize Doppler-shifted echoes to return at the sound frequency to which they are maximally sensitive (Neuweiler, Bruns, & Schuller, 1980; Schnitzler, 1968). The CF bat's Doppler-shift compensation (DSC) reflects tremendous flexibility in vocal production, which also extends to social calls.

The neural circuitry for the vocal control of echolocation and communication sounds in bats appears in some species to operate separately at midbrain and cortical levels, but all descending vocal-motor signals project through a final common pathway to the nucleus ambiguus and, consequently, to the larynx (Fenzl & Schuller, 2005). Thus, though the neural circuits that shape echolocation and communication signal designs may differ, the same motor output system is implicated in the production of both types of calls. In this article, we propose that the same organization principle may hold for echolocation and communication call processing. That is, we hypothesize that early stages of auditory processing of echolocation and social communication signals are largely shared, but at higher stages of the auditory pathway, the neural circuitry for processing functionally distinct vocalizations diverges.

Bat Communication Calls Serve Diverse Functions

As noted in the previous section, bats use their sophisticated audio-vocal systems to localize objects in their surroundings (Griffin, 1958). The bat's auditory scene may not only include its own sonar vocalizations and echoes but also the echolocation sounds emitted by conspecifics and their echo returns. Some reports also suggest that bats use conspecific echolocation vocalizations for social communication (*Rhinolophus spp*. [Kobayasi, Hiryu, Shimozawa, & Riquimaroux, 2012]; *Noctilio albiventris* [Dechmann, Wikelski, van Noordwijk, Voigt, & Voigt-Heucke, 2013]; *Eptesicus fuscus* [Grilliot, Burnett, & Mendonça, 2009]; *Saccopteryx bilineata* [Knörnschild, Feifel, & Kalko, 2013]; *Myotis myotis* [Yovel, Melcon, Franz, Denzinger, & Schnitzler, 2009]; *Myotis capaccinii* [Dorado-Correa, Goerlitz, & Siemers, 2013]; see Bohn & Gillam, 2018, for a review), as these signals can convey information about foraging activity to conspecifics. For many social functions, bats produce specialized vocalizations that relay entirely different types of information, often with acoustic properties distinct from echolocation signals. The chiropteran auditory and nervous system is tasked with processing these signals, extracting relevant information, and coordinating appropriate behavioral responses.

The majority, if not all, of bat species (including nonecholocators) produce a common set of social communication calls: distress, agonistic, and infant isolation vocalizations (see Table 1). Distress calls are common across the animal kingdom and have also been studied in a number of bat species. They are predominantly low-frequency, noisy, "scream-like" calls that are often produced in bouts (Brown, 1976; Carter & Leffer, 2015; Prat et al., 2016; Russ, Jones, Mackie, & Racey, 2004). Agonistic calls are also widespread in bats and commonly take the form of low-frequency, noisy "squawks" (Bohn, Schmidt-French, Ma, & Pollak, 2008; Fernandez, Fasel, Knörnschild, & Richner, 2014; Prat et al., 2016; Schwartz et al., 2007; Walter & Schnitzler, 2017) or buzz-like calls (i.e., a rapid set of downward frequency modulated sweeps; Bohn et al., 2008; Brown, 1976; Pfalzer & Kusch, 2003; Schwartz et al., 2007). For both of these call types, the main information transmitted is the signaler's state (stress level for the former and aggression level for the latter). Recent research has begun to unravel how the receiver encodes and processes information carried by these signals. For example, distress calls provide information about the stress levels of callers and even induce dopaminergic responses in the amygdala of receivers (Mariappan, Bogdanowicz, Marimuthu, & Rajan, 2013). Agonistic calls vary with the level of aggressive intensity of the interaction (Bastian & Schmidt, 2008; Gadziola, Grimsley, Shanbhag, & Wenstrup, 2012; Walter & Schnitzler, 2017) and can potentially encode fitness of the caller (B. Luo et al., 2017).

Infant isolation calls are also widespread in bats, having been described in the majority of families (e.g., Brown, 1976; Brown,

Table 1
General Types of Calls Produced by Bats, Including the Information the Receiver Should Extract From the Signals, Whether Calls Are Produced in Complex Sequences, the Potential Calls Have for Being Learned as Opposed to Innate, and the Acoustic Structure

Call	Information	Sequences	Potential for learning	Form
Distress	Caller state Location	No	Low	Noisy Low frequency
Agonistic	Caller state Competitive ability	No	Low	Noisy Low frequency Buzzes
Isolation	Caller identity Caller state	No	Low	Tonal Frequency modulated
Contact	Caller identity	No	Low–High	Tonal Frequency modulated
Territorial	Caller identity Competitive ability	Short	Low–Medium	Frequency modulated Often downward sweeps
Song	Caller identity Male quality Competitive ability	Long Can be hierarchical	Medium–High	Often sequences Highly varied may include both signature syllables and buzz-like phrases

Brown, & Grinnell, 1983; Matsumura, 1979; Nelson, 1964). Isolation calls are usually tonal, frequency-modulated signals that are produced by infants and may contain signature information used by mothers to identify and care for young (Brown, 1976; Gelfand & McCracken, 1986; Porter, 1979). Studies have shown that mothers can discriminate among isolation call signatures (Bohn, Wilkinson, & Moss, 2007) and/or preferentially respond to their own infant's calls (Balcombe, 1990; Knörnschild et al., 2013; Knörnschild & von Helversen, 2008; Thomson, Fenton, & Barclay, 1985). Remarkably, females appear to be able to rapidly track and update their template of pup calls, as these calls rapidly change during ontogeny (De Fanis & Jones, 1995; Engler, Rose, & Knörnschild, 2017; Knörnschild & von Helversen, 2008).

Beyond these common social call types, bat species vary immensely in the repertoire, complexity, and forms of other communication signals. Here, we discuss three broad categories: social cohesion signals, territorial calls, and mating songs (see Table 1). Social cohesion calls are commonly in the form of contact calls to identify and recruit group mates and or/family members. One feature common to these calls across species is that, like isolation calls, they are individual or group signature signals that are most often tonal and frequency modulated (except *P. hastatus*; see below). For example, a number of species produce maternal directives that are used as a counterpart to isolation calls (e.g., *T. brasiliensis* [Balcombe & McCracken, 1992]; *Phyllostomus discolor* [Esser & Schmidt, 1989]; Figure 1). Social calls are also used by group mates to locate roosting sites in a number of species (*Dermanura watsoni*, *Ectophylla alba* [Gillam & Fenton, 2016]; *Thyroptera tricolor* [Gillam & Chaverri, 2012]; *Antrozous pallidus* [Arnold & Wilkinson, 2011]) and to coordinate foraging (*P. hastatus* [Boughman, 1998; Boughman & Wilkinson, 1998]). In cases in which vocal signatures are group specific and groups are comprised of unrelated individuals, vocal learning may play a role in call acquisition. This is the case in *P. hastatus* (Boughman, 1998) but remains to be determined in other species.

In a number of bat species, individuals use calls to delineate territories and/or claim food. For example, *E. fuscus* produces frequency modulated bouts (FMBs) that are individually distinctive, emitted only by male bats in competitive foraging contexts, and are thought to serve a food claiming function (Wright, Chiu, Xian, Wilkinson, & Moss, 2014; Figure 1). A number of different *Pipistrellus* species emit territorial calls composed of bouts of downward frequency modulated syllables (*P. pipistrellus* [Barlow & Jones, 1997]; *P. pygmaeus* [Jones, 1997]; *P. kuhlii* [Russo & Jones, 1999]; *P. maderensis* [Russo et al., 2009]; *P. nathusii* [Jahelková & Horáček, 2011]). Playbacks have demonstrated that these calls repel conspecifics at foraging sites (Barlow & Jones, 1997) and are also used at breeding territories by some species (Jones, 1997; Russo & Jones, 1999; Russo et al., 2009). In one congener, *P. nathusii*, the relatively simple "territorial call" is combined with three other phrases to produce complex songs during the mating season (see below; Jahelková & Horáček, 2011; Figure 1).

In a few bat species, males produce elaborate songs that serve in mate attraction (see Smotherman et al., 2016, for a review). Notably, these vocalizations can be composed of hundreds of syllables, have multiple types of phrases, and encode diverse types of information (reviewed in Gillam & Fenton, 2016; Smotherman et al., 2016). For example, *P. nathusii* songs are composed of at least four types of phrases, with some phrases being highly similar to the territorial signals of congeners, whereas other phrases clearly contain signature-type signals that are similar to infant-isolation-calls/maternal-directives (longer, with greater variation in frequency-modulated syllables; Jahelková, Horáček, & Bartonička, 2008).

One of the most well-studied singing bats is *Saccopteryx bilineata* (Behr, Knörnschild, & von Helversen, 2009; Behr & von Helversen, 2004; Behr et al., 2006; Bradbury & Vehrencamp, 1977; Davidson & Wilkinson, 2002, 2004; Voigt et al., 2008). *S. bilineata* songs are comprised of over 20 types of syllables and over 60 types of composite syllables (Davidson & Wilkinson, 2002). Again, songs can contain multiple types of information. Some syllables contain geographic and individual signatures (Davidson & Wilkinson, 2002), and the fundamental frequency and length of buzzes in songs are correlated with reproductive success and presumably contain information on male quality and competitive ability (Behr & von Helversen, 2004). Notably, research suggests that vocal learning plays an important role in the development of songs in this species (Knörnschild et al., 2010; Figure 1).

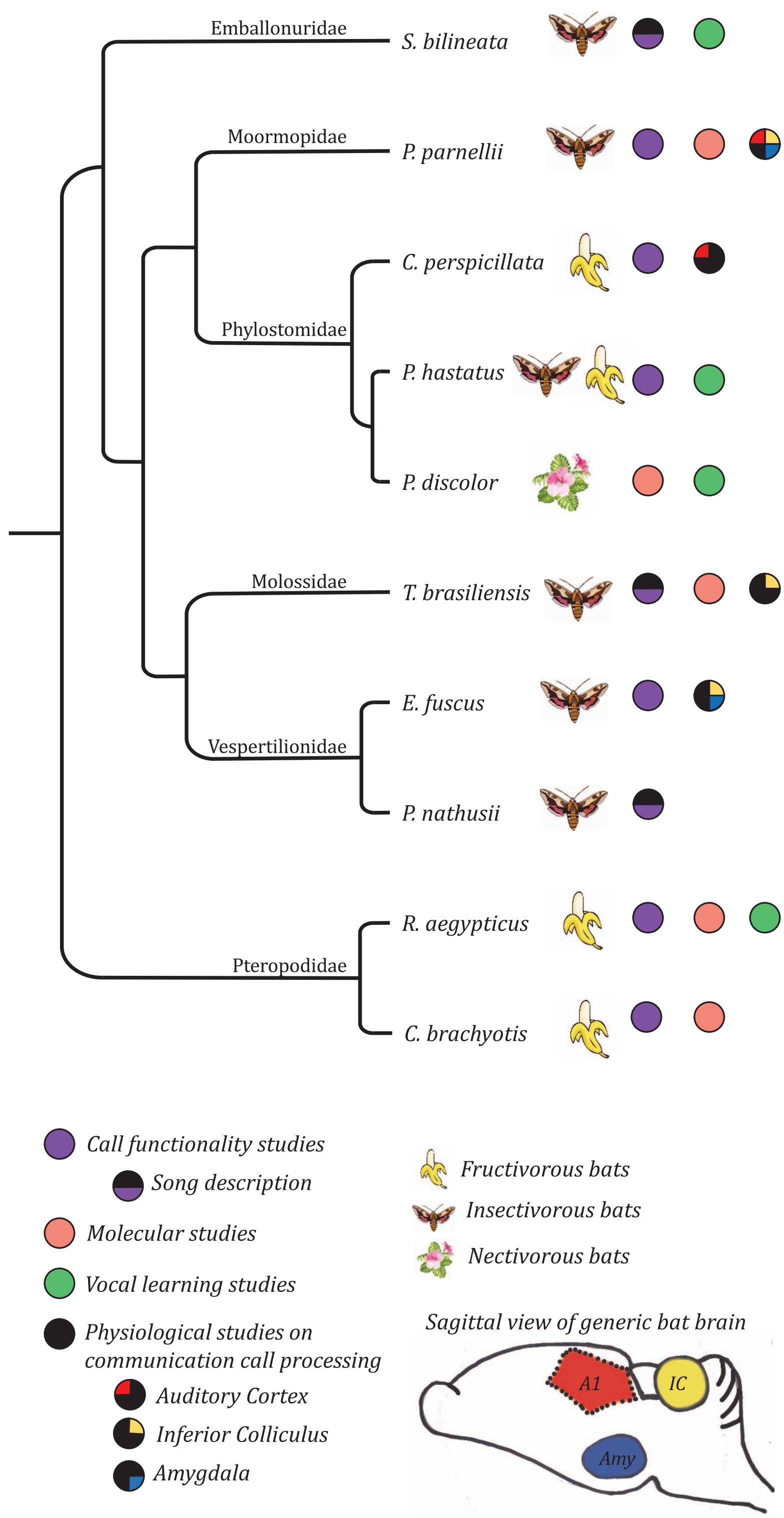

Figure 1. Bat species for which research on communication signals and/or communication signal processing has been predominantly conducted. Phylogenetic relationships shown represent those described by Simmons and Geisler (1998) and Teeling et al. (2018). The names of the represented families are shown on the respective branches of the phylogenetic tree. Type of diet for each species and studies for which each species has been used are represented following the key shown in the figure. The schematic of the generic bat brain is based on a sagittal view of the brain of *Eptesicus fuscus*, the approximate locations of the auditory cortex (A1), inferior colliculus (IC), and amygdala (Amy) are marked in red, yellow, and blue, respectively.

T. brasiliensis is another species that uses complex songs (Figure 1). All songs follow a specific hierarchical structure; they are composed of four types of syllables that are combined to form three types of phrases (Bohn, Moss, & Wilkinson, 2009; Bohn et al., 2008; Figure 2). Syllables and phrases are distinct, discrete, and easily identified across individuals. Songs contain buzz phrases that are nearly indistinguishable from echolocation buzzes (Schwartz et al., 2007; Figure 2) and Chirp A syllable features overlap with echolocation pulses (Bohn et al., 2008). Chirp phrases contain signature syllables that provide identity information; they are highly distinct across individuals but stereotyped within individuals (B syllables; compare Figure 2b, 2c, and 2d). Buzz phrases. on the other hand, likely serve a similar function as *S. bilineata*. Furthermore, similar to birds, songs can be categorized into "song types" based on the number and order of phrases. Although songs can vary from one to over 20 phrases in length, phrase order typically follows specific syntactical rules, and particular phrase combinations are preferred over others depending on social context (Bohn, Smarsh, & Smotherman, 2013). The most compelling feature of this system, however, is song flexibility. Even though song construction follows basic rules, *T. brasiliensis* dynamically varies syllable number, phrase order, and phrase repetitions across from one song rendition to the next (Bohn et al., 2009, Figure 2b and 2c). Complex songs are not ubiquitous in bats; in the three bat species for which we described songs (*P. nathusii*, *T. brasiliensis*, and *S. bilineata*), most other species within their families do not produce elaborate vocalizations with song-like characteristics (Vespertilionidae, Molossidae, and Emballonuridae, respectively; Figure 1). This supports the hypothesis that sophisticated vocalizations, like songs, have evolved independently across bat taxa (Smotherman et al., 2016), which, in turn, provides immense opportunities for comparative research into how the production and processing of complex signals evolves.

Some bat species produce a plethora of call categories beyond those discussed above. For example, at least 16 types of calls produced in specific behavioral contexts have been described in *T. brasiliensis* (Bohn et al., 2008). The acoustic range of vocal communication signals in *T. brasiliensis* is astonishing; call durations range from milliseconds to hundreds of milliseconds, frequencies range from 5 kHz to 80 kHz, forms vary from noisy

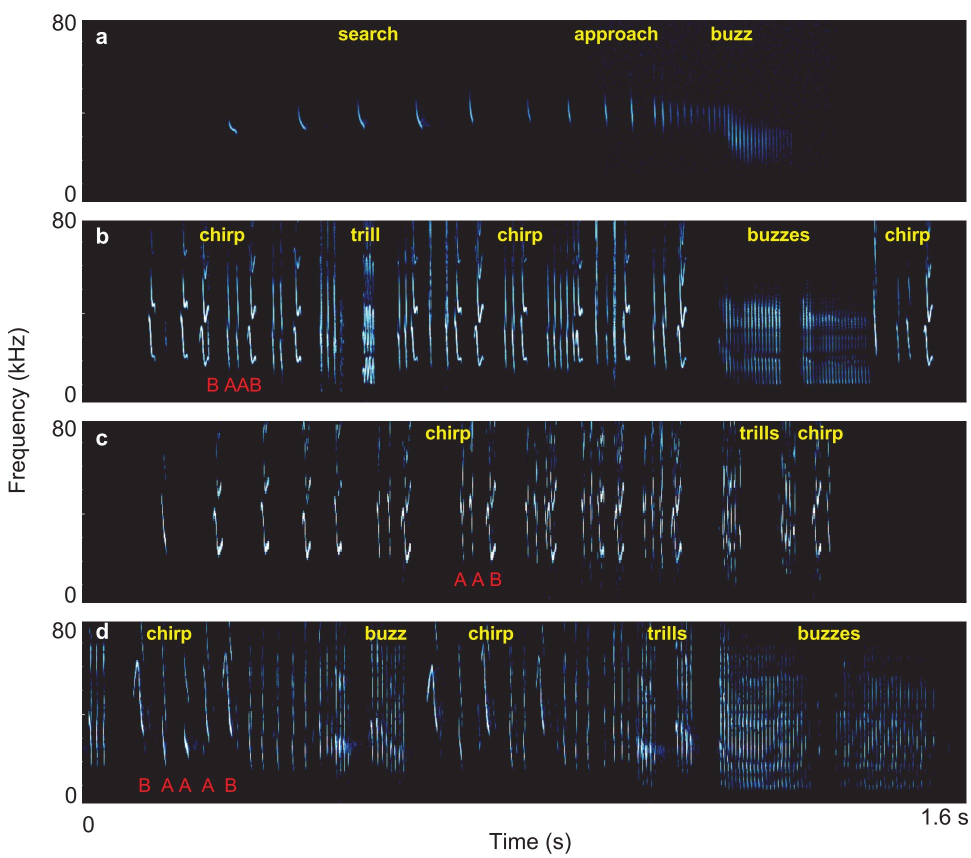

Figure 2. Spectrograms of echolocation and songs in *Tadarida brasiliensis*. (a) Spectrograms (in kHz) of echolocation in the field, and (b-d) songs produced by male bats, *T. brasiliensis* in roost sites. Chirp, trill, and buzz are the three phrase types, and "A" and "B" refer to the two types of syllables that are used in chirp phrases; (b) and (c) are the same bat producing different song types ("chirp-trill-chirp-buzz-chirp" and "chirp-trill-chirp," respectively), illustrating the flexibility of song production from one rendition to the next; (d) is a different male producing a chirp-buzz song type. Note the stereotypy within bats, but divergence between bats, for the "signature" B syllables and the echolocation like properties of A syllables and buzzes produced in purely social contexts.

low-frequency signals to tonal CF to complex spectrotemporal patterns, and some social calls are acoustically indistinguishable (by human scientists) from echolocation pulses (Bohn et al., 2008). Other species show highly diverse vocal repertoires but the social function of these signals remains poorly understood (e.g., *Pteronotus parnellii* [Kanwal, Matsumura, Ohlemiller, & Suga, 1994; but see Clement & Kanwal, 2012]; *Rhinolophus ferrumequinum* [J. Ma, Kobayasi, Zhang, & Metzner, 2006]; *Hipposideros armiger* [Lin et al., 2015]). Indeed, in many species for which call processing has been studied (see below), inter- and intraindividual variation of calls has not been detailed. This is a key factor in determining whether acoustic variants are signatures for the same call (e.g., Type B syllables in *T. brasiliensis*; Figure 2) or entirely different call types.

Although bats are diverse in their use of communication calls, they all serve to transmit social information to elicit appropriate behavioral responses from conspecific receivers. Even in cases in which echolocation-like calls are used in social communication (Figure 2), the acoustic signals carry functionally different information in social and echolocation contexts. This raises the following questions: How does the Chiropteran system process a diverse repertoire of species-specific acoustic signals? To what extent are neural circuits shared for processing echolocation and communication calls? Finally, do bats show neural specializations for analyzing complex acoustic signals, such as songs? Below we review research that lays a foundation to begin addressing these questions.

Auditory Processing of Vocal Signals in Bats

Hearing sensitivity. In a number of bat species, the auditory system shows high sensitivity in at least two spectral bands: a low-frequency region that coincides with the peak spectral band of infant isolation calls and other social vocalizations, and a higher frequency peak that encompasses the spectral band of echolocation sounds (Bohn, Boughman, Wilkinson, & Moss, 2004; Esser & Daucher, 1996; Guppy & Coles, 1988; Wenstrup, 1984). A comparative phylogenetic analysis revealed correlated evolution not only between low-frequency peaks in hearing sensitivity and communication calls but also between low-frequency (communication associated) and high-frequency (echolocation associated) peaks in hearing sensitivity (Bohn et al., 2006). Thus, although social communication and echolocation signals often fall into different spectral regions of the bat audible range, they may have evolved together.

Central nervous system processing of acoustic signals.

Inferior colliculus (IC). The IC is a midbrain structure that serves as a hub for auditory information processing. It receives ascending input from brain stem nuclei (Casseday, Fremouw, & Covey, 2002; Ito, Furuyama, Hase, Kobayasi, & Hiryu, 2018; Ito, Furuyama, Hase, Kobayasi, Hiryu, & Riquimaroux, 2018; Pollak, Wenstrup, & Fuzessey, 1986) as well as descending input from the auditory cortex (E. Gao & Suga, 1998; X. Ma & Suga, 2003; Zhang & Suga, 2005). The IC has been studied extensively with respect to echolocation signal processing in several different bat species. IC neurons are selective to sound frequency and are arranged tonotopically, with neurons tuned to lower frequencies located in dorsal regions and neurons tuned to higher frequencies in ventral regions (*E. fuscus* [Covey, 2005; Poon, Sun, Kamada, & Jen, 1990]; *P. parnellii* [Zook & Casseday, 1985]; *Plecotus auritus* [Coles, Guppy, Anderson, & Schlegel, 1989]; *Carollia perspicillata* [Sterbing, Schmidt, & Rübsamen, 1994]; Figure 1). IC neurons also show differential responses to FM calls that differ in sweep rate and directionality of the sweep; for example, some neurons respond to fast downward sweeps but not to slow or upward sweeps of the same duration and bandwidth (*E. fuscus* [Morrison, Valdizón-Rodríguez, Goldreich, & Faure, 2018]). It is postulated that target range is encoded by delay-tuned neurons that respond selectively to pairs of sounds separated over restricted time intervals between pulses and echoes (*P. parnellii*[Wenstrup & Portfors, 2011]; *C. perspicillata* [Beetz, Kordes, García-Rosales, Kössl, & Hechavarría, 2017]; *E. fuscus* [Macías, Luo, & Moss, 2018]), which could potentially facilitate routing calls through echolocation pathways. It has also been reported in a number of bat species that IC neurons respond selectively to the duration of calls or echoes (*E. fuscus* [Ehrlich, Casseday, & Covey, 1997]; *P. parnellii* [Macías, Mora, Hechavarría, & Kössl, 2011]; *Rhinolophus pusillus* [F. Luo, Metzner, Wu, Zhang, & Chen, 2008]; *A. pallidus* [Fuzessery & Hall, 1999]).

Differences in neural response selectivity outlined above could potentially play a role in the discrimination and processing of communication calls in separate populations of IC neurons. Communication calls are commonly produced at lower frequencies than echolocation sounds, and so frequency-tuned neurons could lay the foundation for separately processing functionally distinct acoustic signals in the IC. Some communication calls may overlap in spectral content but differ in fine spectrotemporal structure from echolocation sounds; thus, differential responses of IC neurons to sweep shape may play a role in the discrimination of these types of calls (Morrison et al., 2018; Salles, Macias, Sundar, Elhilali, & Moss, 2018). Furthermore, communication calls tend to be longer in duration than most echolocation pulses; thus, duration tuned neurons may also contribute to the discrimination of social and biosonar calls.

In a number of bat species, single neurons in the IC show selectivity to the features of communication calls (*T. brasiliensis* [Andoni & Pollak, 2011]; *P. parnellii* [Portfors, 2004]; *E. fuscus* [Salles et al., 2018; Figure 1]). The most extensive research on midbrain mechanisms of communication processing has been conducted on *T. brasiliensis* (reviewed in Pollak, 2011). Selectivity of neurons in the IC to specific communication call spectrotemporal patterns appears to be driven by inhibition from projections of the lateral lemniscus (Klug et al., 2002; Pollak, Andoni, Bohn, & Gittelman, 2013). Furthermore, there is evidence that selective responses to communication calls are modulated by serotonin, most commonly by reducing the response strength but also, in some cases, by increasing spike number (Hurley & Pollak, 2005). In the IC of *P. parnellii*, neurons respond selectively to combinations of tones at specific frequencies (combination sensitivity), which is a feature of neurons implicated in echo ranging but may also contribute to response selectivity to species-specific communication calls (Holmstrom, Roberts, & Portfors, 2007; Portfors, 2004).

It is noteworthy that research findings demonstrate that selectivity to pairs of tones alone cannot account for the responses of some neurons to communication calls. For example, some IC neurons respond to specific calls and also respond to artificial combinations of pure tones that would be present in the calls. However, responses evoked by artificial combination of isolated tones are weaker than responses to natural calls (*P. parnellii* [Brimijoin & O'Neill, 2005]).

These findings led to experiments showing that responses of single neurons in the bat IC show nonlinearities. That is, one tone presented at a specific time separation from another tone could facilitate a neural response (i.e., increase the spike rate), whereas either tone presented in isolation evokes little or no response. The fact that facilitation depends on the timing of sound elements indicates that both spectral and temporal features of acoustic signals shape neural responses. This means that the IC may operate as a spectrotemporal pattern detector (Brimijoin & O'Neill, 2010). Recent studies in *E. fuscus* supports this idea by showing that single units in the IC can be selective to either communication or echolocation sounds that overlap in bandwidth and duration but differ in spectrotemporal features (i.e., changes in frequency over time within the calls; Salles et al., 2018).

Auditory cortex. Information carried by echolocation and communication signals is processed at several interconnected stages of the auditory pathway. Auditory neurons project from the IC to the thalamus to the primary auditory cortex (A1), which then projects back to the IC and other brain areas, such as the amygdala (see Pannese, Grandjean, & Frühholz, 2015, for review). We hypothesize that the acoustic information processing of echolocation and communication signals that guide context-specific action selection depends on neural interactions across all stages of the auditory pathway.

Considerable research on signal processing in the bat central nervous system has focused on A1. In one CF-FM bat species, *P. parnelli*, neurons in A1 have been directly implicated in DSC (see above; Fitzpatrick, Kanwal, Butman, & Suga, 1993). Interestingly, neurons designated as Doppler shift constant frequency (DSCF) neurons appear to also play a role in the processing of communication calls, as they respond to both CF echolocation and FM communication sounds. The strength of the responses to communication calls can be even greater than to the echolocation sounds, and is dictated by the slope, bandwidth, central frequency, and frequency modulation direction (Washington & Kanwal, 2008). Local field potential studies in the same species reveal that population dynamics carry information about call identity (Medvedev & Kanwal, 2004). Furthermore, gamma-band activity (which, in many species, has been correlated with increased attention; Drebitz, Haag, Grothe, Mandon, & Kreiter, 2018) is not only elicited by communication calls but also varies with call type and structure (Medvedev & Kanwal, 2008).

Carollia perspicillata is the only other species of bat for which responses to natural communication calls have been studied in the A1 (Figure 1). Martin, García-Rosales, Beetz, and Hechavarría (2017) reported that neurons in the A1 can only follow the pattern of a natural sequence of distress calls when the calls were presented at intervals longer than 50 ms, indicating that even in rapidly vocalizing animals, cortical neurons track calls with low temporal resolution (<20 Hz). As most studies of the bat A1 have focused on echolocation signal processing (reviewed in Kössl, Hechavarria, Voss, Schaefer, & Vater, 2015), there remain many important questions to address about the mechanisms of acoustic communication sound processing in bats.

Amygdala. The amygdala shares reciprocal connections with the IC and receives input from A1 (see Pannese et al., 2015, for review). In bats, the amygdala could therefore modulate responses in the IC to communication calls through direct projections (Marsh, Fuzessery, Grose, & Wenstrup, 2002). This nucleus, which is part of the limbic system, has been implicated in many mammalian species with affective information processing and emotional responses. In this sense, the amygdala is a key target for the study of communication call processing, as neurons in this structure may encode the emotional valence and behavioral significance of stimuli (see Namburi, Al-Hasani, Calhoon, Bruchas, & Tye, 2016, for review). The role of the amygdala in the processing of communication calls in bats has been studied in *E. fuscus* and *P. parnellii*. In *E. fuscus*, amygdala neurons show different activation patterns with changes in contextual information carried by communication calls (Gadziola et al., 2012; Figure 1). Further research on the amygdala of this species showed that neural firing rate and spike timing together facilitate discrimination of vocal sequences and corresponding behavioral contexts (appeasement or aggression; Gadziola, Shanbhag, & Wenstrup, 2016). In *P. parnellii*, amygdala neuron selectivity to communication calls has been demonstrated, with some neurons excited by at least one type of call and suppressed by other calls. Furthermore, the behavioral function of communication calls influences amygdala neuron firing; calls associated with aggression elicited higher firing rates, whereas those associated with appeasement suppressed firing rates (Naumann & Kanwal, 2011). Combined, these studies indicate that pathways between the IC and amygdala play an important role in modulating the processing of communication calls.

Neural circuits. We hypothesize that separate neural circuits process echolocation and communication vocalizations. Although neurons dedicated to processing biosonar and social signals may be colocalized in some brain structures, their connections to other regions could differ. This hypothesis arises from the observation that echolocation is an active sense, which requires the animal to produce the signals that give rise to echoes returning from objects. Thus, the motor command for call production could activate a circuit dedicated to processing echolocation signals. By contrast, listening to environmental sounds such as communication calls produced by conspecifics involves passive sensing, as the animal does not control the timing or features of acoustic stimuli. Gleaning bats rely largely on sounds generated by their prey to forage and also use echolocation to avoid obstacles (Brewton, Gutierrez, & Razak, 2018). In these bats, passive and active listening channels operate through different thalamocortical pathways. Specifically, neurophysiological data from the gleaning pallid bat reveal that separate regions of the midbrain IC and A1 respond to echolocation signals and environmental noise (*A. pallidus*; Razak, Shen, Zumsteg, & Fuzessery, 2007). It would be of interest to determine if the separation of echolocation and passive listening channels is common across bat species. Indeed, if echolocation sound production activates auditory feedback systems that tune the processing of returning echoes, it could serve to increase the bat's sensitivity and selectivity to returning echoes, while reducing interference from calls and echoes of conspecifics.

Neural circuits dedicated to processing sounds from the environment, including communication calls from conspecifics, may serve to select and activate motor programs for diverse behaviors. For example, auditory neurons that process and respond to rustling sounds from prey moving in the environment can help localize and intercept a meal. Other neurons that process and respond to aggressive calls from a conspecific or a predator can serve to mediate avoidance of a potentially dangerous encounter. Thus, rapid and appropriate behavioral responses may be mediated by selective activation of passive listening channels.

It is also noteworthy that the time scales over which echolocation and communication vocalizations are produced and processed are vastly different. Although echolocation vocalizations can be shorter than 1 ms and produced at extremely short intervals (down to ~5 ms; Elemans et al., 2011), communication calls tend to be an order of magnitude longer (~20–100 ms) in duration and often have much longer interpulse intervals, up to several hundred milliseconds, depending on the type of call, species, and context (Bohn & Gillam, 2018; Bohn et al., 2008). This supports the idea that different pathways may participate in processing echolocation and communication vocalizations: a fast processing pathway for echolocation and a slower pathway for communication sounds.

Finally, we would like to highlight that processing of echolocation sounds requires the extraction of very different types of information from that carried by communication calls. In the case of echolocation signal processing, spatial information about the environment, based largely on echo timing and interaural difference cues, elicits discrete behavioral responses, which change with the bat's distance and direction to targets and obstacles. Communication calls, on the other hand, carry social, identity, emotional, and other information. In most species, social communication calls can vary considerably within and among individuals, especially over time and across behavioral contexts. For example, territorial calls can be combined with other phrases during the mating season to form complex songs (*P. nathusii*; Jahelková & Horáček, 2011), and signature syllables can very immensely across individuals (Figure 2). Thus, we hypothesize that the information processed from communication calls is relayed to brain regions that modulate sound-evoked activity with respect to the emotional content and context of stimuli, which, in turn, can inform behavioral decision-making adaptive behavioral responses.

Neural control of vocalizations in bats. Activation of local populations of neurons through electrical or chemical stimulation has led to the identification of brain areas implicated in different types of vocal signal production (i.e., communication and echolocation). Microstimulation of prefrontal cortex of *P. parnelli* elicited either echolocation-like sounds or communication-like sounds, depending on the locus of activation (Gooler & O'Neill, 1987). Stimulation of midbrain structures revealed differences between the production pathway for echolocation and communication sounds. For example, microstimulation of the superior colliculus (SC) of *E. fuscus* elicited echolocation sounds, whereas microstimulation of the periaqueductal gray (PAG) elicited communication-like vocalizations (Valentine, Sinha, & Moss, 2002). By contrast, microstimulation of the PAG of *P. discolor* elicited both echolocation and communication calls, whereas microstimulation of the paralemniscal area elicited only echolocation vocalizations (Fenzl & Schuller, 2005). In *Rhinolophus rouxi*, microstimulation of the SC elicited echolocation call production but failed to elicit communication calls, which are more complex in structure in this species (Schuller & Radtke-Schuller, 1990). Microstimulation of the amygdala in *P. parnellii* not only elicited agonistic communication calls but, surprisingly, also elicited the production of echolocation sounds (J. Ma & Kanwal, 2014). However, this finding warrants further exploration, given the acoustic similarity between echolocation signals and vocalizations used in social communication. In *P. parnellii* (Clement & Kanwal, 2012) and other bat species, such as *T. brasiliensis* (Bohn et al., 2008; Schwartz et al., 2007), sounds that resemble echolocation signals can in fact be used in different social contexts and/or are embedded in sequences for communication. Identification of the pathways for the production of communicative vocalizations in the brains of bats and characterization of conserved features across species has seen great progress in recent years, but a complete understanding depends on further research in this area (see Schwartz & Smotherman, 2011, for review).

Where to Go: Future Directions and New Approaches

Neurophysiology

Comparative studies of central nervous system processing of acoustic communication signals can serve to guide new lines of investigation of bat auditory processing. For example, studies of marmosets have revealed greater neural responses in auditory cortex to species-specific twitter calls in comparison to synthetic vocalizations of the same type altered in temporal parameters (Wang, Merzenich, Beitel, & Schreiner, 1995). More recent research reveals that subthreshold activity shapes cortical selectivity to communication calls (L. Gao & Wang, 2019), which underscores the importance of conducting intracellular neural recordings to fully understand the neural mechanisms of natural sound processing in bats.

A focus on bat natural acoustic behaviors can also pave the way to a deeper understanding of social communication signal processing. Social calls for a specific function often show variable spectrotemporal parameters among individuals. This observation motivates the following questions: Do neurons in the bat auditory system respond to a wider range of variation of social calls compared to sonar echolocation vocalizations? How and where do neurons process signals to support functional categories that encompass interindividual acoustic variation? Experiments that aim to investigate the neuronal selectivity to different categories of communication calls (i.e., distress, aggression, mating) would provide valuable information about the specifics of acoustic communication processing and how it differs from the processing of echolocation sounds.

In some species, communication calls may overlap in spectrotemporal features with echolocation sounds. How does the bat auditory system separate signals with similar acoustic structure that serve different behavioral functions? This question can be addressed by characterizing neural responses using a range of synthetic sounds constructed from morphed echolocation and communication calls.

Finally, very little is known about how complex vocal sequences are processed in mammals, including bats. Even in *T. brasiliensis*, for which research has examined processing of communication signals, no studies have examined how acoustic context (whether and how syllables are in sequences) or syntax (the number and order of elements/phrases) affects neuronal selectivity to these signals.

Advances in the miniaturization of neural recording devices has permitted neural recordings from bats in flight, which have provided new insights into echolocation signal processing and its use in navigation (Kothari, Wohlgemuth, & Moss, 2018). This technology could be applied to investigate neural processing of communication sounds in free-flying animals and to address the following questions: How does neural selectivity to communication sounds in immobilized bats compare with that recorded from freely behaving animals? And how does social context influence auditory communication processing in free-flying bats?

Vocal Learning and Acoustic Communication

Vocal learning involves the modification of sound production patterns in response to auditory feedback (Janik & Slater, 2000). Comparative studies of vocal learning can yield valuable insights into general mechanisms of audio-vocal feedback control across species, including humans. The value of comparative studies in bats for the understanding of speech and language has also been discussed in detail by Vernes (2017).

Songbirds are a key model system for vocal learning (for reviews, see Brainard & Doupe, 2002; Köppl, Manley, & Konishi, 2000; Mooney, 2009a, 2009b; Prather, 2013; Woolley, 2012), and major advances have been made through both molecular and electrophysiological studies that have not yet been feasible in other species (Tyack, 2008). Studies of nonhuman primates show that auditory input during development has little effect on call parameters (Tyack, 2008), which prompts the search for more appropriate animal models that can yield insights into how mammals acquire and modify their species-specific communication sounds. Many marine mammals have astonishing capabilities for vocal learning, but the techniques to probe the underlying mechanisms in these species are limited (Reichmuth & Casey, 2014).

Bats emerge as a key mammalian model for studies of vocal learning and its role in acoustic communication, because they show diverse and complex social behaviors, and they are well suited for laboratory research. There are many key questions begging for scientific answers. First, are complex vocal sequences learned and how are they are processed in mammals, including bats? Even in *T. brasiliensis*, for which research has characterized acoustic communication signal processing in the central auditory system (e.g., Andoni & Pollak, 2011; Klug et al., 2002; Pollak et al., 2013), no studies have investigated how acoustic context (whether and how syllables are in sequences) or syntax (the number and order of elements/phrases) affects neuronal selectivity to these signals. Furthermore, there is compelling evidence that some bat species learn their communication sounds (reviewed in Knörnschild, 2014). In addition to vocal learning of group-foraging calls in *P. hastatus* (Boughman, 1998; Figure 1) and songs in *S. bilineata* (Knörnschild et al., 2010; Figure 1), maternal directives in *P. discolor* have been the focus of some studies. Early evidence of vocal learning in *P. discolor* (Esser, 1994) has been further supported by the discovery of geographical vocal dialects and (Esser & Schubert, 1998; Figure 1), most recently, the successful training of bats to modify their communication calls based on playbacks of calls with different parameters (Lattenkamp, Vernes, & Wiegrebe, 2018). Notably, these are not the same species for which we have the most extensive research on neural systems (*P. parnellii*, *E. fuscus*, *T. brasiliensis*; Figure 1). Another focus of study for vocal learning is the nonlaryngeal echolocator *Rousettus aegyptiacus*. These bats do use their larynx to produce social vocalization. *R. aegyptiacus* pups reared in isolation do not develop normal adult vocalizations, and during development, playbacks can modulate the parameters of their adult vocalizations (Prat et al., 2016; Figure 1). Questions still remain, however, about the ontogeny, time course, and social context of vocal learning in bats and the underlying neural mechanisms. Further work can lay the groundwork to establish bats as key mammalian models for important scientific advances on the mechanisms of vocal learning, acoustic communication, and other natural acoustic behaviors.

Molecular Studies of Vocal Communication in Bats

Molecular tools have aided the progress of neuroscience for several decades but, until recently, most were available only for standard model species (i.e., mice and flies). This is rapidly changing, as many advances now open the door for unraveling the molecular mechanisms of sensory processing. For example, viral injections that drive the expression of receptors permit optogenetics in diverse animal species (El-Shamayleh, Ni, & Horwitz, 2016; Galvan et al., 2017). This technique allows experimental activation or inactivation of specific neurons and provides insight into how different populations of neurons collectively modulate behavior. Some researchers are currently developing optogenetic tools for studies in bats, and we believe that this work will shed new light on the neural pathways mediating vocal learning (M. Yartsev, personal communication, 2018).

The advances in genomics brought forward the creation of different consortiums to generate the genome of different groups of animals. In particular, the Bat1K consortium aims to generate chromosome-level genomes for all bat species and has, to date, achieved the sequencing of 14 genomes from different species (Teeling et al., 2018). This project not only will have a tremendous impact on bat neuroscience but also will enable new research directions in bat ecology and conservation, epidemiology of bat transmitted diseases, and studies on immunology and longevity.

Although full genomes of many bat species are not yet available, some studies have ventured to study gene expression and key molecules posited to play a role in different aspects of communication. For example, FoxP2 is a transcription factor expressed in multiple tissues, including the brain, and it has been deemed important in human vocal communication (Lai, Fisher, Hurst, Vargha-Khadem, & Monaco, 2001). For this reason, this protein has been studied in detail in relation to vocal learning in different species. Sequencing of this transcription factor in several bat species with contrasting echolocating systems suggest a role of FoxP2 in the development of echolocation (Li, Wang, Rossiter, Jones, & Zhang, 2007; Rodenas-Cuadrado et al., 2018). Other studies in bats focused on the expression pattern in the brain of this protein in two species of vocal learners, *P. discolor* and *R. aegyptiacus* (the former a laryngeal echolocator and the latter a nonlaryngeal echolocator; Figure 1). *Cynopterus brachyotis*, a species that does not use echolocation for navigation, produce multiharmonic distress calls that elevate the levels of different proteins (TH, Nurr-1, DAT, D1DR) in the amygdala of both emitting and receiving bats, whereas this does not happen in bats listening passively to playback of modified distress calls (Mariappan, Bogdanowicz, Raghuram, Marimuthu, & Rajan, 2016; Figure 1). These studies represent the first approaches in the investigation of genes and proteins related to acoustic communication processing and vocal learning in bats, and we propose the need to continue down this avenue of research to deepen knowledge of the molecular pathways involved. For example, using *c-fos* or other immediate early genes to examine and compare active neural regions in bats exposed to communication or echolocation sounds, combined with electrophysiological approaches, could help address questions of neuronal selectivity in these areas.

Other key molecules involved in the modulation of communication call signal processing are hormones and neurotransmitters. Previous studies of *C. brachyotis* showed that distress calls increase the release of dopamine, norepinephrine, serotonin, corticosterone, and ACTH in the amygdala of the emitter and listening bats (Mariappan et al., 2013; Figure 1). A study of *P. parnelli* showed extensive distribution of oxytocin in different brain areas, including the amygdala and the PAG, and considered the potential role of this hormone and vasopressin in vocal communication (Rao & Kanwal, 2004). To our knowledge, the experiments to test how these hormones may modulate auditory processing and vocal production parameters have not been conducted. Follow-up experiments exploring hormonal modulation of communication behavior and gene expression in animals engaged in vocal communication could give further insight into the molecular mechanisms involved in these processes. We believe this to be an exciting research niche and an important step to understanding the mechanisms of acoustic signal processing in bats that rely on sound for communication and echolocation.

Outlook

Bats comprise a diverse and gregarious group of animals that have evolved highly specialized audio-vocal systems for echolocation and acoustic communication. Because most mammals use vocalizations for social communication, echolocation likely evolved from communication call precursors. Over millions of years, evolution has shaped bat vocal motor and sensory processing systems to support echolocation and acoustic communication (Bohn et al., 2006; Smotherman et al., 2016). Bats have evolved auditory systems sensitive to ultrasound, the ability to extract fine temporal and spectral information from echoes, and an audio-vocal feedback system that supports rapid modifications of call production parameters in response to echoes and environmental sounds. Importantly, bats are some of the few mammals in which vocal learning has been characterized. We assert that research on a diverse group of animals such as bats can help identify and elaborate on common mechanisms and specializations for acoustic communication behavior across species.

References

Altringham, J. D., McOwat, T. P., & Hammond, L. (2011). *Bats: From evolution to conservation* (2nd ed.). Oxford, UK: Oxford University Press. http://dx.doi.org/10.1093/acprof:osobl/9780199207114.001.0001

Andoni, S., & Pollak, G. D. (2011). Selectivity for spectral motion as a neural computation for encoding natural communication signals in bat inferior colliculus. *The Journal of Neuroscience, 31,* 16529–16540. http://dx.doi.org/10.1523/JNEUROSCI.1306-11.2011

Arnold, B. D., & Wilkinson, G. S. (2011). Individual specific contact calls of pallid bats (*Antrozous pallidus*) attract conspecifics at roosting sites. *Behavioral Ecology and Sociobiology, 65,* 1581–1593. http://dx.doi.org/10.1007/s00265-011-1168-4

Balcombe, J. (1990). Vocal recognition of pups by mother Mexican free-tailed bats, *Tadarida brasiliensis mexicana*. *Animal Behavior, 39,* 960–966. http://dx.doi.org/10.1016/S0003-3472(05)80961-3

Balcombe, J. P., & McCracken, G. F. (1992). Vocal recognition in Mexican free-tailed bats: Do pups recognize mothers? *Animal Behaviour, 43,* 79–87. http://dx.doi.org/10.1016/S0003-3472(05)80073-9

Barlow, K. E., & Jones, G. (1997). Function of pipistrelle social calls: Field data and a playback experiment. *Animal Behaviour, 53,* 991–999. http://dx.doi.org/10.1006/anbe.1996.0398

Bastian, A., & Schmidt, S. (2008). Affect cues in vocalizations of the bat, *Megaderma lyra,* during agonistic interactions. *The Journal of the Acoustical Society of America, 124,* 598–608. http://dx.doi.org/10.1121/1.2924123

Beetz, M. J., Kordes, S., García-Rosales, F., Kössl, M., & Hechavarría, J. C. (2017). Processing of natural echolocation sequences in the inferior colliculus of Seba's fruit eating bat, Carollia perspicillata. *eNeuro, 4*. http://dx.doi.org/10.1523/ENEURO.0314-17.2017

Behr, O., Knörnschild, M., & von Helversen, O. (2009). Territorial counter-singing in male sac-winged bats (*Saccopteryx bilineata*): Low-frequency songs trigger a stronger response. *Behavioral Ecology and Sociobiology, 63,* 433–442. http://dx.doi.org/10.1007/s00265-008-0677-2

Behr, O., & von Helversen, O. (2004). Bat serenades—Complex courtship songs of the sac-winged bat (*Saccopteryx bilineata*). *Behavioral Ecology and Sociobiology, 56,* 106–115. http://dx.doi.org/10.1007/s00265-004-0768-7

Behr, O., von Helversen, O., Heckel, G., Nagy, M., Voigt, C. C., & Mayer, F. (2006). Territorial songs indicate male quality in the sac-winged bat *Saccopteryx bilineata* (Chiroptera, Emballonuridae). *Behavioral Ecology, 17,* 810–817. http://dx.doi.org/10.1093/beheco/arl013

Betke, M., Hirsh, D. E., Makris, N. C., McCracken, G. F., Procopio, M., Hristov, N. I., . . . Kunz, T. H. (2008). Thermal imaging reveals significantly smaller Brazilian free-tailed bat colonies than previously estimated. *Journal of Mammalogy, 89,* 18–24. http://dx.doi.org/10.1644/07-MAMM-A-011.1

Bohn, K. M., Boughman, J. W., Wilkinson, G. S., & Moss, C. F. (2004). Auditory sensitivity and frequency selectivity in greater spear-nosed bats suggest specializations for acoustic communication. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology, 190,* 185–192. http://dx.doi.org/10.1007/s00359-003-0485-0

Bohn, K. M., & Gillam, E. H. (2018). In-flight social calls: A primer for biologists and managers studying echolocation. *Canadian Journal of Zoology, 96,* 787–800. http://dx.doi.org/10.1139/cjz-2017-0188

Bohn, K. M., Moss, C. F., & Wilkinson, G. S. (2006). Correlated evolution between hearing sensitivity and social calls in bats. *Biology Letters, 2,* 561–564. http://dx.doi.org/10.1098/rsbl.2006.0501

Bohn, K. M., Moss, C. F., & Wilkinson, G. S. (2009). Pup guarding by greater spear-nosed bats. *Behavioral Ecology and Sociobiology, 63,* 1693–1703. http://dx.doi.org/10.1007/s00265-009-0776-8

Bohn, K. M., Schmidt-French, B., Ma, S. T., & Pollak, G. D. (2008). Syllable acoustics, temporal patterns, and call composition vary with behavioral context in Mexican free-tailed bats. *The Journal of the Acoustical Society of America, 124,* 1838–1848. http://dx.doi.org/10.1121/1.2953314

Bohn, K. M., Smarsh, G. C., & Smotherman, M. (2013). Social context evokes rapid changes in bat song syntax. *Animal Behaviour, 85,* 1485–1491. http://dx.doi.org/10.1016/j.anbehav.2013.04.002

Bohn, K. M., Wilkinson, G. S., & Moss, C. F. (2007). Discrimination of infant isolation calls by female greater spear-nosed bats, *Phyllostomus hastatus*. *Animal Behaviour, 73,* 423–432. http://dx.doi.org/10.1016/j.anbehav.2006.09.003

Boughman, J. W. (1998). Vocal learning by greater spear-nosed bats. *Proceedings: Biological Sciences, 265,* 227–233. http://dx.doi.org/10.1098/rspb.1998.0286

Boughman, J. W., & Wilkinson, G. S. (1998). Greater spear-nosed bats discriminate group mates by vocalizations. *Animal Behaviour, 55,* 1717–1732. http://dx.doi.org/10.1006/anbe.1997.0721

Bradbury, J. W., & Vehrencamp, S. L. (1977). Social organization and foraging in emballonurid bats. *Behavioral Ecology and Sociobiology, 2,* 1–17. http://dx.doi.org/10.1007/BF00299284

Brainard, M. S., & Doupe, A. J. (2002). What songbirds teach us about learning. *Nature, 417,* 351–358. http://dx.doi.org/10.1038/417351a

Brewton, D., Gutierrez, V., & Razak, K. A. (2018). Accurate sound localization behavior in a gleaning bat, Antrozous pallidus. *Scientific Reports, 8,* 13457. http://dx.doi.org/10.1038/s41598-018-31606-z

Brimijoin, W. O., & O'Neill, W. E. (2005). On the prediction of sweep rate and directional selectivity for FM sounds from two-tone interactions in the inferior colliculus. *Hearing Research, 210,* 63–79. http://dx.doi.org/10.1016/j.heares.2005.07.005

Brimijoin, W. O., & O'Neill, W. E. (2010). Patterned tone sequences reveal non-linear interactions in auditory spectrotemporal receptive fields in the inferior colliculus. *Hearing Research, 267,* 96–110. http://dx.doi.org/10.1016/j.heares.2010.04.005

Brown, P. (1976). Vocal communication in the pallid bat, Antrozous pallidus. *Zeitschrift für Tierpsychologie, 41,* 34–54. http://dx.doi.org/10.1111/j.1439-0310.1976.tb00469.x

Brown, P. E., Brown, T. W., & Grinnell, A. D. (1983). Echolocation, development, and vocal communication in the lesser bulldog bat, *Noctilio albiventris*. *Behavioral Ecology and Sociobiology, 13,* 287–298. http://dx.doi.org/10.1007/BF00299676

Busnel, R. (Ed.). (1980). *Animal sonar systems*. Boston, MA: Springer. http://dx.doi.org/10.1007/978-1-4684-7254-7

Carter, G., & Leffer, L. (2015). Social grooming in bats: Are vampire bats exceptional? *PLoS ONE, 10,* e0138430. http://dx.doi.org/10.1371/journal.pone.0138430

Casseday, J. H., Fremouw, T., & Covey, E. (2002). The inferior colliculus: A hub for the central auditory system. In D. Oertel, R. R. Fay, & A. N. Popper (Eds.), *Integrative functions in the mammalian auditory pathway* (pp. 238–318). New York, NY: Springer. http://dx.doi.org/10.1007/978-1-4757-3654-0_7

Chaverri, G. (2010). Comparative social network analysis in a leaf-roosting bat. *Behavioral Ecology and Sociobiology, 64,* 1619–1630. http://dx.doi.org/10.1007/s00265-010-0975-3

Chaverri, G., Ancillotto, L., & Russo, D. (2018). Social communication in bats. *Biological Reviews of the Cambridge Philosophical Society, 93,* 1938–1954. http://dx.doi.org/10.1111/brv.12427

Clement, M. J., & Kanwal, J. S. (2012). Simple syllabic calls accompany discrete behavior patterns in captive *Pteronotus parnellii*: An illustration of the motivation-structure hypothesis. *The Scientific World Journal, 2012,* 128695. http://dx.doi.org/10.1100/2012/128695

Coles, R. B., Guppy, A., Anderson, M. E., & Schlegel, P. (1989). Frequency sensitivity and directional hearing in the gleaning bat, *Plecotus auritus* (Linnaeus 1758). *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology, 165,* 269–280. http://dx.doi.org/10.1007/BF00619201

Covey, E. (2005). Neurobiological specializations in echolocating bats. *The Anatomical Record, Part A, Discoveries in Molecular, Cellular, and Evolutionary Biology, 287A,* 1103–1116. http://dx.doi.org/10.1002/ar.a.20254

Davidson, S. M., & Wilkinson, G. S. (2002). Geographic and individual variation in vocalizations by male *Saccopteryx bilineata* (Chiroptera: Emballonuridae). *Journal of Mammalogy, 83,* 526–535. http://dx.doi.org/10.1644/1545-1542(2002)083<0526:GAIVIV>2.0.CO;2

Davidson, S. M., & Wilkinson, G. S. (2004). Function of male song in the greater white-lined bat, *Saccopteryx bilineata*. *Animal Behaviour, 67,* 883–891. http://dx.doi.org/10.1016/j.anbehav.2003.06.016

Dechmann, D. K. N., & Safi, K. (2005). Studying communication in bats. Invited review. *Cognition, Brain, Behavior: An Interdisciplinary Journal, 9,* 479–496.

Dechmann, D. K. N., Wikelski, M., van Noordwijk, H. J., Voigt, C. C., & Voigt-Heucke, S. L. (2013). Metabolic costs of bat echolocation in a non-foraging context support a role in communication. *Frontiers in Physiology, 4,* 66. http://dx.doi.org/10.3389/fphys.2013.00066

De Fanis, E., & Jones, G. (1995). The role of odour in the discrimination of conspecifics by pipistrelle bats. *Animal Behaviour, 49,* 835–839. http://dx.doi.org/10.1016/0003-3472(95)80215-0

Dorado-Correa, A. M., Goerlitz, H. R., & Siemers, B. M. (2013). Interspecific acoustic recognition in two European bat communities. *Frontiers in Physiology, 4,* 192. http://dx.doi.org/10.3389/fphys.2013.00192

Drebitz, E., Haag, M., Grothe, I., Mandon, S., & Kreiter, A. K. (2018). Attention configures synchronization within local neuronal networks for processing of the behaviorally relevant stimulus. *Frontiers in Neural Circuits, 12,* 71. http://dx.doi.org/10.3389/fncir.2018.00071

Ehrlich, D., Casseday, J. H., & Covey, E. (1997). Neural tuning to sound duration in the inferior colliculus of the big brown bat, *Eptesicus fuscus*. *Journal of Neurophysiology, 77,* 2360–2372. http://dx.doi.org/10.1152/jn.1997.77.5.2360

Elemans, C. P. H., Mead, A. F., Jakobsen, L., & Ratcliffe, J. M. (2011). Superfast muscles set maximum call rate in echolocating bats. *Science, 333,* 1885–1888. http://dx.doi.org/10.1126/science.1207309

Elemans, C. P. H., Mead, A. F., Rome, L. C., & Goller, F. (2008). Superfast vocal muscles control song production in songbirds. *PLoS ONE, 3,* e2581. http://dx.doi.org/10.1371/journal.pone.0002581

El-Shamayleh, Y., Ni, A. M., & Horwitz, G. D. (2016). Strategies for targeting primate neural circuits with viral vectors. *Journal of Neurophysiology, 116,* 122–134. http://dx.doi.org/10.1152/jn.00087.2016

Engler, S., Rose, A., & Knörnschild, M. (2017). Isolation call ontogeny in bat pups (*Glossophaga soricina*). *Behaviour, 154,* 267–286. http://dx.doi.org/10.1163/1568539X-00003421

Esser, K. H. (1994). Audio-vocal learning in a non-human mammal: The lesser spear-nosed bat *Phyllostomus discolor*. *Neuroreport, 5,* 1718–1720. http://dx.doi.org/10.1097/00001756-199409080-00007

Esser, K. H., & Daucher, A. (1996). Hearing in the FM-bat *Phyllostomus discolor*: A behavioral audiogram. *Journal of Comparative Physiology. A, Sensory, Neural, and Behavioral Physiology, 178,* 779–785. http://dx.doi.org/10.1007/BF00225826

Esser, K. H., & Schmidt, U. (1989). Mother-infant communication in the lesser spear-nosed bat *Phyllostomus discolor* (Chiroptera, Phyllostomidae)— Evidence for acoustic learning. *Ethology, 82,* 156–168. http://dx.doi.org/10.1111/j.1439-0310.1989.tb00496.x

Esser, K. H., & Schubert, J. (1998). Vocal dialects in the lesser spear-nosed bat *Phyllostomus discolor*. *Naturwissenschaften, 85,* 347–349. http://dx.doi.org/10.1007/s001140050513

Fenton, M. B., & Ratcliffe, J. M. (2017). Sensory biology: Bats united by cochlear development. *Nature Ecology & Evolution, 1,* 46. http://dx.doi.org/10.1038/s41559-016-0046

Fenzl, T., & Schuller, G. (2005). Echolocation calls and communication calls are controlled differentially in the brainstem of the bat *Phyllostomus discolor*. *BMC Biology, 3,* 17. http://dx.doi.org/10.1186/1741-7007-3-17

Fernandez, A. A., Fasel, N., Knörnschild, M., & Richner, H. (2014). When bats are boxing: Aggressive behaviour and communication in male Seba's short-tailed fruit bat. *Animal Behaviour, 98,* 149–156. http://dx.doi.org/10.1016/j.anbehav.2014.10.011

Fitzpatrick, D. C., Kanwal, J. S., Butman, J. A., & Suga, N. (1993). Combination-sensitive neurons in the primary auditory cortex of the mustached bat. *The Journal of Neuroscience, 13,* 931–940. http://dx.doi.org/10.1523/JNEUROSCI.13-03-00931.1993

Fuzessery, Z. M., & Hall, J. C. (1999). Sound duration selectivity in the pallid bat inferior colliculus. *Hearing Research, 137,* 137–154. http://dx.doi.org/10.1016/S0378-5955(99)00133-1

Gadziola, M. A., Grimsley, J. M. S., Shanbhag, S. J., & Wenstrup, J. J. (2012). A novel coding mechanism for social vocalizations in the lateral amygdala. *Journal of Neurophysiology, 107,* 1047–1057. http://dx.doi.org/10.1152/jn.00422.2011

Gadziola, M. A., Shanbhag, S. J., & Wenstrup, J. J. (2016). Two distinct representations of social vocalizations in the basolateral amygdala. *Journal of Neurophysiology, 115,* 868–886. http://dx.doi.org/10.1152/jn.00953.2015

Galvan, A., Stauffer, W. R., Acker, L., El-Shamayleh, Y., Inoue, K.-I., Ohayon, S., & Schmid, M. C. (2017). Nonhuman primate optogenetics: Recent advances and future directions. *The Journal of Neuroscience, 37,* 10894–10903. http://dx.doi.org/10.1523/JNEUROSCI.1839-17.2017

Gao, E., & Suga, N. (1998). Experience-dependent corticofugal adjustment of midbrain frequency map in bat auditory system. *Proceedings of the National Academy of Sciences of the United States of America, 95,* 12663–12670. http://dx.doi.org/10.1073/pnas.95.21.12663

Gao, L., & Wang, X. (2019). Subthreshold activity underlying the diversity and selectivity of the primary auditory cortex studied by intracellular recordings in awake marmosets. *Cerebral Cortex, 29,* 994–1005. http://dx.doi.org/10.1093/cercor/bhy006

Gelfand, D. L., & McCracken, G. F. (1986). Individual variation in the isolation calls of Mexican free-tailed bat pups (*Tadarida brasiliensis mexicana*). *Animal Behaviour, 34,* 1078–1086. http://dx.doi.org/10.1016/S0003-3472(86)80167-1

Gillam, E. H., & Chaverri, G. (2012). Strong individual signatures and weaker group signatures in contact calls of Spix's disc-winged bat, *Thyroptera tricolor*. *Animal Behaviour, 83,* 269–276. http://dx.doi.org/10.1016/j.anbehav.2011.11.002

Gillam, E., & Fenton, M. B. (2016). Roles of acoustic social communication in the lives of bats. In M. B. Fenton, A. D. Grinnell, A. N. Popper, & R. R. Fay (Eds.), *Bat bioacoustics* (pp. 117–139). New York, NY: Springer. http://dx.doi.org/10.1007/978-1-4939-3527-7_5

Gooler, D. M., & O'Neill, W. E. (1987). Topographic representation of vocal frequency demonstrated by microstimulation of anterior cingulate cortex in the echolocating bat, *Pteronotus parnelli parnelli*. *Journal of Comparative Physiology. A, Sensory, Neural, and Behavioral Physiology, 161,* 283–294. http://dx.doi.org/10.1007/BF00615248

Griffin, D. R. (1958). *Listening in the dark: The acoustic orientation of bats and men*. Oxford, UK: Yale University Press.

Grilliot, M. E., Burnett, S. C., & Mendonça, M. T. (2009). Sexual dimorphism in big brown bat (*Eptesicus fuscus*) ultrasonic vocalizations is context dependent. *Journal of Mammalogy, 90,* 203–209. http://dx.doi.org/10.1644/07-MAMM-A-161.1

Guppy, A., & Coles, R. B. (1988). Acoustical and neural aspects of hearing in the Australian gleaning bats, *Macroderma gigas* and *Nyctophilus gouldi*. *Journal of Comparative Physiology. A, Sensory, Neural, and Behavioral Physiology, 162,* 653–668. http://dx.doi.org/10.1007/BF01342641

Holmstrom, L., Roberts, P. D., & Portfors, C. V. (2007). Responses to social vocalizations in the inferior colliculus of the mustached bat are influenced by secondary tuning curves. *Journal of Neurophysiology, 98,* 3461–3472. http://dx.doi.org/10.1152/jn.00638.2007

Hristov, N. I., Betke, M., Theriault, D. E. H., Bagchi, A., & Kunz, T. H. (2010). Seasonal variation in colony size of Brazilian free-tailed bats at Carlsbad Cavern based on thermal imaging. *Journal of Mammalogy, 91,* 183–192. http://dx.doi.org/10.1644/08-MAMM-A-391R.1

Hurley, L. M., & Pollak, G. D. (2005). Serotonin modulates responses to species-specific vocalizations in the inferior colliculus. *Journal of Comparative Physiology A, Neuroethology, Sensory, Neural, and Behavioral Physiology, 191,* 535–546. http://dx.doi.org/10.1007/s00359-005-0623-y

Ito, T., Furuyama, T., Hase, K., Kobayasi, K. I., & Hiryu, S. (2018). Organization of projection from brainstem auditory nuclei to the inferior colliculus of Japanese house bat (*Pipistrellus abramus*). *Brain and Behavior, 8,* e01059. http://dx.doi.org/10.1002/brb3.1059

Ito, T., Furuyama, T., Hase, K., Kobayasi, K. I., Hiryu, S., & Riquimaroux, H. (2018). Organization of subcortical auditory nuclei of Japanese house bat (*Pipistrellus abramus*) identified with cytoarchitecture and molecular expression. *The Journal of Comparative Neurology, 526,* 2824–2844. http://dx.doi.org/10.1002/cne.24529

Jahelková, H., & Horáček, I. (2011). Mating system of a migratory bat, Nathusius' Pipistrelle (*Pipistrellus nathusii*): Different male strategies. *Acta Chiropterologica, 13,* 123–137. http://dx.doi.org/10.3161/150811011X578679

Jahelková, H., Horáček, I., & Bartonička, T. (2008). The advertisement song of *Pipistrellus nathusii* (Chiroptera, Vespertilionidae): A complex message containing acoustic signatures of individuals. *Acta Chiropterologica, 10,* 103–126. http://dx.doi.org/10.3161/150811008X331144

Janik, V. M., & Slater, P. J. B. (2000). The different roles of social learning in vocal communication. *Animal Behaviour, 60,* 1–11. http://dx.doi.org/10.1006/anbe.2000.1410

Jones, G. (1997). Differences in songflight calls and social calls between two phonic types of the vespertilionid bat *Pipistrellus pipistrellus*. *Journal of Zoology, 241,* 315–324. http://dx.doi.org/10.1111/j.1469-7998.1997.tb01962.x

Kanwal, J. S., Matsumura, S., Ohlemiller, K., & Suga, N. (1994). Analysis of acoustic elements and syntax in communication sounds emitted by mustached bats. *The Journal of the Acoustical Society of America, 96,* 1229–1254. http://dx.doi.org/10.1121/1.410273

Kerth, G. (2008). Causes and consequences of sociality in bats. *Bioscience, 58,* 737–746. http://dx.doi.org/10.1641/B580810

Klug, A., Bauer, E. E., Hanson, J. T., Hurley, L., Meitzen, J., & Pollak, G. D. (2002). Response selectivity for species-specific calls in the inferior colliculus of Mexican free-tailed bats is generated by inhibition. *Journal of Neurophysiology, 88,* 1941–1954. http://dx.doi.org/10.1152/jn.2002.88.4.1941

Knörnschild, M. (2014). Vocal production learning in bats. *Current Opinion in Neurobiology, 28,* 80–85. http://dx.doi.org/10.1016/j.conb.2014.06.014

Knörnschild, M., Feifel, M., & Kalko, E. K. V. (2013). Mother–offspring recognition in the bat *Carollia perspicillata*. *Animal Behaviour, 86,* 941–948. http://dx.doi.org/10.1016/j.anbehav.2013.08.011

Knörnschild, M., Nagy, M., Metz, M., Mayer, F., & von Helversen, O. (2010). Complex vocal imitation during ontogeny in a bat. *Biology Letters, 6,* 156–159. http://dx.doi.org/10.1098/rsbl.2009.0685

Knörnschild, M., & von Helversen, O. (2008). Nonmutual vocal mother–pup recognition in the greater sac-winged bat. *Animal Behaviour, 76,* 1001–1009. http://dx.doi.org/10.1016/j.anbehav.2008.05.018

Kobayasi, K. I., Hiryu, S., Shimozawa, R., & Riquimaroux, H. (2012). Vocalization of echolocation-like pulses for interindividual interaction in horseshoe bats (*Rhinolophus ferrumequinum*). *The Journal of the Acoustical Society of America, 132,* EL417. http://dx.doi.org/10.1121/1.4757695

Köppl, C., Manley, G. A., & Konishi, M. (2000). Auditory processing in birds. *Current Opinion in Neurobiology, 10,* 474–481. http://dx.doi.org/10.1016/S0959-4388(00)00110-0

Kössl, M., Hechavarria, J., Voss, C., Schaefer, M., & Vater, M. (2015). Bat auditory cortex – model for general mammalian auditory computation or special design solution for active time perception? *European Journal of Neuroscience, 41,* 518–532. http://dx.doi.org/10.1111/ejn.12801

Kothari, N. B., Wohlgemuth, M. J., & Moss, C. F. (2018). Dynamic representation of 3D auditory space in the midbrain of the free-flying echolocating bat. *eLife, 7,* e29053. http://dx.doi.org/10.7554/eLife.29053

Lai, C. S., Fisher, S. E., Hurst, J. A., Vargha-Khadem, F., & Monaco, A. P. (2001). A forkhead-domain gene is mutated in a severe speech and language disorder. *Nature, 413,* 519–523. http://dx.doi.org/10.1038/35097076

Lattenkamp, E. Z., Vernes, S. C., Wiegrebe, L. (2018). Volitional control of social vocalisations and vocal usage learning in bats. *The Journal of Experimental Biology, 221*(14), jeb180729. http://dx.doi.org/10.1242/jeb.180729

Li, G., Wang, J., Rossiter, S. J., Jones, G., & Zhang, S. (2007). Accelerated FoxP2 evolution in echolocating bats. *PLoS ONE, 2,* e900. http://dx.doi.org/10.1371/journal.pone.0000900

Lin, A., Jiang, T., Kanwal, J. S., Lu, G., Luo, J., Wei, X., . . . Feng, J. (2015). Geographical variation in echolocation vocalizations of the Himalayan leaf-nosed bat: Contribution of morphological variation and cultural drift. *Oikos, 124,* 364–371. http://dx.doi.org/10.1111/oik.01604

Luo, B., Lu, G., Chen, K., Guo, D., Huang, X., Liu, Y., & Feng, J. (2017). Social calls honestly signal female competitive ability in Asian particoloured bats. *Animal Behaviour, 127,* 101–108. http://dx.doi.org/10.1016/j.anbehav.2017.03.012

Luo, F., Metzner, W., Wu, F. J., Zhang, S. Y., & Chen, Q. C. (2008). Duration-sensitive neurons in the inferior colliculus of horseshoe bats: Adaptations for using CF-FM echolocation pulses. *Journal of Neurophysiology, 99,* 284–296. http://dx.doi.org/10.1152/jn.00935.2007

Luo, J., & Moss, C. F. (2017). Echolocating bats rely on audiovocal feedback to adapt sonar signal design. *Proceedings of the National Academy of Sciences of the United States of America, 114,* 10978–10983. http://dx.doi.org/10.1073/pnas.1711892114

Ma, J., & Kanwal, J. S. (2014). Stimulation of the basal and central amygdala in the mustached bat triggers echolocation and agonistic vocalizations within multimodal output. *Frontiers in Physiology, 5,* 55. http://dx.doi.org/10.3389/fphys.2014.00055

Ma, J., Kobayasi, K., Zhang, S., & Metzner, W. (2006). Vocal communication in adult greater horseshoe bats, *Rhinolophus ferrumequinum*. *Journal of Comparative Physiology A, Neuroethology, Sensory, Neural, and Behavioral Physiology, 192,* 535–550. http://dx.doi.org/10.1007/s00359-006-0094-9

Ma, X., & Suga, N. (2003). Augmentation of plasticity of the central auditory system by the basal forebrain and/or somatosensory cortex. *Journal of Neurophysiology, 89,* 90–103. http://dx.doi.org/10.1152/jn.00968.2001

Macías, S., Luo, J., & Moss, C. F. (2018). Natural echolocation sequences evoke echo-delay selectivity in the auditory midbrain of the FM bat, *Eptesicus fuscus*. *Journal of Neurophysiology, 120,* 1323–1339. http://dx.doi.org/10.1152/jn.00160.2018

Macías, S., Mora, E. C., Hechavarría, J. C., & Kössl, M. (2011). Duration tuning in the inferior colliculus of the mustached bat. *Journal of Neurophysiology, 106,* 3119–3128. http://dx.doi.org/10.1152/jn.00294.2011

Mariappan, S., Bogdanowicz, W., Marimuthu, G., & Rajan, K. E. (2013). Distress calls of the greater short-nosed fruit bat *Cynopterus sphinx* activate hypothalamic-pituitary-adrenal (HPA) axis in conspecifics. *Journal of Comparative Physiology A, Neuroethology, Sensory, Neural, and Behavioral Physiology, 199,* 775–783. http://dx.doi.org/10.1007/s00359-013-0838-2

Mariappan, S., Bogdanowicz, W., Raghuram, H., Marimuthu, G., & Rajan, K. E. (2016). Structure of distress call: Implication for specificity and activation of dopaminergic system. *Journal of Comparative Physiology A, Neuroethology, Sensory, Neural, and Behavioral Physiology, 202,* 55–65. http://dx.doi.org/10.1007/s00359-015-1053-0

Marsh, R. A., Fuzessery, Z. M., Grose, C. D., & Wenstrup, J. J. (2002). Projection to the inferior colliculus from the basal nucleus of the amygdala. *The Journal of Neuroscience, 22,* 10449–10460. http://dx.doi.org/10.1523/JNEUROSCI.22-23-10449.2002

Martin, L. M., García-Rosales, F., Beetz, M. J., & Hechavarría, J. C. (2017). Processing of temporally patterned sounds in the auditory cortex of Seba's short-tailed bat, *Carollia perspicillata*. *European Journal of Neuroscience, 46,* 2365–2379. http://dx.doi.org/10.1111/ejn.13702

Matsumura, S. (1979). Mother-infant communication in a horseshoe bat (*Rhinolophus ferrumequinum nippon*): Development of vocalization. *Journal of Mammalogy, 60,* 76–84. http://dx.doi.org/10.2307/1379760

McCracken, G. F. (2003). Estimates of population sizes in summer colonies of Brazilian free-tailed bats (Tadarida brasiliensis). In T. J. O'Shea & M. A. Bogan (Eds.), *Monitoring trends in bat populations of the U.S. and territories: Problems and prospects* (pp. 21–30). Washington, DC: U.S. Department of the Interior, U.S. Geological Survey.

McCracken, G. F., & Bradbury, J. W. (1981). Social organization and kinship in the polygynous bat *Phyllostomus hastatus*. *Behavioral Ecology and Sociobiology, 8,* 11–34. http://dx.doi.org/10.1007/BF00302840

McCracken, G. F., & Wilkinson, G. S. (2000). Bat mating systems. In E. G. Crichton & P. H. Krutzsch (Eds.), *Reproductive biology of bats* (pp. 321–362). London, UK: Academic Press. http://dx.doi.org/10.1016/B978-012195670-7/50009-6

McFarlane, D. A., Rentergem, G. V., Ruina, A., Lundberg, J., & Christenson, K. (2015). Estimating colony size of the wrinkle-lipped bat, *Chaerephon plicatus* (Chiroptera: Molossidae) at Gomantong, Sabah, by quantitative image analysis. *Acta Chiropterologica, 17,* 171–177. http://dx.doi.org/10.3161/15081109ACC2015.17.1.014

Medvedev, A. V., & Kanwal, J. S. (2004). Local field potentials and spiking activity in the primary auditory cortex in response to social calls. *Journal of Neurophysiology, 92,* 52–65. http://dx.doi.org/10.1152/jn.01253.2003

Medvedev, A. V., & Kanwal, J. S. (2008). Communication call-evoked gamma-band activity in the auditory cortex of awake bats is modified by complex acoustic features. *Brain Research, 1188,* 76–86. http://dx.doi.org/10.1016/j.brainres.2007.10.081

Mooney, R. (2009a). Neurobiology of song learning. *Current Opinion in Neurobiology, 19,* 654–660. http://dx.doi.org/10.1016/j.conb.2009.10.004

Mooney, R. (2009b). Neural mechanisms for learned birdsong. *Learning & Memory, 16,* 655–669. http://dx.doi.org/10.1101/lm.1065209

Morrison, J. A., Valdizón-Rodríguez, R., Goldreich, D., & Faure, P. A. (2018). Tuning for rate and duration of frequency-modulated sweeps in the mammalian inferior colliculus. *Journal of Neurophysiology, 120,* 985–997. http://dx.doi.org/10.1152/jn.00065.2018

Nachtigall, P. E., & Moore, P. W. B. (Eds.). (1988). *Animal sonar: Processes and performance*. Boston, MA: Springer. http://dx.doi.org/10.1007/978-1-4684-7493-0

Namburi, P., Al-Hasani, R., Calhoon, G. G., Bruchas, M. R., & Tye, K. M. (2016). Architectural representation of valence in the limbic system. *Neuropsychopharmacol, 41,* 1697–1715. http://dx.doi.org/10.1038/npp.2015.358

Naumann, R. T., & Kanwal, J. S. (2011). Basolateral amygdala responds robustly to social calls: Spiking characteristics of single unit activity. *Journal of Neurophysiology, 105,* 2389–2404. http://dx.doi.org/10.1152/jn.00580.2010

Nelson, J. E. (1964). Vocal communication in Australian flying foxes (Pteropodidae; Megachiroptera). *Zeitschrift für Tierpsychologie, 21,* 857–870. http://dx.doi.org/10.1111/j.1439-0310.1964.tb01224.x

Neuweiler, G., Bruns, V., & Schuller, G. (1980). Ears adapted for the detection of motion, or how echolocating bats have exploited the capacities of the mammalian auditory system. *The Journal of the Acoustical Society of America, 68,* 741–753. http://dx.doi.org/10.1121/1.384812

Neuweiler, G., & Covey, E. (2006). *The biology of bats*. New York, NY: Oxford University Press.

Pannese, A., Grandjean, D., & Frühholz, S. (2015). Subcortical processing in auditory communication. *Hearing Research, 328,* 67–77. http://dx.doi.org/10.1016/j.heares.2015.07.003

Pfalzer, G., & Kusch, J. (2003). Structure and variability of bat social calls: Implications for specificity and individual recognition. *Journal of Zoology, 261,* 21–33. http://dx.doi.org/10.1017/S0952836903003935

Pollak, G. D. (2011). Discriminating among complex signals: The roles of inhibition for creating response selectivities. *Journal of Comparative Physiology A, Neuroethology, Sensory, Neural, and Behavioral Physiology, 197,* 625–640. http://dx.doi.org/10.1007/s00359-010-0602-9

Pollak, G. D., Andoni, S., Bohn, K., & Gittelman, J. X. (2013). The repertoire of communication calls emitted by bats and the ways the calls are processed in the inferior colliculus. In S. A. Helekar (Ed.), *Animal models of speech and language disorders* (pp. 211–239). New York, NY: Springer. http://dx.doi.org/10.1007/978-1-4614-8400-4_8

Pollak, G. D., Wenstrup, J. J., & Fuzessey, Z. M. (1986). Auditory processing in the mustache bat's inferior colliculus. *Trends in Neurosciences, 9,* 556–561. http://dx.doi.org/10.1016/0166-2236(86)90176-1

Poon, P. W., Sun, X., Kamada, T., & Jen, P. H. (1990). Frequency and space representation in the inferior colliculus of the FM bat, *Eptesicus fuscus*. *Experimental Brain Research, 79,* 83–91. http://dx.doi.org/10.1007/BF00228875

Porter, F. L. (1979). Social behavior in the leaf-nosed bat, Carollia perspicillata. *Zeitschrift für Tierpsychologie, 50,* 1–8. http://dx.doi.org/10.1111/j.1439-0310.1979.tb01012.x

Portfors, C. V. (2004). Combination sensitivity and processing of communication calls in the inferior colliculus of the moustached bat *Pteronotus parnellii*. *Anais da Academia Brasileira de Ciências, 76,* 253–257. http://dx.doi.org/10.1590/S0001-37652004000200010

Prat, Y., Azoulay, L., Dor, R., & Yovel, Y. (2017). Crowd vocal learning induces vocal dialects in bats: Playback of conspecifics shapes fundamental frequency usage by pups. *PLoS Biology, 15,* e2002556. http://dx.doi.org/10.1371/journal.pbio.2002556

Prat, Y., Taub, M., & Yovel, Y. (2015). Vocal learning in a social mammal: Demonstrated by isolation and playback experiments in bats. *Science Advances, 1,* e1500019. http://dx.doi.org/10.1126/sciadv.1500019

Prat, Y., Taub, M., & Yovel, Y. (2016). Everyday bat vocalizations contain information about emitter, addressee, context, and behavior. *Scientific Reports, 6,* 39419. http://dx.doi.org/10.1038/srep39419

Prather, J. F. (2013). Auditory signal processing in communication: Perception and performance of vocal sounds. *Hearing Research, 305,* 144–155. http://dx.doi.org/10.1016/j.heares.2013.06.007

Rao, P. D. P., & Kanwal, J. S. (2004). Oxytocin and vasopressin immunoreactivity within the forebrain and limbic-related areas in the mustached bat, *Pteronotus parnellii*. *Brain, Behavior and Evolution, 63,* 151–168. http://dx.doi.org/10.1159/000076241

Ratcliffe, J. M., Elemans, C. P. H., Jakobsen, L., & Surlykke, A. (2013). How the bat got its buzz. *Biology Letters, 9,* 20121031. http://dx.doi.org/10.1098/rsbl.2012.1031

Razak, K. A., Shen, W., Zumsteg, T., & Fuzessery, Z. M. (2007). Parallel thalamocortical pathways for echolocation and passive sound localization in a gleaning bat, *Antrozous pallidus*. *The Journal of Comparative Neurology, 500,* 322–338. http://dx.doi.org/10.1002/cne.21178

Reichmuth, C., & Casey, C. (2014). Vocal learning in seals, sea lions, and walruses. *Current Opinion in Neurobiology, 28,* 66–71. http://dx.doi.org/10.1016/j.conb.2014.06.011

Rodenas-Cuadrado, P. M., Mengede, J., Baas, L., Devanna, P., Schmid, T. A., Yartsev, M., . . . Vernes, S. C. (2018). Mapping the distribution of language related genes FoxP1, FoxP2, and CntnaP2 in the brains of vocal learning bat species. *The Journal of Comparative Neurology, 526,* 1235–1266. http://dx.doi.org/10.1002/cne.24385

Russ, J. M., Jones, G., Mackie, I. J., & Racey, P. A. (2004). Interspecific responses to distress calls in bats (Chiroptera: Vespertilionidae): A function for convergence in call design? *Animal Behaviour, 67,* 1005–1014. http://dx.doi.org/10.1016/j.anbehav.2003.09.003

Russo, D., & Jones, G. (1999). The social calls of Kuhl's pipistrelles *Pipistrellus kuhlii* (Kuhl, 1819): structure and variation (Chiroptera: Vespertilionidae). *Journal of Zoology, 249,* 469–493. http://dx.doi.org/10.1017/S0952836999231202

Russo, D., Teixeira, S., Cistrone, L., Jesus, J., Teixeira, D., Freitas, T., & Jones, G. (2009). Social calls are subject to stabilizing selection in insular bats. *Journal of Biogeography, 36,* 2212–2221. http://dx.doi.org/10.1111/j.1365-2699.2009.02158.x

Safi, K., & Dechmann, D. K. N. (2005). Adaptation of brain regions to habitat complexity: A comparative analysis in bats (Chiroptera). *Proceedings: Biological Sciences, 272,* 179–186. http://dx.doi.org/10.1098/rspb.2004.2924

Salles, A., Macias, S., Sundar, H., Elhilali, M., & Moss, C. F. (2018, November). *Neural discrimination of communication and echolocation calls in the big brown bat (Eptesicus fuscus)*. Poster session presented at the Society for Neuroscience, San Diego, CA.

Schnitzler, H.-U. (1968). Die Ultraschall-Ortungslaute der Hufeisen-Fledermäuse (Chiroptera-Rhinolophidae) in verschiedenen Orientierungssituationen [The ultrasonic sounds of horseshoe bats (Chiroptera-Rhinolophidae) in different orientation situations]. *Zeitschrift fur Vergleichende Physiologie, 57,* 376–408. http://dx.doi.org/10.1007/BF00303062

Schuller, G., & Moss, C. F. (2003). Vocal control and acoustically guided behavior in bats. In J. Thomas, C. F. Moss, & M. Vater (Eds.), *Echolocation in bats and dolphins* (pp. 3–16). Chicago, IL: University of Chicago Press.

Schuller, G., & Radtke-Schuller, S. (1990). Neural control of vocalization in bats: Mapping of brainstem areas with electrical microstimulation eliciting species-specific echolocation calls in the rufous horseshoe bat. *Experimental Brain Research, 79,* 192–206. http://dx.doi.org/10.1007/BF00228889

Schwartz, C. P., & Smotherman, M. S. (2011). Mapping vocalization-related immediate early gene expression in echolocating bats. *Behavioural Brain Research, 224,* 358–368. http://dx.doi.org/10.1016/j.bbr.2011.06.023

Schwartz, C., Tressler, J., Keller, H., Vanzant, M., Ezell, S., & Smotherman, M. (2007). The tiny difference between foraging and communication buzzes uttered by the Mexican free-tailed bat, *Tadarida brasiliensis*. *Journal of Comparative Physiology A, Neuroethology, Sensory, Neural, and Behavioral Physiology, 193,* 853–863. http://dx.doi.org/10.1007/s00359-007-0237-7

Simmons, N. B., Geisler, J. H. (1998). Phylogenetic relationships of Icaronycteris, Archaeonycteris, Hassianycteris, and Palaeochiropteryx to extant bat lineages, with comments on the evolution of echolocation and foraging strategies in Microchiroptera. *Bulletin of the American Museum of Natural History, 235,* 1–82. New York, NY: American Museum of Natural History.

Smotherman, M., Knörnschild, M., Smarsh, G., & Bohn, K. (2016). The origins and diversity of bat songs. *Journal of Comparative Physiology A, Neuroethology, Sensory, Neural, and Behavioral Physiology, 202,* 535–554. http://dx.doi.org/10.1007/s00359-016-1105-0

Sterbing, S. J., Schmidt, U., & Rübsamen, R. (1994). The postnatal development of frequency-place code and tuning characteristics in the auditory midbrain of the phyllostomid bat, *Carollia perspicillata*. *Hearing Research, 76,* 133–146. http://dx.doi.org/10.1016/0378-5955(94)90095-7

Suga, N., & Jen, P. H. (1975). Peripheral control of acoustic signals in the auditory system of echolocating bats. *The Journal of Experimental Biology, 62,* 277–311.

Teeling, E. C., Vernes, S. C., Dávalos, L. M., Ray, D. A., Gilbert, M. T. P., & Myers, E., & Bat1K Consortium. (2018). Bat biology, genomes, and the Bat1K project: To generate chromosome-level genomes for all living bat species. *Annual Review of Animal Biosciences, 6,* 23–46. http://dx.doi.org/10.1146/annurev-animal-022516-022811

Thomas, J., Vater, M., Moss, C. F. (2003). *Echolocation in bats and dolphins*. Chicago, IL: University of Chicago Press.

Thomson, C. E., Fenton, M. B., & Barclay, R. M. R. (1985). The role of infant isolation calls in mother–infant reunions in the little brown bat, *Myotis lucifugus* (Chiroptera: Vespertilionidae). *Canadian Journal of Zoology, 63,* 1982–1988. http://dx.doi.org/10.1139/z85-290

Tsang, S. M., Cirranello, A. L., Bates, P. J. J., & Simmons, N. B. (2016). The roles of taxonomy and systematics in bat conservation. In C. C. Voigt & T. Kingston (Eds.), *Bats in the Anthropocene: Conservation of bats in a changing world* (pp. 503–538). Cham, Switzerland: Springer International. http://dx.doi.org/10.1007/978-3-319-25220-9_16

Tyack, P. L. (2008). Convergence of calls as animals form social bonds, active compensation for noisy communication channels, and the evolution of vocal learning in mammals. *Journal of Comparative Psychology, 122,* 319–331. http://dx.doi.org/10.1037/a0013087

Valentine, D. E., Sinha, S. R., & Moss, C. F. (2002). Orienting responses and vocalizations produced by microstimulation in the superior colliculus of the echolocating bat, *Eptesicus fuscus*. *Journal of Comparative Physiology A, Neuroethology, Sensory, Neural, and Behavioral Physiology, 188,* 89–108. http://dx.doi.org/10.1007/s00359-001-0275-5

Vernes, S. C. (2017). What bats have to say about speech and language. *Psychonomic Bulletin & Review, 24,* 111–117. http://dx.doi.org/10.3758/s13423-016-1060-3

Voigt, C. C., Behr, O., Caspers, B., von Helversen, O., Knörnschild, M., Mayer, F., & Nagy, M. (2008). Songs, scents, and senses: Sexual selection in the greater sac-winged bat, *Saccopteryx bilineata*. *Journal of Mammalogy, 89,* 1401–1410. http://dx.doi.org/10.1644/08-MAMM-S-060.1

Walter, M. H., & Schnitzler, H.-U. (2017). Spectral call features provide information about the aggression level of greater mouse-eared bats (*Myotis myotis*) during agonistic interactions. *Bioacoustics, 28,* 1–25. http://dx.doi.org/10.1080/09524622.2017.1359798

Wang, X., Merzenich, M. M., Beitel, R., & Schreiner, C. E. (1995). Representation of a species-specific vocalization in the primary auditory cortex of the common marmoset: Temporal and spectral characteristics. *Journal of Neurophysiology, 74,* 2685–2706. http://dx.doi.org/10.1152/jn.1995.74.6.2685

Washington, S. D., & Kanwal, J. S. (2008). DSCF neurons within the primary auditory cortex of the mustached bat process frequency modulations present within social calls. *Journal of Neurophysiology, 100,* 3285–3304. http://dx.doi.org/10.1152/jn.90442.2008

Wenstrup, J. J. (1984). Auditory sensitivity in the fish-catching bat, *Noctilio leporinus*. *Journal of Comparative Physiology A, Neuroethology, Sensory, Neural, and Behavioral Physiology, 155,* 91–101. http://dx.doi.org/10.1007/BF00610934

Wenstrup, J. J., & Portfors, C. V. (2011). Neural processing of target distance by echolocating bats: Functional roles of the auditory midbrain. *Neuroscience and Biobehavioral Reviews, 35,* 2073–2083. http://dx.doi.org/10.1016/j.neubiorev.2010.12.015

Wilkinson, G. S. (1985). The social organization of the common vampire bat. *Behavioral Ecology and Sociobiology, 17,* 123–134.

Wilkinson, G. S., Carter, G., Bohn, K. M., Caspers, B., Chaverri, G., Farine, D., . . . Patriquin, K. (2019). Kinship association and social complexity in bats. *Behavioral Ecology and Sociobiology, 73,* 7. http://dx.doi.org/10.1007/s00265-018-2608-1

Woolley, S. M. N. (2012). Early experience shapes vocal neural coding and perception in songbirds. *Developmental Psychobiology, 54,* 612–631. http://dx.doi.org/10.1002/dev.21014

Wright, G. S., Chiu, C., Xian, W., Wilkinson, G. S., & Moss, C. F. (2014). Social calls predict foraging success in big brown bats. *Current Biology, 24,* 885–889. http://dx.doi.org/10.1016/j.cub.2014.02.058

Yovel, Y., Melcon, M. L., Franz, M. O., Denzinger, A., & Schnitzler, H.-U. (2009). The voice of bats: How greater mouse-eared bats recognize individuals based on their echolocation calls. *PLoS Computational Biology, 5,* e1000400. http://dx.doi.org/10.1371/journal.pcbi.1000400

Zhang, Y., & Suga, N. (2005). Corticofugal feedback for collicular plasticity evoked by electric stimulation of the inferior colliculus. *Journal of Neurophysiology, 94,* 2676–2682. http://dx.doi.org/10.1152/jn.00549.2005

Zook, J. M., & Casseday, J. H. (1985). Projections from the cochlear nuclei in the mustache bat, *Pteronotus parnellii*. *The Journal of Comparative Neurology, 237,* 307–324. http://dx.doi.org/10.1002/cne.902370303

Received October 23, 2018
Revision received January 22, 2019
Accepted January 30, 2019 ■