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Echolocation: a personal historical perspective¹

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Echolocation: A Personal Historical Perspective

Alan. D. Grinnell

Abstract:

The remarkable ability of echolocating bats to use echoes of emitted sounds as a substitute for vision is one of the most fascinating stories in neuroethology. Based in part on personal experience, the author discusses key discoveries in the early decades after the discovery of the phenomenon by Griffin and Galambos in 1941. Advances in our understanding of this remarkable phenomenon illustrate well the importance of comparative approaches, technological advances, and the synergistic interaction between behavior and electrophysiology.

Key words: bats, audition, neuroethology, echolocation, behavior

To adequately review the history of our understanding of echolocation is far beyond the scope of this short paper. However, since I was privileged to be a part of the Griffin laboratory when some of the foundational discoveries were being made, it may be of interest to give my personal perspective on what it was like to be a part of the field in the exciting first few decades after the definitive proof that bats used echolocation. A less personal history can be found in a recently published book on Bat Bioacoustics (Grinnell et al. 2016).

As is no doubt true of every field of science---but seems especially so for echolocation---the major advances in this field have come through the conjunction of three crucial elements: insightful individuals with the curiosity and drive to find ways to answer questions, the development or adoption of new technologies that enable new discoveries, and an evolutionary, comparative approach to asking what it is like to be a bat (Nagel 1974). It is also a perfect exemplar of the synergy between behavior and neurophysiology.

A. Early History: From Spallanzani to Griffin's discovery that bats could echolocate flying insects

The first scientific investigations of how bats orient in the dark, and the experiments by Spallanzani and Jurine that established that hearing was necessary (but not realizing that emitted sounds were responsible) constitute a fascinating story. Anyone unfamiliar with it can find it treated in detail in Griffin's classic "Listening in the Dark" (1958). (I take some personal pride in that book, since I helped proof read it. Unlike his children, however, I did not get paid for finding mistakes.) I will take up the story when Donald Griffin first entered the field.

In 1938, improved technology met a "prepared mind." Donald Griffin, an undergraduate at Harvard, had for years been banding bats and tracking their migrations. He knew of Spallanzani's work, but not the speculation, by Hartridge (1920), that bats might orient by using the echoes of emitted sounds above the range of human hearing. Nevertheless, when Griffin learned that a physics professor, G. W. Pierce, had built a piezoelectric salt crystal microphone mounted at the focal point of a parabolic horn that could detect insect sounds above the human range of hearing, he sought out the professor and asked if they could use the apparatus to listen to bats. Voila! A cage full of little brown bats (*Myotis lucifugus* Le Conte, 1831) produced a nearly constant barrage of sound above the range of human hearing. Their apparatus, however, could detect only an occasional sound from a flying bat. Consequently, in a characteristic abundance of caution, they reported only the production of ultrasound by bats, not confirmation of echolocation (Pierce and Griffin 1938).

A couple years later, Griffin met Bob Galambos, a fellow graduate student beginning his doctoral training in the laboratory of Hallowell Davis at Harvard Medical School, and they began to work together on the phenomenon. Soon they had established that when the parabolic horn was pointed directly at a flying bat, they could detect a

stream of brief ultrasonic (then called supersonic) pulses. By repeating experiments much like those done more than 100 years before by Spallanzani, they also established that the ears were necessary for oriented flight and obstacle avoidance. And knowing of the ultrasonic sounds, they tried tying the bat's mouth tightly shut and sealing the edges with collodion. The bats were completely disoriented until at least a small crack in the collodion appeared. Thanks to the Pierce ultrasonic detector and ingenuity of two students, the phenomenon of echolocation had been discovered (Griffin and Galambos 1941; Galambos and Griffin 1942).

I was 5 years old in 1941, which I point out simply to emphasize that the entire modern history of echolocation, from its first discovery to the present vast literature and sophisticated understanding of the principles involved, has happened within one lifetime.

At the time of the initial demonstration of echolocation, Griffin had already started his PhD project on bird migration, which he completed as a Harvard Junior Fellow, then spent most of the next few years working on war-related research, in the process learning a good deal of electronics and communications theory. In the meantime, Galambos (1942) did his PhD work on cochlear microphonics in bats.

In 1945 Griffin accepted a faculty position at Cornell and returned to the study of bats, mainly working on behavior in the lab. A major breakthrough came in the early 1950s, when he took his cumbersome apparatus into the field near Cornell and found, to his absolute amazement, that big brown bats, *Eptesicus fuscus* (Palisot de Beauvois, 1796), were using echolocation to catch insects! This changed everything (Griffin 1953). As he later wrote in describing this revelation:

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)

B. The Second Generation: Behavioral demonstrations of echolocation skills

1. Continuing research in the Griffin lab. In 1953 Griffin returned to Harvard. Not long thereafter, in 1955, in the spring of my freshman year, I joined his lab. This was the happy result of seeking his permission to bypass taking his elementary zoology course and offering, in return, to be an unpaid laboratory assistant. For the next 7 years, I participated in virtually all of the research that he was doing and can write from personal experience about most of the developments. The first lab project I participated in was a study of the sensitivity of echolocation by *Myotis lucifugus* and the long-eared bat *Plecotus townsendii*, determined by the distance at

which their pulse repetition rate increased, indicating detection of arrays of wires of different diameter. The combination of movies to determine the bat's position and recordings of emitted sounds provided calculable thresholds of detection, evidence for emission patterns when facing increasingly difficult tasks, and evidence that for easy tasks, the bats probably detected the targets well before they showed a behavioral response (Grinnell and Griffin 1958).

2. Resistance to “jamming”. Another project was an attempt to “jam” echolocation with loud white noise---a quantifiable simulation of the problem of overcoming acoustic clutter in natural situations. This effort was greatly helped by collaboration with expert engineers, especially J. J. G. McCue, with the resources of MIT's Lincoln Lab behind them. (The Lincoln Labs also helped enormously by developing a light-weight portable bat detector with a new, superior, microphone.) We used *Plecotus* because its emitted sounds are 30-40 db fainter than those of *Myotis* and sweep through a lower range of frequencies. Confronting the bats with banks of 26 Lincoln Lab-built condenser loudspeakers mounted at either end of the flight room, driven non-coherently by four random noise generators and 16 power amplifiers, we could significantly impair the ability to avoid 0.54 mm diameter wires, but not totally jam them. They seemed to be doing considerably better than information theory said was possible. After some consternation, the conclusion was not that bats defy information theory, but rather that bats can overcome the noise by flying more obliquely to the wires, so that echoes profit from the directionality of the bat's ears. Furthermore, the bats use two receivers (ears), which had, by then, been shown to enhance directionality of hearing by binaural interactions (Griffin et al. 1963).

3. Insect capture in flight in the lab The third major behavioral project was to record and photograph insect capture under controlled conditions in the lab. This project depended critically on Griffin's collaboration with two key individuals and powerful new fast photographic technology. Fred Webster, a member of the prominent New England Forbes family, had built a large Quonset hut in the back yard of his Cambridge home and installed a large trampoline, on which he was practicing turning somersaults wearing skis. He fell in love with bats, removed the trampoline, and turned the Quonset hut into a large bat flight facility. David Cahlander was an associate of Harold Edgerton at MIT, who had developed high-speed photographic techniques, for example to capture the image of a bullet as it exited an apple. Griffin's students supplied the necessary manpower to handle and train bats. This project was not only a great success, but it documented flight and echolocation skills that for decades represented the best documentation of echolocation skills that had somehow to be explained. Many are still far from fully explained.

Using predominantly *Myotis* and the faster flying red bats (*Lasiurus borealis* (Müller, 1776)), the bats were trained first to catch fruit flies flying naturally around a suspended bag of ripe fruit. Bats detected fruit flies at a distance of about 50 cm and could catch them---if the fly density was high enough---at a rate as high as 2 flies in half a second. They were then presented with moths released in the same space and,

finally, mealworms shot from a “mealworm gun”. The bats became very skilled at catching both. In fact, once they had learned that everything appearing in that space was edible, they would attack almost anything tossed into the air: a rubber washer, a metal ball bearing, even a tennis ball. Only after learning that not all targets were edible did the bats show their ability to discriminate between different targets. The high-speed multi-flash images revealed previously unimagined athleticism: most catches were in the tail membrane. If, however, the target was a flying moth or a worm thrown up at the last moment, the bat would sometimes scoop them up near the tip of the wing, transfer them to its tail membrane, and thence into its mouth. The bats would even turn somersaults in air to catch a moth or mealworm above their flight path (Webster and Griffin 1962). Maneuvers like these happen too fast to be resolved at normal speed.

Most interesting were experiments to test the bats’ abilities to discriminate between different targets and in the presence of serious clutter. They proved able to isolate and capture, with unimpaired accuracy, one mealworm (usually the upper or nearer) out of a cluster of a dozen or more within approximately a cubic foot of space. They could pick off one target within 2-3 cm of another. They could capture a mealworm in the presence of different numbers of decoys of similar size (spheres, cylinders, discs). Experienced bats could be misled only by something like rolled up adhesive tape that had much the same size and shape as a mealworm. Approach, selection, and capture were normally completed within 0.2-0.5 sec. Plots of moth and bat trajectory suggested that bats were extrapolating the moth’s position to effect most efficient capture. Extensive tests were done where insect capture had to be done in the presence of various types of background “clutter” (solid surfaces of different shapes or yew branches). Although complex backgrounds, such as a yew branch, often deterred the bats, captures could also be made where the target was almost in touch with the source of the clutter (Webster 1963; Webster and Brazier 1965). These observations had an enormous influence on the further development of the field, defining clearly the behavior that had to be explained.

4. Proof that distance determination is based on pulse-echo delay.

From the beginning of the modern era, it was widely believed that the elapsed time between outgoing sound and returning echo was the criterion for distance determination. The final proof that this was the case was nailed down by James Simmons (1973), who perfected forced choice conditioning techniques in which bats (usually *Eptesicus*) were trained to move to the side of a Y-platform that was in the direction of the closer of two targets separated in angle sufficiently that the choice was probably made with different pulses. The bats learned to do this well, finally reaching chance behavior when the two targets differed by about 12 mm at an absolute distance of 30 cm. Simmons then introduced the clever refinement of replacing the real targets with phantom targets, created by recording emitted sounds close to the bat and playing them back from loudspeakers in the two directions after using an electronic delay line to adjust “echo” delay from each phantom target. The curve of success in resolving the delay line-separated phantom

targets matched the curve obtained with real targets almost exactly. QED. Furthermore, the ability to determine which of two targets was closer when the phantom target echoes were presented one at a time, to successive emitted calls, was the same ($\sim 60 \mu\text{s}$) as when the echoes from the two targets were returned simultaneously (Simmons and Lavender 1976). Thus the targets are being perceived as separate objects at different distances, even when the echoes largely overlap in time and each ear would be sensing them as single sounds differing only in subtle aspects of the spectral peaks and notches. Range resolution, determined with targets closer together, has essentially the same $\sim 1 \text{ cm}$ limit (Schnitzler and Henson 1980).

Surprisingly, the discrimination threshold was virtually the same at an absolute distance of 240 cm as at 30 cm! This led to another set of ingenious behavioral experiments by Jim Simmons that raised the ante for neural mechanisms of distance determination. These again employed virtual targets, but now the bats (*Eptesicus fuscus*) were asked to determine which of two targets was at a fixed echo delay (position in space), and which was “jittering” back and forth in delay around the same mean in every other echo. The result implied an ability to detect that jitter down to the μs range or less (Simmons 1979), and even to do this with only frequencies in the first harmonic (Moss and Schnitzler 1989). These results severely strain belief. The main reason for suspending disbelief is that, in natural behavior, bats can discriminate target shapes and resolve one among many in ways that would appear to require almost this much accuracy. This behavior, and the results of the jitter experiment, have led to sophisticated tests and model building in several labs, trying to decide if bats are capable of coherent cross-correlation of the returning echoes with the outgoing signals, i.e. behave essentially as an ideal receiver, or are correlating the waveforms of the two signals (semi-coherent receiver).

Forced choice behavioral tests were clearly very powerful, and during the 1970s and 1980s, many labs joined the search for the limits of different species’ abilities to measure distances, resolve multiple targets with multiple wave fronts, discriminate target dimensions and surface textures, and resolve other complex target features (eg., Simmons 1980; Habersetzer and Vogler 1983, and others, reviewed in Schnitzler and Henson 1980 and Simmons and Grinnell 1988). The capabilities revealed by these experiments often seemed impossible, except that the bats’ natural behavior seemed to require the impossible. What neural adaptations could explain them?

Section E describes the neurophysiological research that first revealed many of these adaptations.

C. Comparative studies of echolocation.

Before turning to the search for neural correlates of echolocation, however, I must mention the immense stimulus to the study of echolocation that came with discovery of the diversity in behavior and call structure of different bats. Möhres (1953), in Germany, had already reported that the horseshoe bat, *Rhinolophus*

ferrumequinum (Schreber, 1774), emitted pulses that were very long (by echolocating bat standards), averaging about 65 ms in duration, and virtually constant in frequency (about 80 kHz)—a sensational and troubling result, given the inevitable overlap between outgoing sound and returning echo. Moreover, Möhres and Kulzer (1956; Kulzer 1956) had discovered that bats of the genus *Rousettus*, in contrast to other Megachiroptera that are entirely visual, not only have excellent night vision, but have secondarily evolved echolocation by tongue clicks. (Reportedly, Sven Dijkgraaf was the first to discover the *Rhinolophus* constant frequency (CF) sound emission, but did not publish the observation. [Uli Schnitzler, pers. comm.]])

Griffin, too, embraced the comparative approach. In the early 1950s, he took his recording apparatus to Panama and obtained the first recordings of most of the families of neotropical bats, discovering that different families of neotropical bats use quite different pulse designs. He described the long CF pulses of *Chilonycteris rubiginosa* (now *Pteronotus parnellii* (Gray, 1843)), which end in a brief downward frequency sweep (FM), hence the term CF-FM pulses. (This turns out to be true of *Rhinolophus* pulses as well.) Griffin tried with little success to record the faint, harmonic-rich sounds of *Carollia* and other Phyllostomids, and described the sounds and extraordinary behavior of the fish-catching bat *Noctilio leporinus* (Linnaeus, 1758). He also extended the trip to Venezuela where he recorded the audible clicks of the oil birds (*Steatornis*) and experimentally proved that they echolocate, much like *Rousettus*. Alvin Novick, an M.D. who had become interested in bats and joined Griffin's lab, continued these studies in Panama and then, in a long trip to Asia and central Africa, recording from both Microchiropterans and *Rousettus*, verifying that the latter echolocate (Griffin and Novick 1955; Novick 1958a,b). He also confirmed Griffin's speculation that Asian cave swiftlets echolocate by clicks much like those of *Steatornis* (Griffin 1958).

These first comparative studies, summarized at an early stage by David Pye (1980), had an enormous impact on the field. Although a great deal of study continued to refine our understanding of the echolocation skills of insectivorous bats like *Myotis* and *Eptesicus*, a large fraction of the work---and excitement--- in the field has come through the comparative study of multiple species that inhabit different niches, employ different echolocation strategies, and emit different kinds of pulses.

This being a personal perspective, I might also add that Griffin arranged opportunities for me to get some foreign, comparative experience in bat research. Through his arrangement, Al Novick and I spent the summer of 1958 in Mexico, housed in the lab of Prof. Bernardo Villa R., collecting, recording, and studying obstacle avoidance abilities in a number of Mexican bats including *Leptonycteris*, *Natalus*, *Glossophaga*, *Desmodus*, and *Myotis* (four of the five *Desmodus* we studied were subsequently found to be rabid). Similarly, Griffin and I and a talented Harvard undergraduate, Clarke Slater, spent part of the summer of 1960 at William Beebe's research station, Simla, in the Arima Valley of Trinidad, where we built a long flight cage with a shallow pool inside it ("Lake Slatell"), and studied echolocation and fish

capture by *Noctilio leporinus*. They proved fast learners, and convinced us that they could not detect a target through the water surface.

D. The importance of technological advances.

It is a cliché that technological advances are often the enabling factor in research breakthroughs, but this truism was never more obvious than in echolocation research. Hartridge had the concept, but echolocation couldn't be proved until an ultrasonic sound detector was available. When the original Pierce Rochelle salt crystal transducers were replaced by a commercially available Western Electric 640AA condenser microphone, suddenly the sensitivity was much greater and the frequency response much better, allowing greater knowledge about harmonics. Moreover, the parabolic horn could be retired and reception became much less directional. Improved amplifiers and filters also helped. Equally importantly, methods of recording underwent a succession of revolutions. In 1938, the only recording device available to Griffin was a chart recorder that could barely resolve pulses up to 100-200/sec. By the 1940s, cathode ray oscilloscopes were available, and allowed much greater temporal resolution of signals, but analysis had to be done on filmed records of oscilloscope traces. Still, this was adequate to reveal that typical pulses lasted only 2-3ms and were frequency modulated, sweeping downward in frequency through approximately an octave. Sometime in the mid 1950s, high-frequency tape recorders became available, and Griffin acquired an Ampex model 307 that could be operated up to 60 inches/s (~150 cm/s). It wasn't until computers entered the scene (and improved rapidly) that any of this work really became "easy."

At the time I arrived on the scene (1955), the situation was only slightly improved. Field recordings involved packing carefully the following equipment into a Navy surplus van (nicknamed "Bluebeard" in honor of its color): A gasoline-powered generator, extra cans of gasoline, about 200 yards of power cable, Western Electric 640AA microphones and preamplifiers, wave generators, amplifiers and electronic filters (at least two of everything), radios, multiple tripods, the 70-pound Ampex tape recorder, soldering iron and other tools and repair supplies, and often mist nets and poles. We had to reach the recording site by mid afternoon to unpack and set everything up in the light, then wait for the bats, hoping that they would appear, that they would be feeding where we anticipated, that everything would work, and that it wouldn't rain. It's no wonder efforts were made, where possible, to study echolocation in the lab.

By the early 1970s, the somewhat more portable and much better Racal Store 4 tape recorders had greatly facilitated both laboratory and field research. Even earlier, memory oscilloscopes helped immensely, especially in the lab, by providing instantaneous feedback that made it possible to customize experiments in real time. The increase in interest in recording bats in the field and, in particular, the advent of integrated circuits and then computer technology led to the introduction of a succession of better and better "bat detectors." Most of us relied on improved

commercially available models; Uli Schnitzler seemed always to have even better, more versatile lab-designed and built detectors. In 2018, the equipment that used to fill a navy truck, and the lab equipment needed to analyze the few minutes of data collected in a day's work, has been replaced and vastly improved on by many alternative, pocket-sized detectors---even a small wafer that plugs into an iPhone---that can instantaneously record and analyze hours, if not days, of data. Brave new world!

E. Neural adaptation for echolocation: The synergy between behavior and neurophysiology

1. Initial searches for neural correlates. That bats can use sound as an accurate substitute for vision in behavior as complicated as insect capture came as a shock to human observers, since it is so foreign to our experience. Even blind humans, who use sound surprisingly effectively as a source of information about their environment, can't do anything equivalent. The question arises: what is different about the auditory system of bats that enables them to do these things? Galambos (1942*b*), as a doctoral student, had recorded cochlear microphonics up to 98 kHz, but no one had followed up on that work. I was privileged to begin the study for neural correlates of echolocation, and since that time, the field has advanced in tandem: usually behavioral experiments have revealed extraordinary abilities that need to be accounted for neurophysiologically. Sometimes unexpected neurophysiological results have anticipated behavioral results.

In the spring of my junior year and the following summer at Woods Hole, where Griffin was on the faculty of the Physiology course and I worked as his assistant, I began recording evoked potentials from the inferior colliculus of anesthetized *Myotis*. Fortunately, the experiments worked from the beginning and Griffin, who did not himself have a background in neurophysiology, let me run with it. Once again, Bob Galambos entered the picture to great advantage. Griffin arranged for me to visit his lab at Walter Reed Naval Hospital in Washington with some bats during spring vacation of my senior year (1958) to record and stimulate with his state-of-the-art set up, which was designed for studying cat audition. The records were beautiful and excited both of us. (That was also where I first met David Hubel, who later became a member of my PhD committee.) I ended up making neural correlates of echolocation my PhD subject. I studied the evoked potentials representing summed activity of different parts of the auditory pathways (mostly the first four neural levels, from the auditory nerve to the input to the inferior colliculus), the activity of clusters of single neuronal responses riding on localized evoked potentials, and the responses of single isolated neurons (Grinnell 1963*a,b,c,d*; Grinnell and Grinnell 1965). The results have long since been superseded, but even those early experiments permitted a number of interesting conclusions.

In 1962, I received my PhD and departed for London and a postdoctoral fellowship in the laboratory of Bernard Katz. Griffin contacted Prof. Y. Katsuki in Tokyo to see if he had someone who could continue the neurophysiology experiments, and Nobuo

Suga was sent to Harvard. He continued the experiments on *Myotis* with steadily improving equipment (especially in the form of much better FM signal generators), and was able to work out circuitry for the kinds of single units I had described and many more at different neural levels (Suga 1964a,b, 1970; Suga and Jen 1975). Within a short time four major independent labs were adding importantly to the behavioral data and seeking neural correlates for echolocation performance: those of Suga and George Pollak and their students in the U.S. and Gerhard Neuweiler and Hans-Ulrich Schnitzler in Germany. Overall, by the early 1980s, convincing neural correlates for the basic skills of echolocation in FM bats had been described.

2. Basic neural correlates of echolocation.

Adaptations for using ultrasound. Bats are sensitive to the ultrasonic frequencies they emit. The bats studied responded to higher frequencies than other animals tested to that point, and showed greatest sensitivity in the ranges of their echolocation sounds, including harmonics (40-50 kHz in *Myotis*, 55-65kHz in *Plecotus*) (Grinnell 1963a). This is unsurprising; but the adaptations of cochlear structure produce a match between greatest sensitivity and emitted frequency even up to 135-150 kHz in the paleotropical CF-FM bat, *Hipposideros galeritus* (Cantor, 1846) (Grinnell and Hagiwara, 1972).

Exaggeration of responses to echoes. The bat peripheral auditory system is specialized for hearing and analyzing echoes. The behavioral results indicated that bats must be able to hear and independently analyze faint echoes down to delays of less than a ms after emission of much louder pulses. This is something humans and other mammals cannot do (Rosenzweig and Rosenblith, 1950). Perhaps the most dramatic adaptation I observed in my initial neurophysiological experiments was extraordinary temporal resolution, which was exaggerated at levels between the auditory nerve and the input to the colliculus, in sharp contrast to neural responses in other mammals. Localized evoked potentials showed separate responses to pairs of tone pips down to intervals of ~0.2 ms, and there was full recovery, and even exaggeration of response, to the second of pairs of sounds at 1-5 ms separation. There were clearly neural mechanisms for facilitating response to echoes, at least up to the level of the inferior colliculus. (Grinnell 1963b).

Adaptations for overcoming forward masking. Moreover, in an experimental *tour de force*, Henson (1965) succeeded in recording cochlear microphonics from flying free-tail bats, showing that contraction of the middle ear muscles slightly preceded emission and reduced sensitivity to emitted sounds by 20-30 db, while recovering rapidly enough to have little effect on responses to echoes. Some facial features may also reduce response to the outgoing sounds. In addition, Suga and Schlegel (1972) found neural circuits that suppress response to emitted sounds. All are nice adaptations for echolocation.

Target localization: distance. Echolocating bats must be able to localize targets accurately in all three dimensions. It was widely believed, and Simmons (1973) soon

proved, that target distance is encoded in the delay between each frequency in the emitted pulse and the same frequency in the returning echo. If there are neural mechanisms for measuring these delays, that requirement is met. Indeed, some single units responded in ways that were clearly adapted for echolocation, eg. only to the second of two sounds, or to both, but with much greater sensitivity to the second of two than to the first, or with responses only to the pair at a restricted interval between the two (what would now be called delay tuning.) (Grinnell 1963b). Subsequent research was to document much more extensively specialized populations of neurons, especially in the inferior colliculus, that responded with extremely stable response latency to a given frequency in both the outgoing sound and returning echo, or to a combination at a specific interval (Suga 1970; Pollak et al. 1977).

Target localization: azimuth and elevation. The criterion for target distance was uncontroversial, but how bats determine the direction of each echo source has been more of a problem. *Eptesicus* are able to detect a shift of 1.5° in the horizontal position of a target (Simmons et al. 1983), about the same as in humans, and of about 3° in the vertical plane---much more accurate than humans (Lawrence and Simmons 1982), consistent with the need of bats to localize targets accurately in 3-dimensional space. The potential cues for horizontal localization are interaural time differences (ITDs) and interaural intensity differences (IIDs). Given the small size of the heads of bats, the (ITD) for a 1-2 degree shift in the horizontal plane would be less than $1\mu\text{s}$ across the midline and even less for changes in angle to either side. On the other hand, as a sound source is moved to different points in the hemisphere in front of a *Myotis* or *Plecotus*, changes in threshold for collicular evoked potentials can be as much as 2 dB per degree, and the figure is much larger for some single units (Grinnell 1963c; Grinnell and Grinnell 1965). This is the case both in the horizontal and vertical axes (directionality imposed largely by pinna structure). Moreover the directionality patterns are highly frequency dependent, and enhanced by inhibition from the contralateral ear. Consequently, it seemed reasonable to postulate that bats, by comparing the relative intensity perceived at the two ears over the range of frequencies used in the FM pulses, can pin-point accurately the source of any given sound (Grinnell and Grinnell 1965; Fuzessery and Pollak 1984; Harnischfeger et al. 1985).

I still believe that binaural comparison of relative perceived loudness at many different frequencies in the echo is the most likely explanation for target localization in both azimuth and elevation, but the extraordinary temporal resolution described above --in the μs range--- keeps alive the idea that ITDs could be the cue used in the horizontal dimension, and that multi-wavefront reflections off the pinna and tragus can be used for vertical localization (Simmons et al. 1983). On the other hand, another strong argument against ITDs being the cue is the observations that in bats, as in other animals, there is a time-intensity trade in the latency of responses in the auditory pathways. This has been reported to be in the range of $8\mu\text{s}/\text{dB}$, and can be as high as $50\mu\text{s}/\text{dB}$ (Harnischfeger et al. 1985; Pollak 1988). Interestingly, some single units in the cortex of *Myotis lucifugus* show a shorter response latency to a

faint sound than to a louder one (paradoxical latency shift) (Sullivan 1982). This probably reflects the effect of inhibitory circuits that help determine echo delay specificity and may help overcome this intensity dependent shift in response time. How bats can simultaneously localize multiple targets from multiple overlapping echoes remains a problem, of course, for this parameter like most others.

An amusing further thought: as a sound source is moved from one side of a bat to the other, the apparent intensity on one side increases as the other decreases, roughly doubling the difference in effectiveness at the two ears. Changes in vertical angle do not enjoy this opposite change in the two ears. One might predict, therefore, that if binaural intensity differences are the cue, localization might be expected to be about twice as accurate in the horizontal as in the vertical plane. That this is reported to be the case is probably entirely accidental.

Selectivity for FM sounds. Although most collicular single units responded to an FM sound whenever it swept through the frequency of the CF tone pip to which it was most sensitive, a few units responded selectively only to downward-sweeping FM sounds (Grinnell and McCue 1963). There were no commercially available FM sweep generators at that time, so these experiments depended on a one-of-a-kind FM pulse generator, built by the Lincoln Labs. This kind of selectivity was more thoroughly explored by Suga (1964a) and by many others. Indeed, it fits into a general picture of specialization/adaptation for echo features used in natural behavior.

3. Long CF-FM bats and Doppler Shift Compensation.

One of the best examples of synergy between behavior and neurophysiology is the discovery and elucidation of the specialized adaptations for echolocation in long CF-FM bats. Griffin (1958), based on the early findings of long CF echolocation signals in *Pteronotus parnellii* and *Rhinolophus ferrumequinum*, speculated that that these bats might somehow use Doppler shift information. In 1965, I found that inferior collicular evoked potentials in *P. parnellii* showed a prominent peak of sensitivity and large magnitude responses around the frequency of the second harmonic of the emitted CF (62-63 kHz), and an even more sharply tuned "off-response" to frequencies just below that (Grinnell 1967,1970). The auditory system was clearly focused on frequencies around the second harmonic.

These surprising neural response made sense with the major discovery by Schnitzler (1968), that, during flight, long CF-FM horseshoe bats compensate for the upward Doppler shift of the echoes of their emitted sounds by lowering the emitted frequency just enough for the 50-100 ms-long CF component of returning echoes to be maintained at a desired reference frequency close to the CF emitted at rest. This Doppler Shift Compensation (DSC) is phenomenally accurate. Over a wide range of flight speeds and Doppler shifts of up to 2 kHz or more, the returning echo is maintained at a constant frequency within 50-100 Hz around 83 kHz---an accuracy of about 0.06%, making it one of the most accurately regulated biological

phenomena known (Simmons 1974; Schuller et al. 1974). Similar DSC was soon also shown in the neotropical mustache bat, *Pteronotus parnellii*, which emits pulses with a long CF component of about 61 kHz. In both cases, the CF terminates in an FM sweep. Doppler shift compensation is so extraordinary, and implies so much specialization, that a large fraction of the behavioral and neurophysiological studies since this discovery have been done with these species. In both species, from the cochlea onward, the auditory pathways are highly specialized for detecting and analyzing frequencies in a narrow band around the emitted CF (Grinnell 1970; Neuweiler 1970, 1980; Pollak et al. 1972, 1979). Indeed, this feature has been well named an “acoustic fovea” (Schuller and Pollak 1979). In the relatively narrow frequency range of Doppler Shift Compensation, single units are phenomenally sharply tuned, with $Q_{10\text{dB}}$ values up to 300-400 (Suga and Jen 1977)!

Thanks to the painstaking work of many anatomists, especially Ada Pye, John Zook, Marianne Vater, Manfred Kössl, John Casseday, and Ellen Covey, there is now a large and fascinating literature on the anatomical specializations of the cochlea and auditory pathways in the CF-FM bats, where, from the cochlea to the auditory cortex there are morphological and physiological specializations for analysis of a narrow band of frequencies around the echo CF component. George Pollak and John Casseday, with their collaborators, have contributed much of what we know about the anatomy, physiology, and pharmacology of the brain stem and midbrain circuitry that helps explain the echolocation-specialized response properties in both FM and CF-FM bats. They also wrote an excellent review of our knowledge as of 1989 (Pollak and Casseday 1989).

The amount of Doppler shift in the echo could in theory give long CF-FM bats information about the azimuth of targets, since the magnitude of the shift is dependent on the target angle relative to the direction of flight. Nevertheless, it seems likely that the FM component is mainly responsible for their target localization in the same way as in FM bats. The directionality of echolocation has been carefully worked out using behavioral criteria in *Rhinolophus ferrumequinum* (Schnitzler and Grinnell 1977; Grinnell and Schnitzler 1977). An interesting complication is that *Rhinolophus* rotates one ear forward, the other back, with (or after) each emission (Griffin et al. 1962). This alternating rapid back and forth movement would have a powerful effect on directionality of hearing. Other bats distort their pinnae, nose leafs, or other facial structures, coupled with pulse emission, no doubt also affecting emission beam pattern and directionality of hearing.

4. Organization of the auditory cortex in CF-FM bats.

This brings me to one of the greatest triumphs of bat neurophysiology. When it became clear that the colliculus and other centers in the auditory systems of *Rhinolophus* sp. and *Pteronotus parnellii* were specialized to have an acoustic fovea (Grinnell, 1967, 1970; Pollak et al. 1972; Suga et al. 1976; Neuweiler and Vater 1977; Pollak and Schuller 1981; Feng and Vater 1985), Suga and his collaborators carried the study into the cortex of *P. parnellii*, and described an extraordinary level of

organization (O'Neill and Suga 1982; Suga et al. 1983; Suga 1984). As one would expect, the emphasis on near-CF frequencies translates into a large fraction of the auditory cortex being devoted to processing of sounds in the range of the 2nd harmonic, around 61-63 kHz (the acoustic fovea). Moreover, this is not simply an enlargement in that portion of the tonotopic map across the auditory cortex. Within that CF-analyzing area there is further concentric organization, with different areas systematically providing information about the first detection of echoes, the angle of incidence of the echo, the relative velocity of the bat relative to the target, and finally to localization of the source of the echo. Nearby areas of the auditory cortex deal with velocity information (the amount of Doppler shift) and the distance of the target. The Doppler shift in principle can provide many forms of information. It turns out, however, that the information the bats appear to be most interested is the flutter in frequency and amplitude of the returning CF echo due to insect wing-beats (Suga and Jen 1977; Schnitzler and Ostwald 1983).

The neural pathways providing this information to the *Pteronotus parnellii* cortex constitute perhaps the most interesting finding. Cortical neurons respond selectively to combinations of the outgoing sounds and returning echoes. The outgoing sound component is the fundamental CF-FM, which in fact is virtually inaudible outside the animal, presumably because it is filtered out by the nasal passages (Suga et al. 1978, 1979). Nevertheless, the fundamental, or an efferent copy, is still perceived by the bat. The emitted sounds consist mainly of the 2nd, 3rd, and 4th harmonics, with the 2nd harmonic being loudest. For measurement of Doppler shift, there is an area in the cortex in which neurons are selectively responsive to specific combinations of the CF₁ in the emitted sound and the CF₂ in the returning echo, while next to this area in the auditory cortex there are parallel arrays of neurons responding to combinations of CF₁/CF₃ and CF₁/CF₄. These areas reflect in spatial organization the existence and degree of flutter in frequency and amplitude of the retuning echo and other information contained in the Doppler shifted CF component. The distance-measuring area consists of three parallel arrays of neurons that respond selectively to combinations of the fundamental FM component in the emitted sounds (FM₁) and the second, third, and 4th harmonics (FM₁/FM₂, FM₁/FM₃, and FM₁/FM₄) of the echo, with neurons spatially arranged with preferred delays between ~0.4 and 20 ms. Thus there are place maps of relative velocity and distance in the cortex (Suga, O'Neill and Manabe 1978; Suga and O'Neill 1979; Suga 1984; Suga and Horikawa 1986). This does not mean that these combinations of echo components are combined with the outgoing self-heard vocalization for the first time in the cortex. Probably they put together in subcortical areas; but they show up most clearly in the cortex. Indeed, a possible spatial map of delay tuned neurons has been found in the area between the posterior and anterior colliculi in *Eptesicus* (Feng et al. 1978).

Final Thoughts:

Virtually all of the references cited in this short review are prior to 1990, coming predominantly from the labs of Griffin and the next generation of researchers, many of whom had been his students or postdoctoral associates. The field has grown

enormously since then, with an exponential growth in the number of labs studying echolocation and the number of papers published. Even for the work prior to 1990, I have barely skimmed the surface, emphasizing what I perceive to be some of the key findings. It would seem that by the mid-1980s most of the fundamental discoveries in the field had been made: the accuracy of detection, localization, and characterization of targets by both FM and CF-FM bats, the diversity of orientation sounds different species emit and their corresponding strategies for extracting information from echoes, and the neural and anatomical adaptations that have co-evolved with behavioral specializations. However, as the third and fourth generation of echolocation investigators have established their own labs, the discoveries keep coming. An increasing emphasis has returned to mechanisms of overcoming clutter, recognition by a bat of its own echoes, simultaneous analysis of echoes from multiple targets, assignment of echoes to the correct outgoing pulse, adaptation of echolocation strategies to different ecological niches, and the richness of the “scene” a bat experiences. The improvement in bat detectors and sound analysis software, which make it much more feasible to monitor bat activity, and the growing awareness of the need to preserve bat populations, has led to a huge increase in bat monitoring and conservation activities, as reflected in the sessions of the meeting giving rise to this volume. There is much reason to be encouraged by these developments, but still much to learn and much cause for worry about the long-term survival of bats.

Echolocation has been a very generous field, and continues to amaze, proving that it is still difficult to fully comprehend what it is like to be a bat.

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