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## Evolutionary aspects of bat echolocation

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**Abstract** This review is yet another attempt to explain how echolocation in bats or bat-like mammals came into existence. Attention is focused on neuronal specializations in the ascending auditory pathway of echolocating bats. Three different mechanisms are considered that may create a specific auditory sensitivity to echos: (1) time-windows of enhanced echo-processing opened by a corollary discharge of neuronal vocalization commands; (2) differentiation and expansion of ensembles of combination-sensitive neurons in the midbrain; and (3) corticofugal top-down modulations. The second part of the review interprets three different types of echolocation as adaptations to ecological niches, and presents the sophisticated cochlear specializations in constant-frequency/frequency-modulated bats as a case study of finely tuned differentiation. It is briefly discussed how a resonant mechanism in the inner ear of constant-frequency/frequency-modulated bats may have evolved in common mammalian cochlea.

**Abbreviations** *AVCN* anteroventral cochlear nucleus · *CF* constant frequency element of an echolocation signal · *DPOAE* distortion product otoacoustic emission · *FM* frequency-modulated echolocation signal · *IC* inferior colliculus · *IHC* inner hair cell · *INLL* intermediate nucleus of the lateral lemniscus · *MSO* medial superior olive · *OAE* otoacoustic emission · *OHC* outer hair cell · *PVCN* posterior ventral cochlear nucleus · *SI* sparsely innervated section of the cochlea · *SOC* superior olivary complex · *VNLL* ventral nucleus of the lateral lemniscus

### Introduction

Biology has remained an integral and unified science in spite of the productive and continuing proliferation of new disciplines incorporating a multitude of highly diverse methods from biochemical protein identification to computer models of ecosystems. It owns its identity to the Darwinian theory of evolution that has been, and still is, verified by countless experimental evidence from the dynamics of complex ecological interactions to the level of molecular interactions in cells and genomes. From petrified records we learn how our extant fauna came into existence, e.g. how reptilian-like creatures may have learned to fly and eventually became birds, and how *Homo sapiens* has evolved from anthropoid primates.

Among mammals bats are unique since they feature two very special achievements: flight and echolocation. Unlike in birds, however, there exists no “archechiropterix” that may show which mammalian precursors developed the ability to fly and to echolocate. The oldest chiropteran skeletons (*Icaronycteris index*) come from Eocene deposits in Wyoming. This record contains a perfect bat with only minor differences to our extant bat fauna. It appears that as far back as 50 million years ago bat species flew and echolocated as efficiently as our extant microchiropteran bat fauna of about 650 species (Neuweiler 2000).

Paleontological records do not disclose how flight and echolocation in bats came into existence. Therefore, one has to compare extant echolocating bats with non-echolocating mammals to understand the mechanisms that enable a brain to interpret the outer world by means of acoustical reflections. Are there any structural and/or physiological specializations that distinguish an echolocating mammal from a non-echolocating one?

An obvious organ to look at is the ear. However, apart from specific modifications in a few highly specialized species (e.g., auditory foveae) the functional structure of the peripheral auditory system including the cochlea and the auditory nerve has been highly

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conserved and is uniform in all mammals including bats and man. This is not the case for the neuronal aspects of audition.

## Adaptations to echolocation

### Neuroanatomical specializations in echolocating bats

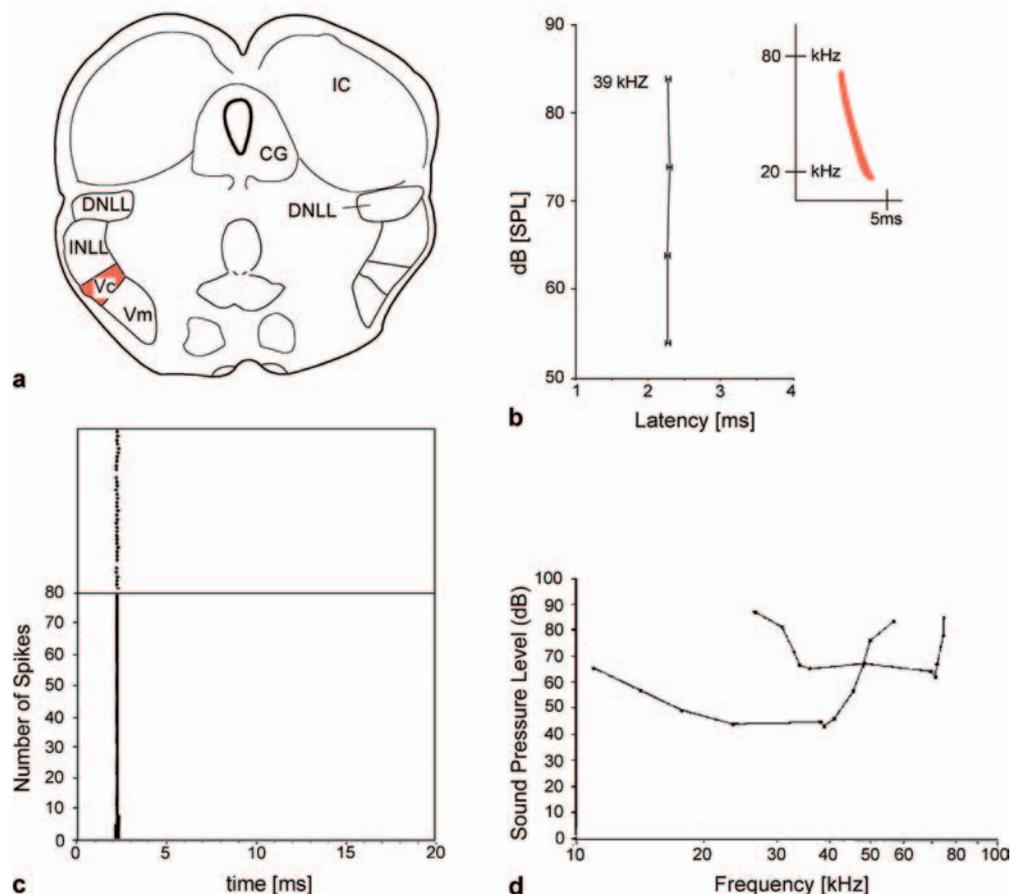
In echolocating bats, the lower brainstem nuclei of the ascending auditory pathway, including the inferior colliculus of the midbrain, are hypertrophied and some of them are differentially structured (Covey and Casseday 1995). First, the anteroventral cochlear nucleus (AVCN) is extremely large. In *Pteronotus*, there is a unique group of large multipolar cells in a marginal zone. Second, unlike in other mammals, there is an additional, direct input from the posterior ventral cochlear nucleus (PVCN) to the superior olivary complex (SOC). Third, in non-echolocating mammals, the medial superior olive (MSO) receives identical inputs from ipsi- and contralateral AVCN. This is considered a prerequisite for processing interaural time differences. In echolocating bats, however, the ipsilateral input is sparse, and in one bat species, *Pteronotus parnellii*, the large majority of MSO-neurons only receives monaural input from the contralateral AVCN (Grothe and Neuweiler 2000). Finally, the monaural ventral and intermediate nuclei of the lateral

lemniscus (VNLL and INLL) are unusually large and conspicuously organized (Fig. 1): the VNLL is differentiated into a multipolar and a columnar section. Columnar neurons receive tonotopically arranged inputs via large calyx-synapses on their cell bodies. This unique columnar organization of neurons with calyx-synapses is also found in echolocating dolphins. The broadly tuned neurons of the columnar VNLL process specifically frequency-modulated (FM) components of echolocation signals. Columnar neurons are intensity invariant and respond with one single spike at constant latencies over a wide range of intensities and frequencies (Fig. 1). Thus, they are ideally suited as time markers. Except for the few cases mentioned above the specific auditory implications for echolocation of these neuroanatomical specialities are not yet known.

### Echo suppression in non-echolocating mammals

In natural situations a human subject or an animal will not only listen to a sound source but also to its multiple reflections (clutter) from reverberant surfaces. In most experimental studies the natural clutter is simplified into a singular lagging reflection following a leading direct sound (Litovsky et al. 1999). The auditory system ensures that reflections fuse with the sound source to one percept. Such perceptual fusion occurs for delays up to

**Fig. 1a–d** Auditory brain stem nuclei and neurons specialized for precise time-coding in the columnar part (*Vc*) of the ventral lemniscal nucleus (VNLL) of the echolocating bat *Eptesicus fuscus*. **a** Schematic map of auditory nuclei in the brainstem. *CG* central gray; *DNLL* dorsal, *INLL* intermediate, *Vc* columnar part, *Vm* multipolar part of the VNLL. *IC* inferior colliculus. **b** Frequency-modulated (FM)-stimulated neurons in *Vc* are intensity invariant and respond with one spike at the same latency. *Inset*: FM echolocation sound of *E. fuscus*. **c** Latencies of single unit responses in *Vc* show no time-jitter. **d** Tuning curves of *Vc*-units are very broad and integrate over most parts of the FM echolocation signal (After Haplea et al. 1994)



5 ms between leading and lagging stimulus. When the delay increases to 8–10 ms for brief sounds, e.g. for clicks, a human listener begins to hear two separate signals. This critical delay is called echo threshold. Apparently, for brief delays perception of echoes as distinct signals is suppressed, and the leading signal dominates the heard sound image. It is hypothesized that a neural gate closes after the first elicited spike, and reopens after a few milliseconds (echo threshold). The gate could be implemented by self- or lateral inhibition (Litkovsky et al. 1999). In cats (Litovsky and Yin 1998), rabbits (Fitzpatrick et al. 1995) and barn owls (Keller and Tagahashi 1996) a majority of single units from the inferior colliculus (IC) showed lag suppression within variable time delays. In these samples the median time delay for lag suppression matches the behaviourally measured echo thresholds. However, since in newborn cats lag suppression is present in the IC, but not behaviourally, it is also suggested that cortical events may be involved (Litovsky 1998).

Echo suppression builds up even more when trains of lead-lag signal pairs are heard, and echo thresholds rise by several milliseconds. Echo thresholds additionally increase when each leading signal is succeeded not by one but by several echoes of various time delays (Yost and Guzman 1996).

Since echolocating bats listen to trains of lead signals (vocalized echolocation sound) followed each by several highly correlated but non-identical lag signals (echoes), they should be heavily afflicted by echo suppression mechanisms as described in humans and a few experimental mammals. A bat would be neurally deaf to echoes returning within about 2.5 ms, i.e. reflected from objects up to at least 40 cm away.

### Echo sensitivity locked to sound emission

Obviously, echolocation requires not only an elimination but a reversal of echo suppression into echo facilitation. Do such echo-facilitating neurons exist? Indeed, Grinnell (1963) discovered echo-facilitation in an evoked potential study of the IC in the bat *Myotis l. lucifugus*.

Theoretically, the most efficient way to implement echo-sensitivity would be the opening of facilitative, auditory gates by a corollary discharge of the neuronal command that triggers vocalization of an echolocation sound. By such a corollary command to the auditory pathway echo-sensitivity would be specifically locked to an emitted echolocation call, and could be limited for a defined time window. Schuller (1979) reported units in the IC of horseshoe bats (*Rhinolophus ferrumequinum*) that vigorously responded to phantom echoes only when the awake bat had vocalized (Fig. 2). In these units, playbacks of echolocation sounds were ineffective without a preceding sound emission by the bat. The specific echo-sensitivity triggered by sound emission vanished for phantom echoes with delays larger than 60 ms (Fig. 2c). Thus, these echo-neurons will respond

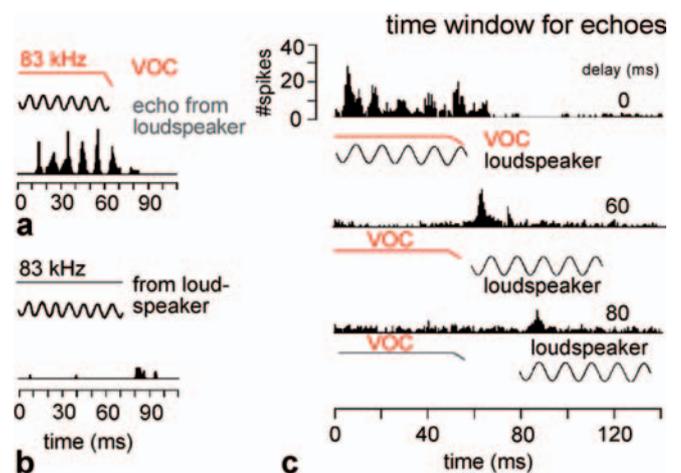
to echoes returning from objects up to a distance of 10 m, and will exclude echoes from targets further away.

This limitation nicely matches the foraging behaviour of horseshoe bats which preferably utilize a sit-and-wait strategy when foraging. From a vantage point within vegetation horseshoe bats initiate pursuit of flying insects passing by at distances of not more than about 7 m (Neuweiler et al. 1987).

Unfortunately, recordings in the ascending auditory pathway of bats that actively emit echolocation signals have been discontinued. Thus, the few IC units reported by Schuller (1979) are the only evidence that auditory units sensitized for echoes by a corollary motor command may exist. These sparse neural data are, however, corroborated by comparative behavioural studies (Roverud and Grinnell 1985; Roverud 1993). Echolocating bats that were trained for a distance-discrimination task failed when they were jammed by intense playbacks of the species' echolocation sounds. Distance discrimination could only be disrupted by species-specific echolocation sounds or signals carrying specific elements of the echolocation sound. Jamming was time-locked to the beginning of vocalizations, and lost its effectiveness beyond echo delays of more than 30 ms. These results from different bat species strongly suggest that a time window of enhanced echo processing locked to sound emission indeed exists.

### Echo sensitivity by combination sensitive neurons

In contrast to the tiny sample of vocalization-triggered auditory echo units, another type of echo-sensitive neuron has been extensively described in large portions



**Fig. 2a–c** Echo-sensitive neuron only triggered by a vocalized echolocation sound recorded from the inferior colliculus of a horseshoe bat. **a** The neuron vigorously responds to a phantom echo (wavy line) played from a loudspeaker when the bat at the same time emits an echolocation sound (VOC). **b** The same neuron is unresponsive when the bat does not vocalize, and both signals are played from a loudspeaker. **c** The specific echo-sensitivity triggered by sound emission vanishes when the echo is delayed by more than 60 ms (time-window for echoes). After Schuller (1979)

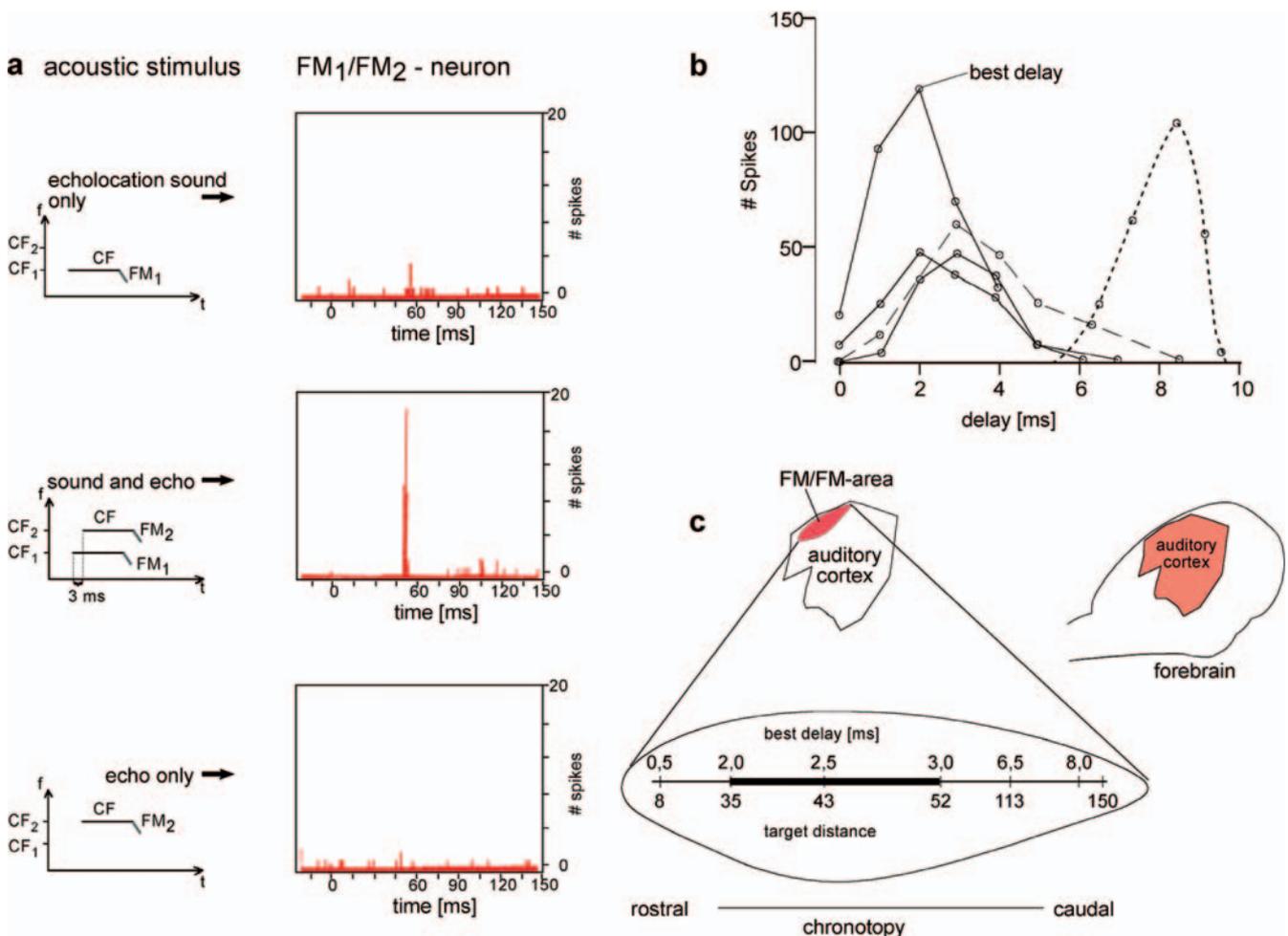
of the IC and higher auditory centres: so called combination-sensitive neurons. These neurons preferably or exclusively answer to a combination of two auditory stimuli (Fig. 3a), e.g. an initial loud FM signal that corresponds to an emitted echolocation signal, and after a specific delay a fainter second FM signal that corresponds to an echo (FM/FM neurons). The so-called best delay between first and second signal to which the neuron responds best is specific for each neuron and ranges between 0 and 20 ms with a majority of best delays below 10 ms (Fig. 3b, c; Portfors and Wenstrup 1999). In terms of a foraging, echolocating bat these data indicate that most of these FM/

FM echo-sensitive neurons should be active when the bat closes in on a target, for instance when pursuing prey at distances shorter than about 2 m. Due to its specific best delays each FM/FM unit will respond only to an echo returning from the appropriate distance; hence, these neurons have been also called “range-finding neurons” (O’Neill and Suga 1982).

According to a recent study in the nuclei of the lateral lemniscus (Portfors and Wenstrup 2001), combination sensitivity seems to be generated in the IC where about 75% of units recorded are combination sensitive; of these 70% are facilitated and 30% inhibited by the first signal.

Echo-sensitive neurons often respond to a first signal mimicking specific parameters of an emitted echolocation sound only after long latencies of ca. 13 ms compared to ca. 7 ms for the second signal (echo). These long latencies to the first stimulus may result from inhibition initiated by the beginning of the first stimulus. These findings support the hypothesis that echo-sensitive neurons are coincidence detectors (Olsen and Suga 1991; Portfors and Wenstrup 2001). Coincidence is most probably achieved by rebound from inhibition elicited by the emitted sound. Duration of inhibition varies and corresponds to the best delay of the units. Combination sensitivity disappears when inhibition is blocked in the inferior colliculus.

**Fig. 3a–c** Combination-sensitivity in the auditory cortex of horseshoe bats. **a** A FM<sub>1</sub>/FM<sub>2</sub> neuron that only responds to a combination of the FM elements of the first harmonic (FM<sub>1</sub> marks the emitted echolocation sound) and the second harmonic (FM<sub>2</sub> marks the returning echo) with a characteristic delay (3 ms). *Upper and lower graph: CF* constant-frequency component. The neuron was stimulated by a CF/FM signal; however, it only responded to the FM component. **b** Delay-tuning curves of five different units in the FM/FM area of the auditory cortex. **c** Arrangement of best delays of FM/FM units in a rostral-caudal chronotopic order. *Bold line:* units with best delays between 2 and 3 ms, corresponding to target distances of 35–52 cm, are overrepresented. After Schuller et al. (1991)



Combination-sensitive neurons that are inhibited will be silent during sound emission; however, by rebound from inhibition they may feed additional excitation into facilitated FM/FM neurons and thus enhance echo-sensitivity (Portfors and Wenstrup 2001).

FM/FM or other echo-sensitive neurons belong to the broad class of combination-sensitive neurons that have been also recorded in higher auditory centres of non-echolocating mammals and of birds. Combination-sensitive neurons respond best to specific temporal relationships between spectrally separate sound elements, and are considered to be coders of species-specific communication signals. A neuron is classified as combination sensitive when its response to the combined stimuli is different by at least 20% from the algebraic sum of responses to each separate element of the combined stimulus (Portfors and Wenstrup 1999).

Apparently, combination sensitivity is a general feature of auditory reception in all mammals and birds, and not specific to echolocating animals. In evolution, echo sensitivity, and hence, echolocation may have been established more by quantitative than by qualitative modifications: combination-sensitive neurons are found in very large aggregations in midbrain and higher auditory centres of bats, whereas in non-echolocating mammals and birds combination sensitivity is far less frequently recorded and is narrowly confined to specific subregions of auditory brain centres. Transformation of combination sensitivity from coding communication sounds to echo coding also implies that temporal relationships are shortened from hundreds to only a few milliseconds, and neuronal spectral filters are tuned to specific echolocation sound elements.

It is unlikely that combination sensitivity in echolocating bats is achieved by the reversal of echo-suppression mechanisms in non-echolocating mammals from an inhibitory to a facilitatory mode, since combination sensitivity and echo suppression coexist in the auditory system of non-echolocating mammals.

Locking time windows of enhanced audition to neuronal commands of sound emission would be the perfect way to generate echo sensitivity. Only one neural study (Schuller 1979) supports such a mechanism. Apparently, listening to the tight time relationship between heard emitted sound and returning echoes is good enough to generate echo sensitivity by modifying combinatory neuronal circuits common to neuronal coding of species-specific communication signals in all mammals and in birds (Margoliash and Fortune 1992; Gehr et al. 2000).

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### Top-down modulation

Theoretically, echo sensitivity could be generated or enhanced in a more flexible way by corticofugal modulation of auditory units. Recent studies (Ma and Suga 2001) have shown that corticofugal efferent innervation to the medial geniculate and IC modulates auditory signal processing in three domains: frequency, time, and

direction. Electrical stimulation of cortical FM/FM neurons enhances the auditory responses of subcortical combination-sensitive neurons matched in best delay to the activated cortical neurons, and sharpens delay tuning without shifting their best delays, whereas it suppresses the auditory responses and shifts the best delays of unmatched subcortical delay-tuned neurons (Yan and Suga 1996).

An earlier study (Kössl and Vater 1989) has demonstrated that norepinephrine markedly diminishes latency jitters in units of cochlear nuclei. This effect was interpreted as a more precise coding of echo timings in alert bats due to the attentive effect of norepinephrergic innervation from locus coeruleus.

Thus, corticofugal modulation activated by echoes, and general modulatory mechanisms of attention such as norepinephrergic or cholinergic inputs from brain stem nuclei primarily serve to focus attention and perceptive power to a sector of the outer world that is of momentary behavioural interest. Auditory sensitivity to echoes will be enhanced, and frequency and time filters will be quickly shaped to actual requirements. Top-down modulation may prove to be a powerful way to adjust the auditory system to actual demands of auditory cognition in echolocation. As in vision, it might also provide learned cognitive templates stored in memory from previous experiences in echolocation. Therefore, studies in top-down modulation in the neural auditory pathway (Yan and Suga 1996) will become a central issue in echolocation research.

Echolocation is a neuronal and not a cochlear achievement. Mechanisms involved in generating echo-sensitivity are still under discussion and include:

1. Time windows of echo-sensitivity triggered by vocal command centers (Fig. 2).
2. Combination sensitivity (Fig. 3) derived from coding species-specific communication signals.
3. Cortical top-down modulation.

In my opinion, echolocation phylogenetically was an adaptation of already existing mechanisms in auditory neuronal processing. In “pre-bats”, the transition from neural combination circuits for sound communication to those for echolocation was probably elicited by nocturnal pursuits of small flying insects. The capacity of flight in turn may have evolved from small insectivorous and arboreal mammals catching nocturnal insects while running along branches and hopping from twig to twig in trees (see also Simmons and Stein 1980; Padian 1985). However, in another line of thinking it is supposed that echolocation evolved in cave dwelling animals.

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### Specialization in evolution: the conquest of ecological niches

Once bats came into existence their functional bauplan did not substantially change for some 50 million years.

Yet, flight combined with echolocation was, and still is, so advantageous to a nocturnal mammal that bats radiated into many ecological niches. Microchiroptera adapted echolocation systems, wing shapes and flight styles (Rayner 1991) to all possible food sources. Some species pursue flying insects at high speeds, others pick up insect prey from the ground, tree bark and twigs, and still others search for frogs, lizards, mice and birds. Among the neotropical phyllostomids there is a large group of bats species specialized for visiting nocturnal flowers for pollen and nectar, or for collecting fruits. The infamous vampire bats can only subsist on blood from mammals and birds. There is no other mammalian order that has tapped such a rich variety of food resources.

Bat species may be differentiated and identified by the frequency range and the time structure of their echolocation calls. These species-specific echolocation systems may be grouped under three broad categories (Fig. 4; Neuweiler 1984).

**Fig. 4** Echolocation systems in bats. *CF/FM*: horseshoe bats, hipposiderids, and the neotropic moustached bat emit multiharmonic echolocation signals consisting of a long pure tone terminated by a brief FM component. *CF/FM* bats often forage within or close to dense vegetation *FM*. Most insectivorous bats foraging on the wing emit brief, downward-FM echolocation signals when approaching and catching a prey (*FM*). They often emit longer and only shallowly modulated signal when they search for prey (not shown) *Click-like*: gleaners bats and some flower visiting bats emit very brief signals over a broad frequency band (click-like). These echolocation sounds are far less intense than those of *FM* and *CF/FM* bats

FM echolocation

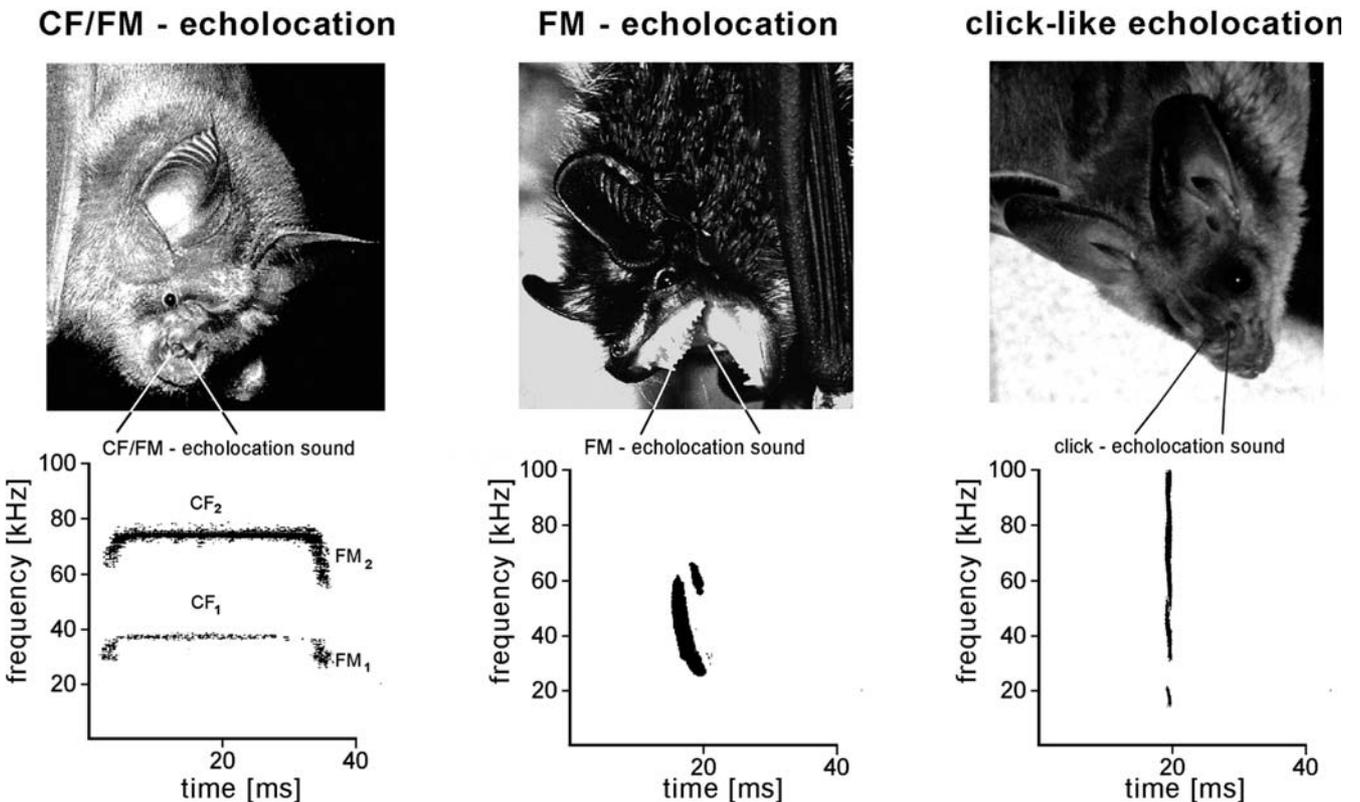
Most bat species pursue insects on the wing. During the approach to and capture of prey these bats emit sequences of brief (several milliseconds) downward FM sounds. FM signals serve as good time-markers in the ascending auditory pathway, and hence are thought to guarantee a precise distance perception in echolocation.

Constant-frequency/frequency-modulated echolocation

The Old World families of horseshoe bats (rhinolophids) and hipposiderids, and one neotropical species, *Pteronotus parnellii*, emit a combined echolocation sound consisting of a rather long (8–60 ms) constant frequency (CF) invariably terminated by a brief FM element. In many species the echolocation sounds start with a brief frequency upward-modulated element that is especially pronounced in commuting flights of the bats (Neuweiler et al. 1987). Thus, the correct signature for these echolocation systems should be *FM/CF/FM*. However, since no specific function could be assigned to the initial FM component this designation has not been endorsed.

*CF/FM* echolocation sounds consist of two or more harmonics. In the moustached bat and in horseshoe bats the second harmonic of the CF component ( $CF_2$  in Fig. 4) is the most intense element of the echolocation signal to which audition is specifically adapted.

*CF/FM* bats preferably, but in no way exclusively, forage wing-beating insects in dense vegetation. They possess an auditory fovea in the cochlea and compensate



Doppler shifts of complete echo signals in order to keep audition of CF<sub>2</sub> echoes within an auditory fovea (see below).

#### Click-like echolocation

A number of bat species that pick up prey from substrates or visit flowers and fruiting vegetation emit faint and very brief signals of submillisecond durations. The ultra-brief sounds consist of several shallowly FM harmonics that add up to a click-like, broadband signal covering a frequency band of up to 80–100 kHz. Based on behavioural experiments it has been suggested that broad-band signals may serve to differentiate textures of targets by the interference pattern (colouration) reflected in broad band echoes (Schmidt 1988; Neuweiler and Schmidt 1993).

In ethoecological studies of neotropical and European bat communities the correlation between foraging niches and type of echolocation signals has been subdivided in a much more detailed way (Schnitzler and Kalko 1998; Kalko and Schnitzler 1998).

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#### Perfect adaptation by auditory specialization: a case study in CF/FM bats

Auditory adaptations to the three categories of echolocation have not been systematically studied with one notable and striking exception, the CF/FM bats, i.e. the moustached bat (*Pteronotus parnellii*) and the rufous horseshoe bat (*Rhinolophus rouxi*). Over the last decades these two bat species have become case studies of sophisticated adaptation of an auditory system to a specific foraging strategy.

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#### Foraging behaviour

The foraging behaviour of the rufous horseshoe bat exemplifies foraging strategies in CF/FM bats (Neuweiler et al. 1987). When these bats leave their caves in the evening they immediately take cover within bushes and commute under the canopy of trees and bushes into the jungle. After a brief period of foraging on the wing the bats spend the night foraging in a sit-and-wait strategy. Each bat occupies its own foraging area and suspends itself from slender twigs. The bat scans the surrounding by emitting continuous sequences of CF/FM signals throughout the night. Whenever an echolocation sound hits a wing-beating insect the bat takes off for a catch and returns with its prey to the very same spot or nearby twigs. The horseshoe bats detect the flying insects against the dense echo clutter reverberated from foliage by echo-glints imposed on the long pure tone component (CF) of the echo by each wing beat of the target. Echo-glints are produced by frequency Doppler shifts induced by the speed of the insect wing, and by an intense mirror

reflection of the impinging sound waves when the moving wing passes through a position perpendicular to the incoming sound waves. Behavioural experiments testified (Link et al. 1986) that horseshoe bats are indeed specialized to wing beat detection, and deaf to non-flying insects. Insects sitting or moving on a substrate do not elicit attacks of horseshoe bats even at close distances. Apparently, the long CF component of the echolocation sound serves as a carrier for glints induced by fluttering prey. However, the modulation depths of such glints amounts to less than 0.25% of the carrier frequency, for instance to maximally 185 Hz on a CF component of 75 kHz emitted by a rufous horseshoe bat.

In order to detect even very tiny glints CF/FM bats have implemented a very narrow cochlear frequency filter tuned to the species-specific and even individual frequency of the CF<sub>2</sub> echo component (Fig. 5). We have called this individually tuned frequency filter an auditory fovea.

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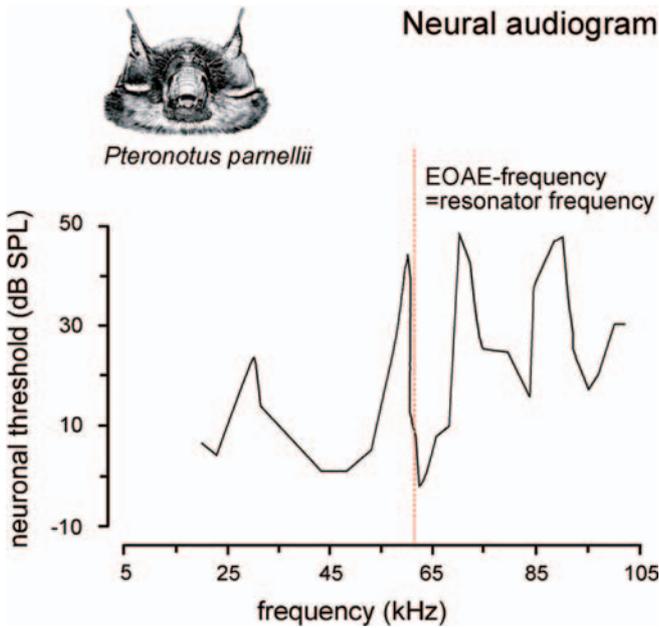
#### Mechanisms of auditory foveae

Structural and functional specialization that produce the extremely narrow frequency filter of the auditory fovea have been most thoroughly studied in *Pteronotus parnellii* (Henson and Henson 1991; Russell and Kössl 1999; for a review see Kössl and Vater 1995) because in the moustached bat the cochlea is experimentally more accessible than in horseshoe bats. The functional principles of an auditory fovea discovered in the moustached bat are assumed to apply with moderate modifications to all CF/FM bats (rhinolophids and hipposiderids).

A complete and precise cochlear frequency map in moustached bats (Fig. 6c) has been obtained on the basis of an inner hair cell frequency map produced by dye-labelling auditory neurons characterized by their best frequency (Kössl and Vater 1985).

The foveal frequency filter in the inner ear of the moustached bat is housed in the extended, large basal cochlear turn and consists of two parts (Fig. 6a): (1) a basal sparsely innervated (SI) zone characterized by structural specializations of the basilar and tectorial membrane. In the SI region the basilar membrane is tuned from 72 to 62 kHz. The frequency of about 62 kHz (CF<sub>2</sub> frequency), is represented at the transition of the SI zone to (2) an adjacent long section of the basilar membrane (CF<sub>2</sub> zone) where the narrow frequency band of the CF<sub>2</sub> echo and its glints induced by wing-beating insects are represented in a widely expanded way.

In the SI zone, the thickness of the basilar membrane is markedly increased by longitudinal fibres that provide mechanical coupling over its length. The tectorial membrane is also highly modified, and shows a beam-like structure (club-shaped in cross-sections) that may easily vibrate since it is only loosely attached to the spiral limbus. Both structural specializations in the basilar and tectorial membrane abruptly disappear at



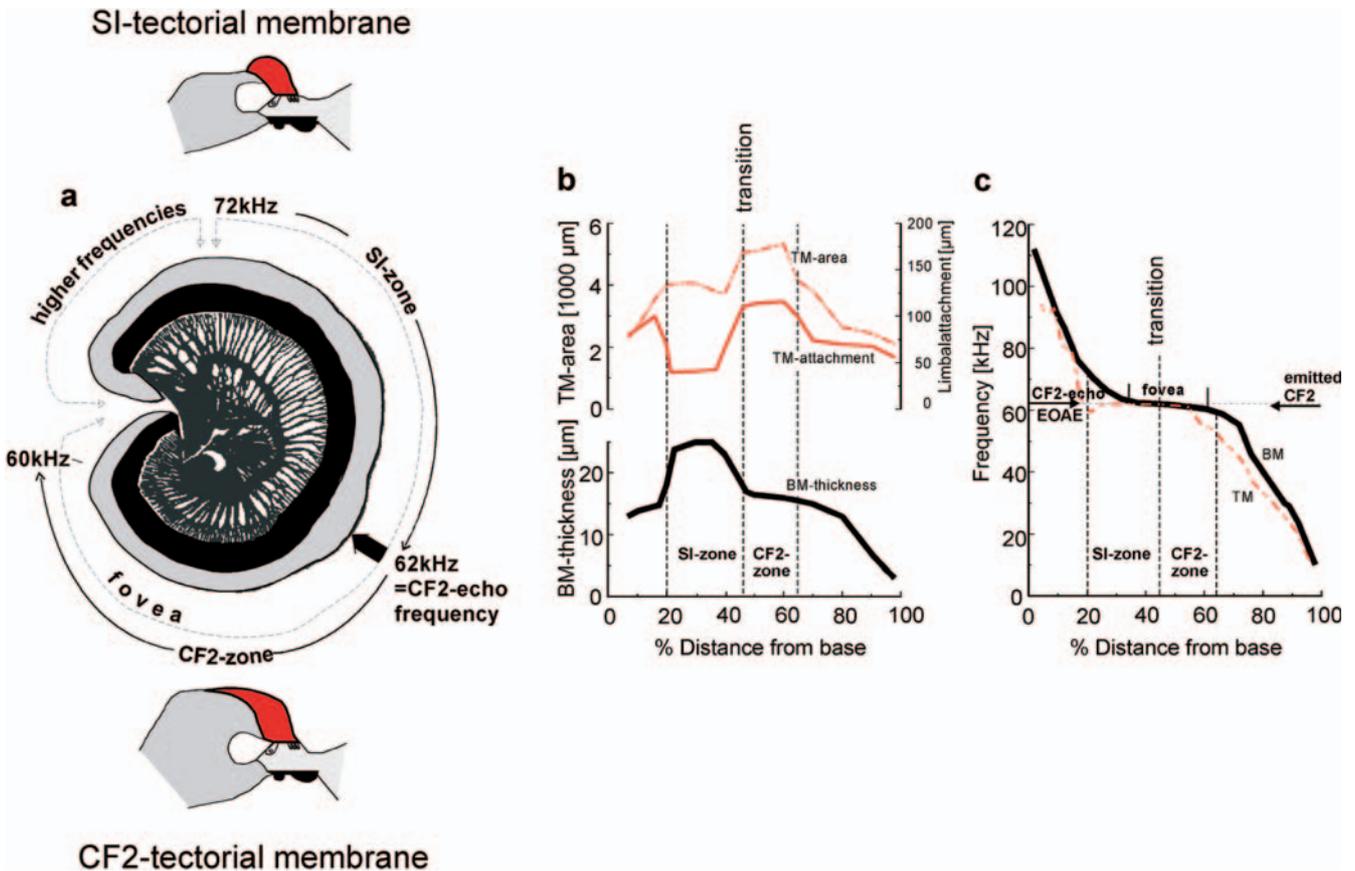
**Fig. 5** The auditory fovea filter in the moustached bat. The audiogram is derived from best thresholds of cochlear nucleus units. *EOAE*: the frequency at which an otoacoustic emission may be evoked or may occur spontaneously. *EOAE* frequency is identical with the frequency of the resonator in the cochlea. *EOAE* frequency is slightly different in each specimen. In the audiogram *EOAE* frequency is normalized to 62.0 kHz (*dotted line*). After Kössl (1994)

the transitory location between SI and CF<sub>2</sub> zones where CF<sub>2</sub> frequencies are represented.

**The frequency tuning of the tectorial membrane**

In all mammals, tectorial and basilar membrane are mechanically coupled by the hair bundles of the outer hair cells (OHCs) that slip into depressions of the tectorial underside. OHCs are electromechanical and amplifying transducers with a strong nonlinearity. It produces distortions that may show up as faint sounds emitted from the inner ear into the outer ear canal where they may be recorded as otoacoustic emissions (OAE). Distortion product otoacoustic emissions (DPOAE)

**Fig. 6a–c** Auditory fovea: the specialized basal turn of the cochlea in moustached bats. **a** A camera lucida drawing of the basal turn. *Dashed lines with arrows* demarcate the specialized zones SI (sparsely innervated) and CF<sub>2</sub> (fovea). *Grey band*: spiral ligament, *black band* basilar membrane; *radial fibres*: innervation of organ of Corti. **b** Structural specializations for a resonant system in the SI zone. Note the abrupt changes in thickness of basilar and tectorial membrane, and in the limbal attachment of the tectorial membrane at the transition between SI and CF<sub>2</sub> zones of the basal cochlear turn. **c** Frequency place map of the basilar membrane (BM) and tectorial membrane (TM) of the complete cochlea. Note the widely expanded representation (fovea) of the narrow frequency band around the CF<sub>2</sub> echolocation frequency which corresponds to that of the evoked or spontaneous otoacoustic emission (CF<sub>2</sub> echo, *EOAE*). From Russell and Kössl (1999)



occur when the ear is stimulated with two closely spaced frequencies  $f_1$  and  $f_2$ . The most pronounced distortion is  $2f_1 - f_2$ . DPOAEs are filtered by the tectorial membrane and, therefore, provide a convenient and noninvasive way of measuring the frequency characteristics of tectorial membranes (Kössl and Vater 1996b). In non-echolocating mammals and in non-specialized regions of the bat cochlea there is a mismatch of the mechanical tuning between basilar and tectorial membrane by about a quarter of an octave at each location (Kössl and Vater 1996b). It is assumed that this slight mismatch contributes to the sharpening of cochlear frequency filters by reducing low-frequency tails in the tuning curves.

DPOAE measurements in FM bats disclosed the same frequency-tuning pattern as in non-echolocating mammals. In CF/FM bats, however, DPOAE-recordings showed a functionally highly specialized tectorial membrane (Fig. 6b, c; Kössl and Vater 1996a). Throughout the SI zone of the cochlea in *P. parnellii* the tectorial membrane is only tuned to the frequency of the CF<sub>2</sub> echolocation sound around 62 kHz. This indicates that a specialized tectorial membrane resonance plays an integral role in enhancing cochlear tuning to CF<sub>2</sub> beyond values normally encountered in non-CF/FM bats and non-echolocating mammals.

### The cochlear resonator in the basal turn of CF/FM bats

This resonating system is also a source for very loud stimulus-evoked or even spontaneous OAEs that are restricted to the CF<sub>2</sub> frequency. In moustached bats OAEs can not be evoked by any other stimulus frequency. When driven by the resonator frequency, a standing wave is generated in the SI zone. The resonant CF<sub>2</sub> filter is also characterized by a minimal threshold and long lasting ringing of cochlear microphonics.

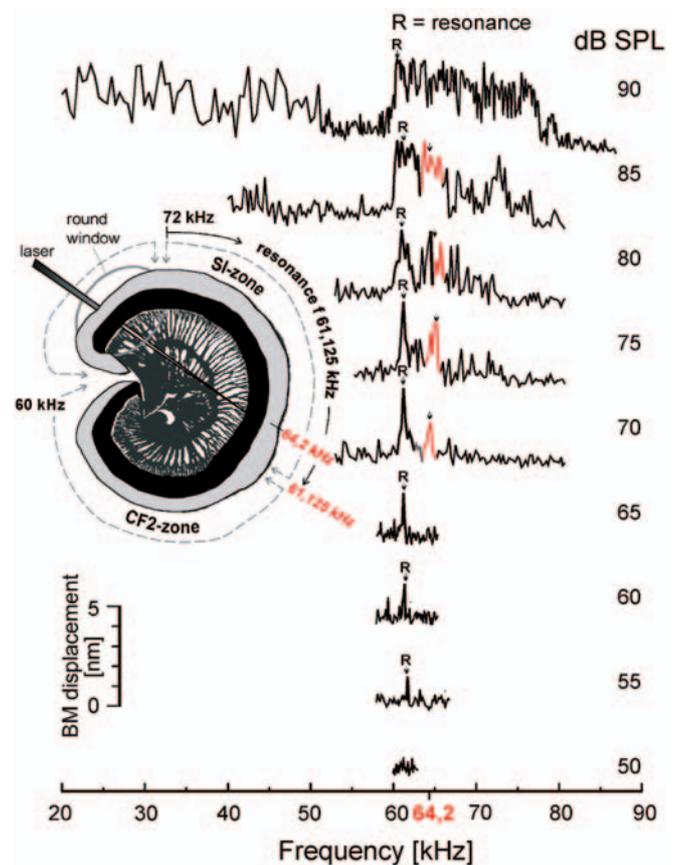
In the moustached bat, the frequency of spontaneous or stimulus-frequency-elicited OAEs is considered as the resonator frequency. In the auditory fovea this resonance frequency is situated about halfway in the very steep sensitivity slope from a high threshold peak at the low-frequency side of the foveal filter to the best frequency of the fovea (CF<sub>2</sub> echo frequency; Fig. 5). The frequency distance between maximal insensitivity and maximal sensitivity only amounts to 1 kHz or less. The insensitivity peak coincides with the so-called resting frequency around 61 kHz, that is the frequency of the CF<sub>2</sub> component emitted by a non-flying moustached bat. The best frequency of the fovea corresponds to the CF<sub>2</sub> echo frequency (Fig. 5) that flying moustached bats actively maintain by an audio-vocal feedback system (Doppler shift compensation) that eliminates Doppler shifts of the complete echo caused by the bats own flight speed. The closely spaced peaks of insensitivity and sensitivity are both considered to be generated by the resonating SI zone (see below).

If a tectorial resonance is the source for the extremely narrowly tuned auditory fovea, how does the SI region

operate with a basilar membrane tuned from 72 to 62 kHz and an overlaying tectorial membrane that only resonates at about 62 Hz?

Measurements of basilar membrane vibrations in the SI zone by noninvasive laser interferometry (Fig. 7; Russell and Kössl 1999) disclosed that (1) each location on the basilar membrane is indeed tuned to a characteristic frequency between 72 kHz at the base of SI zone and 62 kHz at the transition from SI to CF<sub>2</sub> zone; and (2) when the ear was acoustically stimulated by sounds of about 62 kHz the SI zone resonated over its full length.

These pioneering experiments show prove that the SI zone in the cochlea of the moustached bat acts as a resonator tuned to CF<sub>2</sub>. The resonator consists of a tectorial membrane as a driving element, and the longitudinal coupling of the mechanics of the basilar membrane. Both mechanical components are interconnected by the non-



**Fig. 7** Displacement measurements of the basilar membrane at a location where 64.2 kHz are represented in the moustached bat. Vibrations were recorded by laser interferometry in the intact cochlea through the round window while the ear was stimulated by tone pulses of frequencies from 20 to 90 kHz (*abscissa*) and sound levels indicated on the *right vertical axis*. When stimulated with the individual CF<sub>2</sub> frequency of the specimen (61.125 kHz) the 64.2-kHz place of the BM vibrates at even lower sound levels than by stimulations at the place frequency of 64.2 kHz. *R* resonant vibrations; *arrows only*: vibrations elicited by 64.2-kHz stimuli. This is strong evidence for the existence of a resonator tuned to the CF<sub>2</sub> echolocation signal in the SI zone (From Russell and Kössl (1999)

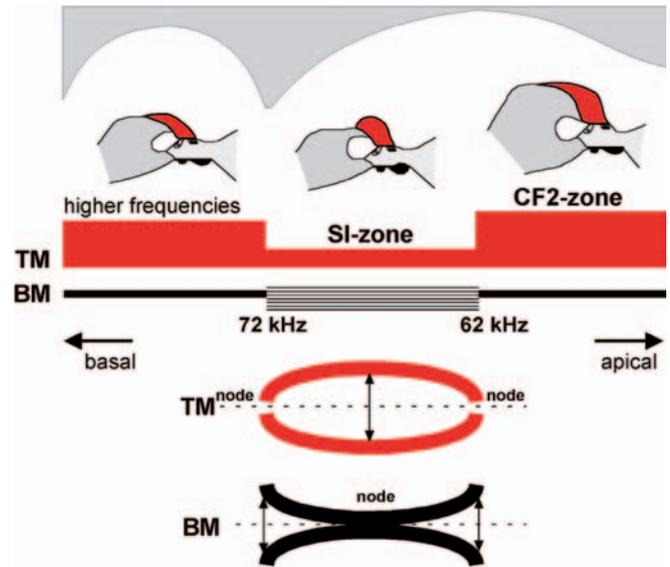
linear dynamics of OHCs. When OHCs are functionally eliminated, evoked OAE at the resonance frequency surprisingly increases in level or convert to spontaneous OAE (Faulstich and Kössl 1997; Kössl and Vater 2000). It seems that the OHCs exert dampening and stabilizing effects in order to prevent damages by an easily over-driven resonator.

The discovery of the resonator in the SI zone of the moustached bat's cochlea generates more problems than it solves:

1. Why is the row of IHCs in the SI region not excited when this complete cochlear section is vibrating at 62 kHz?
2. How can the resonator generate at the same time a closely spaced minimum and maximum of sensitivity?
3. How is resonant power fed into the adjacent CF<sub>2</sub> zone of the auditory fovea?

In order to answer such questions Russell and Kössl (1999) developed a model for the generation of standing wave resonance (Fig. 8). They view the tectorial and basilar membrane as longitudinally spanned strings. The tectorial membrane is fixed at the basal and apical ends of the SI zone (nodes in Fig. 8), whereas the basilar membrane acts as a sturdy string that may freely vibrate at the basal end of the SI zone and at the transition to the foveal CF<sub>2</sub> zone. These are the locations where the longitudinal fibres in the thick basilar membrane section terminate. The authors suggest that the standing wave at 62 kHz is generated by reflections at the two ends of the SI zone. Thus, the response of the cochlea to CF<sub>2</sub> echo components will be sharpened and stabilized by the standing wave resonance. The standing wave will create large cochlear pressure changes at the 62-kHz location of the cochlea, i.e. it will pump energy into the CF<sub>2</sub> zone where the narrow frequency band around 62 kHz is represented in a vastly expanded frequency map of high sensitivity.

It is assumed that the SI zone has two modes of vibration. First, when stimulated by a frequency of 62 kHz the tectorial membrane will strongly resonate and the resonant energy will be released more apically in the CF<sub>2</sub> zone. In the SI zone, due to the loose attachment of the tectorial membrane to the spiral limbus, tectorial and basilar membrane will vibrate together in the transverse plane as a single mass, and the vibration of the tectorial membrane enforces the same movements in the basilar membrane. Since both membranes move as a single entity, only minimal shearing of the sensory hair bundles between the two membranes will occur. Therefore, the inner hair cells of the SI region are not excited by 62 kHz. For frequencies a few hundred Hertz below the resonance frequency of 62 kHz, basilar and tectorial membrane are still locked in their movement and strong oscillations emerge. However the phase of the oscillation has shifted by 180° (as experimentally demonstrated) with the result that now the resonator is in antiphase to the input stimulus and absorbs acoustic energy similar to the situation in commercial mufflers used, e.g. in cars.



**Fig. 8** The Russell-Kössl model of a resonating system in the SI zone as a constituting element of the auditory fovea in the moustached bat. *Upper graph* shows the attachment of the TM to the spiral limbus in the different zones of the basal cochlear turn. *TM bars* symbolize the size of the attachment areas of the TM that is narrow in the SI zone. *BM bars* symbolize thickness of the BM that is thickened by longitudinal fibres in the SI zone. *Lower graph* shows the assumed vibration behaviour when both membranes in the SI zone resonate as a standing wave at 62 kHz. After Russell and Kössl (1999)

In the audiogram this results in a very narrowly tuned peak of insensitivity just below the CF<sub>2</sub> center frequency of the fovea-filter (Fig. 5). Actually, the narrowness of the foveal frequency filter is not owned to very low thresholds but to this insensitivity peak that results in an extremely steep slope at the low frequency side of the filter. Thus, the SI resonator generates a peak of insensitivity and at the same time a peak of sensitivity by pumping energy into the adjacent CF<sub>2</sub> zone of the cochlear basal turn.

2) When the SI zone is driven by other frequencies represented in the SI region (higher frequencies in Figs. 6 and 8) that do not initiate resonant vibrations of the complete tectorial membrane the SI region locally vibrates as a two-mass system in the radial plane as in all other regions of the cochlea and will shear the hair bundles of the hair cells.

These two modes of vibration plausibly explain why the IHCs of the SI zone are not excited by the 62-kHz resonance, yet correctly respond to stimulations at their best frequencies above 62 kHz up to 72 kHz.

It is assumed that this Russell-Kössl model of a cochlear resonator derived from experiments in *P. parnellii* may apply to all CF/FM bats. However, in horseshoe bats resonator-characteristics are not as distinct as in moustached bats: the OAE at the foveal frequency is far less intense, and ringing or the sensitivity peak of microphonics are far less pronounced. These differences might be due to a strong damping of reso-

nator systems in horseshoe bats (Henson et al. 1985; Kössl 1994).

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### Where do the resonators in the cochleae of CF/FM bats come from?

The literature states that in inner ears resonance must not occur. Where, then, do the unique resonators in the basal turns of CF/FM bats phylogenetically come from?

In the New World, *P. parnellii* is the only CF/FM bat so far known. A comparative study in three mormoopid species closely related to the moustached bats disclosed no structural or functional intermediate stages between FM echolocation in related species and the CF/FM system in the moustached bat (Kössl et al. 1999). The only distinct difference between them is the large basal turn of the cochlea with its mechanical specializations described above.

Molecular data suggest that the moustached bat only recently evolved about 4–9 million years ago (Kössl et al. 1999). In rhinolophids and hipposiderids CF/FM echolocation is phylogenetically much older, and this may be the reason why there are about 150 CF/FM species in the Old World and only one in the neotropics. In any case, the auditory foveae in *P. parnellii* and in horseshoe bats are one of the most striking examples of convergent evolution.

It challenges our imagination to conceive evolutionary driving forces initiating mechanical modifications that turned the basal turn of the cochlea not only into a place of high-frequency representation but also into a sharply tuned resonator. One idea postulates that the CF resonators are not the result of specific evolutionary driving forces but were “invented” by an accident which may consist of a change in ontogenetic programs controlling the development of the basilar and tectorial membranes and produce a strong mechanical discontinuity. The consequence could be abrupt changes in acoustical impedance, acoustical reflections and resonant oscillations which could produce a frequency-specific cochlear insensitivity. This speculation is based on a study of OAE-generating mechanisms in other mammals (Shera and Guinan 1999). OAEs are not only measurable in the form of distortion products but may be also elicited by distinct stimulus frequencies or they may even occur spontaneously. Spontaneous or frequency driven OAEs mainly result from reflections of travelling waves at acoustical impedance irregularities occurring haphazardly along the cochlear partition. Coherent reflections from such mechanical discontinuities in the cochlea may create narrow-band cochlear standing waves showing up as OAEs that are recordable in the ear canal. This applies to the resonator in *P. parnellii*: exactly such a very prominent and punctuate mechanical discontinuity at the transition from the SI to the CF<sub>2</sub> zone, and an intense standing wave are the hallmarks of the resonator in the basal cochlear turn of moustached bats.

According to this concept the prominent mechanical discontinuity and its resulting standing wave may have occurred accidentally in one of the forbears of CF/FM bats. The bats may have made the best of it by implementing into their echolocation system the accidental sharp-frequency filtering that results from the resonating wave. In this case, function would follow structure and the bats would have added a CF component to their echolocation call with a frequency defined by the auditory foveal frequency. Vocalization would adapt to an auditory “accident”.

If this scenario were correct, this would be a remarkable process in which an accidental non-functional mishap would be turned into an evolutionary beneficial and highly sophisticated specialization.

In whatever way the auditory foveae with its narrow frequency filtering may have evolved, the cochlear resonators have made CF/FM bats specialists for detecting fluttering targets. In a highly cluttering environment this specialization may be an advantage. However, such sophisticated specializations are evolutionary deadlocks. If, for instance, dense vegetations disappear, the advantage of fluttering target detection disappears as well, and species that predominantly rely on fluttering target detection by CF/FM echolocation may become extinct. Even without anthropogenic impact ecosystems and ecological niches change continuously. Hence, species with sophisticated adaptations to specific niches will disappear and new species answering to new challenges will evolve. As long as there is time enough for newly evolving species to adapt to new environments the turnover of specialized species is a natural process and a driving force of biodiversity. Obviously, specialized animals naturally have a limited time of existence.

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