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Journal of the Acoustical Society of America

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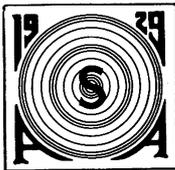
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Ears adapted for the detection of motion, or how echolocating bats have exploited the capacities of the mammalian auditory system

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(Received 23 April 1980; accepted for publication 4 June 1980)

Bats use the rich food resources of the night by specializing in audition. They emit short echolocation sounds and listen to the echoes returning from potential prey. The bat's auditory system analyzes spectral and temporal parameters of echoes for detecting, locating, and identifying a target. Different bat species have solved the problem of acoustic target detection and pattern recognition even in clustered situations by focusing on certain acoustical features of a target. The specialized motion detection by horseshoe bats, for instance, analyzes small echofrequency shifts modulated onto a long constant frequency echolocation signal. These frequency modulations are Doppler shifts within echoes returning from wing beating insects. For detecting modulations as small as 10 Hz or 0.01%, horseshoe bats have in the cochlea an extremely narrow filter ($Q \approx 500$) matched to the carrier frequency (i.e., echolocation sound) of 83 kHz. The filter is realized by structural differentiations of the basilar membrane and the filter frequencies are represented on the basilar membrane in an expanded fashion. We have called this specialized patch of the basilar membrane an "acoustical fovea." The "foveal frequencies" are largely overrepresented in the tonopical arrangement of the ascending auditory pathway. The bats have developed a feedback system which lowers the emitted frequency during flight in such a way that the Doppler shifted echofrequency is kept precisely at a fixed reference frequency of the fovea. This feedback system and other neuronal data disclose an intricate coupling of the auditory and vocalizing system. The evolution of echolocation in bats has driven the analyzing capacities of audition in both frequency and time domain close to theoretical limits. Investigations of such specialized systems give fascinating insights into capacities and possible general principles of auditory information processing.

PACS numbers: 43.10.Ln, 43.80.Lb, 43.63.Th

INTRODUCTION

The process of evolution has been essential for providing a living for all creatures. Every possible niche has been exploited by some animal species and many have become endowed with highly specialized skills which 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 is falling the visually orienting birds give up hunting and the richly laid table of the night sky 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. Whereas birds never managed to develop an adequate substitute for vision, bats have successfully used their larynx and ears for production of sound and the subsequent detection and discrimination of objects in complete darkness. Bats emit short ultrasonic sounds through the open mouth or through the nostrils and listen to the echoes returning from the world around them (Fig. 1).

This acoustical way of perceiving the outer world has been called echolocation by Griffin (1958) who discovered it in 1938.

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 comprise a wide frequency band ranging from as little as 16 kHz up to 150 kHz. Broadband signals are composed either of a steep downward frequency modulation within one or two harmonics or of an array of four to six harmonics in a shallow or short frequency sweep (Fig. 2). These FM components may be preceded or followed by short constant frequency parts. Some bats, e.g., horseshoe bats and mustache bats, emit unusually long echolocation sounds with durations of 30 ms and more. These signals consist of a pure tone terminated by a brief FM component.

Applying optimal filter theory to these echolocation signals, introduced by Simmons (1971) into experimental echolocation research, might give some insight why bats use specifically structured signals for echolocation. Ambiguity functions of the autocorrelated echolocation signals disclose what kind of sound parameters the signals are theoretically best suited for (Fig. 2). In a correlator, for instance, broadband FM signals result in excellent time (target range) resolution with suppression of unwanted sidebands if a certain timecourse of the FM sweep is maintained. By contrast, a pure tone is not well suited for time analysis, but is capable of detecting Doppler shifts.

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.
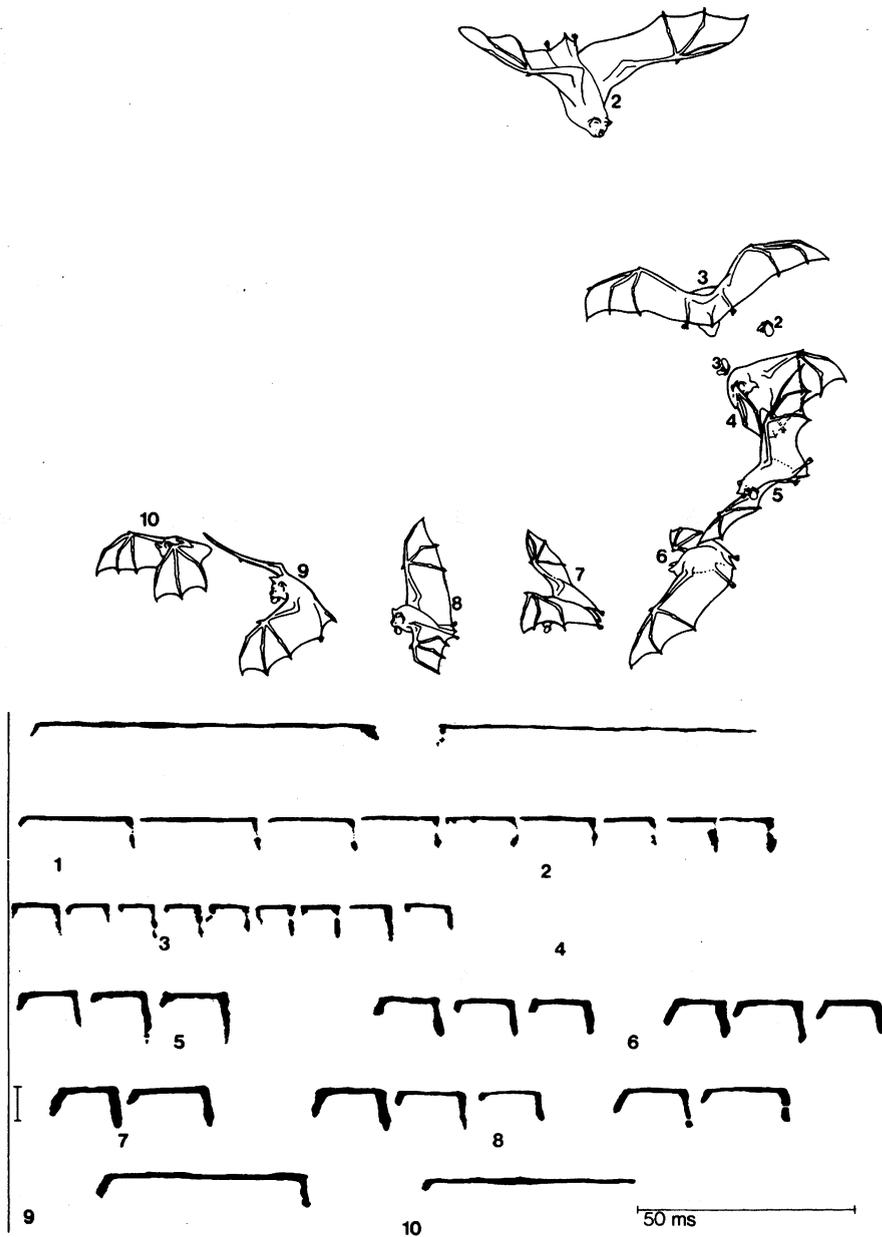
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FIG. 1. An echolocating horseshoe bat, *Rhinolophus ferrumequinum*, catches a moth (at position 4). Spectrograms of the echolocation sounds emitted during flight are shown below. Numbers indicate identical timings as in the flight path (frame No. 1 is not shown). Note: the constant frequency part of the echolocation sound is emphasized during detection of and approach towards the prey (up to No. 4). Frequency of the constant frequency part: 82 kHz, vertical bar: 10 kHz. The complete sequence from No. 1 to No. 10 lasts about 0.9 s. (From Vogler, Frankfurt.)

We use optimal filter theory as a heuristic tool for predicting certain performance capacities of a specific type of echolocation signal even though they may turn out to be suboptimal.

According to signal theory an echolocating bat should select a certain sound structure best adapted to the environmental situation they are active in. Indeed, it appears that some bats have become specialized for detecting and analyzing distinct acoustical features of their prey in order to overcome auditory constraints imposed by a specific environment.

I. MOVEMENT DETECTION BY A PURE TONE CARRIER

Bats hunting within dense foliage or close to any structured background should have difficulties in de-

tecting prey. The background reflects a multitude of time-smeared echoes so that any structure of an echo, like a FM sweep, is more or less lost and the relevant echo from a prey masked by noise. Focusing echolocation on a unique acoustical feature might overcome these difficulties in an echo-cluttered environment. The horseshoe bats, *Rhinolophus spec.*, sometimes hunt close to foliage, walls, etc., i.e., in what would appear to be an echo-cluttered area (Brosset, 1966). These animals conspicuously and invariably emit pure tone echolocation signals of about 83 kHz (Figs. 1 and 2). Since the pure tone is terminated by a short downward FM sweep and the pulse duration is long, the emitted signals are classified as long CF/FM and the horseshoe bats as "CF/FM" bats. In the last ten years we have investigated the auditory system of horseshoe bats and found remarkable adaptations for the analysis of the pure tone component.
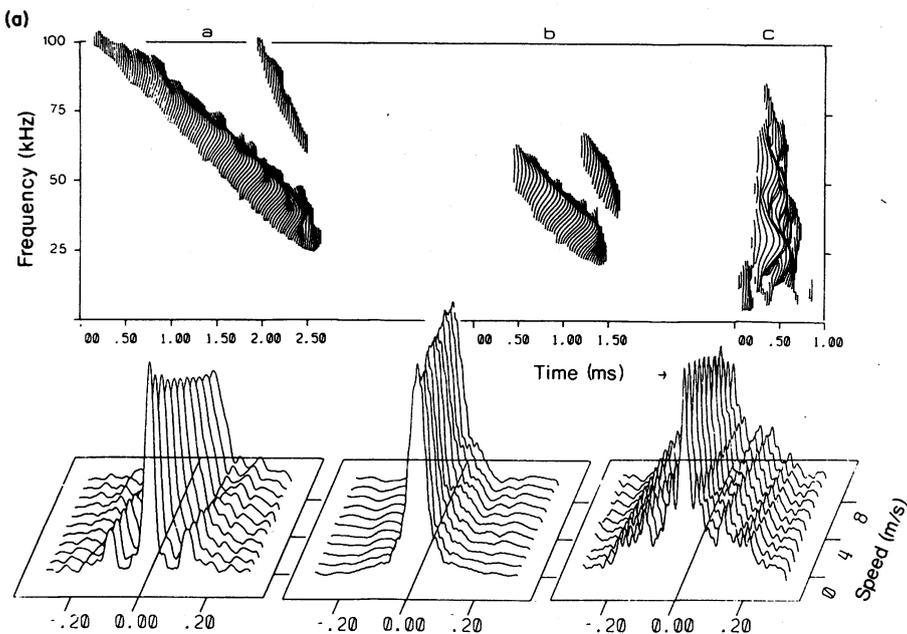
FIG. 2. Spectrogram and ambiguity function of echolocation sounds in bats. (a) Echolocation sounds of *Myotis myotis* during searching flight: a, approach phase: b, and shortly before hitting prey: c. Ambiguity functions below indicate that signals a and b are well suited for time coding (sharp maximum without side bands in the time axis). (b) Echolocation sounds of three bat species, *Rhinolophus ferrumequinum*: a, *Megaderma lyra*: b, and *Taphozous melanopogon*: c. The ambiguity function of the constant frequency part in "a" shows that a pure tone is less suited for time coding, but has a narrowly peaked maximum in the velocity axis (lowest left most graph). [After Beuter in *Animal Sonar Systems*, edited by R. G. Busnel and J. Fish (Plenum, New York, 1980)].
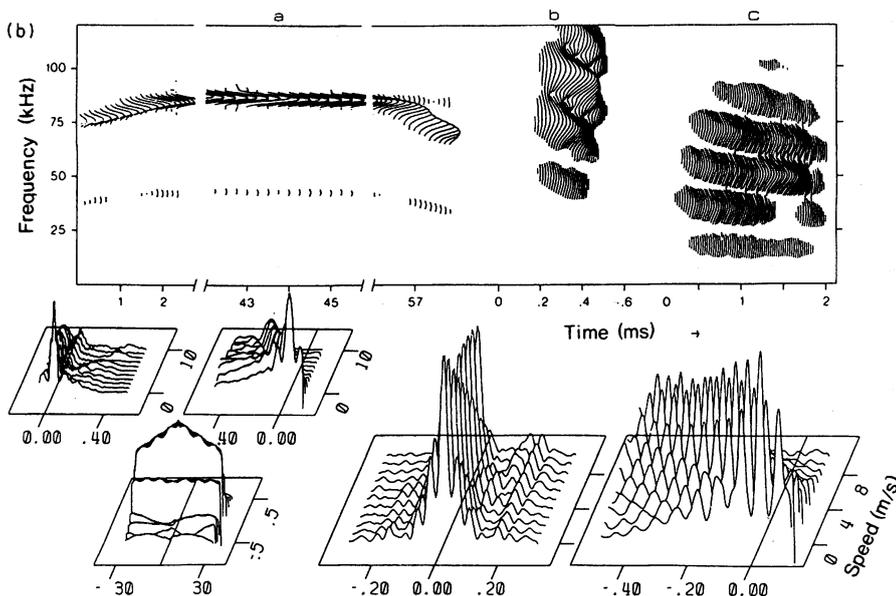
A. The filter

Recordings of audiograms in horseshoe bats, either by collicular evoked potentials or behaviorally, have disclosed a remarkable specialization. The audiogram of this bat is divided into two parts, an ordinary one covering a wide frequency range from a few kHz up to 80 kHz and a second one which is narrowly tuned to a specific frequency around 83 kHz. The latter is separated from the ordinary hearing range by a sharp peak of insensitivity at 81 kHz (Fig. 3, audiogram). The center frequency of this steeply sloped (930 dB/octave)

filter is closely matched to the individual pure tone frequency the bat hears in the echoes returning to its ears. This echo frequency varies between 81.00 and 85.00 kHz, but is individually kept constant with an accuracy of 50 to 200 Hz. The individual echo frequency always closely correlates with the individual center frequency of the filter.

N_1 recordings and the study of tuning curves of auditory nerve fibers and cochlear nucleus neurons [Fig. 3(b)] have demonstrated the filter qualities, with $Q_{10\,dB}$

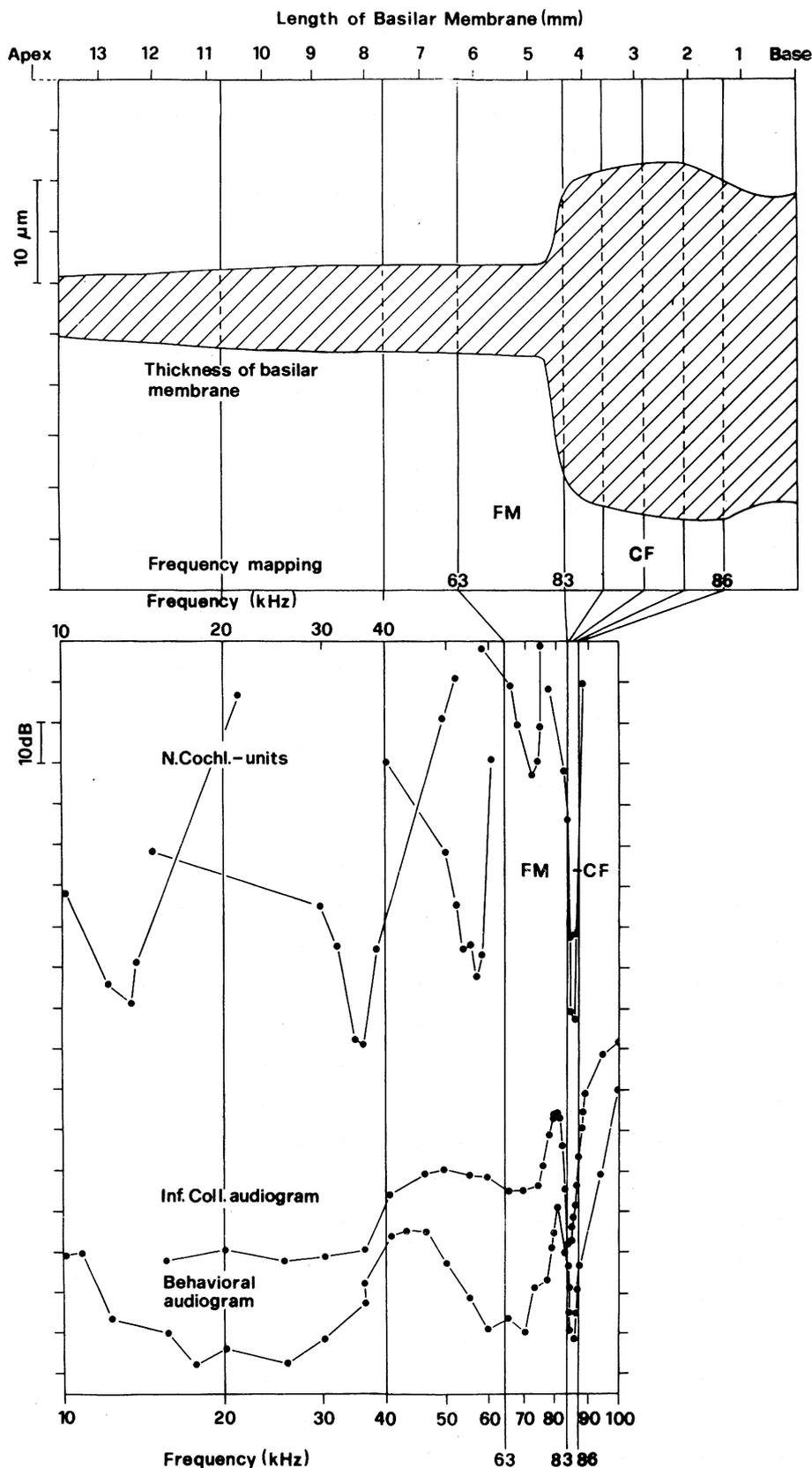**Length of Basilar Membrane (mm)**

Apex 13 12 11 10 9 8 7 6 5 4 3 2 1 Base

10 μm

Thickness of basilar membrane

FM

CF

Frequency mapping

63   83   86

Frequency (kHz)

10   20   30   40

10dB

N. Cochl. – units

FM CF

Inf. Coll. audiogram

Behavioral audiogram

10   20   30   40   50   60 70 80 90 100

Frequency (kHz)

63   83 86

FIG. 3. The filter tuned to the constant frequency part of the echoes in the cochlea of the horseshoe bat, *Rhinolophus ferrumequinum*. Upper graph: Thickness of basilar membrane from base to apex (upper abscissa). Lower abscissa: Frequency representation on the basilar membrane as determined by frequency mapping. CF: frequency range of the constant frequency part of the echoes. FM: frequency range of the final frequency modulated part of the echoes. Lower graph: Behavioral and inferior collicular audiogram and tuning curves of single cochlear nucleus units. Ordinate: thresholds in relative dB units. Note: precise correlation of sharp tuning in the 83- to 86-kHz range with its representation on the thickened part of the basilar membrane. (After Bruns and Schmieszek, 1980.)

values of up to 500, must be determined by structures which reside within the cochlea.

Morphological studies of the cochlea of Rhinolophus have disclosed several marked specializations within the basal part of the basilar membrane (BM) where

frequencies above 80 kHz are represented. 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 unusually long and yet never touch the tectorial membrane, whereas those of

the outer hair cells are very short and clearly imprint the tectorial membrane (Bruns and Goldbach, 1980). In the specialized region the BM becomes progressively narrower as it extends from the oval window up to a distance of 4.3 mm toward the apex (Bruns, 1976a). After this point the membrane progressively widens in the usual mammalian fashion.

The pectinate zone of the BM and the secondary osseous spiral lamina attaching the BM to the outer wall of the cochlea are greatly thickened (Fig. 4) (Bruns, 1976a). Whereas the inner margin of the BM is rigidly attached to the primary osseous spiral lamina, the outer anchoring system of the BM appears to be made elastic and soft by a very thin bony connection of the outer BM margin to the outer cochlear wall and by a large spiral ligament devoid of any of the radial fibers which commonly fix the BM to the outer wall (Bruns, 1980) (Fig. 4).

These differentiations of mechanically important BM structures should greatly influence the mechanical properties of that part of the organ of Corti. All of these structural specializations abruptly disappear about 4.3 mm apical to the oval window (Fig. 3). This sudden and convergent change in mechanical components should introduce a steep discontinuity into the commonly uniform gradient of mechanical properties of the BM,
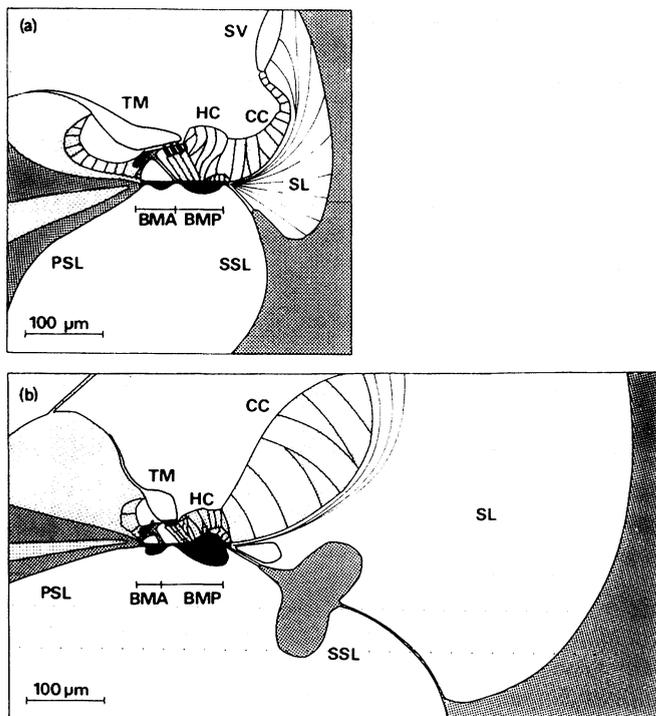

FIG. 4. Schematic cross sections through the cochlea of bats. (a) Generalized cross section through the basal turns of the cochlea of rat, mouse, and bats emitting frequency modulated orientation sounds. (b) Cross section through the specialized basal region (filter region) of the cochlea in horseshoe bat, *Rhinolophus ferrumequinum*. BMA: arcuate zone of basilar membrane, carrying the inner hair cells. BMP: pectinate zone of BM, carrying the outer hair cells. CC: Claudius cells. HC: Hensen's cells, PSL: Primary spiral lamina. SSL: Secondary spiral lamina. SL: Spiral ligament. SV: Stria vascularis. TM: Tectorial membrane. (From Bruns, 1979b.)

e.g., stiffness gradient. A continuous stiffness gradient of the BM is said to be the basis for the uniform pattern of logarithmic frequency representation in the mammalian cochlea.

We suspected that a discontinuity of the mechanical gradient correlates with the narrow 83-kHz filter, and indeed frequency mapping by the swollen nuclei method has disclosed that the frequency of 83 kHz is represented on the BM exactly at the 4.3-mm site where the large thickenings and other structural peculiarities abruptly vanish (Fig. 3) (Bruns 1976b).

Because of the precise correlation of the 83-kHz filter with structural anomalities of the BM, we postulate that the filter is of a mechanical nature. We do not know the mechanisms resulting in narrow filtering, but vibration measurements of the BM by a capacitance probe have disclosed a peculiar vibration pattern of the specialized part of the BM and this pattern is confined to frequencies above 80 kHz (Wilson, 1977). For these frequencies the outer and inner part of the BM no longer vibrate uniformly, but start to move out of phase, vibrating in a 180° antiphase mode for the center frequency of the filter around 83 kHz and reaching 360°, i.e., vibrating in phase again, for frequencies above 86 kHz. This antiphasic deflection of the BM for filter frequencies is congruent with the weak structural coupling of the outer BM margin to the cochlea wall in the specialized basal part of the cochlea. Based on Steele's model of BM vibrations, Bruns (1979b) suggested a mode of independent vibration of the outer part of the specialized BM part caused by the loose connection of the BM to the outer cochlea wall. It would account for the possibility of antiphasic motion, the low deflection amplitudes measured, and, yet, low thresholds due to large shearing angles for hair cells tuned to the filter frequencies.

It is tempting to deduce a general second mechanical filter for the mammalian cochlea from these findings, but since the mechanical parameters have not been measured, we will refrain from any speculations. *The studies noted above show that a frequency analysis and resolution of unprecedented precision is achieved in the periphery and as we have proposed by the micromechanics of the cochlea. This assumption of a purely mechanical frequency analysis in the mammalian auditory system is consistent with Sellick's conclusions from his intracellular hair cell recordings (Sellick, 1979).*

B. An acoustical fovea

Frequency mapping in the cochlea of the horseshoe bat has yielded another surprising result. The narrow frequency band from 82 to 86 kHz is represented on the BM in a vastly expanded fashion (Bruns, 1976b). The complete specialized basal length from oval window up to 4.3 mm toward the apex is allotted to this narrow frequency band of 4000 Hz (Fig. 5 and Fig. 3). Such a length is usually covered by a complete octave e.g., for 80 to 40 kHz, in horseshoe bats. Since the bat actively maintains the echofrequency within this special frequency band by a feedback system explained later, we have called this expanded region of the cochlea an
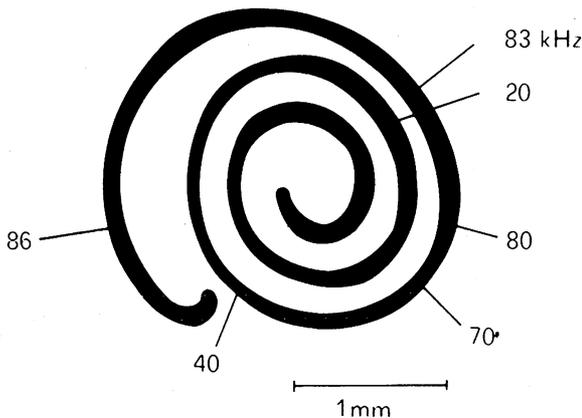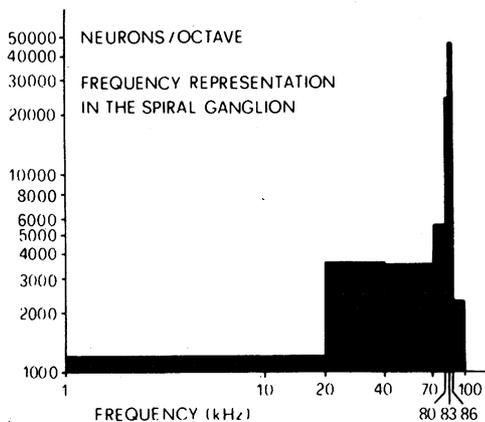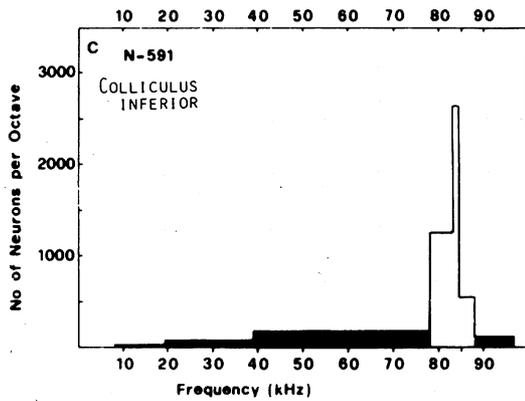
acoustic fovea (Schuller and Pollak, 1979; Bruns, 1979a).

As in the visual system the peripheral expansion of cochlear frequency analysis is fully preserved in the auditory centers up to the auditory cortex. In Rhinolophus, 20% of the 16 000 afferent fibers in the cochlear nerve come from the foveal part of the organ of Corti (Bruns and Schmieszek, 1980), and in all auditory nuclei so far studied, a disproportionally vast number of units have best frequencies (BF) within the 82- to 86-kHz band, e.g., 23% of 600 units studied in a systematic scan of the colliculus inferior (Fig. 5) (Pollak and Schuller, in preparation).

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

(1) *Frequency analysis is achieved and completed by mechanical filter mechanisms of the cochlea. No further neuronal filtering is mandatory.*

(2) *Overrepresentation of biologically relevant frequency bands in the tonotopy of auditory nuclei result from corresponding overrepresentation in the cochlear filter bank either by expanded frequency representation or specific innervation patterns or both. Overrepresentation would then become a mere special case of the general fact that all auditory nuclei are organized in a tonotopic fashion, always originating in the corresponding orderly representation of the frequencies on the BM.*

(3) *In mammalian species the mechanical fine structure of the cochlea can be differentiated. 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.*

C. Foveal frequency stabilization by auditory-laryngeal feedback

Let us return to the problem how the echolocating horseshoe bat can use the long constant frequency echo of 83 kHz. As outlined above, the cochlea and consequently the auditory nuclei are specifically matched to receive this narrow frequency band, and they achieve an unprecedented fine frequency resolution [$Q_{10\,dB}$ values up to 500 compared to maximally 20–30 in other bats and mammals (Neuweiler and Vater, 1977)]. The center frequency of the cochlear fovea is morphologically fixed and cannot be shifted. For a hunting bat this fact could have disastrous results since the bat's flight speed (of up to 4 m/s) will Doppler shift an echo to a higher frequency. The faster the bat flies, the higher the Doppler shift and the less likelihood of a matching of the echo frequency with that of the auditory fovea. The echo tones would range between 86 and 87 kHz, clearly outside the optimum of the cochlear fovea, which is fixed at about 83 kHz.

The horseshoe bat has solved this problem by applying a feedback system for sound emission (Schnitzler, 1968). Whenever the frequency of the echo (CF and FM component) is higher than a distinct "reference-fre-

FIG. 5. The acoustic fovea in horseshoe bats, *Rhinolophus ferrumequinum*. Lowest graph: Frequency representation on the basilar membrane which is projected into the transmodiolar plane. The frequency range of the constant frequency part of the echoes is greatly expanded (83–86 kHz). Upper graphs: Neuronal frequency representation in spiral ganglion and colliculus inferior. Ordinate: Number of neurons/octave. Abscissa: Best frequency of units (in spiral ganglion determined by its afferent origin on the basilar membrane). Note: Overrepresentation of the foveal frequency band is preserved in the ascending auditory pathway. (From Bruns and Schmieszek, 1980; Schuller and Pollak, 1979.)

quency" (nearly identical to the center frequency of the cochlear fovea), the flying bat will decrease the frequency of the next emitted sounds by a corresponding amount. By means of this feedback system between auditory and vocal centers the CF echo frequency is precisely maintained at the center frequency of the acoustic fovea with an accuracy of 50 to 200 Hz or a deviation from the reference frequency by only 0.06% (Fig. 6) (Schuller, Beuter, and Schnitzler, 1974). For perceiving the deviation from the reference frequency, the bat must have a time overlap of the emitted sound and returning echo (Schuller, 1977). It is an open issue if the necessity of overlap is due to a minimal time window triggered by the onset of vocalization or by interference of frequencies in the emitted pulse and returning echo.

Only echo frequencies above the reference frequency are compensated for. Echo frequencies below the reference frequency would only occur if the bat flew backwards. The feedback system operates as a sample and hold device (Schuller and Suga, 1976a). The last heard echo frequency is stored irrespective of the duration of the delay before the next sound emission.

The system reacts sluggishly and needs about 340 ms to compensate for a shift of 1000 Hz. This slowness prevents the compensating mechanism from eliminating brief Doppler shifts within an echo tone. Such minor Doppler shifts imposed onto the CF component of the echo may be of considerable interest to the bat as described below.

The emitted frequency is precisely tuned by the activity of the cricothyroid muscles and the superior laryngeal nerves innervating them—the higher their activity, the higher the emitted frequency (Schuller and Suga, 1976b).

By this feedback mechanism the bat effectively uncouples its movement-sensitive echolocation system from its own traveling speed. Laryngeal muscle activity continuously keeps the echo frequency within the acous-
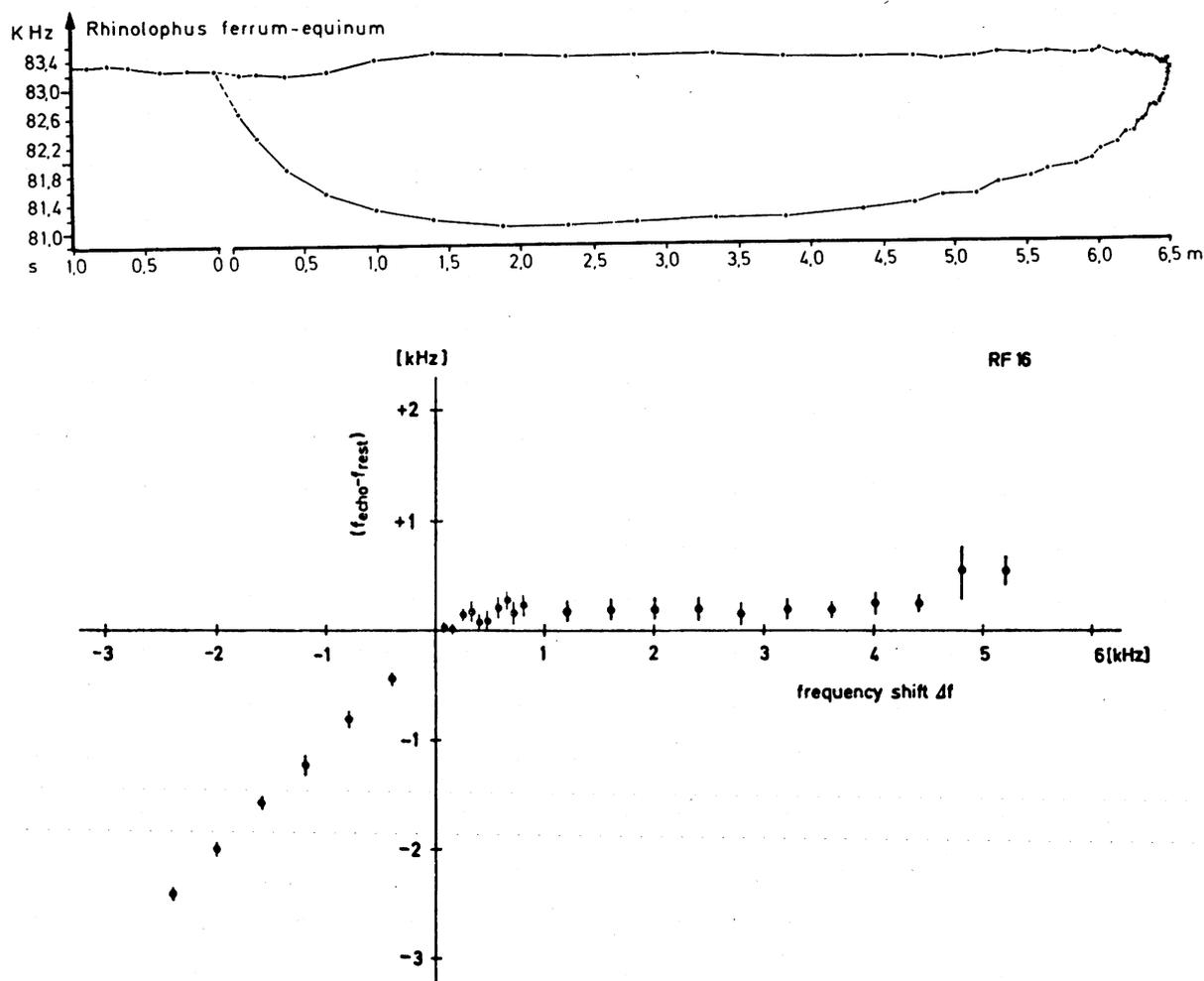

FIG. 6. Stabilization of the echo frequency within the acoustic fovea by a feedback system. Upper graph: A horseshoe bat, emitting 83.3 kHz, flies from a starting point (0 0 on abscissa) to a landing post (6.5-m distance). The emitted frequency before takeoff is 83.3 kHz (ordinate). As soon as the bat starts flying the emitted frequency (lower trace) is lowered in such a way that the echo frequency (upper trace) is kept constant within the foveal frequency. (After Schnitzler, 1968) Lower graph: Capacity of the feedback system. A horseshoe bat receives artificially frequency shifted echoes (Δf, abscissa). The bat reacts by lowering its emitted sound frequency so that the echo frequency is kept constant and close to the frequency emitted in nonflying situations ($f_{echo} - f_{rest}$ ordinate). Frequency shifts of more than 5–6 kHz and shifts below the f_{rest} (negative quadrant) are not compensated for. (From Schuller *et al.*, 1974.)

tic fovea of the ear, just as eye tracking movements stabilize the image of an object on the fovea of the retina. Because of this analogy we have called the expanded representation of the filter frequencies from 82 to 86 kHz an acoustic fovea (Schuller and Pollak, 1979).

D. Movement—Sensitivity of auditory neurons

Although Rhinolophus has solved the problem of maintaining the echo frequency precisely within the receiving filter, one still does not know how the bats specifically detect moving prey by listening to echoes. As already noted above, there exists a large overrepresentation of neurons tuned to the narrow foveal range (82–86 kHz). Many of these neutrons have extremely narrow response areas resulting in Q_{10dB} values of 500 or more (Fig. 7) (Suga, Neuweiler, and Möller, 1976). These types of single unit tuning curves are preserved from the cochlear nuclei to the cortex. These neurons consequently are sensitive to minute frequency modulations of the BF, even to modulations in the range of ±10 to 20 Hz, i.e., 0.02% of the carrier frequency of 83 000 kHz. The neurons tuned to the foveal frequencies are principally sensitive to minor Doppler shifts inflicted onto

echoes from moving prey (Schuller, 1979a).

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 (Fig. 8).

Many of the FM-sensitive foveal units reduce or lose their FM-encoding capacities for stimuli with sound pressure levels above 50 to 70 dB SPL (Fig. 9) (Pollak and Schuller, in preparation). This may be considered an adaptation to echo listening since echoes commonly are faint.

Some neurons appear to be specialized for reacting only to behaviorally relevant frequency modulations. In analogy to the visual system one may call these units "movement-specialized" neurons. These experiments have shown that the auditory nervous system is capable of detecting and analyzing moving targets by modulations of a pure tone echo reflected from a moving prey. Behaviorial experiments in *Pteronotus parnellii* (Goldman
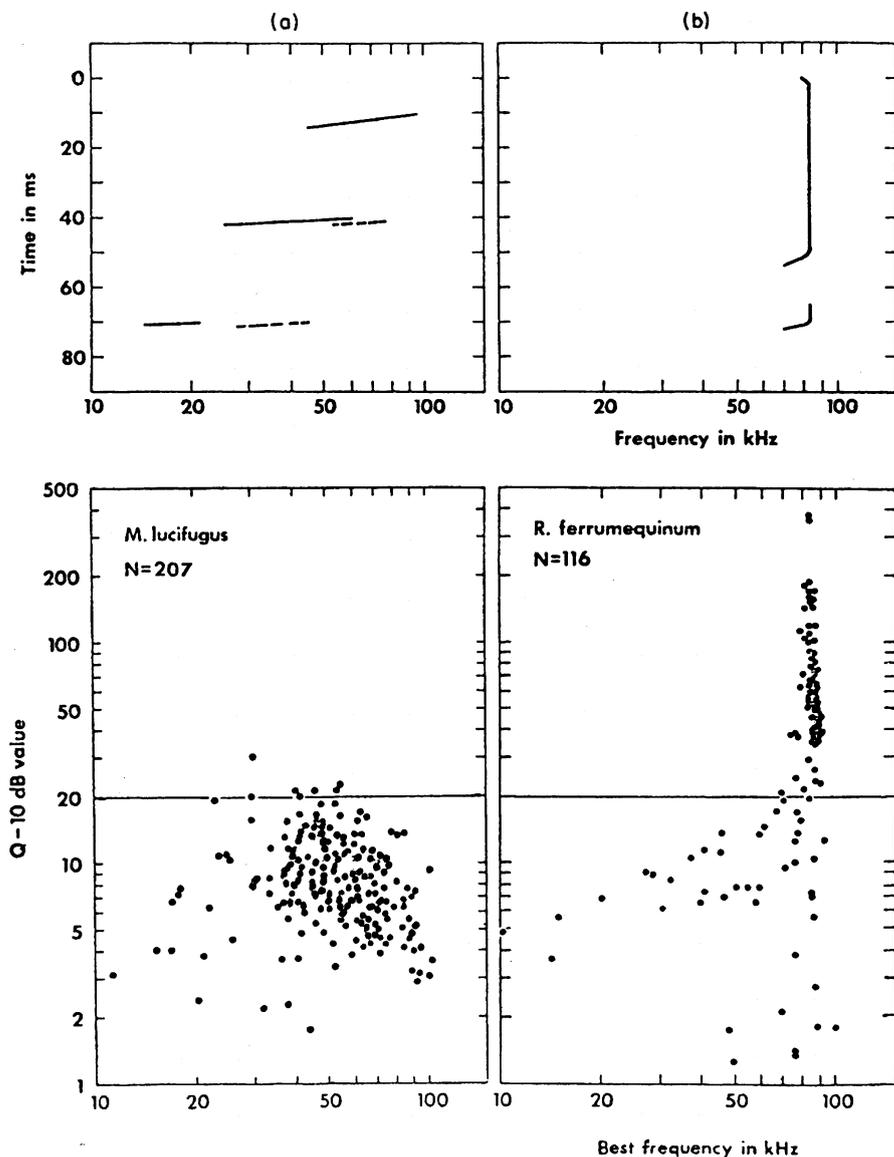

FIG. 7. Comparison of $Q_{10 dB}$ values of cochlear nucleus units in *Myotis lucifugus*, a bat emitting frequency modulated signals, and in the horseshoe bat, *Rhinolophus ferrumequinum*. Upper graph: Spectrograms of the orientation sounds in *Myotis lucifugus* (a) and *Rhinolophus ferrumequinum* (b). Lower graph: Q values (best frequency divided by width of the tuning curve 10 dB above threshold for best frequency) for units with different best frequencies. Note the exceptionally high Q values for the foveal frequency range in the horseshoe bat. (From Suga, Neuweiler, and Möller, 1976.)
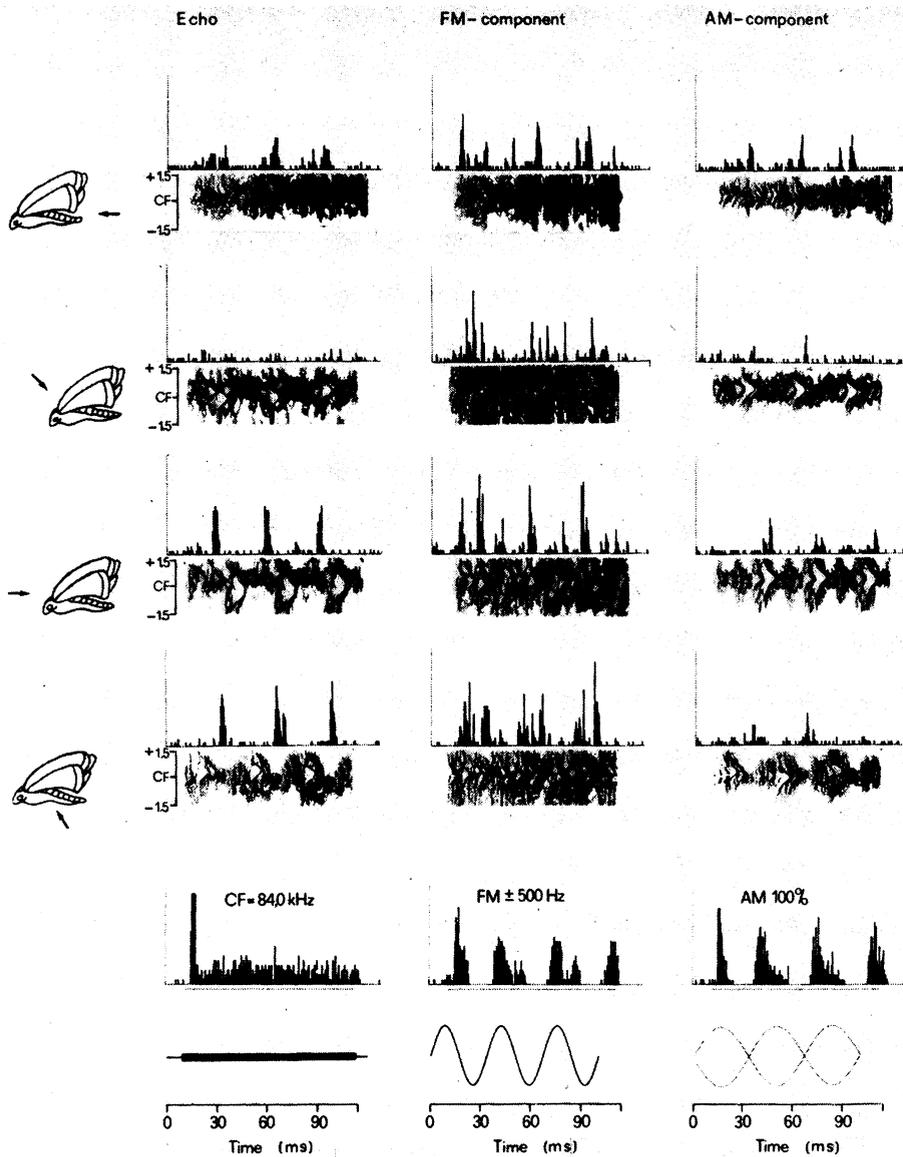
FIG. 8. Responses (PST histograms) of an inferior collicular neuron in the horseshoe bat to echoes reflected from a wing beating moth. The moth was "echolocated" by a 84-kHz pure tone of different directions as indicated by arrows. Below each PST histogram is the spectrogram of the echo stimulus (CF = 84 kHz, frequency modulation range maximally ± 1.5 kHz). Left column: response to the complete echoes. Middle column: response to the FM component and right-column response to the amplitude modulated component of the echoes. Lowest row: response to the pure tone carrier frequency alone (left), to a sinusoidal frequency modulation of the carrier by ± 500 Hz (middle) and to a 100% amplitude modulation of the carrier frequency. (From Schuller, in preparation.)

and Henson, 1977), another bat emitting a long pure tone component, and in horseshoe bats corroborate the neurophysiological results. Both bats immediately detect and catch a wing beating insect, but do not seem to detect it when the prey stays motionless.

Thus according to experimental evidence a long pure tone echolocation sound is a specialized signal for detecting and analyzing movements of a target (Fig. 8). The signal is optimal for bats hunting close to dense backgrounds. The time-smeared cascades of echoes reflected from trees, foliage, walls, etc. 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 (Fig. 8) (see also Neuweiler, 1980). These acoustical markers alert the echolocating bat to the prey and evoke catching behavior (Fig. 1). Bats might even identify different prey by characteristic echo modulations, but this assumption has never been tested.

E. Neuronal specializations for echo listening

A laboratory situation where a bat's ear is exposed to a single stimulus in a quiet surrounding is a far cry from the real auditory world with which an echolocating bat is confronted. The horseshoe bat emits a pure tone of about 60 ms in duration and the echoes start to return when 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 (Möller, 1978). In inferior collicular neurons tuned from 82 to 86 kHz the well-known suppression of the response to a second tone by a first tone completely vanishes when the frequency of the first tone ranges between 82 and 78 kHz (Fig. 10). This actually is the frequency band 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.
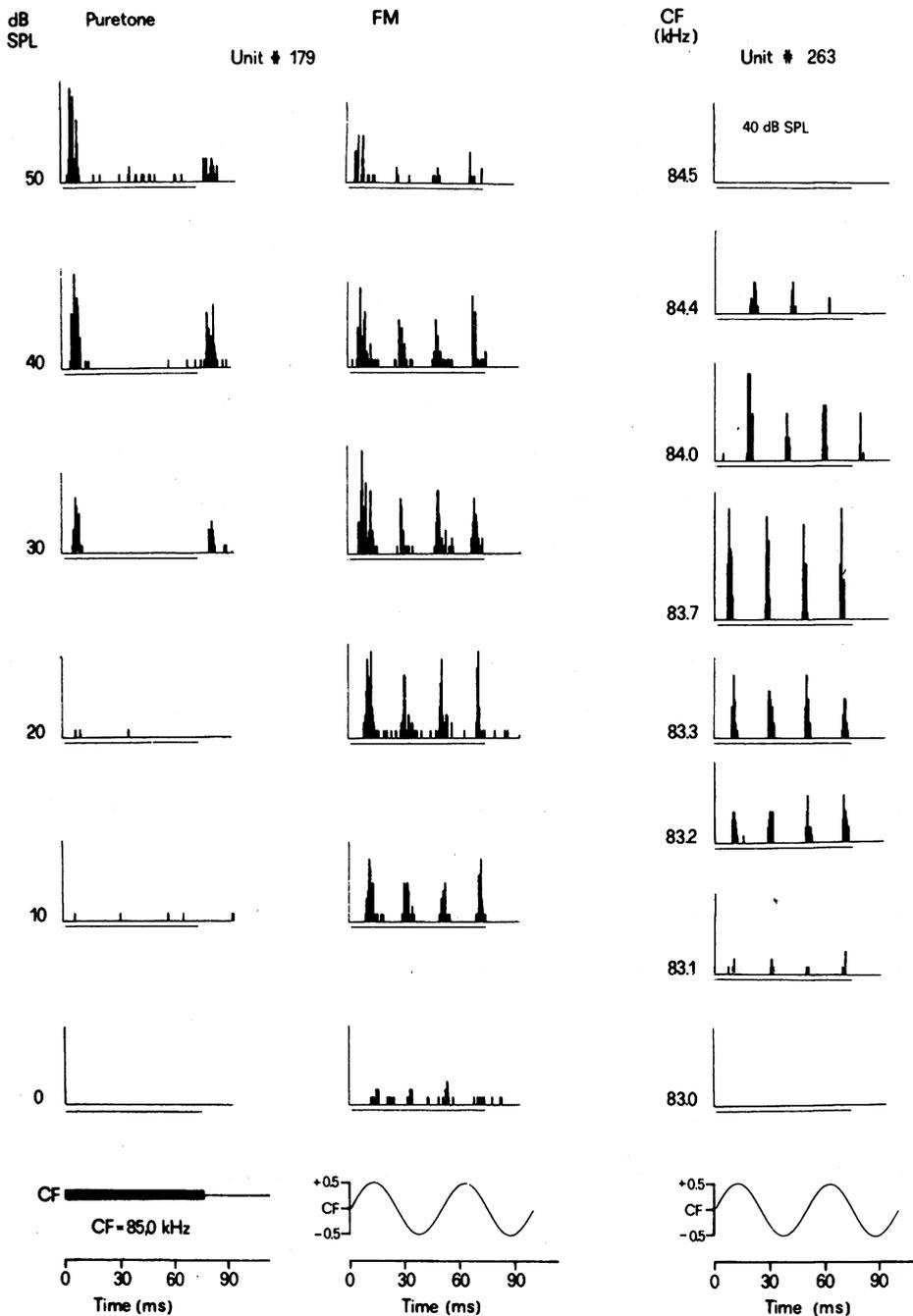
FIG. 9. Neuronal adaptations to processing of frequency modulations in the constant frequency part of the echoes (CF) in collicular units of horseshoe bats. Ordinate: Stimulus intensity in dB SPL. Left column: response to the carrier frequency alone. Middle column: response to a sinusoidal frequency modulation of the carrier. Note: Encoding of frequency modulations is best at lower intensities (echoes). Right column: Dependency of FM encoding from the carrier frequency (CF) demonstrated in another unit. (From Pollak and Schuller, in preparation.)

Moreover, in the foveal neurons the emitted pure tone frequencies of 82 to 78 kHz not only prevent suppression but also facilitate the response to the second (echo) signal as demonstrated by single unit and evoked potential recordings (Fig. 10). This is a remarkably precise adaptation to a specific behavioral situation.

However, unlike in the experiments described, the echolocating bat is not only listening to overlapping signals but also actively vocalizing. Since the Doppler shift compensation system must have neuronal pathways from auditory to vocalizing centers, it might well be that vice versa vocalization centers actively alter the encoding capacities of auditory neurons in an adaptive manner. Recently Schuller (1979b) succeeded in recording the activity of inferior collicular neurons while

eliciting normal echolocation sounds. He described a few neurons which were specifically influenced by neural centers associated with vocalization (Fig. 11). Some of these neurons only responded to an electronically simulated frequency modulated echo when it overlapped with an ongoing vocalization. The FM-encoding capacity was lost when the echo ceased to overlap the echolocation sound. Since the duration of the electrically elicited echolocation sounds could not be varied, it remains an open question if overlap is the required condition or if vocalization triggers a fixed, time window enhancing FM encoding. Substituting the vocalized signal by a playback signal of the same frequency, duration, and intensity failed to elicit the specific responsiveness of these units to FM echoes. It is therefore concluded that the centers associated with vocalization
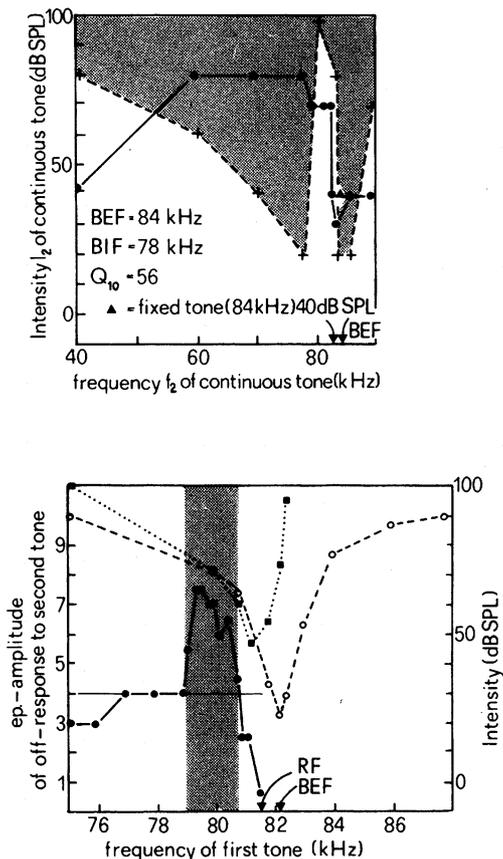
FIG. 10. Lack of inhibition and enhancement of response by two-tone stimulation in inferior colliculus neurons of *Rhinolophus ferrumequinum*. Top: Response to a fixed tone (echo) is inhibited by a continuous tone (shaded area) except to a narrow frequency range of 78–82 kHz, corresponding to the frequencies actually emitted by a flying horseshoe bat. Solid line: tuning curve of the unit. BEF: Best excitatory frequency. BIF: Best inhibitory frequency. Bottom: Frequency range of a first tone (hatched column) causing facilitation of response to a second fixed tone (echo) as shown by evoked potential amplitudes (solid line, black dots). Fixed tone: 60 dB SPL, frequency at reference frequency RF, i.e., frequency of the echo, preceded by a first tone of variable frequency (abscissa) and 90 dB SPL. Delay time between both stimuli 10 ms. Horizontal left bar marks evoked potential amplitude for fixed tone alone. Right-hand ordinate: threshold of EP to single tone stimulation. Broken line and open circles: Threshold curve for on-response. (From J. Möller, 1978.)

may specifically alter the responsiveness of auditory neurons.

[Recent results of O'Neill and Suga (1979) with cortical neurons indicate that a lower harmonic of an echolocation sound may have specific triggering capacities for the responsiveness of neurons in another pure tone emitting bat, *Pteronotus parnellii*. This harmonic effect cannot be ruled out completely in the above described experiment. However, in horseshoe bats unlike in Pteronotus the lower harmonic is very faint or absent and therefore it is unlikely that the described effects in Rhinolophus are caused by the first harmonic of the pulse.]

In a bat which is hunting insects these neurons would

be alerted to the behaviorally relevant echo features, i.e., modulations of the pure tone carrier frequency by the wingbeats of a prey. This would occur for a limited time span only, and this time span corresponds to the time that echoes could be expected to return. When the bat is not echolocating, these neurons apparently are shut off.

F. Conclusions

The cochlear investigations and neurophysiological experiments show that the auditory system of the horseshoe bat is indeed adapted to detect and analyze moving prey against a noisy background. The adaptive value of echolocation with a pure tone is the exploitation of food resources in noise-cluttered (multiple echoes) environments such as foliages, bushes, etc. It also complies to signal theory asking for pure tone signals in such a difficult signal retrieving situation.

The movement sensitivity of echolocation is brought about by applying a pure tone signal carrying movement-induced modulations in the echoes reflected from potential prey. The cochlea of the horseshoe bat has an acoustical fovea built into the organ of Corti. The fovea deals with the echo-carrier frequency and results in an extremely fine frequency resolution within the narrow frequency range of 82 to 86 kHz.

This foveal frequency band is vastly overrepresented throughout the ascending auditory pathways. Onto the peripheral adaptations several neuronal specializations are superimposed and they converge towards the same end—movement direction.

The auditory studies in echolocating bats not only show the remarkable precision and high degree of specialization attained in a biological signal receiving system, but they also disclose the advantage of studying specialized systems for learning about general principles. Further evidence for this notion comes from general qualities of audition in echo-locating bats.

II. TIME—ENCODING IN ECHOLOCATION

Distance of a target from a bat is measured by the round trip traveling time of the sound, from the instant of pulse emission to the reception of the echo. In a behavioral experiment it was shown that echolocating bats differentiate time lags between two echoes, as small as 60 μs, corresponding to a distance difference of 1 cm between two targets (Simmons, 1973).

The localization of an echo source is probably measured by an interaction of binaural cues and positioning of the movable and highly directional pinnae. It is generally accepted that directionality in the horizontal plane is coded by binaural intensity and time differences.

Animals with large heads and consequently large interaural distances are considered to analyze time differences; whereas, small mammals such as bats having interaural distances of about 15 to 20 mm would depend to a large degree on binaural intensity cues. However, a recent study in our lab showed that in the
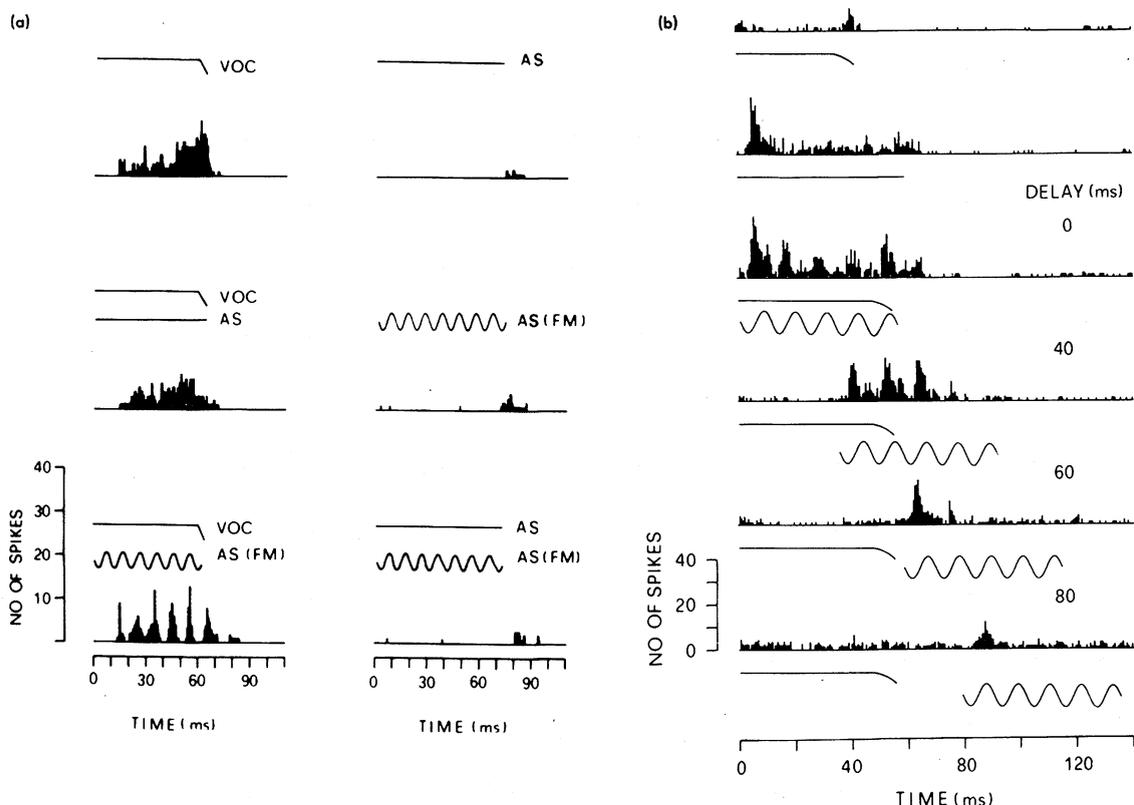
FIG. 11. Vocalization of echolocation sounds (VOC) influences responsiveness of inferior colliculus neurons in horseshoe bats. (a) Left column: Responses (PST histograms) of a unit to vocalization alone (VOC) and to vocalization combined with simulated echoes (VOC and AS), AS= same frequency and intensity as constant frequency part of VOC; AS (FM): same as AS, but frequency modulated by ± 500 Hz. Right column: Responses to the same stimuli but without vocalization. Note: FM-encoding capacity is lost when the bat is not vocalizing (compare histograms in bottom row). (b) Time relationship between vocalization and FM encoding. Upper histogram: Response to vocalization alone; second histogram: response to a pure tone of 1-kHz higher frequency and same intensity as in vocalization. Lower histograms: responses to vocalization and simulated frequency modulated echo. As shown by the delays of the echo, the FM stimulus is only encoded during vocalization. (From Schuller, 1979.)

inferior colliculus and medial olivary nucleus of an FM bat there are neurons encoding binaural time delay in the microsecond range. *Seven of 70 neurons recorded showed markedly different spike counts when a pure tone arrived 15 μs later at the ipsi than at the contralateral ear or vice versa (Harnischfeger, 1980).*

Apart from demonstrating that some mammalian neurons have the capacity to handle time differences in the microsecond range the study also indicates that fine time coding might be achieved with signals that would not appear to be optimal. The signals used were pure tones in the range of 18 to 61 kHz, of 2-ms duration and rise and fall times of 500 μs. Apparently the neurons get the timing information from the envelope of the signals. Due to the high frequencies, phase differences can be ruled out as possible time cues in this experiment.

III. SPECTRUM—ANALYSIS IN ECHOLOCATION

In many discrimination tasks bats performed remarkably well in acoustically differentiating the echoes from objects of different shape, size, and texture. In fact, resolution and fine structure of an acoustical world in the bat might match that of our own richly structured visual one.

This is demonstrated by an accidental result in a discrimination experiment, designed by Simmons et al. (1974), where bats had to differentiate echoes from holes of different depths drilled into otherwise identical Plexiglas plates (Fiedler, Hahersetzer, and Vogler, 1980). When offered two plates with identical hole depths in control experiments, the bats invariably chose at random, but in one case they did not and continued to prefer one of the two plates. A scanning electron microscopical inspection disclosed that in the prefered plate the holes were drilled by a worn out tool resulting in *ringlike, 20- to 50-μm-high ridges* on the bottom of the holes, whereas the bottoms in the other plate were plane. Apparently bats do acoustically recognize the complex echo patterns from objects with fine textural differences.

Broadband echoes returning from targets structured in depth show conspicuous blackouts in the frequency spectrum (Simmons et al., 1974; Beuter, 1980). These spectral troughs result from interferences of echoes returning from the surface and the depth of a target. In the above mentioned experiments the smaller the hole depth is, the greater the spacing of the troughs of a broadband echo spectrum are, and thus they should be easily discriminated by a frequency analyzing system. Therefore frequency analysis of a broadband echo should yield information on the fine texture of a target,

whereas a coarse structure may be analyzed in the time domain (Beuter, 1980).

The remarkable performances in differentiating objects by blind men using sonar aids and the sensations they report (Kay, 1980) indicate that fine frequency and time analysis demonstrated to exist in audition of bats might be a general feature of mammalian auditory systems. The examples of good auditory analysis in both frequency and time domain corroborates our notion that echolocating bats have not invented something new, but simply exploit and refine the capacities of the mammalian auditory system. Therefore we believe that the bats have something to tell, not only to the zoologist, but also to any scholar interested in audition.

ACKNOWLEDGMENTS

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