What's It Like to Be a Bat? Ask Jim Simmons

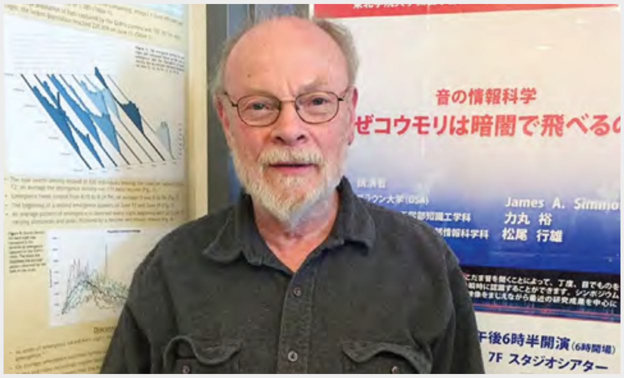
Cynthia F. Moss and Laura N. Kloepper

Imagine conducting research so groundbreaking that a team of international scientists convene a workshop titled Hard Data and Speculations to discuss your publications. This workshop lasts five days, focuses on an in-depth breakdown of your data, includes lively debate, and ends in an official signing of a declaration. Now imagine that the story of this declaration continues to be told to new generations of acousticians with whispers of awe. Who could be the great scientist behind this incredible legend?

"Pay no attention to the man behind the curtain," says James (Jim) Simmons (**Figure 1**) with a twinkle in his eye. This phrase is one of Jim's often-quipped taglines as he shows his bat laboratory and explains his research on the extraordinary sonar imaging of echolocating bats. For those who don't recognize this line, it comes from a scene in the motion picture *The Wizard of Oz* (see bit.ly/3vysQQA) when Dorothy's dog Toto reveals that a supernatural talking head is just an illusion created by a man operating a device behind a curtain.

This phrase has a double meaning to Jim. First, he uses the phrase to warn his audience about aspects of the bat's sonar imaging that may appear supernatural or beyond the grasp of human understanding. Second, Jim often conducts his research in his bat flight laboratory while hiding behind a curtain with his sophisticated electronic equipment. But don't let this jokester fool you; we should absolutely pay attention to the man behind the curtain because through his work on bat sonar imaging over the past six decades, Jim has revealed the extraordinary sensory capabilities of bats, developed sonar-processing models that are incorporated into bioinspired design, and touched the lives of countless students and colleagues who have been fortunate to know his work.

Figure 1. *Jim Simmons at a poster session in Japan in 2014. Photo by Laura N. Kloepper, reproduced with permission.*



The Discovery of Echolocation

Surprisingly, *so*und *na*vigation and *r*anging (SONAR) was an established technology nearly three decades before Galambos (1942) and Griffin (1958) demonstrated at Harvard University, Cambridge, Massachusetts, in the 1930s that bats produce ultrasonic calls and process echo returns with their ears. In the late eighteenth century, Spallanzani (1794) postulated that bats relied on sound to navigate, but at the time, there were no devices to formally test this idea, and human ears cannot detect the ultrasonic cries of bats. Spallanzani conducted experiments that separately eliminated the bat's use of vision, touch, and hearing to explore the relative importance of these senses to its navigation. He found that interfering with the bat's hearing had the most detrimental effects on navigation, but the sensory information these animals used to avoid obstacles and capture prey remained a mystery. More than a century later, with the use of specialized equipment provided by G. W. Pierce, a physics professor at Harvard University, Griffin and Galambos (1941) demonstrated that bats could steer around fine wires and discriminate edible and inedible targets by producing ultrasonic calls and listening to echoes from objects in the surroundings. They also showed that taping the bat's mouth closed or plugging its ears interfered with its ability to navigate. Griffin (1944, 1958) coined this remarkable active sensing behavior, echolocation. The reader can find modern reviews of bat

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echolocation in *Acoustics Today* (Simmons, 2017) and volumes of the *Springer Handbook of Auditory Research* (*SHAR*) series, such as *Hearing by Bats* (Popper and Fay, 1995), *Biosonar* (Surlykke et al., 2014), and *Bat Bioacoustics* (Fenton et al., 2016).

Graduate Training at Princeton University

After completing his undergraduate degree in psychology and chemistry in 1965 at Lafayette College, Easton, Pennsylvania, Jim launched his scientific career as a graduate student (1965–1969) at Princeton University, Princeton, New Jersey, in the laboratory of Ernest Glen Wever (see acousticstoday.org/7408-2), a renowned auditory scientist whose research program explored mechanisms of hearing in a wide range of species. Graduate students in Wever's laboratory during Jim's tenure at Princeton University studied a variety of organisms, including fish (Richard R. Fay), cats (James Saunders), and dolphins (James McCormick). Wever also hosted many senior scientists and visitors who contributed to a vibrant interdisciplinary laboratory environment. In an era when audio technology was in its infancy, Wever made connections with Bell Telephone Laboratories researchers, who provided state-of-the art equipment for the measurement and analysis of sound. This equipment, along with custom devices, was essential to the success of Jim's doctoral research.

As a graduate student, Jim learned that Wever had a colony of bats waiting for a research question, and he decided to unravel the mysteries of echolocation in these animals. Such experiments would take tremendous creativity and perseverance, and Jim rose to the challenge. Jim adapted classic psychoacoustic methods to measure range difference discrimination thresholds in bats. The success of these experiments depended on Jim's astute observations of bat natural behaviors. He designed a task that required a bat to fly or crawl toward a trained stimulus. Jim presented the bat with two objects, one closer and one further away and rewarded the bat with a tasty insect for approaching the closer object. He gradually decreased the difference in distance between the two objects and determined the minimum range difference that bats could reliably discriminate (see ***Target Range Discrimination Experiments***). Researchers around the world have since adopted Jim's behavioral methods to address a wide range of scientific questions on sonar perception in bats.

Important Visitors to Wever's Laboratory at Princeton

At the time Jim was conducting his thesis research, spatial perception by echolocation was not well understood, and one of the exciting moments of his graduate career came when a skeptical Nobel Laureate, Georg von Békésy (see acousticstoday.org/7302-2), traveled from Harvard University to visit Wever's laboratory at Princeton University. von Békésy (1960), who made important and fundamental discoveries about the transduction of sound in the inner ear, did not believe that the bat auditory system operated fast enough to support echolocation. Griffin, who was already greatly impressed by Jim's research, took the train from The Rockefeller University, New York, New York, to Princeton University in a plot to quash von Békésy's doubts about bat biosonar. Jim's demonstrations of his behavioral research methods and bat sonar range discrimination performance curves convinced von Békésy not only that the bat auditory system operated on a fast enough timescale to use echolocation for navigation but also to estimate target distance from echo delay. It was not until some years later that Jim found out that this exchange was a setup. Wever and Griffin both knew the significance of Jim's discoveries and wanted von Békésy to see Jim's work firsthand. Jim's trailblazing dissertation *Perception of Target Distance by Echolocating Bats* demonstrated the extraordinary abilities of bats to determine target distance from the delay of echo returns (see Simmons, 1973) and laid the foundation for decades of sophisticated behavioral studies of animal sonar in air and underwater.

Not all visitors to Wever's laboratory were scientists. One noteworthy visitor during Jim's time at Princeton University was the philosopher Thomas Nagel (see bit.ly/3HeKrzt), who later went on to publish his famous essay, "What Is It Like to Be a Bat?" In his essay, Nagel (1974) used the example of a bat to make his argument that the subjective mind of another cannot be accessed. In the era when Jim met Nagel, the scientific community shunned any notions that one might consider the mental state or consciousness of an animal, but psychophysical measurements relating the physical dimensions of a stimulus and animal performance were considered objective and rigorous. In this vein, Jim took a scientific approach to shed light on the images represented in the bat's sonar receiver. Was Jim's work inspiration for Nagel's essay? One will never be certain, but

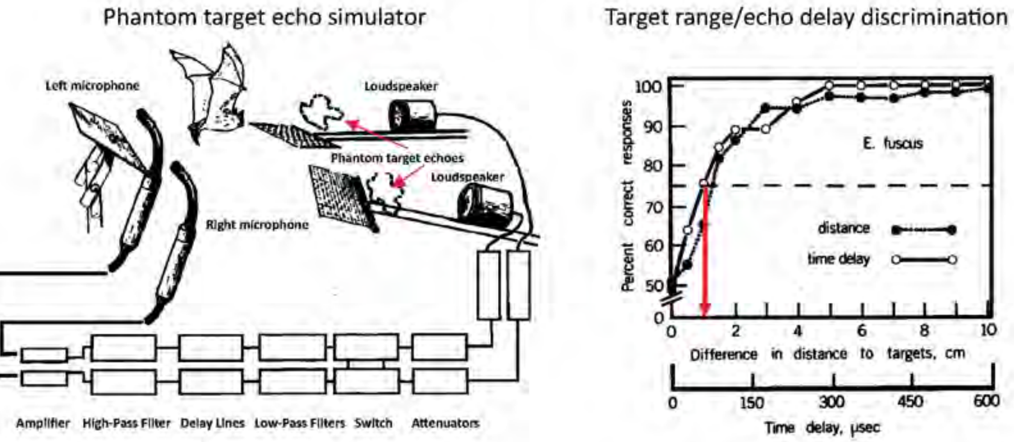


Figure 2. ***Left:*** *methods used to simulate echoes at different delays. The bat produced echolocation calls, which were picked up by microphones to its left and right. The signals were amplified, filtered, delayed, and played back through loudspeakers to generate phantom target echoes. The bat was trained in a two-alternative forced-choice procedure to approach the closer phantom target, i.e., playback echoes with the shorter delay, for a food reward.* ***Right:*** *comparison of the bat's performance (percent correct) in discriminating the difference in distance of two physical targets (**solid circles, dotted line**) and the echo delay of two phantom targets (**open circles, solid line**).* ***Vertical red arrow:*** *range difference (~1 cm) or echo delay difference (~ 60 μs) yielding 75% correct performance. The alignment of the two performance curves for physical object distance and playback echo delay discrimination demonstrates that bats use echo delay to determine target distance. Figures from Simmons, 1973.*

the timing of Nagel's visit, five years prior to his published essay, raises the intriguing possibility.

Jim's Work Leading to the Declaration of Sandbjerg

Target Range Discrimination Experiments

At the time Jim began his experiments on sonar ranging in bats, there were competing theories on the acoustic cues bats use to measure distance. Pye (1961) proposed that bats relied on beat frequencies that arise from overlap between outgoing sonar calls and returning echoes to determine target distance; however, Cahlander et al. (1964) reported that the frequency-modulated (FM) calls produced by insectivorous bats rarely overlap with returning echoes, thus debunking the beat theory of sonar ranging.

Jim's psychophysical experiments provided conclusive evidence in support of the hypothesis that bats use the time delay between sonar call and echo to measure target distance. He showed this through careful two-alternative forced choice (2AFC) psychophysical experiments that required the bat to discriminate between the arrival time of two electronically delayed playbacks of the animal's sonar calls, "phantom target" echoes. Jim discovered that the bat's performance depended on the echo delay difference between two playback echoes, showing almost 100% correct choices for delay differences greater than 300 μs and falling to chance for delay differences of 0 (**Figure 2**). Jim also demonstrated that bats could discriminate echo delay differences as small as 60 μs, which corresponds to range differences of approximately 1 cm. Importantly, he did these experiments with both phantom and physical targets to further test the notion that bats rely on echo delay to measure target distance.

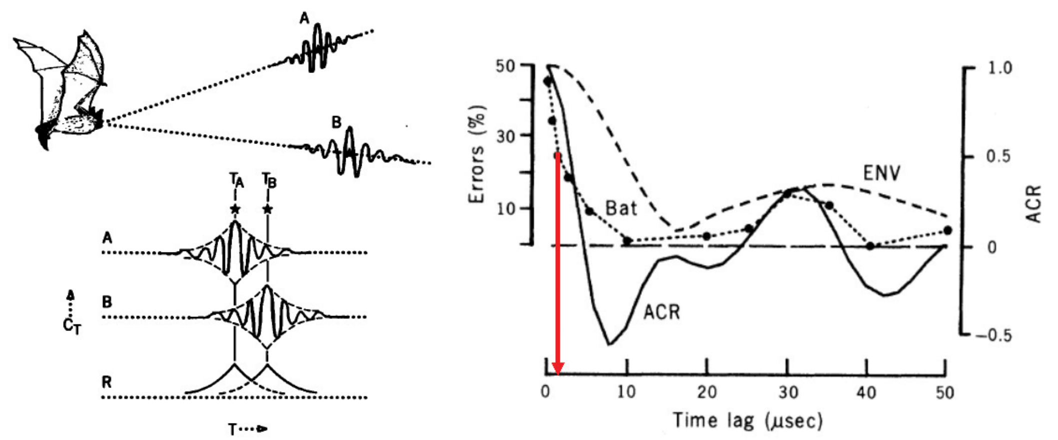
Further experiments carried out by Jim showed that a bat's ranging performance depended on the bandwidth of its echolocation signals. Again, using psychophysical approaches, he explored the echo delay discrimination abilities in four different species of bats that use echolocation signals with varying bandwidth (Simmons, 1973). Jim found that bats using broadband echolocation signals, such as the big brown bat *Eptesicus fuscus*, show finer range discrimination performance than bats that use narrowband echolocation signals, such as the greater horseshoe bat *Rhinolophus ferrumequinum*. These comparative data were consistent with Jim's hypothesis that bats perceive target distance by cross-correlating the outgoing call and returning echo, yielding a time-domain readout of target range or echo arrival time from the envelope of the correlation function. This is referred to as a matched filter operation, whereby the arrival time of returning echoes is measured from the peak of the cross-correlation function (see Woodward, 1953).

This matched filter operation can take the form of a semicoherent or coherent ideal receiver. A semicoherent ideal receiver encodes the envelope of the cross-correlation function, and a coherent ideal receiver encodes the fine structure (phase) of the cross-correlation function (for more explanation, see Simmons and Stein, 1980; Skolnik, 2002). Jim noted that the cross-correlation functions of broadband echolocation signals show a sharper peak in time than those of narrowband echolocation signals, and the bats' range discrimination performance curves parallel the envelope of their species-specific sonar correlation functions. These observations led Jim to posit in his 1973 paper that bats operate as semicoherent ideal receivers.

Microsecond Discrimination of Jitter in Echo Delay

Jim also observed that the bats made head movements when performing the 2AFC range difference discrimination tasks and hypothesized that head movements could smear the bat's perception of target distance. Without the influence of head movements on range discrimination, perhaps bats would show greater performance and potentially reveal that they operate as ideal coherent receivers. Jim came up with a new experimental paradigm that asked the bat to measure target distance (or echo delay) without moving its head. This task required the bat to discriminate between echoes that alternated in delay between successive echoes (a jittering target) from echoes that returned at consistent delays (a stationary target). The comparable experiment for a human would be to discriminate between dots at a fixed distance and dots that alternate between two distances, separated by millimeters or even micrometers. The results showed that bats could discriminate changes in echo delay of less than 1 µs, corresponding to a change in distance in the micrometer range.

Figure 3. ***Left:*** *relationship between the positions of targets in range (or delay) and the location of the central peaks in the cross-correlation functions for outgoing sounds and returning echoes for two targets, A and B, at different distances from the bat. This schematic is intended to provide the reader with an intuitive understanding of Simmons's interpretation of sonar ranging by bats, i.e., the animal cross-correlates its sonar call and returning echo to estimate echo delay.* T_A*, time of arrival of echo A;* T_B*, time of arrival of echo B following the operation of a receiver (R). From Simmons, 1973.* ***Right:*** *jitter discrimination task required the bat to differentiate between two playback stimuli, one containing echoes that alternated in delay (a jittering target) and one containing echoes that returned at stable delays (a stationary target). Jitter values ranged from 0 to 50 µs. The bat's percentage errors were plotted as a function of the jitter in echo delay (time lag) in microseconds. Note that the bat in this task successfully discriminated jitter in echo delay on the order of 1 µs, referencing a 75% correct (25% error) criterion (vertical red arrow).* ***Dotted line:*** *envelope of the autocorrelation function (ENV);* ***solid line:*** *fine structure of the autocorrelation function (ACR). Note that the rise in errors at 30 µs corresponds to the sidelobe of the fine structure of the correlation function. Because the bat's performance aligns with the fine structure of the correlation function, Simmons argues that bats perceive the phase of echo returns and hence operate as ideal sonar receivers. From Simmons, 1979.*



Furthermore, bats showed a rise in errors at around 30 µs. These findings led Jim to infer that the echolocating bat operates as a coherent ideal sonar receiver that represents the fine structure (phase) of the time-domain representation of target distance. In this scenario, the bat measures target distance from the peak of the correlation function along the delay axis (**Figure 3**) but is also sensitive to interference from sidelobes. In the jitter discrimination experiment, the bat appeared to sometimes confuse the central peak of the correlation function with the sidelobe when the echo delay alternated by 30 µs. In other words, Jim posited that the bat did not reliably discriminate 30-µs jitter in echo delay because it is sensitive to the fine structure (phase) of the correlation function, occasionally confusing the central peak and the sidelobe. Interested readers are referred to Skolnik (2002) for more background on sonar receivers.

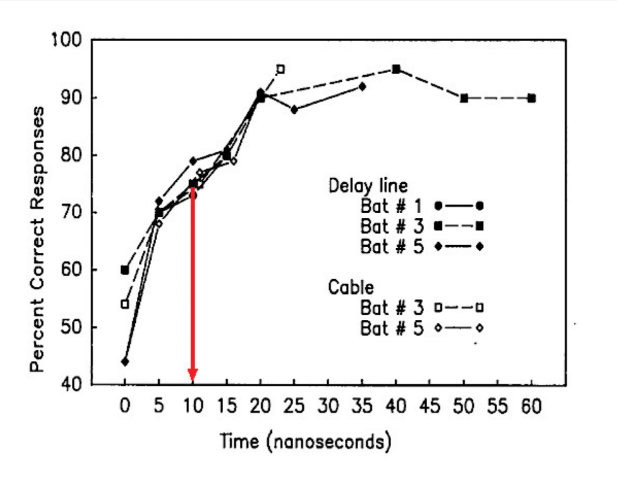
Jim's stunning report that bats discriminate jitter in echo delay of less than 1 µs and show sensitivity to the phase of the correlation function was published in *Science* (Simmons, 1979). These findings and their interpretation that the bat operates as an ideal sonar receiver stirred a great debate among scientists in the field (see the controversial paper by Beedholm and Møhl, 1998), largely because coding of phase in the auditory system is believed to be limited to sound frequencies below 5 kHz, not in the ultrasound range used by bats. For readers who would like to learn more, Jim published a review in *Acoustics Today* (Simmons, 2017).

Replication of Jitter Discrimination Experiments

Among those who challenged the interpretation of Jim's 1979 jitter discrimination data was Hans-Ulrich (Uli) Schnitzler. Uli argued that there are strict criteria for specifying the operation of an ideal sonar receiver and the shape of the psychophysical performance curve cannot substitute for these criteria (see Skolnik, 2002). He also noted that the analog delay lines that were used to generate microsecond jitter in echo arrival times could have generated spectral cues rather than echo delay for the bats to perform the discrimination task (see Moss and Schnitzler, 1995). Uli arranged for his electronics shop to build a digital delay line to replicate Jim's experiments, eliminating the possibility of spectral artifacts. Experiments in Uli's laboratory confirmed that bats can indeed discriminate jitter in echo arrival time of less than 1 µs (Moss and Schnitzler, 1989).

Uli and his colleagues at the University of Tübingen, Tübingen, Germany, then went on to demonstrate with the same apparatus that bats can discriminate the phase of echo returns (Menne et al., 1989). Because these experiments were conducted with a digital delay line, the spectral artifact criticism associated with analog delay lines could be tossed aside, but these latter experiments yielded jitter discrimination performance curves that differed from those in Jim's 1979 report. Namely, the rise in range discrimination errors at 30 µs was absent in the data from Uli's laboratory. The source of this discrepancy in data from the two laboratories remains a

Figure 4. *Bat's performance detecting jitter in the delay of playback echoes. The bat produced echolocation calls, which were picked up by two microphones, electronically delayed, and played back through two loudspeakers, one placed to the left and the other to right of the bat's observation position. On each trial, one loudspeaker returned echoes at a fixed delay and the other loudspeaker returned echoes that alternated in delay from one broadcast to the next, simulating a target that jittered in range. The jittering target was randomly presented through the left or right loudspeaker on successive trials, and the bat was rewarded for crawling toward the jittering target. In this experiment, jitter ranged from 0 to 60 ns, more than an order of magnitude smaller than the jitter values tested in Simmons' (1979) experiment. The bat's performance ranged from ~50% (chance) in control trials with 0 ns jitter to ~90% correct with jitter values greater than 20 ns. Jitter in echo delay was produced in two ways, using either an analog delay line or cables of different lengths. Note that in this experiment, the bat's jitter discrimination threshold was about 10 ns (***vertical red arrow***), referencing a 75% correct performance criterion. From Simmons et al., 1990.*



Declaration of Sandbjerg

On this the 12th day of August, anno 1994,

it is agreed:

Under the assumption that in a jitter experiment a bat compensates for all errors caused by its own movements during the measuring process, the 40-ns threshold obtained at a 36 dB S/N ratio can be understood ONLY on the basis of a coherent receiver.

Signed by:

Witnessed by:

Bertel Møhl

Sabine Schmidt

Rolf Müller

Figure 5. ***Left:*** *signing the Declaration of Sandbjerg in Sønderborg, Denmark, in 1994. Photo of (**left to right**) Cynthia F. Moss, Johns Hopkins University, Baltimore, Maryland; Hans-Ulrich Schnitzler, University of Tübingen, Tübingen, Germany; James Simmons, Brown University, Providence, Rhode Island; and Lee Miller, University of Southern Denmark Odense, Denmark,* ***Right:*** *Jim Simmons signed the declaration,* Under the assumption that in a jitter experiment a bat compensates for all errors caused by its own movements during the measuring process, the 40-ns threshold obtained at a 36 dB S/N ratio can be understood ONLY on the basis of a coherent receiver. *All others who signed below were witnesses. Photo by Annemarie Surlykke, University of Southern Denmark Odense, Denmark, reproduced with permission.*

mystery today, but Jim and Uli appreciate each other as scientists and colleagues. They are always happy to have a beer together after an intense scientific debate.

Nanosecond Discrimination of Jitter in Echo Delay and the Declaration of Sandbjerg

Jim continued to measure sonar jitter discrimination thresholds and reported that big brown bats can discriminate echo delay changes on the order of 10 ns (**Figure 4**) (Simmons et al., 1990). This astonishing result sparked further debate, and in 1994, Uli Schnitzler, Annemarie Surlykke, Bertel Møhl, Lee Miller, and Cindy Moss organized a workshop to explore the scientific issues. The workshop, titled Spatial Perception in Echolocating Bats: Hard Data and Speculations, took place over 5 days at Sandbjerg Manor, Sønderborg, Denmark. Each day consisted of multihour discussion sessions of papers (largely from Jim's laboratory) and written summaries of discussion.

The workshop concluded with a signing of the Declaration of Sandbjerg that states *Under the assumption that in a jitter experiment a bat compensates for all errors caused by its own movements during the measuring process, the 40-ns threshold obtained at a 36 dB S/N ratio can be understood ONLY on the basis of a coherent receiver*. Jim undersigned this statement (see **Figure 5**). Although the scientific issues were far from resolved after this meeting, the discussion was stimulating and spirits were high. Over the years since this workshop, researchers have continued to argue these points and mostly agree to disagree.

Jim's Additional Contributions to Knowledge of Bat Echolocation

Along with Jim's fundamental contributions to our understanding of bat perception by sonar that led to the Declaration of Sandbjerg, he also conducted groundbreaking neurophysiological experiments in echolocating bats soon after he began his first faculty position in the Psychology Department at Washington University, St. Louis, Missouri. Also at Washington University at the same time was the renowned auditory physiologist and former postdoc of Donald Griffin, Nobuo Suga (see **Figure 6**).

Range-Tuned Neurons

Discussions with Griffin and Suga inspired Jim to probe the neurophysiological underpinnings of echo ranging in bats, and his 1978 paper with coauthors Albert Feng and Shelley Kick led the way for decades of research on this problem (Feng et al., 1978). Feng et al. described

Figure 6. *Photo of (**left to right**) James Simmons, featured in this article; Donald Griffin, the modern-day discoverer of echolocation in bats; and Nobuo Suga, an eminent auditory neurophysiologist, taken at Washington University, St. Louis, Missouri, in the 1970s. Photo by a student in the laboratory, used with permission from James Simmons.*

the response properties of auditory neurons in the bat midbrain intercollicular nucleus that exhibit the response characteristic known as "echo delay tuning" or "range tuning," which may serve as the neural substrate for target distance coding. Echo delay-tuned neurons show little or no response to single sounds but show facilitated responses to pairs of sounds, simulating echolocation calls and echoes, separated by a restricted range of time delays. This remarkable discovery sparked decades of research in bat auditory neurophysiology. Echo delay-tuned neurons in the bat brain have since been identified in many other stations of the auditory pathway in passively listening bats (reviewed by Covey, 2005; Ulanovsky and Moss, 2008; Suga, 2015; Wohlgemuth et al., 2016). Only recently have experimental methods advanced to show that neurons in the bat midbrain superior colliculus encode the three-dimensional (3D) location of physical objects by responding to echoes from calls produced by the actively echolocating bat (Kothari et al., 2018).

Sonar Gain Control

Jim also made the fundamental discovery that bat sonar exhibits an automatic gain control in which the bat's auditory system changes sensitivity according to the delay of the receiving echo, and this adjustment serves to stabilize the perception of echo amplitude over changing distance. Using psychophysical methods, Jim observed that the hearing sensitivity of the big brown bat (*Eptesicus fuscus*) decreases before each sonar pulse is emitted and then recovers in a logarithmic fashion to compensate for the two-way transmission loss of sonar returns, thereby stabilizing the bat's estimate of echo arrival time, which is the bat's cue for target distance (Kick and Simmons, 1984; Simmons et al., 1992). Early experiments required the bat to detect spheres presented at different distances and revealed that the detection threshold increased with a decreasing target distance over a range of about 1.5 m (Kick, 1982). Later experiments transmitted playbacks of the bat's calls to simulate echoes from objects at different distances (Simmons et al., 1992). The playback experiments showed the same trend, a change in threshold with echo delay, corresponding to target distance. The bat's gain control is key to its extraordinary sonar-ranging performance and has important implications for applications in sonar technology. It has also been demonstrated in echolocating marine mammals (Au and Benoit-Bird, 2003).

Acoustic Clutter Rejection

Jim's research has also offered insight to the ways echolocating bats deal with acoustic clutter. When a bat is seeking insect prey in the vicinity of vegetation, each sonar call returns echoes from the target of interest along with a stream of echoes from branches, leaves, and other objects in the vicinity. A study Jim conducted with collaborators at Doshisha University, Kyoto, Japan, led to the discovery that FM bats operating in dense clutter shift the spectral content of successive sonar calls to tag individual returns within echo streams (Hiryu et al., 2010). In this scenario, one echo stream overlaps with the next and the bat's frequency adjustments to its sonar emissions serve to ensure accurate call-echo assignment, which is needed to measure object distances in complex environments. Additional experiments from Jim's laboratory suggest that the directional characteristics of the bat's echolocation calls and its hearing may serve to mitigate clutter interference. They posit that off-axis echoes may be perceived by the bat as "blurry" due to the frequency-dependent directionality of sonar signals and the dependence of auditory-response latencies on echo amplitude. Because bats point their sonar directly at selected targets where echo returns are the strongest and sharpest, blurry object echoes off to the side would not interrupt processing of the selected target along the midline (Bates et al., 2011).

Figure 7. ***Left:*** *Jim Simmons delivering his lecture at the Pioneers in Echolocation session at the Active Sensing Meeting at the Weizmann Institute of Science in Rehovot, Israel, in January 2023. Photo by Cynthia F. Moss, reproduced with permission.* ***Right:*** *Pioneers of Echolocation (***left to right***): Jim Simmons, Uli Schnitzler, and Alan Grinnell. Photo by Annette Denzinger, reproduced with permission.*

Jim Today

Jim, today in his 80s, remains active in science. In January 2023, Jim was recognized in a special Pioneers in Echolocation session of an international meeting on Active Sensing, held at the Weizmann Institute of Science, Rehovot, Israel (**Figure 7**). There, he enjoyed lively discussions with his scientific challenger Uli Schnitzler and long-time colleague and former graduate student of Donald Griffin, Alan Grinnell.

Jim has a long history of supporting students and early-career researchers, both through formal and informal mentoring. He has made several extended visits to Japan where he mentored students and collaborated with faculty on animal bioacoustics research. Some Japanese students and colleagues traveled to Providence, Rhode Island, to wrap up their projects in Jim's laboratory at Brown University.

Jim's knowledge and enthusiasm for bats is infectious, and his impact can be summed up by the quotation from Uli: "Jim Simmons has provoked me to think more than any other individual in the field."

Jim is an avid reader of history and enjoys the outdoors, particularly field expeditions to listen in on bat activity. He collaborates on research with his wife Andrea, and the two have published over 20 papers together. They are proud parents of Jessica and Ryan and grandparents of six-year-old AJ.

Acknowledgments

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