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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.

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

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☆ In honour of Donald R. Griffin, Frederic A. Webster and Charles R. Michael (1960) ‘The echolocation of flying insects by bats’ (**8,** 141–154).

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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

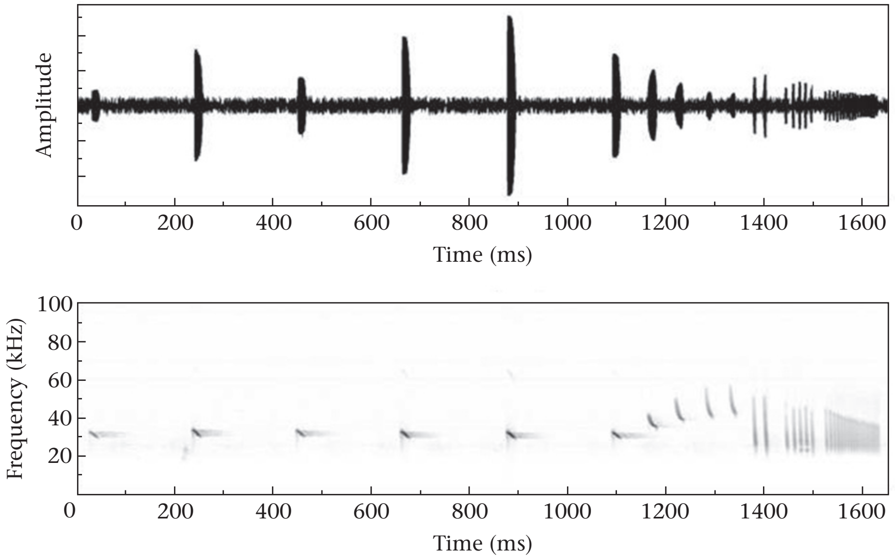

Figure 2. A feeding buzz recorded from a black mastiff bat, *Molossus rufus*, foraging in Belize.