



Early milestones in the understanding of echolocation in bats

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Abstract

Almost 80 years ago, Griffin and Galambos discovered the phenomenon of echolocation in bats. Since then, the field has grown exponentially as new generations of investigators have joined the chase and technological advances have revolutionized working with ultrasound in the laboratory and in the field. Today our understanding of the diversity of behavioral and neural adaptations for echolocation constitutes one of the paramount triumphs of neuroethology. At the invitation of the editor in chief, I here review some of the important milestones in the discovery and early understanding of echolocation in bats through about the mid-1980s.

Keywords Echolocation · History · Bats · Animal sonar · Orientation

Foundational discoveries of behavioral skills

Initial studies

Echolocation is one of the most fascinating phenomena in animal behavior, and its understanding is one of the triumphs of neuroethology. The story begins when the great Italian physiologist, Lazzaro Spallanzani, became interested in bats. Spallanzani was a polymath with insatiable curiosity, an insistence on repeatable experimental evidence, and the protection of the church. At a time when science was still guided mainly by Aristotle, he was a careful, rigorous experimentalist, best known for proving that digestion is chemical, that animals can be artificially inseminated, and—50 years before Pasteur—that spontaneous generation does not occur in a heated broth after sealing the flask. He also became interested in bats and found that they could avoid obstacles in flight and lead apparently normal lives even after their eyes had been removed. In an extensive series of ingenious experiments, he and his Swiss friend and counterpart, Louis Jurine, established that hearing was the sense that enabled blinded bats to avoid obstacles, but they did not realize that emitted sounds were involved. The preeminent naturalist of

the time, Prof. G. Cuvier, refused to believe them, and his influence appears to have stifled interest in the subject for the next 100 years.

In 1908, a young American zoologist at Indiana University repeated many of the experiments of Spallanzani and Jurine, additionally quantifying bats' orientation abilities by testing their ability to avoid vertically stretched wires in a flight room. He verified their remarkable ability to orient without vision, but not when deafened, concluding that “the sixth sense of bats is located in the inner ear” (Hahn 1908). Not long after this, stimulated by the Titanic disaster in 1912, Sir Hiram Maxim, a well-known inventor, wrote a letter to *Scientific American* proposing that low-frequency sound generators be mounted on the hulls of ships to detect icebergs, the way bats use their wing-beat sounds to detect obstacles (Maxim 1912). He was wrong about bats, but the idea of sonar was born. A few years later, Hartridge (1920) pointed out that low frequencies would not work for bats because the obstacles they had to avoid were too small to reflect significant echoes at low frequencies. Ultrasonic frequencies might work, however,...and the concept of echolocation was born. This colorful story has been described in detail by MacArthur (2000), but a very readable account is provided by Griffin (1958) in his much honored classic, *Listening in the Dark*.

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The discovery of echolocation

Ultrasound

Donald Griffin grew up in New England, at one time wondering which he wanted most—to become a fur trapper or a sea captain. The first of these ambitions led to a growing interest in mammals, including bats. A summer working with a bird banding group led him to use bird bands with bats to study their movements between colony sites, their homing capabilities, and their annual migrations back and forth between Cape Cod in the summer and caves in western Massachusetts and Vermont where they hibernated in the winter. As a junior at Harvard, he was aware of Spallanzani's demonstration that blinded bats flew as well as ever, and he knew of Hahn's experiments, but he had not read Hartridge's paper proposing that bats might use ultrasound (then called supersound) to orient. He had clearly been thinking and talking about the problem; however, for when he learned that a physics professor (George W. Pierce) had developed a piezoelectric salt crystal microphone capable of detecting the ultrasounds produced by insects, he sought out the professor and asked if they could try his apparatus on bats. When the parabolic horn of the detector was pointed at a cage full of active little brown bats (*Myotis lucifugus*), they found that the bats were producing a steady barrage of ultrasound covering a wide range of frequencies. Controls showed that these were not simply the sounds of bat claws scratching the wire mesh in the cage, but rather streams of discrete sounds. With the chart recording technology of the day, Pierce and Griffin could tell only that the sounds were brief, lasting less than 100 ms. To their disappointment, however, they could rarely detect ultrasonic pulses from flying bats, so limited their conclusions to the discovery that bats could produce pulses of ultrasound (Pierce and Griffin 1938).

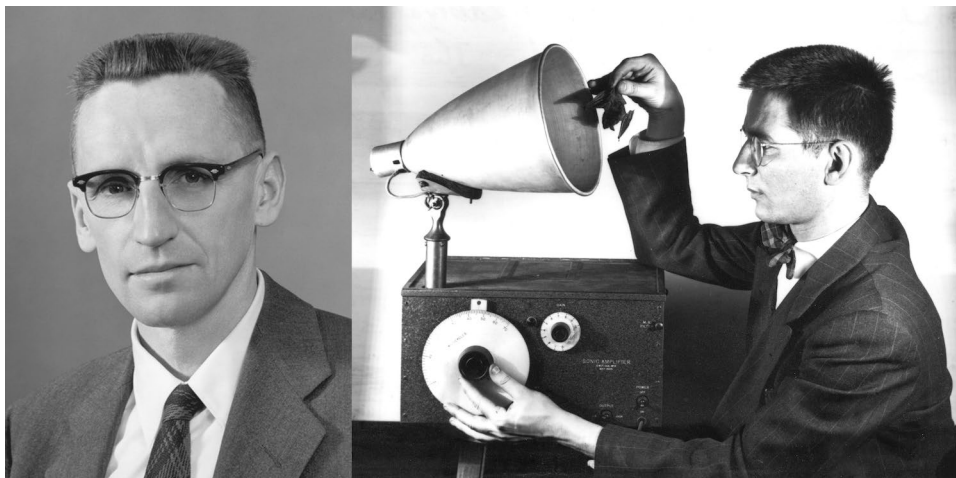
Echolocation

The next advance came only after Griffin had begun his PhD work on homing and migration in birds. In his first year of graduate school, he encountered another graduate student, Robert Galambos, who expressed interest in the bat project, and they embarked on a more thorough set of experiments. Almost immediately, they discovered that if the Pierce detector's parabolic horn was pointed directly at a flying bat, the detector picked up a stream of ultrasonic pulses. They repeated many of Spallanzani's experiments with the added refinement of using arrays of wires as Hahn (1908) had, enabling them to quantify the bats' obstacle avoidance capabilities. As expected, the ears were necessary for obstacle avoidance. More importantly, knowing that the bats were emitting ultrasonic pulses during flight, they tied the mouth shut and sealed it tightly with collodion. Bats with normal hearing but mouths sealed were completely disoriented until even a tiny crack appeared in the collodion. Clearly both the emitted pulses and hearing were necessary. Echolocation (a term coined by Griffin 1944) had been proved (Griffin and Galambos 1941; Galambos and Griffin 1942) (Fig. 1).

Dijkgraaf

It should be mentioned that Sven Dijkgraaf, working in German-occupied Holland without access to current scientific journals or to equipment sensitive to ultrasound, independently concluded that bats emitted sounds and used the echoes for orientation (Dijkgraaf 1946). He had repeated many of the Spallanzani experiments and, in addition, heard faint sounds, which he called *Ticklaute*, as bats flew by. His findings required keen observation and acute insight.

Fig. 1 Donald Griffin in the early 1950s (left) and Robert Galambos, about 1941, with a bat and the Pierce detector



Hearing ultrasound: cochlear microphonics to 98 kHz

After their discovery that bats did indeed orient and avoid obstacles by echolocation, Griffin and Galambos somewhat surprisingly decided that the former would return to his PhD project on homing in herring gulls and common terns, while Galambos, who was just beginning his graduate studies on the physiology of hearing in the laboratory of Prof. Hallowell Davis in the Harvard Medical School, would study bat hearing. Griffin did pioneering work on homing, including following homing birds in airplanes, but his findings are extraneous to this review. Galambos found that the sensitivity and magnitude of the cochlear microphonics in several species of bats were greatest at ultrasonic frequencies of 30–50 kHz, and could be recorded up to 98 kHz, thus covering the range of emitted frequencies (Galambos 1942; Griffin 1958). Further work on the physiology of hearing in bats would come only about 15 years later.

Characterizing the emitted orientation sounds

Pulses are brief, loud, and sweep downward in frequency

After Griffin had earned his doctorate, he worked in several capacities in the war effort (in the course of which he learned a great deal about communications theory and psychoacoustics). In 1945, he accepted a faculty position at Cornell. To us, and to him in retrospect, it is hard to comprehend why he and others in the field did not immediately dive into the study of echolocation after the 1941 papers. As he put it: "... after these basic facts had been generally accepted there was what now seems in retrospect an incredible lack of interest in further studies of echolocation... 'Isn't it time you turned your attention to something really important and forget all about those silly bats?'" (Griffin 1980). He acknowledged later that this attitude had, in fact, significantly dulled his enthusiasm for the subject.

However, at Cornell, after some years of continued work on the sensory basis of bird navigation and on communication between honey bees, the latter after learning of von Frisch's remarkable findings on the dance language of bees, by 1950 he felt it was time to return to bats. Among other studies, he used the best methods available at the time to characterize the sounds emitted by hand-held and flying bats. This involved displaying the sounds on an oscilloscope, photographing the traces, and laboriously measuring pulse durations and intercycle periods to quantify the emission pattern and frequencies in the pulses. He showed that in *Myotis lucifugus* the pulses lasted 1–5 ms (average 2.3 ms), with gradual onset and termination, and were frequency modulated, sweeping downward in an orderly way from around 80–40 kHz (Griffin 1947, 1950). In other species

the range differed, but pulses still swept through approximately an octave. Some recordings showed frequencies up to ~150 kHz, which were judged to be associated with harmonics of the fundamental sweep. Moreover, many of the pulses were extremely loud. With corrections for the declining sensitivity of microphones at high frequencies, the emitted intensity in handheld *Myotis* measured 5–10 cm from the mouth averaged 109 dB relative to the normal reference level of 0.0002 dyne/cm². Early attempts to record flying bats indicated that emitted intensities were also very loud and directionally beamed, especially at high frequencies (Griffin 1950).

Pulses are produced in the larynx

Griffin, with the collaboration of Al Novick, a recent M.D. turned bat enthusiast, went on to establish that emission was laryngeal and to work out in some detail the function of the laryngeal muscles and vocal cords in shaping the sounds (Novick 1955; Griffin 1958).

Field recordings and the capture of flying insects using echolocation

Technological challenges to field recording in the 1950s

Wire avoidance experiments, both by Hahn (1908) and by Griffin and his students at Cornell, had shown that bats could detect and avoid wires down to about 0.25 mm diameter. But could bats catch insects using echolocation? Spallanzani had already shown that insectivorous bats could feed successfully even after being blinded. Griffin had attempted to demonstrate insect capture in the lab with both flying and tethered insects and healthy, free-flying bats, with no success. When equipment became available that could be taken into the field, therefore, he did so. This was no trivial undertaking in 1951, and would have been quite impossible before introduction of the Western Electric 640AA condenser microphone, which was much more sensitive than the Pierce detector and detected sounds to almost 200 kHz, albeit with a drop off of 12 dB in sensitivity/octave above 12 kHz. Field recording still required a portable generator (and can of gasoline), the microphone and preamplifier, amplifiers, electronic filters, wave generators, tripods, hundreds of feet of cables, soldering iron and other tools for on-site repairs, a radio modified to serve as a rectifier to translate bat pulses into audible clicks, an oscilloscope and a camera to photograph the screen face...plus spares of many instruments. It largely filled the back of a van and required hours to set up and check out, followed by hoping that it would not rain and that bats would be feeding within range of the microphone.

Echolocation is used to catch flying insects!

The results were unambiguous; foraging *Eptesicus* were emitting pulses during their pursuit and capture of flying insects, and the emissions showed the same buzzes that occurred in the lab when bats avoided wires. As Griffin later wrote:

We had always thought of echolocation as a collision warning system, and it seemed out of the question that small insects could return strong enough echoes to be audible to a rapidly moving bat. It is difficult to realize three decades later how much of a change in viewpoint was necessitated by this evidence that bats use echolocation not only for locating and avoiding stationary obstacles but for their hunting of small rapidly moving insect prey. Echolocation of stationary obstacles had seemed remarkable enough, but our scientific imaginations had simply failed to consider, even speculatively, this other possibility with such far-reaching ramifications (Griffin 1983, p. 138).

In a further personal communication to me, Griffin added:

I consider this was the most important scientific discovery which I can claim to have made entirely on my own.

Technological advances enable field research

Field recordings have since taken their place as one of the most important sources of information about echolocation capabilities and the versatility of echolocation strategies (see below). As in so many other fields, this has been made possible by progressive improvements in technology: first, the development in the mid-1950s of tape recorders capable of recording ultrasound—initially the 70 pound Ampex 307 that could be operated at tape speeds up to 60 ips, which replaced the field oscilloscope and camera, later (in the 1970s) the more versatile (and slightly lighter) Racal Store 4 tape recorder. Integrated circuits permitted the development of lighter, more sophisticated filters and amplifiers, and—most importantly—the design of new and better bat detectors that used microphones and battery-operated circuits that were more sensitive and relatively flat across a wide range of ultrasonic frequencies. With the advent of computer circuitry, a succession of new detectors with tremendous built-in analytical power and instant displays of sonograms and other information have revolutionized the field. Now recording and analytical power vastly exceeding that of a whole acoustics laboratory in

the 1950s can be found in a thin wafer that plugs into an iPhone. Technological advances have been key to most of the breakthroughs in understanding echolocation.

The diversity in echolocation sounds

Comparative studies of tropical species

Griffin was aware that bats other than those he had been studying exhibited quite different behavior and morphology (e.g., ear structure and nose leaves and other complex nasal structures), and wondered whether other species used brief, downward sweeping FM sounds similar to those of *Myotis* and *Eptesicus*. Griffin's Harvard colleague, Georg von Békésy, the premier auditory expert of the time, told him that it would be a waste of time to examine other kinds of bats, since their sounds are merely noise bursts and a bat is a bat (Griffin 1983). Undeterred, in 1950 he traveled to Panama and observed and recorded from representatives of most of the families of neotropical bats. The following year, his collaborator Al Novick continued the studies in Panama, and subsequently did similar analyses of the echolocation sounds of paleotropical bats (Griffin and Novick 1955; Novick 1958b). The diversity was extreme. It must be kept in mind that analysis of sounds still required photographing oscilloscope traces. Moreover, most of their recordings were of hand-held bats. Hence, their findings have long since been superseded; but the basic finding of diversity was unambiguous, and the dilemmas posed by this diversity were a strong stimulus to the field. In particular, several of the neotropical species used relatively long pulses, especially the emballonurids and *Chilonycteris rubiginosa* (now *Pteronotus parnellii*), which had pulses up to 15–30 ms long that seemed to be of almost constant frequency. How could bats handle the overlap of emitted pulse and returning echo?

Rhinolophus and long “constant frequency” sounds

These data reinforced the exciting and surprising findings that emerged from Germany at about the same time. Möhres (1953) and Möhres and Kulzer (1956) reported that horseshoe bats emitted much longer (average 65 ms) constant frequency (CF) pulses—around 80 kHz in the greater horseshoe bat (*Rhinolophus ferrumequinum*) and 100 kHz in the lesser horseshoe bat (*R. hipposideros*). Moreover, the emitted beam was highly directional. Dijkgraaf (1946) had already shown that horseshoe bats are obligatory nose breathers and emit sounds through their nostrils.

CF signals can be long or short, and all end in FM sweeps

Subsequent research with superior instrumentation showed, of course, that the “CF bats”, both old world and new world,

were in fact “CF-FM bats”, with the long CF component ending in a distinct downward sweep. Moreover, if *Rhinolophus ferrumequinum* and *Pteronotus parnellii* are defined as long CF-FM bats, with CF components longer than 10 ms, there are many “short CF-FM” bats, with CF components < 10 ms in duration (Grinnell 1970; Grinnell and Hagiwara 1972). Even vespertilionid bats like *Eptesicus* produce nearly CF signals when they are flying in open space and searching for prey. They and other “quasi-CF” bats, such as the Emballonuridae and Molossidae, alter their emitted pulses dramatically during flight maneuvers and produce FM sweeps during insect pursuit and capture. Indeed, the variability and flexibility in emitted pulse structure is making it increasingly difficult to fit bats into neat pulse emission categories. As Griffin and colleagues noted in 1960, all bats change their pulse structure and emission pattern according to their behavioral state—search, approach, and terminal phase (Griffin et al. 1960). The ruling principle, however, is that all echolocating bats use sounds containing brief broadband components when they are avoiding obstacles or pursuing prey and need accurate target localization (Fig. 2).

Echolocation by tongue click: *Rousettus*, oilbirds, and cave swifts

It should also be mentioned that bats of the family Pteropidae, the flying foxes, have excellent night vision and do not echolocate (Novick 1958a). The one known exception to this generalization is the genus *Rousettus*, members of which live in caves and tombs and, in addition to excellent night vision, have secondarily evolved echolocation by clicking their tongues (Kulzer 1956; Novick 1958a). Griffin (1953a, b) had earlier shown that the neotropical oilbird, *Steatornis*, also echolocates by tongue clicks when in total darkness.

The studies from the Griffin and Möhres labs in the early 1950s were the opening salvo of a comparative approach that continues to this day. Much progress had been made in describing this diversity when Pye reviewed the subject in 1980 (Pye 1980). The diversity in echolocation signal design that has evolved over the millennia, and the corresponding diversity in echolocation strategies, ecological niches, and neural adaptations, have guided and enriched the field ever since.

The sensitivity of echolocation

In the spring of 1955, not long after Griffin had returned to Harvard from Cornell, I joined his lab—the serendipitous

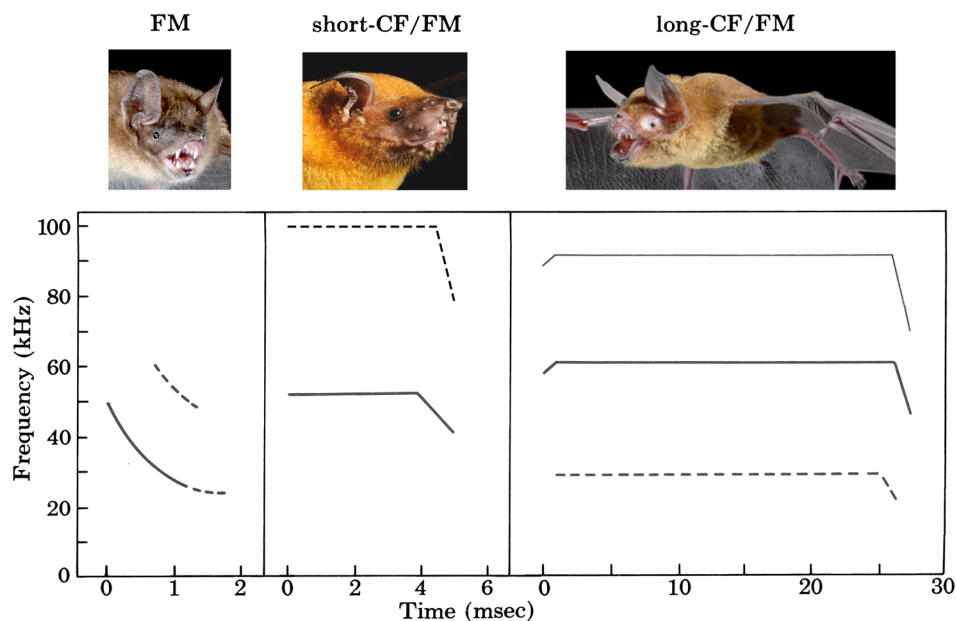


Fig. 2 Early categorization of emitted echolocation sounds into FM, short CF-FM (CF < 10 ms), and long CF-FM (CF > 10 ms) types. Dashed lines represent fainter pulse components. We know now that there are many variants on these, and that most bats can alter pulse structure greatly depending on the echolocation context. *Myotis*, *Plecotus*, and *Eptesicus* are characteristic FM bats. *Noctilio* and most species of *Pteronotus* are short CF-FM bats, and *Pteronotus parnellii*

(with pulses of 30–50 ms) and *Rhinolophus ferrumequinum* (with pulses up to 60–100 ms) are long CF-FM bats. Shown above each pulse type are facial portraits of bats emitting that type: *Eptesicus* sp (FM), *Noctilio leporinus* (short CF-FM) and *Pteronotus parnellii* (after Simmons 1974, with permission of the Acoustical Society of America) (Photos by Brock Fenton)

result of offering to be his unpaid laboratory assistant after he had allowed me to skip taking his introductory zoology course. For the next 7 years I was involved in all of the projects in the Griffin lab, including reading page proofs of *Listening in the Dark*. My first project was a refinement on wire avoidance experiments, using the distance at which bats (*Myotis* and *Plecotus*) changed their pulse emission pattern to judge the distance and echo intensity at which they first detected wires of different diameters. This distance ranged from 214 cm for 3-mm-diameter wires down to 88 cm for 0.18-mm wires. Bats successfully avoided the latter, but sometimes with only 3–4 pulses after detection. Interestingly, the calculated echo strength when the emission rate first shifted from search to approach phase would have been much greater for 3 mm, or even 1.7 mm wires, than for 0.18 mm wires (Grinnell and Griffin 1958).

CF-FM bats reportedly do better than purely FM bats at detecting thin wires. The threshold wire diameter for avoidance by *Rhinolophus ferrumequinum* is about 0.05–0.08 mm (Schnitzler 1967). Three explanations for this difference are that (a) the absolute intensity of *Rhinolophus* emitted sounds is greater than those of *Myotis*, (b) most of the energy in the pulse is packed into a single, high frequency that reflects well off thin wires, thanks to the fourth-power dependence of echo intensity on frequency in the region of Rayleigh scatter where target dimensions are small compared with wavelength (Griffin 1958), and (c) a large fraction of the auditory nervous system is narrowly tuned to frequencies around that emitted CF (see below).

Bats do phenomenally well at overcoming interference/clutter or jamming noise

For detection and analysis of echoes, bats must be able to overcome two major forms of interference: forward masking due to the loud emitted sounds, and backward masking by the clutter of often-overlapping echoes from objects and potential targets around them.

Forward masking

Cahlander, McCue and Webster (1964) confirmed that bats shortened pulse duration sufficiently during approach to an obstacle to prevent overlap of outgoing sounds with returning echoes. Nevertheless, the much louder outgoing sound would be expected to greatly suppress response to echoes. Moreover, the obviously overlapping outgoing sounds and returning echoes of CF bats like *Rhinolophus* clearly violated the principle that pulse duration was regulated to avoid overlap.

Backward masking

The interference represented by the myriad echoes returning from ground, vegetation, man-made obstacles such as buildings and telephone wires, potentially multiple flying insects in the same area as targets of interest—not to mention the emitted sounds of other bats and the echoes of their sounds off all the same objects—represents perhaps the greatest challenge of echolocation. How bats achieve this is still largely to be explained.

Jamming avoidance

The difficulty of controlling and quantifying interference led Griffin and collaborators to attempt to “jam” echolocation by producing as uniform a field of non-coherent loud white noise as possible covering the frequencies used by flying bats as they tried to avoid an array of vertically strung wires at 45-cm spacing, in rows 1 m apart (Griffin et al. 1963). Happily, this effort was joined by the MIT Lincoln Laboratory, a source of invaluable engineering expertise, which had already developed a new, superior bat detector. The noise field was generated by 26 Lincoln Lab-built condenser loudspeakers at either end of the flight room, driven by 16 power amplifiers with non-coherent inputs by 4 random noise generators. *Plecotus rafinesquii*, which emit pulses 30–40 dB less intense than those of *Myotis lucifugus*, were used. Their wire avoidance could be reduced to chance for wires smaller than 0.54 mm diameter, and significantly degraded up to 1.07 mm wires. From careful measurements of the bandwidth and intensity of the emitted cries (which increased with increase in noise intensity) and the noise intensity under different filtering conditions, it was determined that the critical ratio of the peak signal energy (E), compared with the noise power/cycle bandwidth (N_o), which should be about +10 dB for the observed false alarm rate (~0.01%) (Helstrom 1960), was in fact approximately –5 dB! The explanation for this value is not that bats are doing better than information theory, but rather that using two receivers (ears), with binaural inhibitory interactions between them (Grinnell 1963), and by flying at an oblique angle toward the wires, taking advantage of the directionality of the ears, bats can overcome the 15 dB disadvantage (Griffin et al. 1963). Filtering of the noise bandwidth showed that the bats were also using both fundamental and second harmonic components of their cries.

Insect capture in the lab

A major step forward in understanding echolocation came with success in achieving insect capture by flying bats under controlled conditions in the lab. The lab, in this case, was a large Quonset hut converted from a trampoline studio into

a bat flight facility by its owner, Fred Webster, in nearby Cambridge, MA. Also critical was the collaboration of David Cahlander, an expert at high speed photography from the laboratory of Harold Edgerton at MIT. Given the large flight space, bats (*Myotis*, *Eptesicus*, *Rhinolophus ferrum-equinum* and the faster flying red bats, *Lasiurus borealis*) readily learned to catch fruit flies around a hanging bag of rotting fruit. High-speed movies and multi-flash still images revealed unexpected flight maneuvers and details of insect capture that could not be resolved by eye at normal speed, while simultaneous recordings of emitted sounds showed that the bats detected fruit flies at about 50 cm distance and sometimes caught two within half a second. Free-flying moths released in the same space were also readily caught, with the bats apparently extrapolating the moth's trajectory and taking the most direct path to intercept it. From the moment the moth was detected, the bat's head was turned directly at the insect as its position was being tracked.

To control better the position of insect capture, the targets were changed to mealworms, projected into the air by a portable "mealworm gun" that allowed the camera to be focused at a predictable spot. The resulting films showed that capture is usually in the tail membranes, from which the insect is transferred almost immediately to the mouth. If a worm was tossed up at the last moment, however, the bats proved to be remarkable aerial gymnasts: able to flip upside down to catch the worm above them in a tail membrane, or reach out to scoop it up in the wing membrane and immediately transfer it to the tail membrane or sometimes directly to the mouth. It was clear that the bats could localize targets with great precision in all three dimensions (Webster and Griffin 1962).

Once the bats had learned to catch mealworms, some of them generalized the task and would attack anything projected into the air in that general area—even tennis balls. However, after a few encounters with inedible objects, they exhibited remarkable skills at discrimination, distinguishing mealworms from virtually any other object except for rolled-up adhesive tape simulating a mealworm in size and shape. Moreover, they could resolve and catch a mealworm among the clutter of multiple objects of similar size but different shape (small spheres, disks, cylinders that differed in length or diameter from mealworms) or isolate and catch one mealworm in a cluster of a dozen or more mealworms in the same cubic foot of air space (Fig. 3). They would usually pick off targets near the edges of the cluster, and tended to veer away from the whole cluster when there were 25 or more worms in the cluster. Complex backgrounds, such as tree branches, also tended to deter the bats, but some captures occurred when insects were among the branches. In nature, the bats studied tend to be open space foragers, so other species that

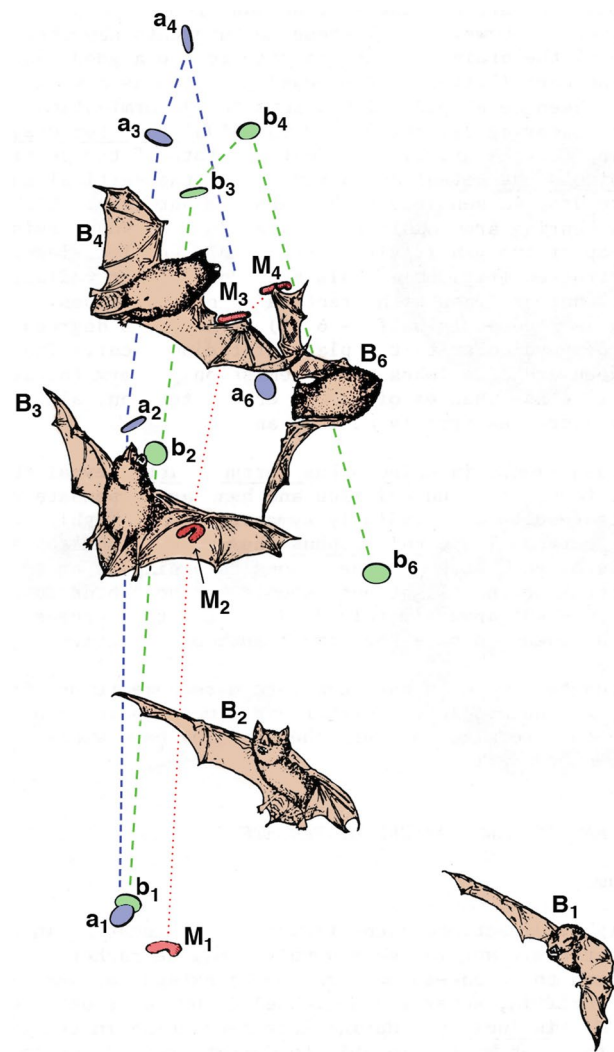


Fig. 3 Tracings of multiflash images of a *Myotis* (B1–B6) discriminating, pursuing and capturing a mealworm (M1–M4) tossed into the air along with three disks (a 1–6, b 1–6, c not shown). The mealworm was caught at the time of image 5 (not shown) and is in the bat's tail membrane in image 6 (modified from Schnitzler and Henson 1980, after Webster and Durlach 1963)

hunt near or within the canopy would probably do even better at these tasks (Webster 1967).

These insect capture/discrimination experiments are described mainly in a series of reports for the Air Force (Webster 1963; Webster and Brazier 1965, 1968), but the experimental results are still state of the art. In particular, the ability to track and catch a mealworm in the presence of multiple similar-sized inanimate targets within a few inches in space constitutes what perhaps remains the most convincing evidence for the ability to resolve the presence, location, and nature of multiple targets simultaneously with echoes of emitted sounds. At the time, these findings were the clearest evidence yet that bats seem capable of the impossible. We are still looking for explanations.

Frascati

An important milestone in the early study of echolocation was the first of several NATO-sponsored international symposia on echolocation, hosted by René-Guy Busnel and held in a chateau in Frascati, Italy, in 1966. This was the first major meeting focused both on bat and cetacean echolocation, and it introduced the second generation of German bat experts (Gerhard Neuweiler and Uli Schnitzler) to the rest of the field. They were to play a major role in future developments. Indeed, the review of the behavioral capabilities of echolocating bats by Schnitzler and Henson (1980), presented at the second NATO conference, held in Jersey in 1979, still stands as one of the most thorough, thoughtful summations of the field. It should also be mentioned that an active group of Russian scientists contributed valuable behavioral experiments with both FM and CF-FM bats in the late 1960s and early 1970s (e.g., Airapetianz and Konstatinov 1970, 1974; Konstantinov et al. 1976).

Target range determination is extremely accurate and done by measuring the interval between emitted sounds and returning echoes

Simmons and proof the pulse–echo delay is the criterion

A breakthrough in studying echolocation skills occurred when Jim Simmons trained *Eptesicus* in a forced choice experiment to move to the side of a Y-shaped platform corresponding to the closer of two targets located about 20° on either side of the midline at an overall distance of 30 cm. With a 75% correct criterion, the threshold discriminable distance was 12–13 mm (~70 μs difference in echo arrival time). He then replaced real targets with “phantom” targets...returning “echoes” of the emitted sounds picked up by microphones near the platform and played back by loudspeakers in the two directions at delays set by electronic delay lines. The performance of the bats was the same, whether the discrimination was between real or phantom targets, proving, as most had thought, that echo delay is in fact the criterion for range determination (Simmons 1973) (Fig. 4). Moreover, at least for targets separated in space, the overlapping echoes were being interpreted as two discrete targets at different distances, rather than range resolution, since the threshold difference was the same when the echoes from the two sides were presented successively rather than simultaneously (Simmons and Lavender 1976). In this case, the time/distance measurements had to be made independently and mentally compared with the delay of echoes from the other direction to pulses emitted 50–100 ms apart.

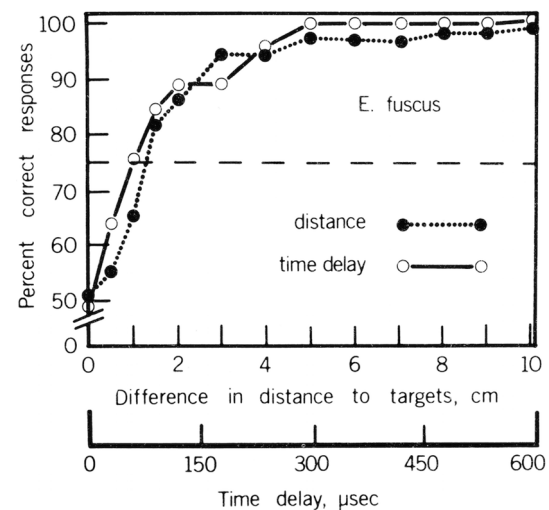


Fig. 4 Ability of eight *Eptesicus* (filled circles) to discriminate differences in distance between two real targets, compared with the ability of an *Eptesicus* to discriminate differences in time delay between “echoes” from virtual targets created by delay lines. Both at the overall distance of 30 cm (from Simmons 1973, with permission of the Acoustical Society of America)

The “jitter” experiment

Surprisingly, Simmons found that the threshold discriminable distance was essentially the same at a distance of 240 cm as it was at 30 cm. Psychophysics and information theory says this should not be the case. This led him to devise a different task that would eliminate the potential problem of head movement—asking the bat to determine which of two phantom targets returned echoes that “jittered” back and forth between echoes. When the time difference in delay (the jitter) between successive echoes was made smaller and smaller, approaching the constant delay time of the echo from the other phantom target, *Eptesicus* was found to be able to discriminate jitter as small as 1–2 μs, or even less (Simmons 1979, and see also; Moss and Schnitzler 1989)! This confounding finding was highly controversial, especially since the jitter was in the delay of echoes of different pulses, emitted 50–100 ms apart. The main reason for suspending disbelief is the phenomenal ability of bats to discriminate the size and shape of targets and capture targets amid surrounding clutter, or to discriminate subtle surface features of targets (Simmons 1974; Habersetzer and Vogler 1983; Schmidt 1988), although this is very likely done via the presence of spectral cues introduced by overlapping echo glints. These findings led quickly to a number of ingenious experiments, in different labs, designed to test the degree to which bats are capable of phase discrimination at ultrasonic frequencies and of using the fine structure of the cross-correlation function for emitted sounds and echoes (Simmons 1980; Simmons and Stein 1980; Schnitzler

and Henson 1980; Altes 1981; Menne and Hackbarth 1986; Mohl 1986). This debate continues.

“Automatic gain control”

Noting that the recovery of sensitivity after pulse emission in *Eptesicus* (approximately 11 dB per doubling of distance) was roughly equivalent to the decrease in emitted pulse intensity as a bat approached a target, Kick and Simmons (1984) proposed the concept of “automatic gain control”.

Long-CF/FM bats use Doppler shift information

The long-CF/FM bats were already known to be in a separate category because of the emitted pulses, which would overlap with returning echoes for most of their duration. Griffin (1958) had noted that these pulses would be susceptible to Doppler shift. Still, one of the most seminal findings in the history of echolocation studies was Schnitzler’s (1968) discovery that flying *Rhinolophus ferrumequinum* lower the frequency of their CF component just enough to compensate for the upward Doppler shift of returning echoes (Fig. 5). (Downward shifts in echo frequency elicit no reaction.) The compensation can be as much as 8 kHz, depending on flight and target speed (Schnitzler and Henson 1980). This “Doppler Shift Compensation” (DSC) maintains echo frequency constant about 50–100 Hz above that of the normal resting frequency (~83 kHz) produced by a stationary bat, and regulates emitted frequency to compensate for Doppler shift with an accuracy of ~0.06% (Schnitzler 1973; Schuller et al. 1974). This makes it perhaps the most accurately regulated biological phenomenon known.

The New World long CF/FM bat, *Pteronotus parnellii*, also shows accurate DSC (Schnitzler 1970; Henson et al. 1982), although *P. parnellii* is not related phylogenetically to *Rhinolophus* (Teeling et al. 2016), indicating that the behavior has been independently evolved. Gustafson and Schnitzler (1979) found that hipposiderid bats also employ DSC. Short-CF-emitting bats do not DS compensate, although the short CF component is doubtless important for their echolocation (Roverud and Grinnell 1985a).

The CF component in principle provides information about the direction of objects returning echoes relative to the flight path, and the closing speed between bat and targets, but it appears that its main use is in detection of echo sources and recognition of (perhaps identification of) potential prey by the modulations in intensity and frequency of the echo CF due to insect wing-beats (Schnitzler 1970). Schnitzler and Flieger (1983) showed that *Rhinolophus* can detect frequency oscillations of only 12 Hz around the carrier 83 kHz CF. Surprisingly, a bat emitting 2–4 ms FM pulses was found to be almost as accurate at discriminating wing-beat flutter (Sum and Menne 1988).

Directionality of echolocation

The insect capture experiments showed that flying bats could localize targets to within a few degrees in all three dimensions. The directionality of echolocation depends on the shape of the beam of emitted sound and on the directionality of hearing. Initial attempts to measure the directionality of the beam in *Myotis* (Griffin 1958) mainly illustrated the difficulty of doing so rigorously, but did show that high frequencies were more narrowly beamed than lower frequencies. Technological advances such as good, cheap microphones,

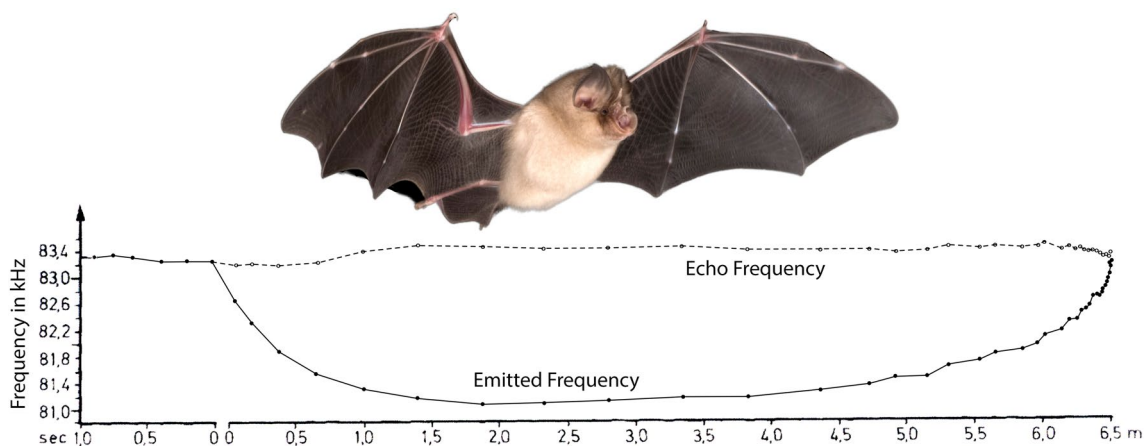


Fig. 5 The emitted frequency of a *Rhinolophus ferrumequinum* before and after it took off at time 0 to fly to a landing spot 6.5 m distant. As it changed flight speed, it changed its emitted frequency by up to about 2 kHz to compensate for Doppler shift of echoes from the

wall it was approaching, with the result that the CF frequency of the returning echoes was maintained almost constant around 83.3 kHz (modified from Schnitzler 1968). (Photo: Brock Fenton)

high-resolution video cameras, and computer analysis programs have solved many of the problems.

The most complete early analysis of the combination of directionality of emission and of hearing was done in two *R. ferrumequinum*, with head fixed in place (although ears and nose structures could still be moved), that spontaneously emitted a stream of pulses. Directionality of emission was quantified by comparing the intensity recorded at many points in the hemisphere the bat was facing, normalized for each pulse to the intensity recorded at another microphone directly in front of the bat (Schnitzler and Grinnell 1977). Directionality of hearing was tested in the same two bats by determining the intensity of simultaneous noise pulses coming from different directions needed to prevent the behavioral response of Doppler shift compensation to sinusoidally frequency-modulated “echoes” coming from directly ahead (Grinnell and Schnitzler 1977). The combined directionality of echolocation at the CF frequency showed a drop off of about 20 dB in the 30° to either side of the midline, and about 10–15 dB in the 30° above and below the axis (Grinnell and Schnitzler 1977). Directionality was less at lower frequencies and was clearly dependent on ear shape and position. Strongly affecting directionality, and probably facilitating vertical localization, *Rhinolophus* characteristically flicks its ears in opposite directions, forward and back, with or between each pulse emission (Griffin et al. 1962). Ear movements are probably an integral feature of echolocation in most species.

Early discoveries of neural adaptations for echolocation

First experiments

The remarkable echolocation capabilities of bats showed that bats were obtaining information from echoes equivalent to what a swallow or flycatcher acquired through vision: accurate information about the shape, distance, direction, and movement velocity of flying insects in cluttered space. Given the very limited ability of humans to obtain information from echoes, it is not surprising that there was resistance to imagining, let alone accepting, that bats could do these things. So what is different about their auditory systems that enable them to echolocate? How do they analyze echoes to get the information they need?

In the spring of 1957, my junior year at Harvard, I prevailed upon Griffin to let me start searching for neural specializations for echolocation. His lab was not equipped for electrophysiology, and neither of us was experienced in the techniques, but I managed to put together a setup, and began looking for the appropriate neural adaptations that could help explain the phenomenon. I first used fine silver

wires, insulated to near the tip, to record gross evoked potentials from the inferior colliculus, later refining the recording to localized evoked potentials and clusters of single units using etched tungsten wires insulated near the tip, and finally to single unit responses using glass micropipettes. Again, Bob Galambos played an important role in studies of echolocation. Griffin arranged that I take some bats to Walter Reed, where Galambos had his state-of-the-art equipment for studying cat auditory neurophysiology, and to look at responses in bats. They were by far the best recordings I had obtained to that point. I was inspired, and Griffin was sold on the project.

As was the case for field recordings of echolocating bats, equipment for producing sound stimuli and recording responses imposed severe limitations. FM sound generators did not exist, and adequate loudspeakers were just being developed by our Lincoln Lab associates. It took several electronic instruments to generate and shape pulses of ultrasound; and the state-of-the-art (Grass Instruments) DC physiological preamplifiers were notoriously unstable.

The skills to be explained initially were sensitive detection of ultrasound in the frequency range the bats emitted, the ability to detect faint echoes immediately after (if not during) much louder emitted sounds, and mechanisms for locating each source of echoes to within about 1–2 cm² in three-dimensional space.

Bats are most sensitive in the range of ultrasound they emit

Evoked potential “audiograms”, determined by measuring the intensity of tone pips of different frequency at which a threshold response is first seen, are much easier to obtain than behavioral audiograms. If the evoked potentials reflect the summed response of most of the neurons at any given level of the auditory system, such audiograms correspond well in shape to audiograms derived from behavioral tests, although the latter tend to show greater absolute sensitivity, since they reflect the maximum sensitivity of the awake, motivated animal. Comparable neural recordings of localized evoked potentials or the responses of single units are more properly called tuning curves.

Based initially on inferior collicular evoked potential “audiograms” in *Myotis* and *Plecotus* (Grinnell 1963), augmented later by similar data from neotropical (Grinnell 1970) and paleotropical bats (Grinnell and Hagiwara 1972), electrophysiological experiments soon established that bat hearing is broadly sensitive over the range of ultrasound they emit, e.g., around 30–80 kHz in *Myotis lucifugus*. This is no surprise, since it is well known that smaller mammals hear high frequencies. However, bats push this to the extreme. Where the emitted pulses contain prominent second and higher harmonics, there are peaks in sensitivity in the range

of those harmonics as well as the fundamental. Greatest sensitivity can be at frequencies as high as 140–150 kHz where this corresponds to the peak energy in the emitted sounds (Grinnell 1970; Grinnell and Hagiwara 1972). Higher frequencies provide stronger echoes off small targets, at the expense of greater atmospheric attenuation (see Griffin 1958, for a thorough discussion of this relationship). The specific bandwidths used by different species are determined by a variety of factors that are only now receiving the importance they deserve: the optimal frequencies and pulse structures for procuring the particular kind of prey/food item the bats have evolved to utilize, the habitat in which they hunt, partitioning of the echolocation spectrum between bats that cohabit the same echolocation niche, and the selective pressure for insectivorous bats to use frequencies to which potential insect prey are not sensitive.

Structural specializations for echolocation

In addition to obvious specializations like large ears with prominent tragi (the spear-shaped flap of skin projecting in front of the external meatus) and complex nose leaves, the auditory nervous system is hypertrophied and specialized from the inner ear to the auditory cortex. (A large literature on the contributions of Ada Pye, John Zook, Marianne Vater, Manfred Kössl, John Casseday, Ellen Covey, and others is summarized by Pollak and Casseday 1989). The fact that the inferior colliculus protrudes as a prominent bulging mass between the cortex and the cerebellum on the dorsal surface of the brain is a major reason that electrophysiological recording was first done on that nucleus. Again, long-CF-FM bats fall into a separate (and extreme) category. Their auditory systems show extraordinarily sharp tuning to one or more of the CF harmonics, usually the 2nd, 3rd, and 4th harmonics, with dips in sensitivity between them (Grinnell 1967, 1970; Neuweiler 1970). It was shown in *Rhinolophus ferrumequinum* that the extremely sharp tuning to the CF components of the emitted pulses begins with dramatic morphological specializations in the cochlea, including basilar membrane width, thickness, and innervation density (Bruns 1976; Neuweiler 1980). Morphological specializations are less evident in the cochlea of *Pteronotus parnellii* (Henson 1978), but physiological responses show equally or even more clear-cut emphasis on the CF frequencies of the emitted sounds, from the cochlear microphonics (Pollak et al. 1972; Schnitzler et al. 1976), through all of the auditory nuclei to the auditory cortex (Suga et al. 1976; Suga and Jen 1977; Schuller and Pollak 1979; Suga and O'Neill 1979; Pollak et al. 1979, 1986). Prominent “off responses” to CF pulses and slow decay of the cochlear microphonics in long-CF-FM bats indicate that there is resonance of the basilar membrane at those narrow frequency bands (Grinnell 1970; Suga et al. 1975; Schnitzler et al. 1976).

Extraordinary frequency resolution in CF-FM bats

Single unit recordings, done predominantly at the level of the inferior colliculus, are characteristic of those described in other mammals, with V-shaped tuning curves bordered by inhibitory inputs which in some cases suppress response at intensities only 10–20 dB above threshold (Grinnell 1963; Suga 1964b; Pollak 1980). The Q_{10dB} value, a measure of the sharpness of tuning based on the bandwidth of the tuning curve divided by the best frequency 10 dB above threshold, is somewhat larger in FM bats (up to about 20) than in most other mammals (5–10), but again, CF/FM bats are in a class by themselves, with single units tuned outrageously sharply around the CF (Q_{10dB} values up to 300 or more!) (Suga and Jen 1977; Neuweiler and Vater 1977; Möller et al. 1978). Clearly frequency resolution around the CF is important to these bats (Fig. 6).

It is important to emphasize that localization of targets in space and identification of their shape and surface characteristics require a broad range of frequencies, normally carried in the FM component of the calls. Thus, in both FM and CF-FM bats, the FM component is emphasized after target detection, becoming steeper and often sweeping through a broader range of frequencies, while the CF component is shortened (but not eliminated). In all bats, the auditory system has to be sensitive to frequencies in the FM component of the call and capable of fine frequency discrimination. Moreover, neural circuitry results in single neurons that are selectively sensitive to FM downward sweeping sounds (Grinnell and McCue 1963; Suga 1964a).

Neural adaptations for responding sensitively to echoes

Suppression of response to emitted sounds

The problem of resolving and analyzing echoes immediately after a louder outgoing sound (forward masking) was mentioned above. One of the adaptations helping overcome this problem was revealed by Henson (1965) and Henson et al. (1982), who performed a beautiful set of experiments in which he recorded cochlear microphonics from flying free-tail bats and showed that rapid middle ear muscle contraction just before and during emission reduced sensitivity to the emitted sound by 20–30 dB, while rapid relaxation restored sensitivity within 1–2 ms following emission, facilitating echo analysis. (This confirmed an hypothesis by Hartridge 1945.) Suga and Schlegel (1972) later described a neural circuit that even more precisely suppresses response to emitted sounds by approximately 15 dB, and there may be multiple circuits performing the same function.

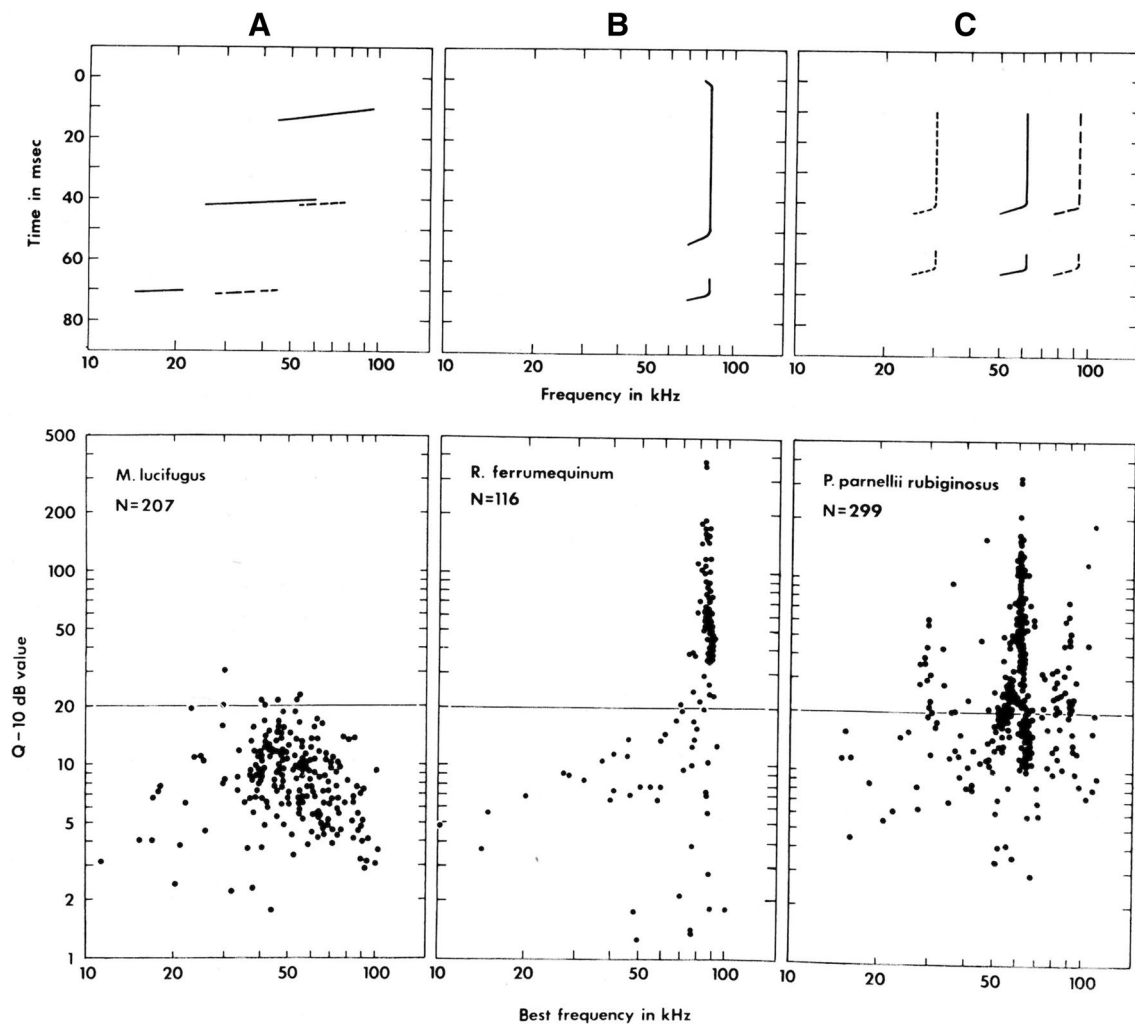


Fig. 6 Q-10 dB values for single cochlear nerve fibers in a typical FM bat (a) and the two most studied CF-FM bats (b, c). Each point represents the width of the tuning curve of the unit 10 dB above threshold at the best frequency, a measure of the sharpness of tuning of the unit. Frequencies in the emitted pulses are shown in the top panels. Units in *Myotis* show best frequencies distributed almost equally through-

out the emitted FM cries (80–40 kHz) and show only moderately sharp tuning. In contrast, peripheral units in *Rhinolophus* and *Pteronotus* show phenomenally high Q-10 dB values at the frequencies of their primary CF components, with a correspondingly 30 large fraction of units tuned to those frequencies (from Suga and Jen 1976, with permission)

Facilitation of response to echoes

Complementing these mechanisms is the finding that the auditory nervous system in echolocating bats has evolved to recover sensitivity remarkably rapidly after exposure to a loud sound. This was apparent in the very first recordings of evoked potentials from the *Myotis* inferior colliculus (Grinnell 1963; Suga 1964a). In contrast to humans and most other mammals studied, where response to echoes is greatly reduced for 5–10 ms after a loud sound, bats showed a detectable evoked response to the second of 2 identical tone pips at as little as 0.2 ms, full recovery within 2 ms, and often a period of exaggerated response at

intervals up to 10 ms or more. This facilitation of response to the second of two stimuli is due to neural mechanisms, since the response to the “echo” recovered much more quickly at the level of N_4 (the input to the inferior colliculus, coming mainly from the lateral lemniscus) than at N_1 or N_2 (summed responses of the auditory nerve and cochlear nuclei) (Fig. 7). Rapid recovery and facilitation of responsiveness at the level of N_4 to the second of two sounds is apparently characteristic of all echolocating bats, including *Rousettus*, but not non-echolocating bats. (Grinnell 1970; Grinnell and Hagiwara 1972; Hagiwara and Grinnell 1972). This is surely one of the most dramatic and important neural adaptations for echolocation.

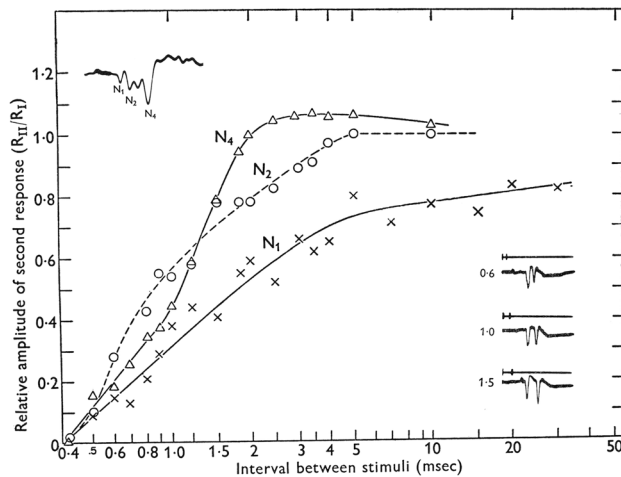


Fig. 7 Average recovery curves for the evoked potentials N1 (auditory nerve), N2 (cochlear nuclei) and N4 (lateral lemniscus) to pairs of identical tone pips (0.2–5 ms duration, 50 kHz, 40 dB above threshold) as a function of inter-stimulus interval, measured with a gross electrode in the posterior colliculus of anesthetized *Plecotus townsendii*. Recovery was greatly facilitated at levels central to the auditory nerve input, in contrast to non-echolocating mammals. Lower right: traces showing facilitated recovery of localized N4 recorded with a microelectrode in the colliculus of a *Myotis lucifugus*. (All from Grinnell 1963.) Comparable CNS facilitation is seen in Rousettus, but not in non-echolocating flying foxes (Hagiwara and Grinnell 1972)

Delay-tuned neurons and target range

Early recordings of single unit responses in the colliculus were consistent with the evoked potential data, showing facilitation of response to the second of two identical sounds. Most collicular units, unlike those at more peripheral levels, responded with only a single spike to a sound in the appropriate narrow frequency band and a given latency. In a sub-set of these neurons, the response latency, especially to FM pulses, was nearly constant over a wide range of supra-threshold intensities (Suga 1970; Pollak et al. 1977). A number of investigators (Grinnell 1963; Suga 1970; Pollak et al. 1977; Feng et al. 1978; Sullivan 1982) reported a variety of single unit behaviors in FM bats that provide a good neural substrate for measurement of pulse–echo delay—units that responded poorly to either the first or second of a pair of sounds alone, but strongly to the pair, even when the “echo” was as much as 50 dB fainter than the initial sound. Those selective for short delays tended to have narrower “time windows” than those selective for longer delays (up to ~30 ms). Subsequent research has, of course, added many details about the circuitry involved and additional behavior encoding echo delay.

Although the delay tuning of any given neuron was usually accurate only to a few ms, it is important to emphasize that the time measurement is being made redundantly by

neurons narrowly tuned throughout the entire bandwidth of the FM sweep of the pulse–echo pair, including harmonics. Some very intriguing data suggest that more than 90 separate frequency channels of no more than 50–100 Hz bandwidth must be present in artificial echoes for the lesser fisherman bat, *Noctilio albiventris*, to react as if it is hearing echoes of its own emitted sounds (Roverud 1993). Averaging delay-tuned populations over that many channels could plausibly provide a measure of target range well within the ~1 cm distance reported in Simmons’s 1973 paper. How to accomplish a delay time accuracy of 1–2 μ s (Simmons 1979) is something else again.

Ranging in the long-CF/FM bat *Pteronotus parnellii* was shown to be done by quite different mechanisms. This beautiful story is described below.

Hearing is highly directional, frequency dependent, and sharpened by interaural inhibition

Localization in the azimuth

Insect capture in the field and in the lab had established that target localization was exceedingly accurate not only in range but in azimuth and elevation as well. Subsequent behavioral laboratory measurements suggested that *Eptesicus* can resolve an angular difference of about 1.5° on the azimuth (Simmons et al. 1983) and about 3° in elevation (Lawrence and Simmons 1982). This is comparable to human capability in the horizontal plane, much better than human performance in the vertical dimension. So how do the bats do it?

Binaural differences in arrival time (ITD) and intensity (IID) are the principal criteria available for discrimination of sound direction on the horizontal axis. Wavefront arrival time and phase cues are useful at low frequencies, up to perhaps 5–8 kHz, with binaural intensity differences becoming more important at higher frequencies, where phase information is no longer available and sound shadows cast by the ears and head create larger IIDs (Grothe et al. 2010). For most mammals, with ears separated by 5–10 cm or more, the maximum ITD is hundreds of μ s and a discriminable difference of $1\text{--}2^\circ$ in sound direction around the midline represents an ITD of 5–10 μ s or more. For bats, however, with ears about 1 cm apart, the equivalent figure would be 1–2 μ s. The temporal resolution of echo delays by bats is so spectacular that the ability to resolve ITDs of this magnitude is not unreasonable. Moreover, there are data supportive of bats’ ability to cross correlate signal waveforms, if not use phase information directly even at ultrasonic frequencies (Simmons 1979).

On the other hand, an ITD of 0.5–1 μ s/degree for sounds coming from near the midline would seem a poor criterion compared with interaural intensity differences (IIDs).

Measurements of directionality of the N_4 evoked potential input to the IC at different frequencies in the range of the emissions of *Myotis* and *Plecotus* showed changes in threshold averaging about 0.5–1 dB/degree between the midline and 30° to the side. Directionality is frequency dependent—greatest at the highest frequencies used in the emitted sounds. Moreover, as the sensitivity/responsiveness increases in the inferior colliculus on one side, it decreases in the contralateral pathway, so binaural comparison at any level effectively doubles the measured directionality. The steepness of directionality is further increased by strong lateral inhibition between the two pathways (Grinnell 1963; Fuzessery and Pollak 1985; Wenstrup et al. 1986).

The difficulties of using small ITDs to determine sound direction on the azimuth is further complicated by the property, common to nervous systems, that as the intensity of a stimulus increases, the latency of response decreases. Measurements of this time–intensity trading relationship in bats have reported between 8 and 50 μ s shifts/dB change in intensity (Harnischfeger et al. 1985; Pollak 1988). Preserving and making accurate angular judgments based on 1–2 μ s ITDs become quite improbable, whereas comparing the relative level of excitation in the binaural auditory pathways, especially when it can be done redundantly at all of the frequencies in a returning echo, would constitute an extremely accurate mechanism.

At the level of the inferior colliculus, early studies showed many single units with extraordinarily sharp cut-offs of response when a sound source was shifted along the azimuth. Changes of 4–5 dB/degree were common in several vespertilionid (Grinnell 1963) and hipposiderid species (Grinnell and Hagiwara 1972). These data, reinforced by similar findings from other labs and other species in the late 1970s and 1980s (see especially Fuzessery and Pollak 1985 and; Wenstrup et al. 1986), have led to general acceptance of the idea that sound localization on the horizontal axis is done by binaural intensity comparison. Indeed, subsequent research showed that there is a functional map of azimuth in the inferior colliculus of *Pteronotus parnellii* (Wenstrup et al. 1986).

Target localization in the vertical dimension

Localization in elevation is nearly as accurate. Again, given the sharp tuning and spectacular temporal resolution of bats, it is possible that spectral notches or multi-wavefront reflections off the ridges and folds on the external ear structures could provide information in the vertical axis (Simmons et al. 1983). But measurements of global directionality of hearing show that sensitivity is frequency dependent and varies as sharply in the vertical dimension as side-to-side (Grinnell and Grinnell 1965; Grinnell and; Schnitzler 1973). If a bat is able to make binaural comparisons of the intensity

of echoes at most or all frequencies in the returning echo, the information exists to pinpoint accurately the direction of a sound source arriving from anywhere in front of the bat (Grinnell and Grinnell 1965; Fuzessery and Pollak 1984, 1985). Whether this is how bats do it remains uncertain.

Combination-sensitive units and organization of the auditory nervous system in long-CF/FM bats

The use of long-CF/FM sounds by *Rhinolophus sp.* and *Pteronotus parnellii* has co-evolved with a constellation of fascinating adaptations of the auditory nervous system. From modified structures in the cochlea that grossly overrepresent frequencies around the emitted CF, to complicated circuitry in subcortical centers, and finally to the organization of the auditory cortex, the entire auditory nervous system is specialized for obtaining information from the CF (and nearby FM) components of echoes—like an “acoustic fovea” (Pollak et al. 1972; Suga et al. 1975; Neuweiler and Vater 1977; Schuller and Pollak 1979). In *P. parnellii*, where this has been particularly thoroughly studied by Suga and his colleagues, the emitted sounds consist of the 2nd, 3rd, and 4th harmonics, with the 2nd (~61 kHz eventually sweeping down to ~49 kHz) being much the loudest. There is a 1st harmonic as well, but it appears to be suppressed by anti-resonance in the vocal tract, and little if any is emitted. The 1st harmonic, or an efference copy of it, is clearly perceived by the bat, however, since its analysis of echoes is partitioned into parallel pathways that compare combinations of the CF and FM components in the 2nd, 3rd, and 4th harmonics of echoes with the CF_1 and FM_1 in the fundamental, which are not present in the echoes.

The auditory cortex of *P. parnellii* illustrates clearly the importance of both the CF and FM echo components and of redundancy in information extraction. There is a tonotopic map across much of the auditory cortex, with a greatly enlarged region dedicated to analysis of frequencies around 61 kHz (the CF_2 echo component), extracting information about the presence of targets, the amount of Doppler shift, the source direction of echoes, and target size. Nearby, there are separate cortical regions dedicated to a systematic mapping of units responsive selectively to combinations of the “emitted” CF_1 and progressively Doppler-shifted echo CF_2 , adjacent to a region mapping CF_1/CF_3 . These areas appear to be devoted to detecting echoes and determining accurately the degree of Doppler shift (relative velocity, subtended angle, and wing-beat amplitude and frequency of targets). Two nearby regions each contains three adjacent spatial maps of target distance, between about 7 cm and 3 m, based on delay-tuned neuronal inputs, comparing each frequency in the non-emitted FM_1 with delays of hearing those frequencies in FM_2 , FM_3 , and FM_4 (Fig. 8) (Suga

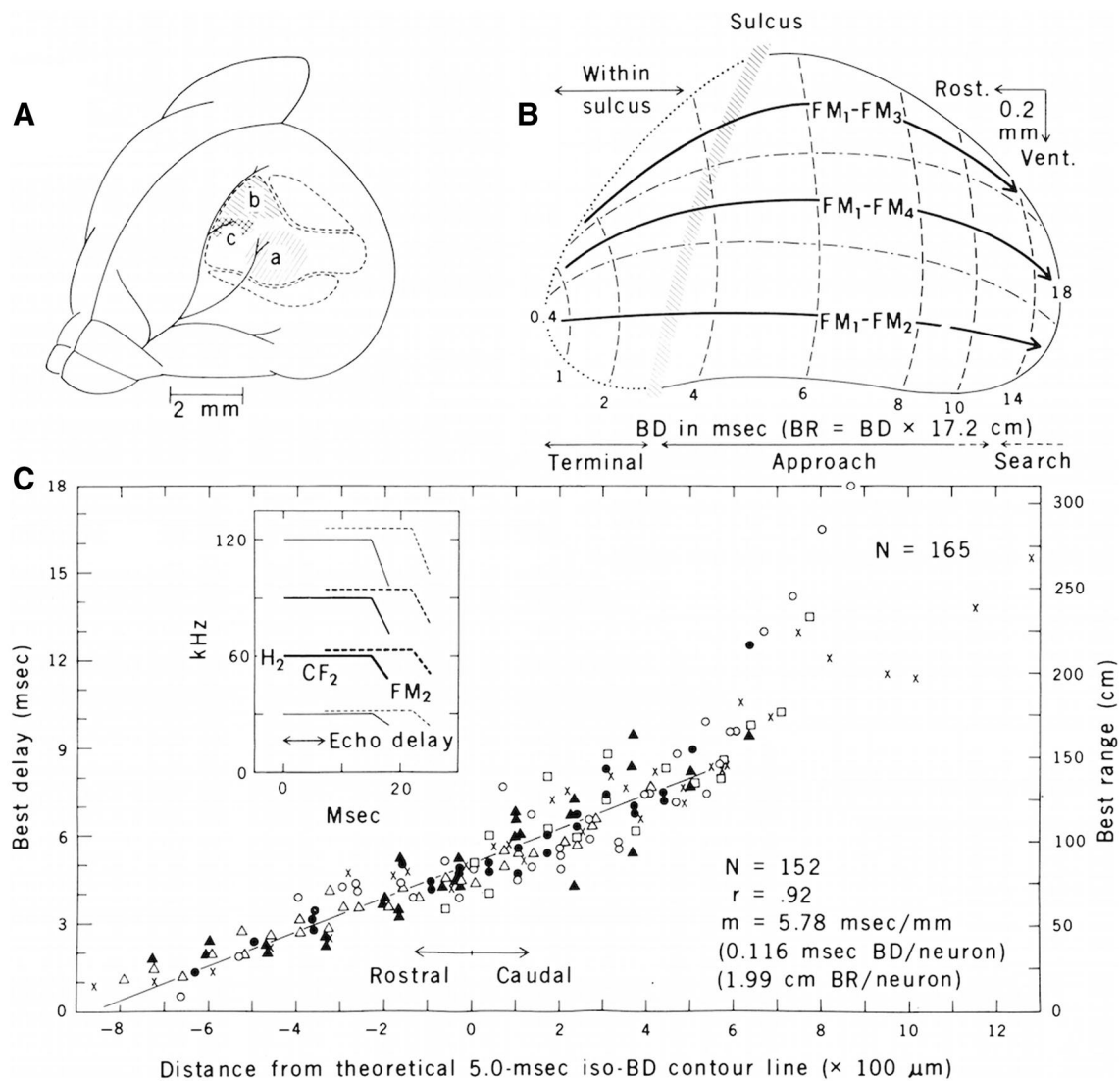


Fig. 8 Part of the auditory cortex of *P. parnellii*. **a** Area a represents a tonotopic map with the large circular shaded area devoted to frequencies around the CF. Area c contains neurons specific for different combinations of emitted CF1 and echo CF2, CF3, or CF4, quantifying the amount of Doppler shift. **b** Area b is shown in greater detail. It consists of three adjacent areas in which distance is place-mapped

redundantly by neurons systematically tuned to combinations of the emitted FM1 and echo FM2, FM4, and FM3 at different delays from 0.4 to 18 ms, corresponding to target distances of 7 to 310 cm. The results of measurements from 152 neurons in 6 different bats (different symbols) are plotted in **c**. (from Suga and O'Neill 1979, with permission)

1977; Suga and O'Neill 1979; Suga et al. 1983; Suga and Horikawa 1986).

The specificity of the response parameters of each cortical area is clearly adapted to the types of signals used and the ecological niche the bats occupy (hunting within the canopy in the case of *P. parnellii*). Undoubtedly, similarly sophisticated circuitry has been evolved in other species using different types of signals, but most have not been studied electrophysiologically. One can make predictions, however, based on behavior. For example, in the short-CF-FM bat *Noctilio albiventris*, behavioral experiments suggest that there are populations of delay-tuned neurons that require

(or are facilitated by) short CF signals in addition to the FM sweep (Roverud and Grinnell 1985b), and a similar population is indicated in the long-CF/FM bat, *Rhinolophus rouxi* (Roverud 1988).

Final thoughts

In the 50 years since Pierce and Griffin detected the production of ultrasound by bats, the number of published studies has grown exponentially. What I have described was just the beginning of a lively and fascinating field. While most of the

fundamental principles of echolocation and many of the neural mechanisms that made them possible were established in that early period, there were—and still remain—many unanswered questions such as how bats hunting in cluttered environments can separately analyze overlapping echoes from multiple targets to localize each and discriminate targets to pursue from all the others to be avoided. And bats never fail to surprise. What has kept the field particularly fresh and fascinating is the seemingly endless diversity of echolocation strategies and adaptations evolved by different species to exploit specific foraging environments and lifestyles. Familiar species turn out to be more flexible and sophisticated in their echolocation skills than we appreciated, requiring additional, unanticipated adaptations. And each time a new species is looked at carefully, it is found to be doing things slightly differently than others—behavior that often challenges belief. There is no danger that these challenges, or the thrill of confronting them, will end soon.

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