Anniversary Essay

Questions, ideas and tools: lessons from bat echolocation☆

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In their 1960 paper about bats using echolocation to find and track flying insects, Donald R. Griffin, Fredric A. Webster and Charles R. Michael (*Animal Behaviour*, **8**, 141–154) changed the face of research on this behaviour. They moved the field of echolocation from documenting that this animal or that one could echolocate to demonstrating an adaptive value of echolocation. They used experiments with captive bats, fruit flies, mosquitoes and crane flies to illustrate how bats used a 'feeding buzz' as they closed with their prey. The topic remains current today, and one of the first papers in *Nature* in 2013 (Jacobsen et al., **493**, 93–96) presented more information about feeding buzzes building on the platform that Griffin et al. had established. In the intervening period, literally thousands of papers have been published about echolocation, demonstrating how curious minds, technological advances and basic information about natural history can result in diversification of a field of research. We have learned that bats can use echolocation to recognize water surfaces and to find insect prey on spider webs. The continuum between orientation and social functions of echolocation means that this behaviour not only influences foraging and negotiating obstacle paths, but is also a cue that brings individuals together. Acoustic wars between bats and potential insect prey have further enriched the discipline by identifying acoustic measures and countermeasures used by the players. Parallel studies with toothed whales have provided further examples of the enrichment that echolocation brings to the lives of animals and those who study them.

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In the physical sciences there is ongoing discussion about whether new ideas or new tools drive changes in disciplines (Dyson 2012). When this dichotomy is applied to studies of echolocation by bats, I find it difficult to support either position, because observing natural systems and asking questions appears to be just as important as ideas and tools. In the late 1700s, Lazarro Spallanzani tried to answer questions about how bats and owls operated successfully at night. His tools included a room, heavy drapes (to keep out the light), a candle, ribbons and bells. He also had different methods (some of them reversible) to deprive or limit the sensory capabilities of captive bats and owls. Ribbons and bells allowed him to monitor the flight behaviour of bats and their ability to avoid obstacles in the dark. Wax and brass tubes inserted into the ears of bats allowed him to control auditory cues. Results acquired with this tool kit allowed Spallanzani to propose that bats could see with their ears, but it did not allow him to explain how they did so. This was the basis of 'Spallanzani's bat problem', and it set the stage for the discovery of echolocation.

Echolocation proved to be an eye-opening finding about animal behaviour. Donald Redfield Griffin (1944) coined the term echolocation (the process of locating obstacles by means of echoes) and founded a field of research that covers the spectrum from behaviour, neurobiology and anatomy to ecology, physiology and genetics. Griffin and his colleagues, the physicist George Washington Pierce and the neurophysiologist Robert Carl Galambos (Pierce & Griffin 1938; Griffin & Galambos 1941; Galambos & Griffin 1942) are synonymous with echolocation and their solution to Spallanzani's bat problem that dated from 1794. Griffin's (1958) book *Listening in the Dark* tells the story of the discovery of echolocation. The topic was explored at biosonar meetings convened in 1966 (Italy: Busnel 1967), 1978 (Ile de Jersey: Busnel & Fish 1980), 1986 (Nachtigall & Moore 1988), 1998 (Portugal: Thomas et al. 2004) and 2009 (Japan: special volume, *Journal of the Acoustical Society of America*).

In 1960, Griffin, Webster and Michael reported how hunting bats used echolocation to find flying insects, providing a clear indication of an advantage that echolocation could confer on bats. They reported that several bat species bats used echolocation to detect, track and precisely locate flying insects under laboratory conditions (Fig. 1). Griffin et al. (1960) described 'feeding buzzes', the high pulse repetition rates (Fig. 2) associated with attacks on prey, and noted differences in rates of emission of calls by bats

Figure 1. A flying little brown bat with open mouth and forward pointing ears.

during search, approach and terminal phases of hunting across an attack sequence on a flying insect. This description remains in general use and is a topic of ongoing research (e.g. Jakobsen et al. 2013; Ratcliffe et al. 2013). The year 1960 also saw a change in the trajectory of growth in the numbers of papers published about echolocation (Grinnell 1980). Between 1938 (Pierce & Griffin) and 1960, 45 papers had been published; by 1978, 520 papers (Grinnell 1980). The first paper about echolocation by toothed whales, specifically porpoises, was published by Norris et al. (1961).

The richness of echolocation as a topic is reflected by the diversity of journals publishing papers on this sensory capability (see References). Here, I focus on bats and echolocation, building from the foundation set by Griffin et al. (1960). My main focus is animal behaviour directly or indirectly involving echolocation, including some examples of connections to neurobiology and neuroethology.

ECHOLOCATION BEHAVIOUR

Most bats, species in the order Chiroptera, echolocate by producing vocal signals in their larynges. Unlike flight, echolocation is not a characteristic of all bats. Most species of flying foxes and their Old World relatives (family Pteropodidae) do not echolocate. The

exception is two or three species of rousette bats (*Rousettus*) whose echolocation signals are tongue clicks rather than signals produced by passing air over vocal folds in the larynx (Altringham 2011).

The diversity of bats is reflected in their faces. Egyptian rousette bats, *Rousettus aegyptiacus* (Pteropodidae), has a dog-like face (Fig. 3a), while a Pallas' mastiff bat, *Molossus molossus* (Molossidae), has relatively large ears (Fig. 3b) but no other obvious facial features related to echolocation. Fleshy noseleafs occur in several families of bats, including Geoffroy's horseshoe bat, *Rhinolophus clivosus* (Rhinolophidae; Fig. 3c), and a large-eared woolly bat, *Chrotopterus auritus* (Phyllostomidae; Fig. 3d). Other bats, such as an Antillean ghost-faced bat, *Mormoops blainvillii* (Mormoopidae; Fig. 3e), have flaps of skin and various structures in the ear that probably are related to echolocation. A vampire bat, *Desmodus rotundus* (Phyllostomidae; Fig. 3f), lacks the typical prominent noseleaf of most phyllostomids.

Laryngeal echolocation of bats hunting a range of insect prey is well documented, including the characteristic increase in pulse repetition rates (feeding buzzes) during attacks on prey (e.g. Kalko 1995; Schnitzler & Kalko 2001). Bats such as greater bulldog bat, *Noctilio leporinus* (Noctilionidae), use echolocation to detect and track fish swimming near (and breaking) the water's surface (Suthers 1967; Schnitzler et al. 1994). Other bats such as long-legged bat, *Macrophyllum macrophyllum* (Phyllostomidae), hunt for and take prey from the water's surface (Brinkløv et al. 2010), or from spiders' webs (Natterer's bat, *Myotis nattereri*, Vespertilionidae; Siemers & Schnitzler 2000). Yet others rely more on prey-generated sounds, sometimes combined with echolocation to detect and assess prey (e.g. greater false vampire bat, *Megaderma lyra*, Megadermatidae: Ratcliffe et al. 2005; Hemprich's big-eared bat, *Otonycteris hemprichii*, Vespertilionidae: Holderied et al. 2011).

Echolocating bats use a range of signals when searching for insect prey (Kalko & Schnitzler 1993; Schnitzler & Kalko 2001; Maltby et al. 2009; Fig. 4). The sounds range from being frequency modulated (FM) (broadband or narrowband) to near or even constant frequency (CF). While FM sweeps tend to go from high to low frequency, this is not always the case. Some bats use very short duration (<1 ms long), steep FM signals, which may or may not include harmonics of the fundamental vocal element (see below). Simmons & Stein (1980) suggested how bats could use different signal designs to their advantage in locating prey. The variety of
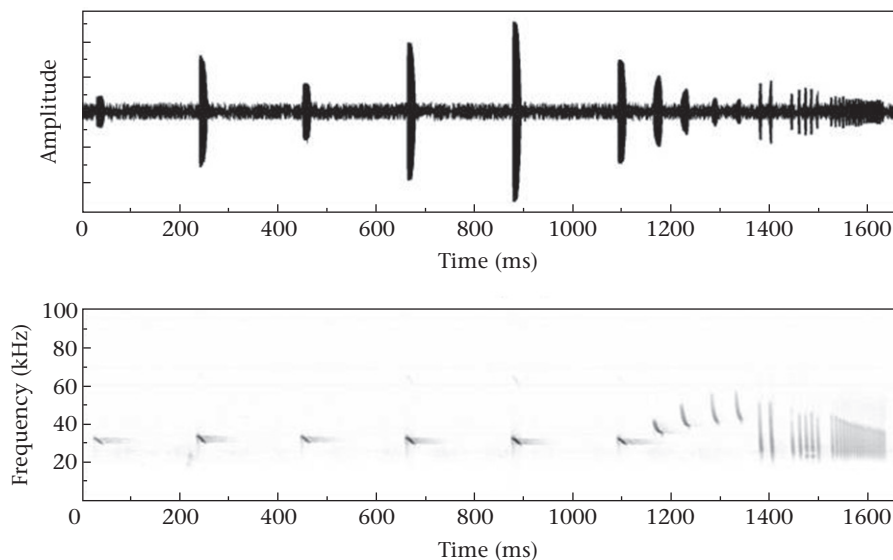
Figure 2. A feeding buzz recorded from a black mastiff bat, *Molossus rufus*, foraging in Belize.

Figure 3. (a) Two Egyptian rousettes, which have dog-like faces typical of pteropodids. (b) The faces of some bats (e.g. Pallas' mastiff bat) lack noseleafs or flaps of skin. Leaf-like structures on the noses and faces of bats are common in other bats: (c) Geoffroy's horseshoe bat and (d) big-eared woolly bat. (e) An Antillean ghost-faced bat has flaps of skin around the mouth and a variety of structures in the ear. (f) Vampire bats have modified noseleafs.

signal emissions used in echolocation has become clearer as more species are studied in the field (e.g. Kingston et al. 1999; Guillén-Servent & Ibáñez 2007; Mora et al. 2011).

The diversity of echolocation behaviour in bats and toothed whales is astonishing. The discovery that bats use echolocation to recognize water surfaces in the laboratory (Grief & Siemers 2010) and in the field (Russo et al. 2012) demonstrated that this mode of orientation was not limited to detecting obstacles or potential food. Furthermore, more recent studies have demonstrated that the tongue-click echolocation of Egyptian rousettes (Fig. 3a) is as sophisticated as that of bats that use laryngeal echolocation (Yovel et al. 2010).

THE TRAIL ONWARD FROM GRIFFIN ET AL. (1960)

Since 1960 as well as 2000, there have been dramatic changes in our views about the evolutionary history, phylogeny and classification of bats. The discovery of extremely well preserved Eocene fossils (e.g. *Icaronycteris index*: Jepsen 1966; *Onychonycteris finneyi*:

Simmons et al. 2008; Fig. 5) established that the radiation of bats was well underway by the Middle Eocene (Simmons & Geisler 1998). Phylogenetic studies revealed that bats (Chiroptera) are monophyletic (Simmons & Geisler 1998) and should be classified into two suborders, Yinpterochiroptera and Yangochiroptera (Teeling et al. 2005). Note, however, that these two suborders are not equivalent to the earlier suborders, Megachiroptera and Microchiroptera. Several families that had been classified in Microchiroptera (Rhinopomatidae, Craseonycteridae, Megadermatidae, Rhinolophidae and Hipposideridae) are now placed with Pteropodidae in the Yinpterochiroptera. Echolocation is at the heart of the debate. Was echolocation an ancestral trait? Did it evolve more than once?
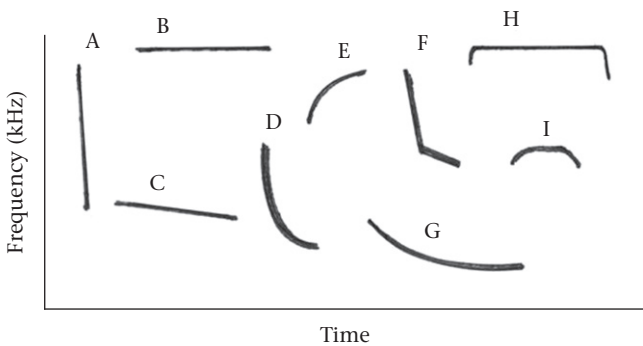
Figure 4. Echolocation calls produced by laryngeally echolocating bats searching for targets vary considerably with respect to patterns of frequency change over time. Included are frequency modulated (FM) calls that may be steep (A, D) or shallow (C, G) or some combination (F). Others are narrowband, dominated by a single frequency (B, H) or may be slightly broader in bandwidth (I, C). Calls that combine constant frequency (CF) and FM sweeps (H) are typical of high duty cycle echolocators.
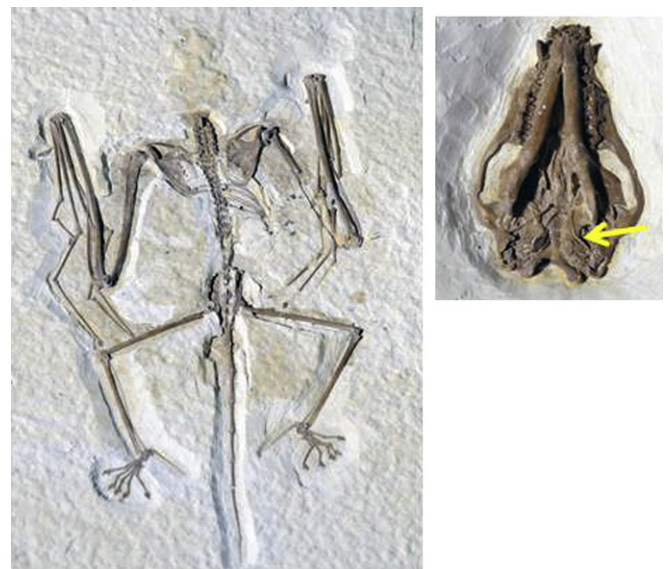
Figure 5. One of two fossil *Onychonycteris finneyi* specimens known. The postcranial skeleton is typical 'bat' although each of the fingers has a small claw, which is not a feature of modern bats. The skull (on the opposite side of the slab) is well preserved (if flattened). Note stylohyal bone, which is well developed (arrow).

As usual in discussions of phylogeny, not everyone agrees with this new classification of bats. When we turn to molecular genetics for an answer (Brenner 2012), the situation does not get any clearer. Li et al. (2007) reported that the *FoxP2* (foxhead box protein P2 transcription factor) gene is very diverse in echolocating bats, apparently supporting the 'new' phylogeny. Later, Li et al. (2008) reported that the hearing gene, *Prestin*, did not show the same level of support for the new phylogeny of bats.

Tools

Changes in instrumentation and software have played an enormous role in research on echolocation. Pierce's sonic detector (Pierce & Griffin 1938) was fundamental to the discovery that bats emitted vocalizations with frequencies well above the range of human hearing (i.e. ultrasonic). The Holgate, one of the first commercially available bat detectors, appeared around 1963. Previously, researchers had to construct their own ultrasonic detectors, and even in 1979, some of the best equipment was custom made (Simmons et al. 1979). Initially the echolocation calls of bats were presented only in the time domain as oscillograms (Griffin 1958). Later calls were recorded on magnetic tape with recorders running at 76.2 or 152.4 cm/s. Griffin usually had a sly smile when he referred to the heavy tape recorders used in the work as 'portable' because they had handles. Even the smaller and lighter ones weighed more than 20 kg without the power supply. In 2012, many different bat detectors were available commercially, along with software for recording, analysing and synthesizing echolocation calls from about 10 kHz to more than 200 kHz (e.g. Adams et al. 2012).

At the Animal Sonar Systems meetings in 1966, 1978 and 1986, colleagues studying bat echolocation reported the results of many field experiments and observations. Meanwhile, most of the echolocation data for odontocetes came from captive animals. One reason for the discrepancy is the higher diversity of echolocating bats (~1000 species) compared with that of odontocete whales (~68 species). A second reason is the reality that it is much easier to work with a 5, 10, 30 or 100 g bat than it is a 65 kg porpoise or a 5000 kg killer whale. Furthermore, work with bats involves far less paperwork and orders of magnitude less money, infrastructure and personnel.

However, work with trained odontocetes provided a wealth of detail that was not usually available for bats. The ability of belugas, *Delphinapterus leucas*, to detect targets in clutter and the ability of bottlenose dolphins, *Tursiops truncatus*, to distinguish among targets was obvious in captive animals (Au 1988), but would have been extremely difficult to detect in wild animals. The results of the work with belugas and bottlenose dolphins gave an indication of what was to come, whether the focus was odontocetes or bats.

By 2009 in Japan, technological developments meant that field data (video and recordings) became available for a wide range of cetaceans, demonstrating, for example, the ubiquity of feeding buzzes in species that use echolocation to detect, track and identify prey (e.g. Miller et al. 2004; Johnson et al. 2006, 2009; Madsen et al. 2007; Arranz et al. 2011).

Frequency of Echolocation Signals

Acoustic signals associated with echolocating bats eluded Spallanzani because most of the acoustic energy was ultrasonic. Svend Dijkgraaf monitored the acoustic signals of bats by listening for the 'Ticklaute' (ticking sound) that accompanied the production of each echolocation pulse (Dijkgraaf 1943, 1946). Using Pierce's sonic detector (Pierce & Griffin 1938), Griffin was able to monitor the echolocation calls of the bats he studied, and listened to a different assortment of sounds that had been unavailable to and unimaginable by Spallanzani. Furthermore, using tools of neurophysiology, Griffin & Galambos (1941) demonstrated that bats also heard the ultrasonic sounds they emitted. Both are examples of tools making a big difference in advancing science.

Echolocating bats use a range of frequencies in their signals (8 kHz to >200 kHz; Altringham 2011), some of which are not 'ultrasonic' because humans can hear them (e.g. large-eared free-tailed bats (Molossidae); plain-nosed bats (Vespertilionidae) such as spotted bats, *Euderma maculatum*). Thus, it is inaccurate to refer to echolocation in general, or to bat echolocation in particular, as ultrasonic. All echolocating birds produce clicks that are audible to humans (e.g. Fullard et al. 2010). Echolocation refers to using echoes of emitted sounds to form images of one's surroundings and it is not dependent on using ultrasonic frequencies.

Call Intensity and Range

The strength (amplitude) of echolocation signals strongly influences the range over which an echolocating bat can use sound emissions to detect insect-sized targets. It remains difficult to measure the decibel (dB) sound pressure level (SPL) of bat echolocation calls because most are very short in duration, shorter than the response time of equipment used to measure intensity. When call intensities have been measured, many bats exceed 110 dB SPL measured at 10 cm in front of the mouth (Griffin 1958). Early on it was obvious that some bats produce very high-intensity echolocation signals. Others, the so-called 'whispering bats', produced low-intensity calls, which were much more difficult to detect with the bat detectors of the time. New World leaf-nosed bats (Phyllostomidae) appeared to be whispering bats, but Mora & Macías (2007) showed that not all phyllostomid species whispered while echolocating. More recent studies using arrays of microphones show that both fruit- and animal-eating phyllostomids produce echolocation calls that are more intense than previously expected (e.g. Brinkløv et al. 2009, 2010).

Having details of call intensity and knowing which frequencies dominated echolocation calls allowed Lawrence & Simmons (1982) to illustrate the impact of atmospheric attenuation on the operational range of echolocation in air. Using a behavioural assay, Kick (1982) showed that echolocating big brown bats, *Eptesicus fuscus* (Vespertilionidae) first detected a 19 mm diameter sphere at a distance of 5 m. Using a combination of video and microphone recordings, Holderied et al. (2005) suggested that the call intensity of Botta's serotine, *Eptesicus bottae* (Vespertilionidae) was over 130 dB SPL at 10 cm. They determined that an echolocating Botta's serotine first detected an insect-sized target at about 20 m. Surlykke & Kalko (2008) used a three-microphone array operated with two video cameras to document insect detection distances of 20–60 m for a variety of Neotropical bats. It is clear now that aerial insectivorous bats produce echolocation calls that are about 125–140 dB SPL at 10 cm (e.g. Surlykke & Kalko 2008). Furthermore, whispering phyllostomid species produce echolocation calls that are about 100–110 dB SPL at 10 cm (e.g. Brinkløv et al. 2010).

The change of proposed detection distances is important because it provides a better indication of the temporal challenges that bats face while hunting insects on the wing. For example, if a bat's maximum detection distance is 5 m, and the bat flies at 5 m/s, it would have very little echo-processing time, and a seemingly insurmountable challenge. Even with a 30 m detection distance, a bat flying 5 m/s would have only 6 s from first detection to contact with a target (± the distance/time covered by the flying insect after detection). And to complicate matters further, many species of bats fly much faster than 5 m/s (e.g. silver-haired bats, *Lasionycteris noctivagans*; McGuire et al. 2011).

Sonar Beam

The use of arrays of microphones to monitor the behaviour of echolocators has greatly expanded our knowledge of the behaviour of bats and odontocetes (e.g. Madsen et al. 2007, 2010). More detailed information about the intensity of bats' echolocation calls (e.g. Surlykke & Kalko 2008) is one example of how this approach has advanced our knowledge. Moreover, Jakobsen & Surlykke (2010) showed how vespertilionid bats dynamically control the width of the biosonar beam (Fig. 6) when pursuing prey. Jakobsen et al. (2013) demonstrated that perceptual control of the biosonar beam provides a better explanation for why many echolocating bats emit ultrasonic signals than do theories involving prey size and wavelengths of sounds.

Harmonics

While the echolocation calls of some laryngeally echolocating bats are dominated by a single acoustic element (fundamental frequency), many other species use harmonics (overtones) in addition to the fundamental (Fenton et al. 2011). For example, the use of harmonics is prevalent and consistent in sheath-tailed bats (Emballonuridae), while in others, such as free-tailed bats (Molossidae), use of harmonics is more variable. In species such as a big brown bat, individuals flying in different situations vary their use of harmonics (Fenton et al. 2011). Work with captive animals clearly illustrates how big brown bats vary their use of harmonics when detecting targets in clutter (Hiryu et al. 2010; Bates & Simmons 2011; Bates et al. 2011) or in the presence of echolocating conspecifics within the same air space (Chiu et al. 2010).

Two common themes emerge from the accumulating evidence. First, many laryngeally echolocating bats actively control call design such as signal bandwidth through the use harmonics, adjusting their echolocation signals according to the situation(s) in which they are operating. Second, good-quality recordings, often from microphones arranged in an array, are necessary to consistently detect the presence of harmonics. Bats must be close enough to the microphones and flying within the microphone's lobe of sensitivity for full details of signal bandwidth to be revealed. Because of limitations in the type of equipment available for studying bat echolocation, these levels of details about bat calls were not readily accessible to Griffin et al. (1960).

Bat Hearing

Bats accomplish amazing feats with echolocation, usually without major changes to the mammalian auditory system (Neuweiler et al.

Figure 6. The acoustic beam of a flying bat illustrating how the bat changes the beam (reprinted with permission from Ratcliffe et al. 2013).

1980; Neuweiler 1989). Neural and behavioural audiograms (Fig. 7) reveal that almost all bats show typical tuning curves for mammals, differing mainly in the range of frequencies across which the animals are sensitive. Among bats, the exceptions to this are high duty cycle echolocators that show a sharply tuned area of sensitivity (Fig. 7), termed the 'acoustic fovea' (Schuller & Pollack 1979). These zones of sensitivity are a function of mechanical tuning of the basilar membrane combined with populations of exquisitely sensitive, narrowly tuned neurons (Neuweiler 2000). Specialized central auditory neurons have also been reported in other bats, but they are not unique to bats or to echolocation. Included in the brain are both neurons tuned to signal duration (duration-tuned: Faure et al. 2003; Aubie et al. 2012) and neurons tuned to delay between pulse and echo (delay-tuned: Portfors & Wenstrup 1999). In the brain, both the inferior colliculus and the auditory cortex are central to auditory scene processing by echolocating bats, although the details are known for only a few species (Neuweiler 2000).

An adaptation essential to echolocation is ensuring that the loud outgoing signal does not mask or deafen the sound emitter to the usually much fainter returning echoes. Jen & Suga (1976) demonstrated that little brown bats, *Myotis lucifugus* (Vespertilionidae) avoided self-deafening by slightly disarticulating the middle ear ossicles (malleus, incus and stapes) the moment before an echolocation pulse was produced. The bones were rearticulated the moment after the call ended. Note that the bat did not turn off its auditory system during pulse production, because the outgoing call had to be registered in the brain for future comparison with returning echoes. Therefore, self-dampening (attenuating) is a more accurate description than is self-deafening because the bat's ears are up to 20 dB less sensitive during signal production than when the bat is not calling. Differences between what the bat says and what it hears are integral to the process of echolocation.

Typical echolocators, including most bats, separate pulse and echo in time. These echolocators typically produce echolocation calls of short duration separated by long periods of silence, which are said to be calls of low duty cycle. Some other bats (horseshoe bats, Rhinolophidae; Old World leaf-nosed bats, Hipposideridae; and Parnell's moustached bat, *Pteronotus parnellii*; Mormoopidae) separate pulse and echo in frequency. They produce calls of longer duration separated by short periods of silence, and these calls are said to be of high duty cycle. The calls of high duty cycle bats are dominated by a single (constant) frequency (CF). This approach to echolocation exploits Doppler shifts in echo frequency that naturally occur when the sound emitter is moving relative to the receiver. The process in high duty cycle bats depends upon Doppler shift compensation, which involves lowering the CF frequency of the outgoing signal to compensate for the Doppler-shifted increase in frequency of the returning echo. The bat's goal is to maintain the frequency in the returning echoes at the centre of the acoustic fovea (Smotherman & Guillén-Servent 2008). High duty cycle echolocation appears to be a specialization for detecting fluttering insects within foliage (Lazure & Fenton 2011) that has evolved twice in bats (Teeling 2009). It may be a specialization associated with collecting more details about fluttering targets in clutter (Fenton et al. 2012).

Most echolocating bats are oral emitters, broadcasting signals through the open mouth (Fig. 8a). Others, such as rhinolophids, hipposiderids and phyllostomids, are thought to emit signals through their nostrils (Fig. 8b) (Pedersen 1998). However, photographs of flying bats suggest that some phyllostomids fly with open mouths (Fig. 8c).

Echolocation and Communication

Griffin et al. (1960) found that bats could detect and track insect prey even in the presence of background noise. Lesser bulldog bats,
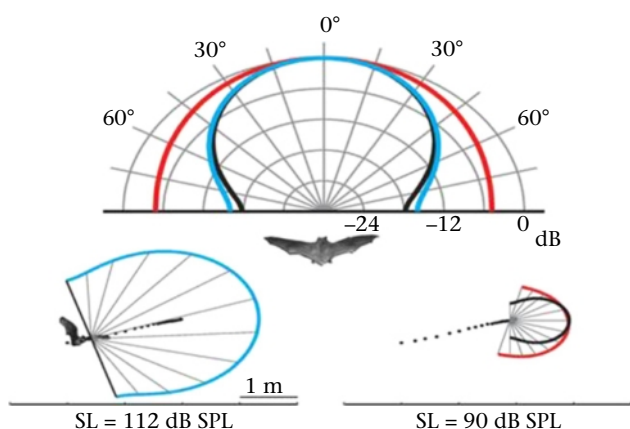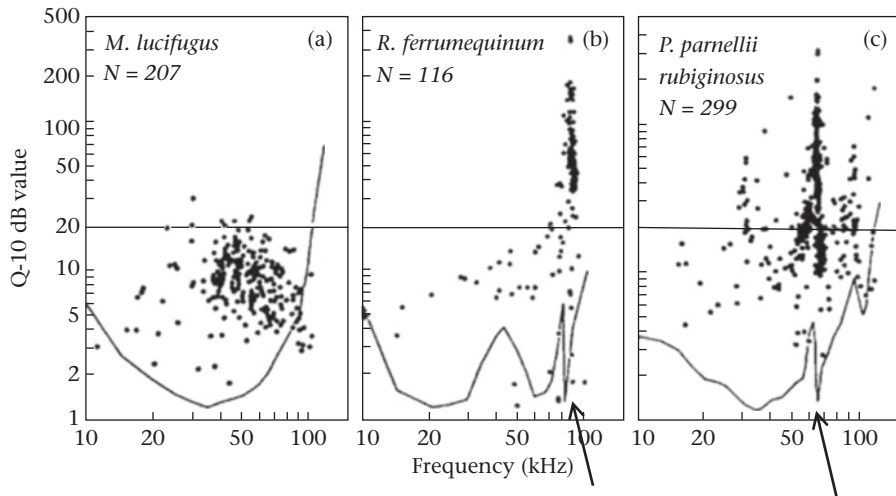
Figure 7. Audiograms of a little brown bat (*M. lucifugus*), a greater horseshoe bat (*R. ferrumequinum*) and a Parnell's moustached bat (*P. parnellii*) comparing a typical low duty cycle bat (a), and two high duty cycle bats (b, c) with acoustic fovea (arrows). Reprinted with permission from Schnitzler & Denzinger (2011).

Noctilio albiventris (Noctilionidae) emit echolocation calls that start with a narrowband FM component and end with a steep downward FM sweep. The initial narrowband component opens windows of reception in the bat's auditory system, setting the stage to receive later-arriving echoes. Presenting flying lesser bulldog bats with a well-timed narrowband signal effectively jams their echolocation by mismatching the timing of signal production and reception (Roverud & Grinnell 1985). Puechmaille et al. (2011) suggested that this phenomenon could explain divergence in echolocation calls in bumblebee bats, *Craseonycteris thonglongyai* (Craseonycteridae). Specifically, the calls of bumblebee bats and those of sympatric Himalayan whiskered bats, *Myotis siligorensis* (Vespertilionidae) are similar enough that the same jamming mechanism could influence the effectiveness of the echolocation of bumblebee bats. These examples illustrate that there can be more to echolocation signals than collecting information about targets.

It is now widely recognized that the signal that one bat uses to collect information about its surroundings also can serve in communication (e.g. Jones & Siemers 2011). The possibility that bats listen to the echolocation calls of other bats was discussed by Griffin (1958) based on his observations of foraging eastern red bats, *Lasiurus borealis* (Vespertilionidae). Möhres (1967) reported that captive greater horseshoe bats, *Rhinolophus ferrumequinum* (Rhinolophidae) used the echolocation calls of preferred individuals to identify and locate their roost-mates. The intensity of many echolocation calls, the rates at which they are produced and the information contained in the echoes (even for bat biologists) all suggest that echolocation calls serve an intraspecific communication function. Barclay (1982) used playback presentations to demonstrate this in little brown bats, and since then the topic has received much more attention. Chiu et al. (2008) demonstrated that big brown bats flying with conspecifics may not echolocate. Furthermore, individual bats may adjust their echolocation calls according to the situation in which they are operating, which could represent either jamming avoidance (Gillam et al. 2007) and/or some form of air traffic control (Ratcliffe et al. 2004; Ulanovsky et al. 2004). Monitoring echolocation calls could allow group hunting (Dechmann et al. 2009), maintain group cohesion (Dechmann et al. 2010; Voight-Heucke et al. 2010), or advertise the location of roosts (Ruczynski et al. 2007). High call repetition rates, such as feeding buzzes associated with attacks on prey, also occur in social interactions (Swartz et al. 2007; Bayefsky-Anand et al.
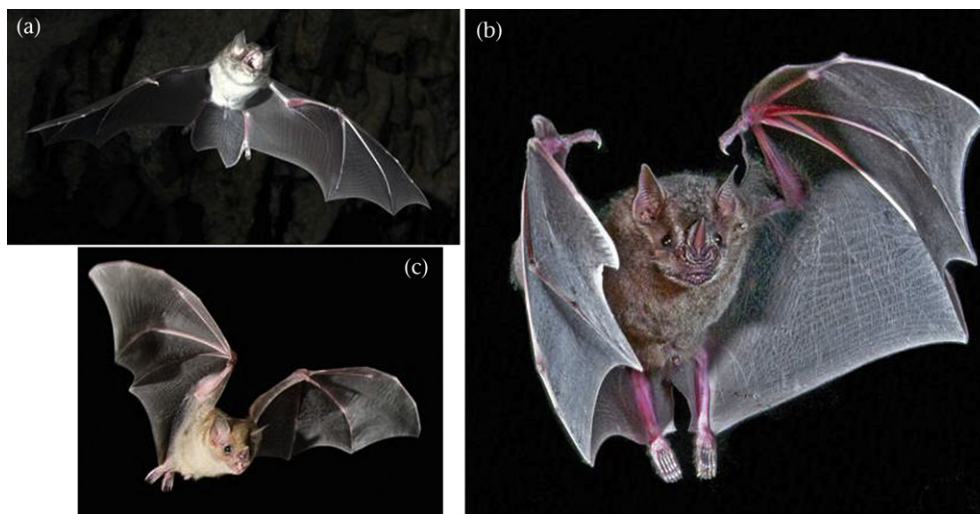
Figure 8. (a) A Parnell's moustached bat, *Pteronotus parnellii* (Mormoopidae), flying inside St Clair cave in Jamaica with its mouth wide open. (b) A Jamaican fruit bat, *Artibeus jamaicensis* (Phyllostomidae), flying with its mouth closed. (c) Another phyllostomid, a little yellow-shouldered bat, *Sturnira lilium*, flying with its mouth partly open.

2008). Selection for effective communication has been suggested for the diversification of some bats (Kingston & Rossiter 2004).

Information Leakage

One of the best known consequences of bat echolocation is the ability of some insects to detect the bats' calls and use this information to avoid or evade attacks (Roeder 1967). Ears for detecting the echolocation calls of bats have evolved independently in at least five orders of insects (Lepidoptera, Neuroptera, Orthoptera, Coleoptera and Mantodea; Faure et al. 2009). In insects such as moths, one to four auditory neurons transmit information from the ear to the central nervous system to coordinate startle and escape behaviours (Roeder 1967; Fullard et al. 2003). While bat-detecting ears usually occur in pairs, most praying mantids have a single ear (Yager 1990). The audiograms (behavioural or neural) of moths and other insects suggest that bats might reduce their conspicuousness to insects by mismatching the frequencies of echolocation calls and the hearing sensitivities of insects (e.g. Fenton & Fullard 1979). Echolocation calls dominated by very high or very low frequencies may be almost inaudible to at least some moths (Fig. 9) (Fullard et al. 2007). The ears of moths, however, are energy transducers that operate by integrating signal intensity across duration. Therefore, to the ear of the moth, high CF frequency, long duration calls of some high duty cycle bats may be as conspicuous as lower frequency, shorter duration calls of some low duty cycle bats (Jacobs et al. 2008).

Some tiger moths (Arctiidae) produce clicks of extremely short duration in response to an attacking bat, an interaction that can involve advertising bad taste (e.g. Acharya & Fenton 1992; Barber & Conner 2007) and/or interfering with the bats' echolocation (Ratcliffe & Fullard 2005; Corcoran et al. 2009; Corcoran & Connor 2012). Arctiids show specializations for protecting themselves against visually hunting, diurnal predators as well as echolocating nocturnal predators (Ratcliffe & Nydam 2008). By adopting a 'stealth' approach to echolocation, bats such as barbastelles, *Barbastella barbastellus* (Vespertilionidae) evade detection by moths (Goertlitz et al. 2010). Parallel developments in echolocation-mediated predator−prey interactions among odontocetes and their prey are now becoming known (Barrett-Lennard et al. 1996; Deecke et al. 2005).

Anatomy

Some specializations for echolocation are obvious in the faces of bats (Fig. 3), including prominent noseleafs and structures around the mouth (Hartley & Suthers 1987; Vanderelst et al. 2010), as well as large and conspicuous ears (Obrist et al. 1993). Furthermore, other obvious structures around the noseleaf and ears, such as the grooves of rhinolophids (Zhuang & Müller 2006) or the tragus and ear margins, play a role in echolocation (Müller 2004; Müller et al. 2006; Gao et al. 2011). Inflations along the vocal tract can also influence signal structure (Suthers et al. 1988). Other specializations are less conspicuous, such as those associated with the larynx (Griffiths 1978) or the stylohyal bone, which connects the larynx to the tympanic bone as part of the hyoid chain (Veselka et al. 2010). Superfast muscles are fundamental to the production of very fast echolocation call rates (50 to >100 Hz) observed in feeding (and other) buzzes (Elemans et al. 2011).

Other Sensory Modalities

Vision

None of the more than 1200 species of extant bats is blind, and some species see very well (Suthers 1970; Bell 1985). Bradbury &
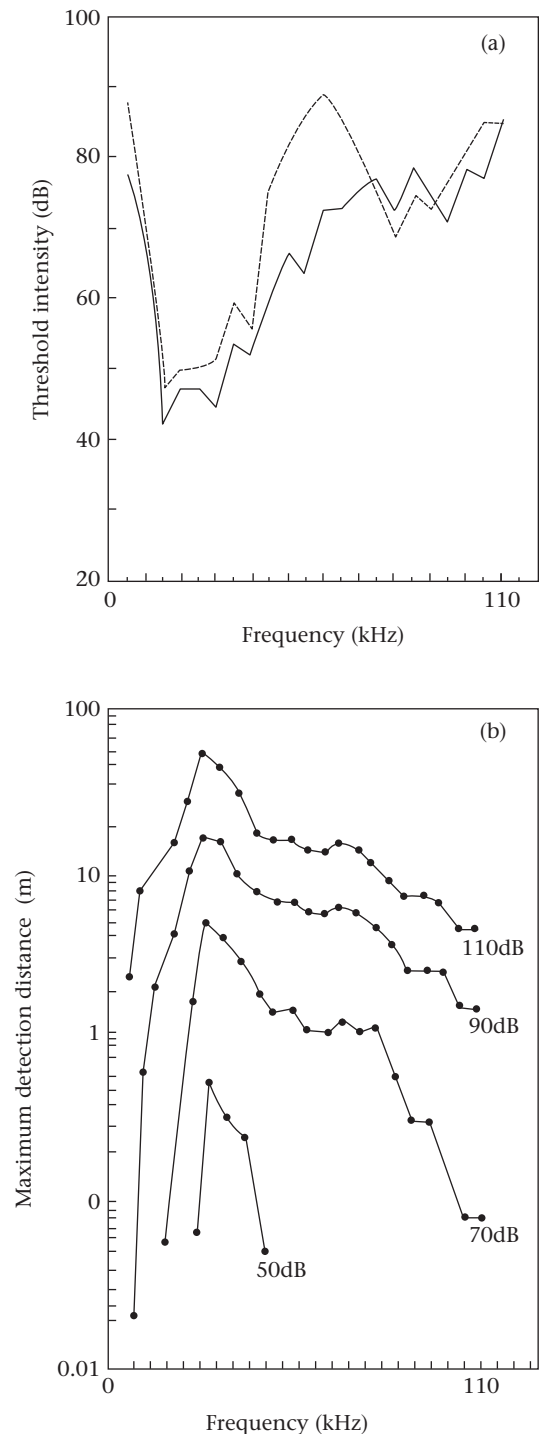
Figure 9. Audiograms of (a) two moths, *Spilosoma prima* (dashed line) and *Phragmatobia assimilis* (solid line), demonstrate that both species hear best in the frequencies dominating the echolocation calls of sympatric bats. Inverting the audiograms (b) and considering hearing thresholds, illustrates the distances at which different echolocation calls would be detected by these moths and how initial call intensity affects distance of detection (reprinted with permission from Fenton & Fullard 1979).

Nottebohm (1969) showed that little brown bats continued to echolocate even when flying in well lighted conditions, but both California leaf-nosed bats, *Macrotus californicus* (Phyllostomidae) and pallid bats, *Antrozous pallidus* (Vespertilionidae) stop echolocating when the lighting is good, the equivalent of a clear moonless night (Bell 1985). Big brown bats integrate information

acquired from vision and echolocation (e.g. Horowitz et al. 2004), but for most species we lack details about how vision and echolocation interact. At least some species of nectar-feeding bats see in the ultraviolet spectrum (Winter et al. 2003; Muller et al. 2009), but the significance of this ability remains relatively unstudied.

Infrared

The discovery that vampire bats, *Desmodus rotundus* (Phyllostomidae), have infrared sensors on their noseleafs (Kurten & Schmidt 1982; Kurten et al. 1984) and can detect a heat source of 32 °C from 13 cm added another dimension to the sensory world of bats. Gracheva et al. (2011) demonstrated that modified nociceptors (TRPV1, Transient Receptor Potential Vanilloid 1) on the edge of the noseleaf in vampire bats are heat detectors. In other mammals, TRPV1 detect noxious temperatures (>43 °C), and in vampire bats, the temperature threshold for activity is reduced. It remains unknown whether the other species of vampires (*Diaemus youngii*, *Diphylla ecaudata*; Phyllostomidae) or other predatory bats also have infrared detectors.

Sense of touch

Spallanzani had considered the possibility that bats had an exceptional sense of touch that might account for their ability to negotiate an obstacle course in the dark (Griffin 1958). Chadha et al. (2011) demonstrated that hairs on the wings of big brown bats are sensors integral to monitoring air movement across the wing membrane. Using a depilatory cream, Chadha and colleagues showed that captive big brown bats lost their ability to make precise aerial manoeuvres after these sensory hairs were removed. The manoeuvrability returned when the hairs grew back. This work and others from the same laboratory (Sterbing-D'Angelo et al. 2011) demonstrated that bats collect sensory information from a variety of sources. Further research on the arrangement of sensory hairs suggests functional diversity in this feature among bats (S. Swartz, personal communication).

NEXT STEPS AND CONTEXTS

Many questions about bats and echolocation promise to be endlessly interesting. One of my favourites is whether or not laryngeal echolocation evolved simultaneously in bats, or if one or the other came first? Speakman & Racey (1991) suggested that by coordinating pulse production with the downstroke in flight, bats minimized the cost of producing intense vocalizations. Voigt & Lewanzik (2012) supported this position and argued that echolocation and flight evolved simultaneously. Fenton et al. (1995) supported the idea that echolocation evolved first because it would have given the ancestors of bats access to nocturnal flying insects, a food supply not readily available to diurnal insectivores hunting by vision. Simmons et al. (2008) articulated the view that flight evolved before echolocation. Only additional evidence, perhaps in the form of fossils, might settle (or complicate) this matter.

How do bats synchronize input from vision and echolocation (not to mention, touch and olfaction)? If you monitor sounds produced by a little brown bat flying around in a room during the day two things usually are obvious. First, the bat does not collide with objects/obstacles in the room. Second, it emits echolocation calls and often produces buzzes (landing buzzes) as it approaches a landing site. Then, after some time, the bat, still echolocating, often flies directly into a window (whether glass or screen), apparently having switched from echolocation to vision. But what if the bat was an echolocator with larger eyes and more acute vision (e.g. a California leaf-nosed bat)?

How do bats that eat fruit, nectar and pollen or blood use echolocation? von Helversen & von Helversen (1999) reported ultrasonic nectar guides in some bat-pollinated flowers. Simon et al. (2011) reported a leaf modified as a beacon to attract echolocating bats to flowers. Questions about how much fruit-eating bats depend upon echolocation to detect or assess food remain unanswered, although some phyllostomids produce echolocation calls as they approach fruit trees (e.g. Brinkløv et al. 2011) while others appear to depend on both acoustics and olfaction to identify figs (Korine & Kalko 2006). At present we do not know whether/how vampire bats use echolocation when hunting.

How do bats thwart the hearing-based defences of their prey? Barbastelles use echolocation calls not readily detectable by moths with bat-detecting ears (Goertlitz et al. 2010), but eastern red bats also catch tympanate moths (Clare et al. 2011) that should have the ability to detect the bats' echolocation calls. Then, there are bat-eating bats (e.g. in Australia, Southeast Asia and India, sub-Saharan Africa and the Neotropics). Do bat-eating bats use echolocation to detect, identify and track prey? Or do they sit or fly quietly while monitoring a prey's behaviour via its echolocation calls?

Griffin's curiosity about migration and orientation underlay the work that led to the discovery of echolocation. The fact that even small (<10 g) insectivorous bats may live very long lives (>30 years) in the wild (e.g. Keen & Hitchcock 1980; Podlutsky et al. 2005) and move considerable distances between summer and winter grounds makes the life history of bats even more fascinating. Although detailed studies are available for relatively few species, we know that some species are long-lived social animals. Social units in roosts may be centres of information exchange (Wilkinson 1992). Moreover, many bats in a roost are often the most important thermoregulatory resource there (e.g. Willis & Brigham 2007). Bats learn by watching other bats (Gaudet & Fenton 1984), behaviour that involves integrating multiple sensory cues, including echolocation (Page et al. 2012) associated with social living.

Data on remotely monitoring bat activity by recorded echolocation calls suggest that more discoveries await. Extensive nocturnal activity of bats during the depths of winter on the prairies in Canada (Lausen & Barclay 2006) is intriguing. It suggests the presence of hibernacula unknown to us, and it implies that energy budgets of hibernating bats may not be as tight as we previously presumed (e.g. Thomas et al. 1990).

The discovery that Egyptian rousettes have and use a large-scale visual space map (Tsoar et al. 2012) again raises questions about bat orientation and migration (Griffin 1970). Isotope analysis has provided evidence of long-distance migration by some bats (Cryan et al. 2004; Fraser et al. 2012) and has raised questions about their flight patterns (McGuire et al. 2011) and physiology (McGuire et al. 2013). This leaves unanswered questions about what cues migratory and other bats use in large-scale navigation, perhaps the lure that originally drew Griffin to bats.

Moss et al. (2011) emphasized that sensorimotor systems are fundamental to echolocation and reflect a combination of sonar signals and the bat's perception of the complex scene revealed by the differences between sonar signals and echoes. Active control of vocalizations, including, for example, the addition of harmonics, are fundamental to the operation of echolocation. This is the situation that Griffin et al. (1960) first revealed. So far, bats appear to have the high duty cycle approach to echolocation to themselves.

Griffin often referred to echolocation as the 'magic well' because every time you delve into the topic, you come up with something new to explore. Bats are a magic well for the same reason. The combination of bats and echolocation is particularly alluring,

offering many parallels and convergences with odontocetes and the other animals that face similar sensory challenges.

Acknowledgments

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