

How bats detect flying insects

During their evolution, the echolocating bats have developed an "auditory fovea" to fully exploit the capacities of their ears, which permits them to find and feast on the rich variety of insects that fly at night.

Gerhard Neuweiler



In the process of evolution every possible niche for survival has been exploited by some animal species. Whenever there is a biological area that produces a surplus it becomes advantageous for some species to adapt itself to make use of that surplus; many species have thus become endowed with highly specialized skills that have given them exclusive access to some hidden treasures.

In warm regions the air is filled with insects, and many birds prey on them during the daytime. When night falls the visually orienting birds give up hunting and the richly laid table of the night air would be largely untouched were it not for a special group of mammals, the bats. Like birds they are also endowed with wings and have become skillful fliers. But whereas birds never managed to develop an adequate substitute for vision (thus limiting, for example, owls to prey larger than the insects), bats have successfully used their larynx and ears for production of sound and the subsequent detection and discrimination of objects in complete darkness. Bats, such as the horseshoe bat shown in figure 1, emit short ultrasonic sounds through the open mouth

or through the nostrils and listen to the echoes returning from the world around them. This acoustical way of perceiving the outer world has been called "echolocation" by Donald Griffin who discovered it in 1938. In figure 2 we show a sequence of spectrograms of the sounds emitted by a horseshoe bat as it catches a moth.

Bats are a remarkably diverse group of animals and they emit a variety of differently structured echolocation signals. Some species alter the signal structure in response to different acoustical situations. Commonly the signals last a few milliseconds and make up a wide frequency band, ranging from 16 kHz up to 150 kHz. Broad-band signals are composed either of a steep downward frequency modulation within one or two octaves or of an array of four to six harmonics in a shallow or short frequency sweep. Figure 3 shows a sample of the variety of sounds emitted by one bat as well as the sounds made by different species of bat.

Detection of motion

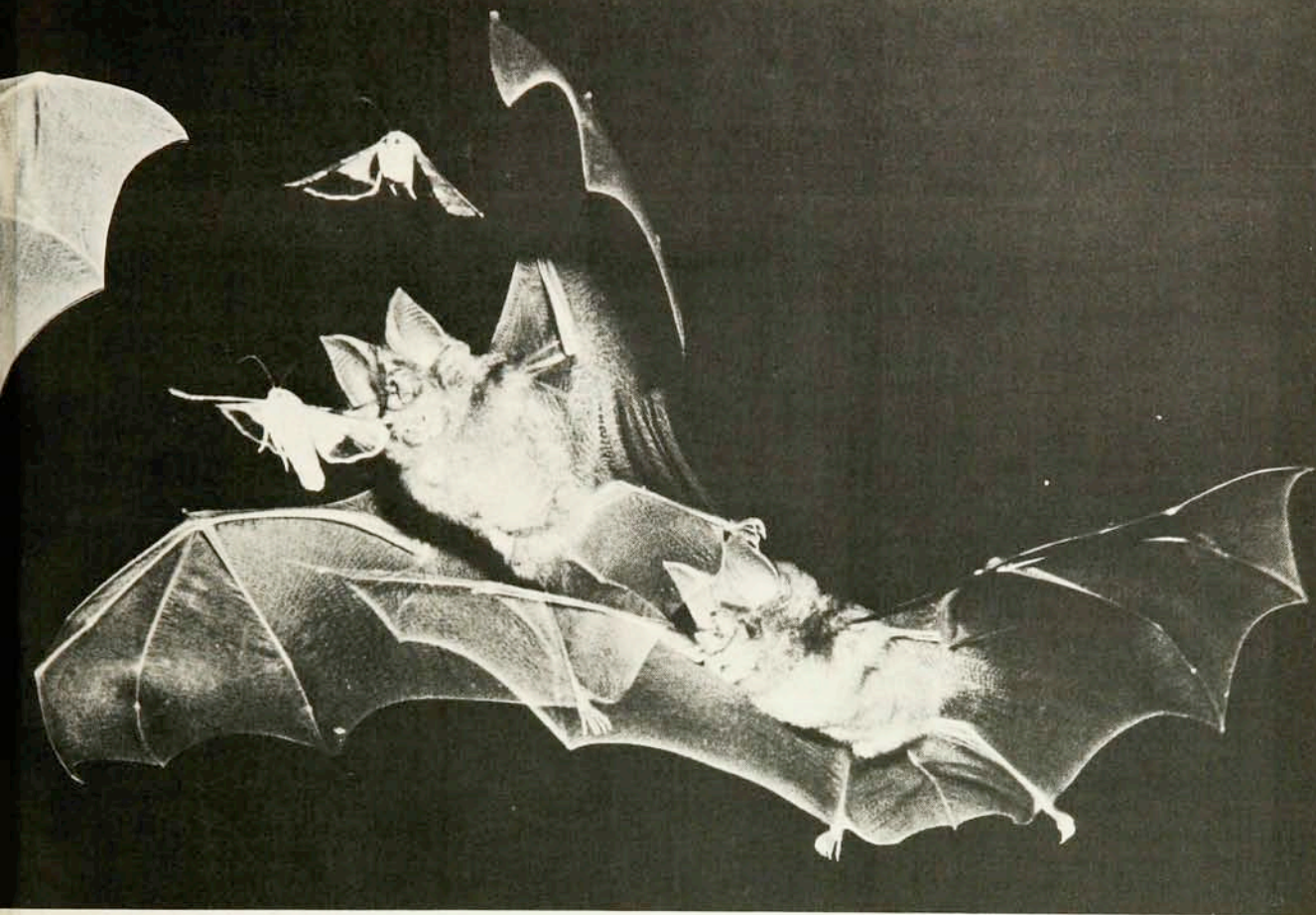
We might expect that bats hunting within dense foliage or close to any structured background would have difficulties in detecting prey. The background reflects a multitude of time-smearred echoes so that any structure of an echo, like a frequency-modulation

sweep, is more or less lost and the relevant echo from a prey is masked by noise. Focusing echolocation on a unique acoustical feature might overcome these difficulties in an echo-cluttered environment. The horseshoe bats, genus *Rhinolophus*, sometimes hunt close to foliage, walls and the like, in what would appear to be an environment cluttered with irrelevant echoes. These animals conspicuously and invariably emit an echolocation signal that consists of a pure tone of about 83 kHz (the "carrier frequency" component) followed by a short downward glissando or chirp (the "frequency modulated" component). Because of the structure of their emitted sounds, horseshoe bats may be called "CF/FM" bats.

Over the last ten years, in our laboratory in Frankfurt we have investigated the auditory system of horseshoe bats and found remarkable adaptations for the analysis of the pure-tone component.

According to signal theory, an echolocating bat should select a structure for the sound it emits that is best adapted to extract useful information from its environment. Indeed, this appears to be the case. Some bats, *Rhinolophus* among them, have become specialized for detecting and analyzing distinct acoustic features in the

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echoes from their prey, thus overcoming auditory constraints imposed by the environment.

An analogous problem of course exists in radar and sonar work, and various theories have been developed to extract the maximum information from the returned echo. One such theory is optimal-filter theory, which was first applied to the problem of echolocation in experiments by James A. Simmons. The theory can be used to show that a broad-band frequency-modulated signal can produce excellent time resolution (or, equivalently, excellent distance determinations) if the fm sweep maintains a certain time course. By contrast, a pure tone is not well suited for time analysis but is excellent for detecting motion *via* the Doppler shift.

Although the concept of optimal filtering has stimulated much discussion and experimentation, it should be emphasized that so far no physiological evidence exists for saying that bats utilize optimal filtering. We use optimal-filter theory as a heuristic tool for predicting certain performance capacities of a specific type of echolocation signal, even though the signals may in fact be suboptimal.

An auditory filter

The response of a bat's auditory system as a function of the frequency of

the sound can be determined either from its behavior or by measuring the electric potential evoked in the inferior colliculus, where signals from the auditory nerve come for preliminary processing on their way to the auditory cortex. Such "audiograms" for horseshoe bats have disclosed a remarkable specialization: the audiogram is divided into two parts, an ordinary one covering a wide frequency range from a few kHz to 80 kHz and a second one narrowly tuned to a specific frequency around 83 kHz (see figure 4). (The two ranges are separated by a sharp peak of insensitivity at around 81 kHz.)

The echoes the bat hears from stationary objects have a frequency near 83 kHz. Although the echo frequency varies from bat to bat, individual bats keep it constant (to within about 50 to 200 Hz) somewhere in the range of 81.00–85.00 kHz. The center frequency of the narrowly-tuned region always coincides with the echo frequency.

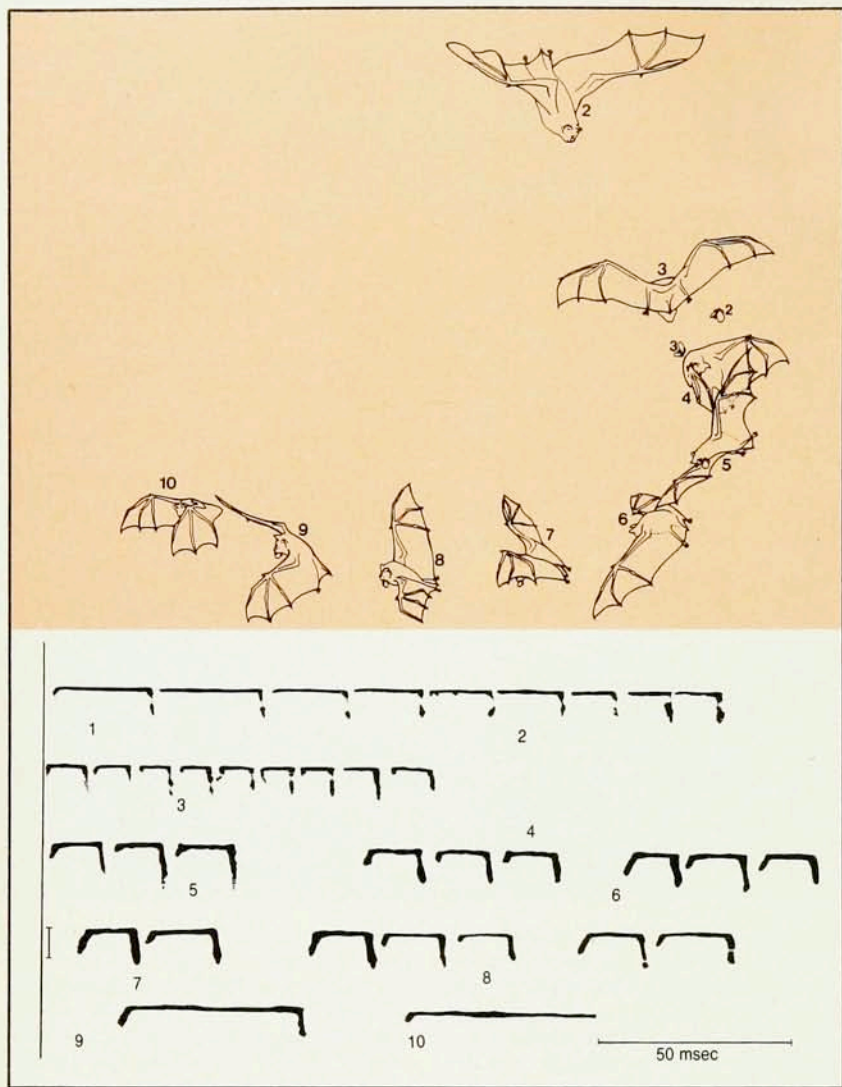
The auditory filters in the bat are remarkably sharply tuned. The response of an individual neuron in the cochlear nucleus rises and falls at about 930 db/octave and its Q -factor has values of up to 500 ($Q_{10\text{db}}$) compared with the Q -values of 20–30 for other bats and mammals. Studies of the response of cochlear neurons have demonstrated that the filter is mechanical;

it is determined by structures within the cochlea.

Morphological studies of the cochlea of *Rhinolophus* have disclosed several peculiarities within that part of the basilar membrane where frequencies above 80 kHz are represented (see the box on page 37). Within this specialized part the inner hair cells do not form a closely spaced continuous row but stand isolated with their receptor surfaces widely and conspicuously spaced. Their stereocilia are usually long and yet never touch the tectorial membrane, whereas those of the outer hair cells are very short and clearly imprint the tectorial membrane. Furthermore, the basilar membrane in most mammalian cochleas widens from the base of the cochlea at the oval window to the apex; however, in the specialized region the basilar membrane becomes *narrower*, widening again in the usual fashion from this region on to the apex.

The manner in which the basilar membrane attaches to the outer wall is also peculiar within the basal region. Generally, the basilar membrane is anchored to the outer wall by a

A horseshoe bat, *Rhinolophus ferrumequinum*, hunting a noctuid moth. This stroboscopic photo (flash rate of 10/sec) was taken by Martin Trappe, Marburg. Figure 1



An echolocating horseshoe bat catches a moth at (4) and eats it. The spectrograms below show the sounds emitted by the bat at each of the numbered positions. The complete sequence 1-10 (flash 1 caught the bat off-camera) lasted about 1 sec. (Courtesy of B. Vogler, Frankfurt) Figure 2

responds precisely to the section of the basilar membrane that is weakly coupled to the outer wall of the cochlea. Mechanical models of the basilar membrane suggest that the vibrations of this section also have a small amplitude.

The mechanical structure of the membrane itself thus appears to suffice to produce the filter we have found. Such a mechanical filter is, furthermore, completely consistent with the conclusions Peter M. Sellick drew from his intracellular recordings from the hair cells in the organ of Corti.

An acoustic fovea

The frequency mapping in the horseshoe bat's cochlea has produced another surprising result: The frequency range from 82 to 86 kHz is represented on the basilar membrane in a vastly expanded fashion. The complete length of the membrane from its base at the oval window up to 4.3 mm toward the apex is allotted to this 4-kHz-wide band. (At these frequencies such an interval is less than a semitone.) In the rest of the cochlea such a length serves to represent an entire octave. Because this is just the frequency range of the echoes heard by the bat, we have called this expanded region an "acoustic fovea."

As in the visual system, where the fovea of the retina is mapped onto an expanded region of the brain's visual centers, the acoustic fovea is also mapped onto disproportionately large regions in the auditory centers up to the auditory region of the cerebral cortex. In *Rhinolophus* more than 20% of the 16 000 afferent fibers in the cochlear nerve come from the foveal part of the organ of Corti, and in all the auditory nuclei studied so far a disproportionately large number of neurons are best excited by frequencies in the band from 82 to 86 kHz. For example, in the inferior colliculus (one of the way-stations for nerve impulses from the cochlea to the auditory cortex) 23% of some 600 cells that were studied in a systematic scan responded best to frequencies in this range. (See figure 4c.)

From these results we can advance three hypotheses about mammalian auditory systems:

- The frequency analysis of incoming sounds is entirely performed by mechanical systems in the cochlea; no further filtering is necessary.
- The overrepresentation of biologically important frequency ranges be-

spiral ligament containing elastic radial fibers; in the specialized region the anchoring system appears to be made flexible and soft by a very thin bony connection and by a large spiral ligament that contains no radial fibers.

All of these structural peculiarities disappear abruptly at the same point along the basilar membrane, about 4.3 mm away from the oval window toward the apex. The differences in structure that we have mentioned should greatly influence the mechanical properties, and consequently the acoustical response, of the organ of Corti. A continuous stiffness gradient of the basilar membrane is said to be the basis for the uniform pattern of logarithmic frequency representation in the mammalian cochlea. The abrupt changes in the structures should introduce a correspondingly steep discontinuity in the commonly uniform gradient of mechanical properties—especially the stiffness—of the basilar membrane.

Frequency mapping of the cochlea

also shows that the 83-kHz frequency range is represented within the first 4.3 mm from the oval window, ending at the same site where the structural peculiarities vanish.

Because of the precise correlation of the 83 kHz frequency region with structural anomalies of the basilar membrane we postulate that the filter has a mechanical nature. We do not know the mechanisms that produce the narrow-band filter, but vibration measurements of the basilar membrane with capacitance probes have disclosed a peculiar vibration pattern of the specialized part of the membrane on which frequencies above 80 kHz are represented.

For these frequencies the outer and inner parts of the membrane no longer vibrate uniformly, but when the frequency is increased above 80 kHz, they start to move out of phase, vibrating completely out of phase at around 83 kHz and vibrating in phase again for frequencies above 86 kHz. This out-of-phase deflection of the membrane cor-

Structure of the cochlea

In mammals, the external ear, ear canal and eardrum, the three small auditory ossicles and the oval window all serve to focus and transfer pressure waves in the air to the fluid in the cochlea. The cochlea itself is a spiral chamber hollowed out of the bone and bisected by a membrane, the basilar membrane, which runs almost the full length of the cochlea. There is a small hole in the basilar membrane at the apex of the cochlea, so that the upper and lower halves can, in fact communicate. The top figure at left shows schematically the cross section of a typical cochlea in a small mammal.

The basilar membrane is attached, on the inside of the cochlea, to a thin bony lamina that projects from the inner wall of the chamber. The transducer that converts the information carried by pressure waves into nerve impulses is the organ of Corti, which is carried by the basilar membrane near the spiral bone. Projecting over the organ of Corti, and also attached to the edge of the spiral bone, is the tectorial membrane. The middle figure at left shows in detail the typical arrangement of these organs in bats, mice and similar mammals.

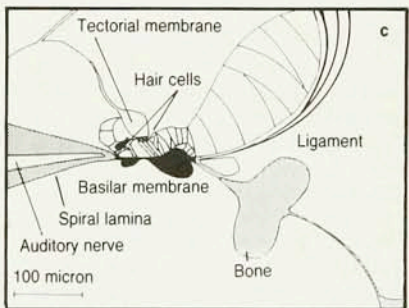
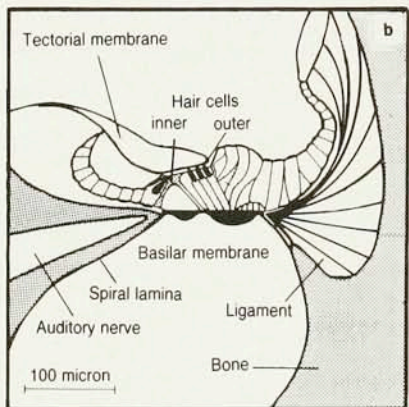
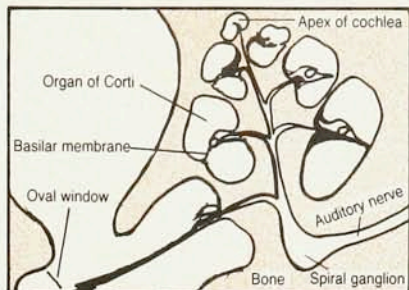
The organ of Corti contains several rows of "hair cells," which are special sensory cells that fire when the cilia they carry are bent. When sound waves reach the ear, waves are set up in the fluid of the cochlea, and the basilar and tectorial membranes vibrate with respect to each other. The tectorial membrane then shears the hair cells; these in turn stimulate, at their base,

the dendrites of neurons whose axons carry the nerve impulses to the spiral ganglion near the axis of the cochlea. The axons of the nerve cells in this ganglion form the acoustic nerve. They ultimately reach neurons in the cochlear nucleus of the brainstem. From there axons project into other regions of the brain, chiefly the auditory regions of the cerebral hemispheres (in fact, of the opposite hemisphere from the side on which the ear is located).

The basilar and tectorial membranes of all mammals change their mass and stiffness continuously from the basal to the apical end. For example, the basilar membrane widens from the base to the apex (the bony shelf narrows, as does the diameter of the cochlea). Thus, each section of the cochlea has different mechanical properties, so that each component frequency of input sound excites a different section of the cochlea.

The output of the organ of Corti as a function of distance thus represents the frequency spectrum of the incident sound. The highest frequencies are represented at the basal end, the lowest at the apex of the cochlea.

In bats, as the text describes, the basal end of the basilar membrane differs from the other regions. It is, for example, thicker and more loosely attached. The third figure at left shows the organ of Corti near the basal end (that is, in the "acoustic fovea") of the cochlea in a horseshoe bat. The alterations from the typical case (figure b) are evident.



gins in the cochlea by a mechanical specialization that expands the segment on which the range is represented, by a specialized innervation pattern that allows more neurons to be packed into that segment, or by a combination of these mechanisms. The overrepresentation at higher centers of the brain would then merely be a reflection of the general fact that the higher sensory centers contain orderly representations of their sensory fields.

► The cochlea of mammals may have a differentiated fine structure. The acoustic fovea of the horseshoe bat's ear may be only one highly specialized case. There is no reason why other species cannot or should not have modified their cochlea in such a manner that frequency resolution matches their behavioral demands.

Frequency stabilization

Let us return to the problem of how the echolocating horseshoe bat can use the long, constant-frequency echo at 83 kHz. As I have outlined, the cochlea

the long, constant-frequency echo at 83 kHz. As I have outlined, the cochlea and the auditory nuclei are specialized to receive this narrow frequency band, and they achieve an unprecedentedly fine frequency resolution. The center frequency of the cochlear fovea is morphologically fixed and cannot be shifted. For a hunting bat, the echo is Doppler-shifted to a higher frequency, which could have disastrous results. The faster the bat flies (and it can fly up to 12 m/sec) the larger is the Doppler shift and the less does the echo frequency match with the auditory fovea. The echo tones would range between 86 and 87 kHz, a frequency clearly outside the optimum of the cochlear fovea, which is fixed at about 83 kHz.

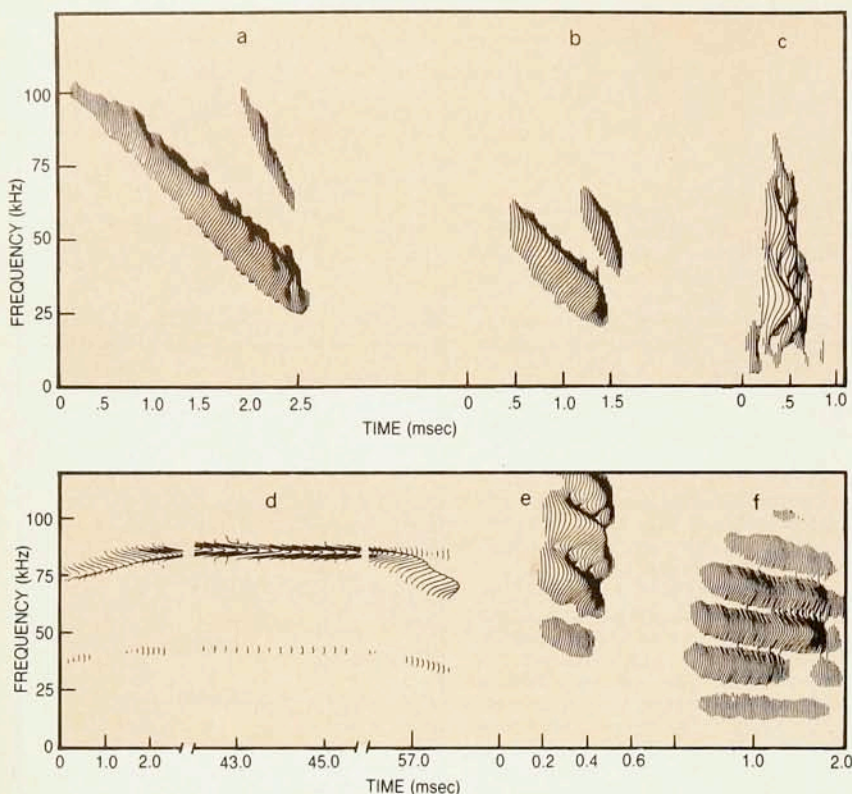
As Hans U. Schreiber has shown, the horseshoe bat has solved this problem by applying a feedback system for sound emission: Whenever the frequency of the echo is higher than a distinct "reference frequency" (nearly identical to the center frequency of the cochlear fovea) the flying bat decreases

the frequency of the next emitted sound by a corresponding amount. In this way the bat maintains the echo frequency at the center of the acoustic fovea with an accuracy of 50 to 200 Hz (this corresponds to a deviation of only 0.06% from the center frequency).

During a brief flight of 6.5 m, for example, one bat (*Rhinolophus euryale*) kept the echo around 104.2 kHz while the emitted frequency dropped as low as 101.7 kHz in the course of the flight. Generally the bat was able to compensate for its own motion smoothly and consistently, and the only erratic fluctuations in the echo frequency came during its landing maneuvers.

For the bat to perceive the deviation of the echo from the reference frequency there must be a time overlap of the emitted sound and the returning echo. We do not know whether this requirement arises from the need for an interference between the two sounds.

The feedback system only compensates for echo frequencies above the reference frequency—echo frequencies



Acoustic spectrograms of echolocation sounds. The top graphs show the sounds of *Myotis myotis* (a) during search, (b) approaching prey and (c) just before capturing prey. The bottom graphs show the sounds of (d) *Rhinolophus ferrumequinum*, (e) *Megaderma lyra* and (f) *Thaphozous melanopogon*. Further analysis indicates that (a) and (b) are well suited for time or distance measurements, while (d) is well suited for velocity measurements.

Figure 3

system one may call these units "movement-specialized" neurons.

The measurements of the response of collicular neurons have shown that the auditory nervous system is capable of detecting and analyzing moving targets by analyzing modulations of a pure-tone echo reflected from a moving prey. Behavioral experiments both in *Pteronotus parnellii*—another bat that emits a long, pure-tone component—and in horseshoe bats corroborate the neurophysiological results: Both bats immediately detect and catch an insect that is beating its wings but apparently do not detect it when the prey stays motionless.

The experimental evidence thus shows that a long pure-tone sound serves the horseshoe bat (and probably other bats as well) for detecting and analyzing the motions of a target. The signal is, in fact, optimal for bats that fly close to a dense background. The time-smeared cascades of echoes reflected from trees, foliage, walls and so forth, appear as long, pure tones of a relatively fixed frequency or—when the background is randomly moving—of a narrow frequency band. But any insect flying within or close to the background will conspicuously pop out from the echo carrier frequency because of rhythmic modulations, as the neural responses shown in figure 5 clearly demonstrate. These acoustical markers alert the echolocating bat to the prey and evoke prey-catching behavior, such as that shown in figure 2. Bats might even identify different prey by characteristic echo modulations, but this assumption has never been tested experimentally.

Neuronal specialization

A laboratory situation where a bat's ear is exposed to a single stimulus in quiet surroundings is a far cry from the real auditory work with which an echolocating bat is confronted. However, the artificial situation is extremely useful for investigating the details of the mechanisms by which the bat finds prey.

Of course, in such a situation, one wants to make the stimulus as close to the natural one as possible, consistent with the requirement that the stimulus and response be simple to analyze. The horseshoe bat emits a pure tone of about 60 msec duration, and the echoes

below the reference frequency would only occur if the bat flew backwards. By feeding artificial echoes to the bat, one can measure the capacity of this feedback-compensation system. Such measurements show clearly that the bat maintains a constant emission frequency if the "echo" has a higher pitch than the emitted sound, while pure-tone echoes shifted as much as 5 or 6 kHz below the reference frequency cause the bat to shift its emitted signal by a compensating amount; the bat compensates less well for larger frequency shifts.

The feedback system operates as a sample and hold device, storing the most recent echo frequency irrespective of the duration of the delay before the next sound emission. The system reacts sluggishly and needs about 340 msec to compensate for a shift of 1000 Hz. This slowness prevents the compensating mechanism from eliminating brief Doppler shifts within a single echo. Such minor Doppler shifts may have considerable interest for the bat, as we shall see.

The emitted frequency is precisely tuned by the activity of the crico-thyroid muscles and the superior laryngeal nerves innervating them.

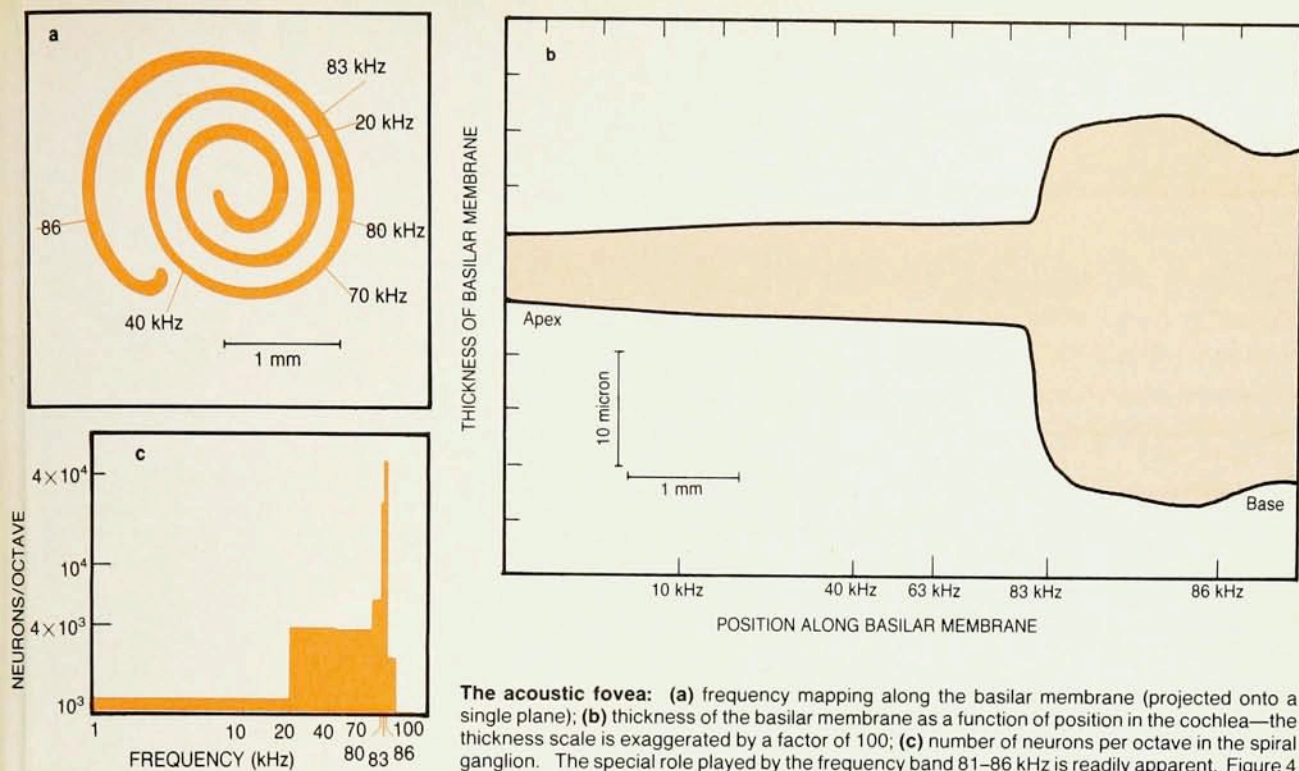
This feedback system effectively uncouples the bat's echolocation system from its own motion. Just as the oculomotor muscles produce tracking motions to keep an image stabilized on the fovea of the retina, the laryngeal muscles adjust their tension to maintain the echo frequency in the acoustic fovea.

Let us now examine the adaptations that let the bat specifically detect moving prey from the variations of the received echoes.

As I have said, there is a large overrepresentation of neurons that respond best to frequencies in the range 82–86 kHz, and these neurons are extremely sharply tuned. This highly specific, frequency-sensitive response is preserved from the cochlear nuclei to the cerebral cortex. We thus expect this part of the auditory system to be sensitive to minute frequency modulations of the returning echo, even to frequency modulations of ± 10 or 20 Hz—that is, 0.02% of the carrier frequency (about 1/30 of a semitone). The neurons of the organ of Corti in the foveal region are thus exquisitely sensitive to the Doppler shifts of echoes from moving prey.

A fluttering moth imposes a complex pattern of frequency and amplitude modulations onto the echo-carrier frequency. Neurophysiological evidence suggests that the foveal neurons indeed faithfully encode these patterns and thus the rhythm of the prey's wing beat. In figure 5 we show the response of a single neuron in the inferior colliculus of a horseshoe bat to the echoes from a moth in various orientations, as well as to the amplitude-modulated and frequency-modulated components of the echoes.

Some neurons in the colliculus appear to be specialized for reacting only to behaviorally relevant frequency modulations. By analogy to the visual



The acoustic fovea: (a) frequency mapping along the basilar membrane (projected onto a single plane); (b) thickness of the basilar membrane as a function of position in the cochlea—the thickness scale is exaggerated by a factor of 100; (c) number of neurons per octave in the spiral ganglion. The special role played by the frequency band 81–86 kHz is readily apparent. Figure 4

start to return while the bat is still vocalizing. Thus the bat's ear usually hears simultaneously a mixture of outgoing sound and returning echoes.

Experiments with overlapping or persisting two-tone stimuli disclosed that the neuronal auditory system of the horseshoe bat is adapted to this situation. Neurons of the inferior colliculus that are tuned to a frequency between 82 and 86 kHz show a curious anomaly: Auditory neurons in general (in most mammals) strongly suppress their response to a second tone after responding to a first tone; for the foveal neurons in bats this suppression completely vanishes when the frequency of the first tone ranges between 82 and 78 kHz. This actually is the frequency band in which a flying horseshoe bat is emitting. Due to the Doppler-compensation system, the emitted frequency will always be up to 4 kHz below the echo frequency.

Our experiments have shown that in the foveal neurons, pure-tone frequencies of 82 to 78 kHz not only do not suppress, but even facilitate the response to the second (echo) signal. This is a remarkable adaptation to a specific behavioral and biological situation.

In the real world, of course, the echolocating bat is not only listening to overlapping signals but is also actively vocalizing. Because the system that compensates for the Doppler shift of the echoes must have neuronal pathways from auditory to vocalizing centers, it may well be that there are pathways in the opposite direction that permit vocalization to alter the way auditory neurons

receive and process information.

Recently Gerd Schuller in our laboratory has found neurons in the inferior colliculus that respond to a frequency-modulated echo only when it overlaps with an ongoing vocalization. Because the duration of the electrically elicited echolocation sounds could not be varied it was impossible to determine whether the required condition is the overlap itself or if vocalization triggers a fixed time window that enhances the sensitivity of these neurons. Substituting the vocalized signal with a play-back signal of the same frequency, duration and intensity failed to elicit the specific responsiveness of these neurons to frequency-modulated echoes. Thus it is probably the centers associated with vocalization, and not the sound that is heard, that specifically alter the responsiveness of auditory neurons. (Recent results for another bat have suggested that it is a lower harmonic of an echolocation sound that triggers the responsiveness of certain neurons. The lower harmonic emitted by horseshoe bats is very faint, however, so that this is an unlikely mechanism.)

Neurons that are sensitive to frequency modulations of the returning echoes only while the bat is vocalizing would clearly be useful for locating prey; their insensitivity at other times reduces the amount of irrelevant information or noise that the bat has to worry about.

Time encoding

The bat measures the distance of a target from the round-trip time of the

echolocation sound, from the instant of pulse emission to the first hearing of the echo. Simmons has shown (by behavioral experiments) that echolocating bats differentiate time lags as small as 60 microsec, which corresponds to a distance of 1 cm between two targets.

To determine the direction of an echo source the bat probably relies on slight differences in the intensity of the echoes in its two ears as well as differences in echo intensity as it moves its external ears, which are very sensitive.

Larger animals, of course, can determine the direction of a sound from the time difference between hearing it with each ear, but for small animals, such as bats, it has generally been assumed that these time differences are too small; small animals would thus have to depend to a large degree on binaural intensity cues. However, a recent study in our lab showed that in the inferior colliculus and medial olivary nucleus of an FM-bat there are neurons that encode binaural time delays in the microsecond range. Seven of the neurons we examined showed markedly different responses when a pure tone arrived 15 microsec later at one ear than the other.

Apart from demonstrating that some mammalian neurons have the capacity to handle time differences in the microsecond range, the study also indicates that the bat can detect time differences with signals that do not have the optimal sound structure. The signals were pure tones in the range of 18 to 61 kHz, with a duration of 2

msec and rise and fall times of 500 microsec. Apparently the neurons get the timing information from the envelope of the signals. Because of the high frequencies involved, phase differences can be ruled out as possible time cues in this experiment.

Spectrum analysis

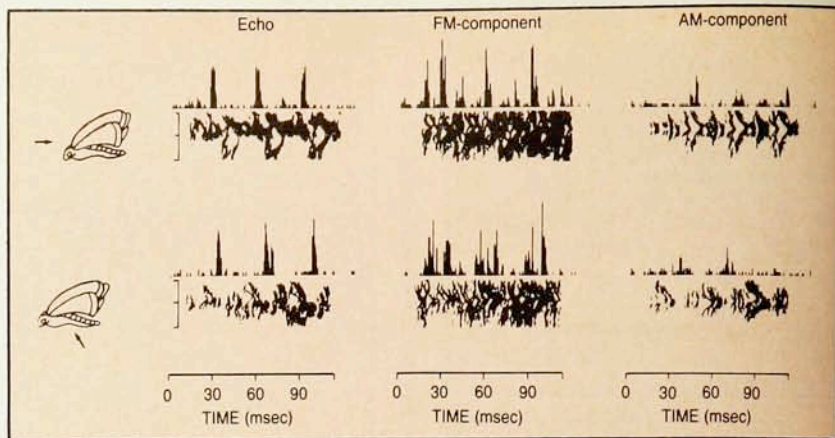
Bats have performed remarkably well in acoustically differentiating the echoes from objects of different shape, size and texture. In fact, the resolution and fine structure of the bat's acoustical world might match that of our own richly structured visual world.

The remarkable degree to which bats can detect fine structural detail was demonstrated by an accidental result in a discrimination experiment performed in my laboratory and originally designed Simmons and his collaborators. Bats were trained to differentiate echoes from holes drilled to different depths in otherwise identical plexiglass plates.

When they were offered two plates with identical hole depths (in control experiments) the bats apparently chose at random, but in one case they did not and continued to prefer one of the two plates. An inspection with a scanning electron microscope disclosed that in the preferred plate the holes were drilled by a worn-out tool that produced ring-shaped ridges, about 20 to 50 microns high, on the bottom of the holes, whereas the holes in the other plate had smooth bottoms. Apparently bats recognize the complex echo patterns from objects with fine differences in texture.

One characteristic that bats may use to differentiate textures is the fact that targets with some structure in depth return broadband echoes with conspicuous blank sections in their spectra. These spectral troughs result from interferences of echoes returned from the front and deeper surfaces of the target. In the experiments to differentiate holes, the shallower the hole the greater is the spacing of the troughs in the echo spectrum, and the more readily should the bat's frequency-analysis system be able to differentiate them. Frequency analysis of a broadband echo should thus yield information on the fine texture of a target while a delay-time analysis of the echoes should yield information about its coarse structure. As figure 2 shows, horseshoe bats terminate many of their echolocation pulses with a broad frequency sweep suitable for just this purpose.

The investigations of the cochlea and of the auditory centers in the brain that I have described here show that the auditory system of the horseshoe bat is indeed adapted to detect and analyze moving prey against a noisy background. Echolocation with a pure-tone



Response of a neuron in the inferior colliculus of a horseshoe bat. The echoes were produced by 84-kHz tones reflected from a moth in the orientation shown at left. The spectrograms below the responses show the actual echo, and its frequency-modulated and amplitude-modulated components. Note that the neuron is most sensitive to the FM component. Figure 5

signal is an adaptation to exploit food resources in environments cluttered with noise (multiple echoes) from foliage, bushes and other structures. The auditory system of the bat, in turn, is adapted to obtain a great deal of very subtle information from the echoes. In particular, the acoustic fovea and the associated neurophysiological adaptations give the horseshoe bat an extremely fine frequency resolution around the carrier frequency for the echoes, 82–86 kHz. Specialized neuronal circuits then enhance the relevant information (concerning potential prey) and suppress noise.

The remarkable performances in differentiating objects by blind men using sonar aids and the sensations that they report both indicate that the fine frequency and time analysis which bats can perform may to some extent be a general feature of mammalian auditory systems. The examples of good auditory analysis in both the frequency and time domains corroborates our notion that echolocating bats have not invented something new but have simply exploited and refined the capacities of the mammalian auditory system. I believe that the bats have something to tell, not only to the zoologist, but also to any scholar interested in audition.

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