J Comp Physiol A (1990) 166:711–720

Journal of Comparative Physiology A Sensory, Neural, and Behavioral Physiology

Resonance phenomena in the cochlea of the mustache bat and their contribution to neuronal response characteristics in the cochlear nucleus

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Accepted October, 10, 1989

Summary. The cochlea of the mustache bat, *Pteronotus parnellii*, is very sensitive and sharply tuned to the frequency range of the dominant second harmonic of the echolocation call around 61 kHz. About 900 Hz above this frequency the cochlear microphonic potential (CM) reaches its maximum amplitude and lowest threshold. At exactly the same frequency, pronounced evoked otoacoustic emissions (OAE) can be measured in the outer ear canal, indicating mechanical resonance. The CM amplitude maximum and the OAE are most severely masked by simultaneous exposure to tones within the range from about 61–62 kHz up to about 70 kHz. The data suggest that the mechanism of mechanical resonance involves cochlear loci basal to the 61 kHz position.

The resonance contributes to auditory sensitivity and sharp tuning: At the frequency of the OAE, single unit responses in the cochlear nucleus have the lowest thresholds. Maximum tuning sharpness occurs at frequencies about 300 Hz below the OAE-frequency, where the threshold is about 10 dB less sensitive than at the OAE-frequency. In addition, in the frequency range around the OAE-frequency several specialized neuronal response features can be related to mechanical resonance: Long lasting excitation after the end of the stimulus, asymmetrical tuning curves with a shallow high frequency slope and phasic 'on-off' neuronal response patterns. In particular the latter phenomenon indicates the occurrence of local mechanical cancellations in the cochlea.

Key words: Mustache bat – *Pteronotus parnellii* – Cochlea – Resonance phenomena

Abbreviations: *CF* constant frequency component of echolocation calls; *CM* cochlear microphonic potential; *FM* frequency modulated component of echolocation calls; *N1* compound action potential of the auditory nerve; *OAE* octoacoustic emission; *SEOAE:* synchronous evoked OAE

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Introduction

The mustache bat, *Pteronotus parnellii* uses echolocation for environmental imaging and for detecting insects. Nearly all of the information that is important for imaging the surroundings is coded in the echoes of the emitted calls which consist of a long constant frequency (CF) component followed by a downward frequency modulated (FM) component. The call is composed of 4 harmonics with the most intense second harmonic CF_2 component at about 61 kHz (Suga 1984). Measurements of cochlear microphonic potentials (CM) and of the compound action potential of the auditory nerve (N1) reveal sharp absolute threshold minima in the 60 kHz range (Pollak et al. 1972; Suga et al. 1975; Pollak et al. 1979) and indicate that the cochlea is especially designed for an optimized perception of a narrow frequency band important for echolocation. This specialization provides an opportunity to study cochlear mechanisms for high sensitivity and sharp tuning in their most highly developed form. At about 61 kHz the CM responses of *Pteronotus* show oscillations lasting several ms after the end of the stimulus, indicating a relatively undamped resonance system (Suga et al. 1975; Suga and Jen 1977). This is corroborated by the presence of pronounced otoacoustic emissions (OAEs) close to 61 kHz in *Pteronotus* which are of higher amplitude than in any other mammal (Henson et al. 1985; Kössl and Vater 1985a). A mechanical resonator in the cochlea is the most likely origin of these events. In the cochlea, there are hydromechanical specializations at, and basal to, the representation of 61 kHz, which could participate in the creation of cochlear reflections and reverberating mechanical oscillations (Kössl and Vater 1985a, b). Close to 61 kHz the evoked neural potentials show pronounced off-components (Grinnell 1970; Pollak et al. 1979), and single unit responses are found in the cochlear nucleus consisting of phasic activity at the onset and the offset of the tone stimulus (Suga et al. 1975). As suggested by Suga et al. (1975), these on-off responses most probably are

caused by mechanical suppression and release of suppression in the cochlea. The present study compares the cochlear phenomena of CM, OAE and N1 in single subjects and relates them to properties of neurons in the cochlear nucleus, the first synaptic relay in the ascending auditory system in order to assess how peripheral auditory processing is influenced by cochlear resonance.

Materials and methods

Sixteen mustache bats, *Pteronotus parnellii*, captured in Jamaica were used for neurophysiological recordings. Prior to each experiment the constant frequency component of the second harmonic (CF_2) was measured in the nonflying animal. This frequency is referred to as resting frequency. The resting frequency was measured with a frequency to voltage converter (100 Hz resolution, 20 to 40 individual calls) and was in all cases below the OAE-frequency. Shortly after each measurement of the resting frequency (10 to 20 min later) OAEs were recorded according to the methods described in Kössl and Vater (1985a). The evoking stimulus was a continuous tone generated by a HP 3594A oscillator and delivered with a condenser loudspeaker. The frequency of the stimulus was shifted upwards with a rate of 100 Hz/s. A microphone adapted to the outer ear canal measured the frequency response which was further analyzed by a HP 3590A wave analyzer with a frequency resolution of 10 Hz. The OAE could be recognized by characteristic interference patterns in the frequency response which are due to interactions of the incoming stimulus with the outgoing otoacoustic emission at a specific frequency range. Otoacoustic emissions measured in this way are termed synchronous evoked OAE (SEOAE). Recordings of cochlear potentials, anaesthesia and surgical procedures followed previously published protocols (Henson et al. 1985; Kössl and Vater 1985a). Cochlear microphonic potentials and N1 (compound action potentials of the auditory nerve) were measured with a glass-insulated tungsten electrode introduced into the cochlea via the cochlear aqueduct (Henson and Pollak 1972). Immediately after recording a stable CM, the electrode was advanced no further to prevent damage to the cochlea. Then the electrode was chronically implanted. To determine the thresholds of CM and N1 potentials, short tone pulses of 10 ms duration with 0.1 ms rise-fall times were used. Acoustic stimuli were delivered with a condenser loudspeaker located at a distance of 15 cm from the ipsilateral ear at optimal azimuth angle. The recorded responses were highpass filtered (cutoff frequency; 10 kHz) to obtain CM potentials, and bandpass filtered (100 Hz – 5 kHz) to yield N1 potentials. The signals were digitized and averaged over 32 presentations using a PDP 11/23 computer. Cochlear potentials and otoacoustic emissions could be measured in the same animal for up to 7 weeks.

In 14 bats, single and multi unit activity in the cochlear nucleus was recorded in systematic series of penetrations using glasspipettes filled with 1.5 to 3 *M* KCl (impedance 4 to 10 MΩ). The cochlear nucleus was approached through the cerebellum according to stereotactic coordinates (Feng and Vater 1985; Kössl and Vater 1985b). In each animal the location of the recording site was marked by an injection of HRP, or by electrolytic lesions (2–3 μA per 2–5 min). Further data specifying the HRP-injection sites, resting frequency and OAE-frequency of the individual bats are given in Kössl and Vater (1990, Table 1). During neurophysiological recordings pure tone stimuli of 20 to 30 ms duration were used with rise-fall times of 1 ms. The neuronal responses were averaged over 40 presentations and post-stimulus-time (PST) histograms were constructed using a bin width of 200 μs. Both the measurement of cochlear potentials and recordings in the cochlear nucleus were obtained from awake animals one or more days after recovery from surgery with wounds locally anaesthetized with lidocaine.

Results

Evidence for specialized mechanical processing in the cochlea

In order to compare CM, N1-potentials and OAEs, it was essential to record all of these phenomena in the same specimen. Pooling data across different individuals is complicated by the fact, that different bats have slightly different echolocation and OAE-frequencies. Measurements of CM- and OAE-amplitudes were taken in short succession (within 10 s) to avoid frequency shifts in the same animal.

The cochlea of *Pteronotus* produces one strong OAE with a frequency close to 61 kHz. A characteristic set of OAE response curves (recorded as synchronous evoked OAE) is given in the upper part of Fig. 1. Interference between the incoming sound and the evoked emission resulted in a maximum of sound pressure level followed by a sharp minimum. At an input stimulus level of about 50 dB SPL the maximum was located at 61.75 kHz, the minimum at 61.92 kHz. The inflexion point, i.e. the point of maximal slope between maximum and minimum of the interference pattern at 61.80 kHz will be defined as the OAE-frequency. CM-measurements in the same bat using the same succession of stimulus levels (lower part of Fig. 1) show that the OAE-frequency is identical with the frequency that evokes a distinct maximum in CM-amplitude. The frequency of the OAEs, evoked by a stimulus level of 50 dB SPL, was on the average (14 bats) 61.45 ± 0.72 kHz and was 880 ± 400 Hz above the individual resting frequencies. The decrease in the depth of the interference maxima and minima with increasing stimulus level (Fig. 1) indicates a saturation at emission levels of about 70 dB SPL, which occurs at input stimulus levels around 80 dB SPL, as shown by Kössl and Vater (1985a). OAEs and the CM-maximum had a similar saturation behaviour and shifted to lower frequencies with increasing stimulus level. The frequencies of the OAE and CM-maximum were identical, and remained constant, in a given individual, for the measuring period of 2 to 7 weeks in each of 3 animals which were studied in detail.

To gain information about the mechanisms by which the OAE and the sharply tuned CM-amplitude maximum are generated, in a single animal a continuous pure tone was used as a masking stimulus and applied simultaneously to the stimulus which evoked OAE and CM (Fig. 2). The CM-maximum and the amplitude of the OAE, derived from the depth of the interference patterns (Kössl and Vater 1985a), were attenuated by masker frequencies between 60 and 74 kHz. The strongest attenuation was seen with maskers at the OAE-frequency (61.80 kHz) and also between 66 and 70 kHz, indicating that the cochlear locations representing 66–70 kHz participate in the generation of the OAE.

The threshold curves for the CM and the N1-potential shown in Fig. 3 were obtained in the same animal

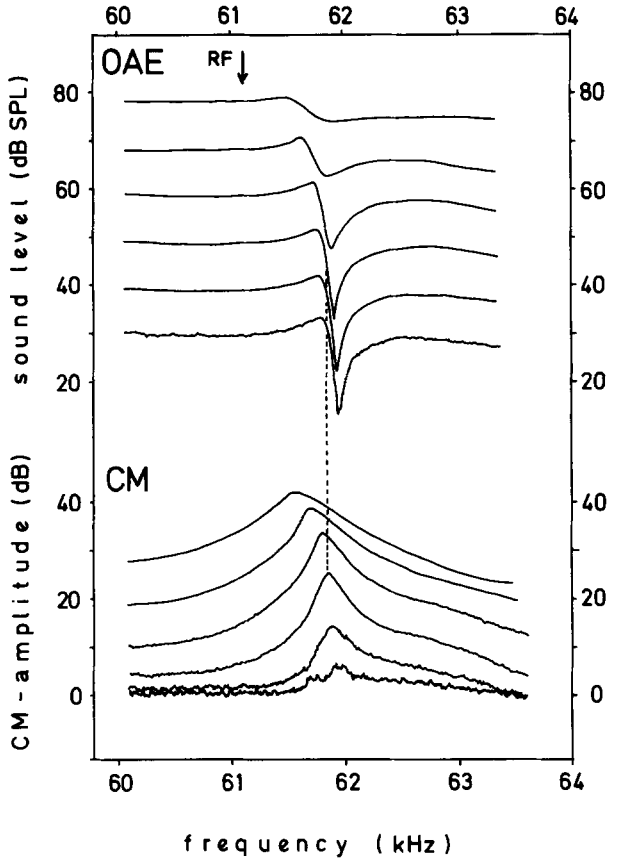

Fig. 1. Otoacoustic emissions and CM-amplitude versus frequency curves recorded from a single individual using stimulus levels between 30 dB SPL (lowest traces) and 80 dB SPL (highest traces). *Upper part:* otoacoustic emissions were measured as synchronous evoked otoacoustic emissions (SEOAE). Due to interference between the continuous tone stimulus and the cochlear emission, a maximum and minimum in the sound level are visible about 700 Hz above the resting frequency (RF). With stimulus levels above 60 dB SPL, the maxima and minima decrease which indicates a saturation of the emission. *Lower part:* The corresponding measurements of CM-amplitude, using the same stimuli as above, show a distinct maximum at a frequency coinciding with the inflexion point of the SEOAE interference pattern

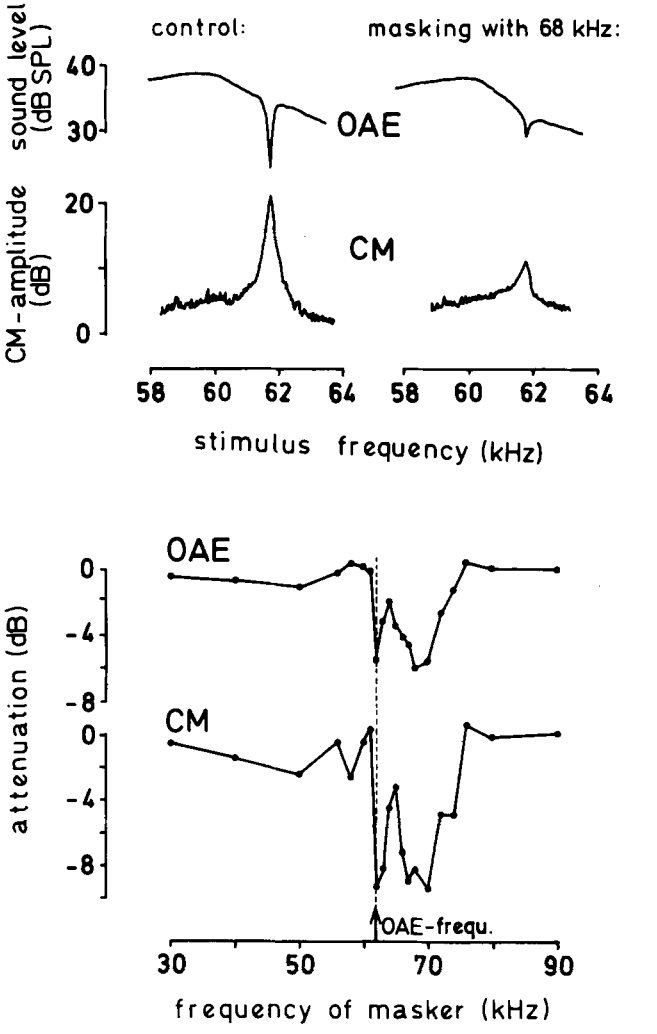

Fig. 2. Measurements of the CM-amplitude and OAE-levels during simultaneous exposure to acoustic maskers. *Upper part:* masking with a continuous pure tone at 68 kHz, 50 dB SPL, diminishes both the OAE and the CM-maximum elicited by a stimulus of 35 dB SPL. *Lower part:* Frequency specificity of masking effects: the masker frequencies most effective in suppressing CMs and OAE are those at 62 kHz and between 66 and 70 kHz

at the same time and could be reproduced at 3 consecutive days. The frequency of both the OAE and the maximum of CM amplitude coincided exactly with that of the absolute minimum of the CM threshold at 61.80 kHz. In *Pteronotus* the N1-potential consists of an on-component and a substantial off-component both of which occur over narrow frequency bands (Grinnell 1970; Suga et al. 1975; Suga and Jen 1977; Pollak et al. 1979). In contrast to the minimum threshold of the CM, the N1-on threshold showed an absolute minimum at 64 kHz about 2.2 kHz above the frequency of the OAE. The N1-off threshold curve showed pronounced minima at about 30, 60, and 90 kHz, and an insensitivity at 70 kHz. The absolute minimum was located at 61.3 kHz and the high frequency slope was very steep. At the OAE-frequency of 61.80 kHz the N1-off threshold is already more than 20 dB above its minimum value.

Best frequencies and tuning characteristic of neurons in the cochlear nucleus

Single unit recordings were obtained from the anteroventral cochlear nucleus and the adjacent marginal cell group (total number of units: 698). In the anteroventral cochlear nucleus inhibitory interactions are less pronounced than in the dorsal CN (cat: Evans and Nelson 1973a, b) and therefore the neurons were expected to reflect properties of auditory nerve fibers relatively unaltered. Most of the units had primary-like responses similar to auditory nerve fiber activity and their temporal response patterns are described by Kössl and Vater (1990). We will present mainly the extensive single unit recordings obtained in one bat (151 units; resting frequency: 61.4 kHz; OAE: 61.90 kHz) which are representative for the data from the other 13 animals.

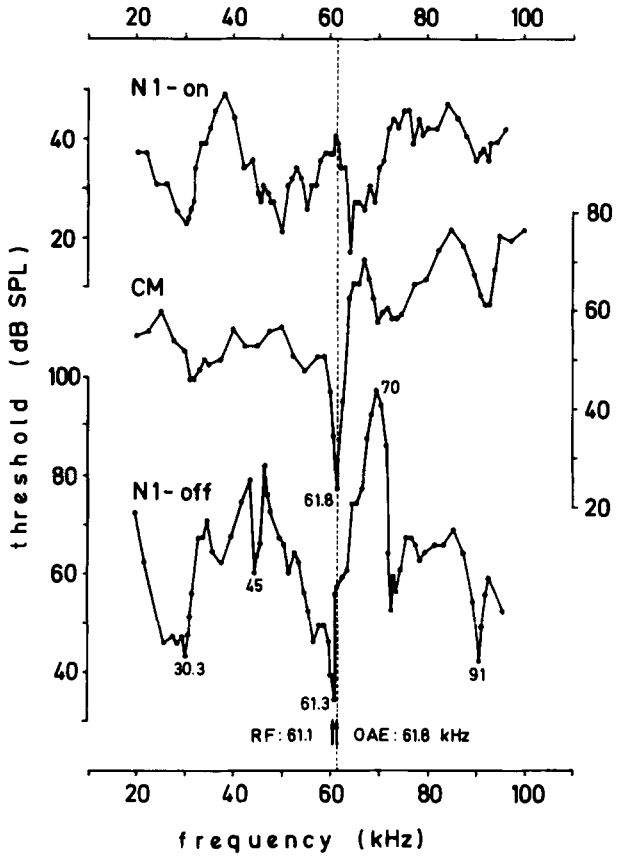

Fig. 3. Threshold curves for N1-on, N1-off, and CM-potentials. The absolute minima of all 3 curves are located above the resting frequency (RF): the N1-off minimum is only 200 Hz above the RF, the CM-minimum about 700 Hz above the RF, and the N1-on minimum about 2.2 kHz above the RF. The N1-off threshold curve shows distinct relative minima at 30.3, 45 and 90 kHz and an absolute maximum at 70 kHz

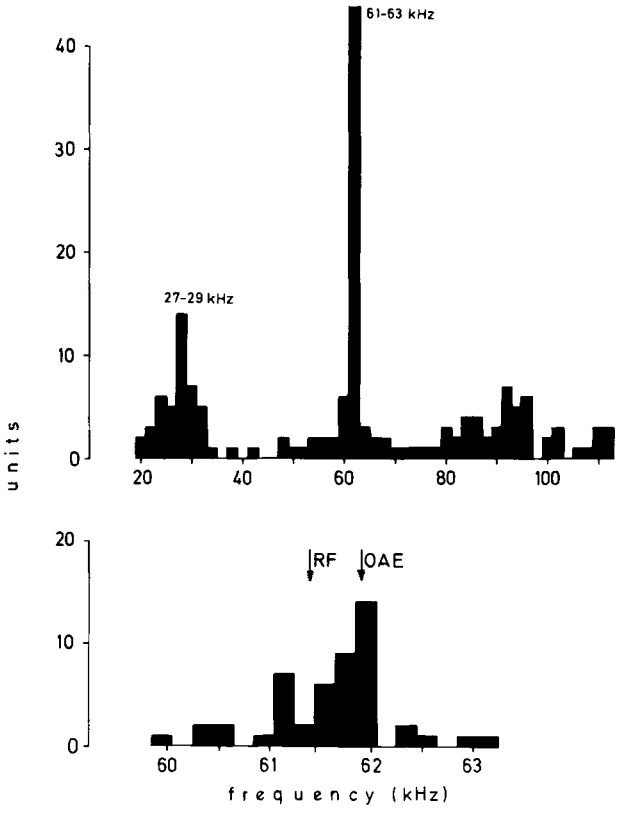

Fig. 4. Distribution of best frequencies of 151 single neurons obtained in the anteroventral CN and the marginal cell group of one animal. Most neurons are tuned to a narrow frequency range close to the frequency of the otoacoustic emission (OAE). The upper graph shows the entire range of frequencies tested; in the lower graph the frequency range between 60–63 kHz is expanded to show the details of the distribution relative to resting frequency (RF) and OAE-frequency

The best frequencies of single units (defined by the frequency of the lowest response threshold) ranged from 19 to 113 kHz (7.7–116 kHz for the total population of neurons recorded in 14 bats). Approximately 30% of the neurons responded best to frequencies within a frequency range between 61 and 63 kHz (Fig. 4). In addition to this overrepresented range, units with best frequencies between 20–34 kHz and 90–97 kHz were encountered in relatively larger numbers than those of intermediate frequencies. The lower part of Fig. 4 shows that, for neurons responding within the 60 kHz range, most of the best frequencies lay above the resting frequency close to the OAE-frequency. This result is corroborated by the distribution of best frequencies in the range of the resting frequency derived from 362 neurons pooled over all experiments (Fig. 5). The best frequencies were normalized either to the individual's resting frequency (left) or its OAE-frequency (right). The correlation with the OAE-frequency is better as indicated by the presence of a sharp maximum in the corresponding distribution histogram. The distribution maxima were 350 Hz above the resting frequency (Fig. 5, left) and 50 Hz below the OAE-frequency (Fig. 5, right).

The most sensitive neurons with thresholds close to 0 dB SPL, had best frequencies close to the frequency of the OAE at 61.90 kHz (Figs. 6, 7). In addition relatively sensitive neurons with thresholds below 20 dB SPL had best frequencies at 19–25 kHz, 40–50 kHz, 82 kHz, and between 93–97 kHz. At frequencies slightly below the CF_2- and CF_3-range, the thresholds were elevated considerably. These bands of insensitivity are about 5 to 7 kHz wide and the thresholds are elevated by 20 to 30 dB. The sample of neurons with best frequencies slightly above 30 kHz (CF_1-range) was too small to clearly demonstrate a similar relation between an insensitivity band and an adjacent high sensitivity area for the first harmonic frequencies.

The sharpness of the tuning curve is characterized by the $Q_{10\,dB}$ value which is the quotient of best frequency divided by the width of the tuning curve 10 dB above the minimum threshold. Neurons in two narrow frequency bands, namely 60.4–62.1 kHz and 90.4–

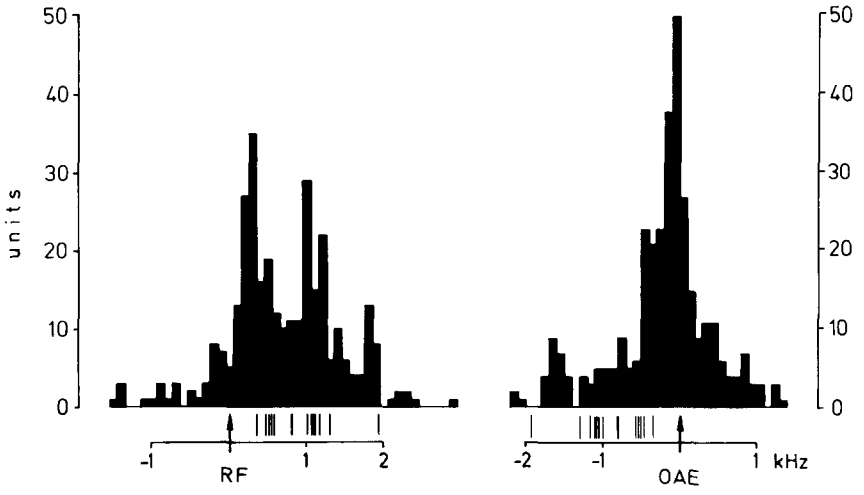

Fig. 5. Distribution of best frequencies of 362 neurons tuned to the range of the resting frequency (RF) and OAE-frequency, representing pooled data from 14 animals. The BFs were normalized to the RF (left) and the OAE-frequency (right) of the individual bats. The vertical bars below the histograms indicate the frequencies of individual OAEs (left) and RFs (right). The maximum peaks are either 350 Hz above the RF (left) or 50 Hz below the OAE (right). Normalization to the OAE produces a tighter distribution peak

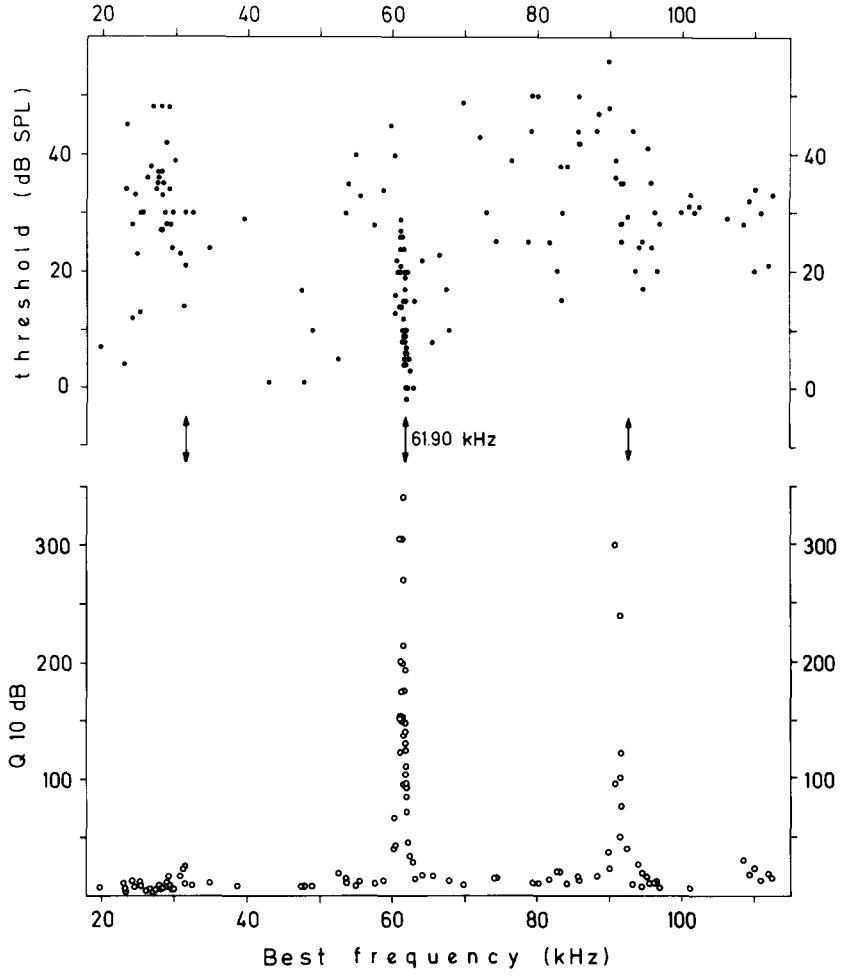

Fig. 6. Distribution of minimal thresholds (upper part, filled circles) and $Q_{10\,dB}$ values (lower part, open circles) of single CN-neurons of one animal for the entire frequency range tested; frequency of the OAE was at 61.90 kHz

92.0 kHz, which correspond closely to the CF_2- and CF_3-range, respectively, were most sharply tuned with $Q_{10\,dB}$ values between 50 and 340 (Fig. 6, lower graph). In the CF_1 frequency range, the maximum $Q_{10\,dB}$ values were about 35. This is not a significantly elevated $Q_{10\,dB}$ value such as is found at the $CF_{2,3}$ frequencies but it is within the range found by Suga and colleagues (Suga et al. 1975: 30, 44; Suga and Jen 1977: 50). Maximum sharpness of tuning did not exactly coincide with maximum sensitivity: the most sharply tuned CF_2 neurons, with $Q_{10\,dB}$ values above 250, had best frequencies between 61.20 and 61.75 kHz (maximum at 61.65 kHz).

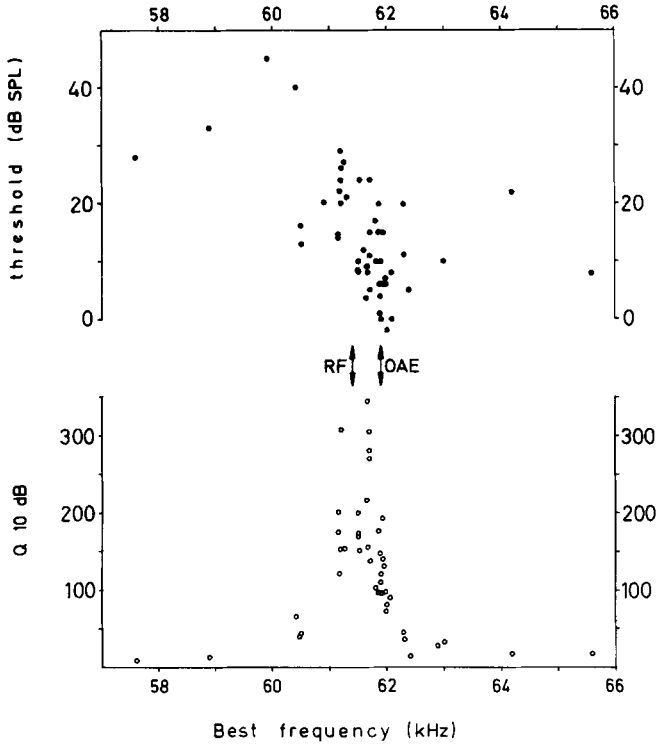

Fig. 7. Expanded plot of the distributions of minimal thresholds (upper part) and $Q_{10\,dB}$ values (lower part) of single neurons tuned to frequencies between 56–66 kHz. The best frequencies of the most sensitive neurons are at or slightly above the OAE-frequency (61.90 kHz), whereas the most sharply tuned neurons with highest $Q_{10\,dB}$ values have best frequencies below the OAE-frequency

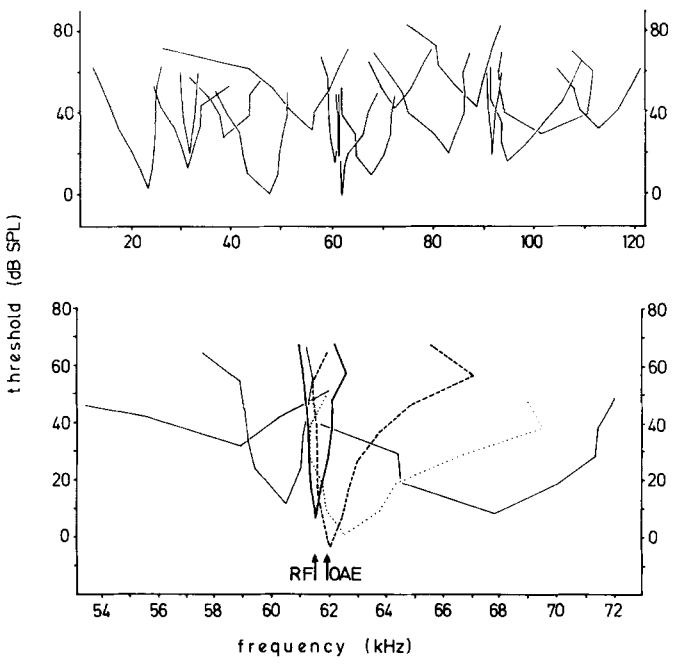

Fig. 8. Tuning curves of single neurons throughout the entire frequency range (upper part). Tuning curves for the 60 kHz range are depicted on an expanded frequency scale (lower part). Below the OAE-frequency, i.e. close to the resting frequency (RF), the tuning curves are symmetrical, at and above the OAE-frequency the high frequency slopes are more shallow, below the RF the low frequency slopes are more shallow

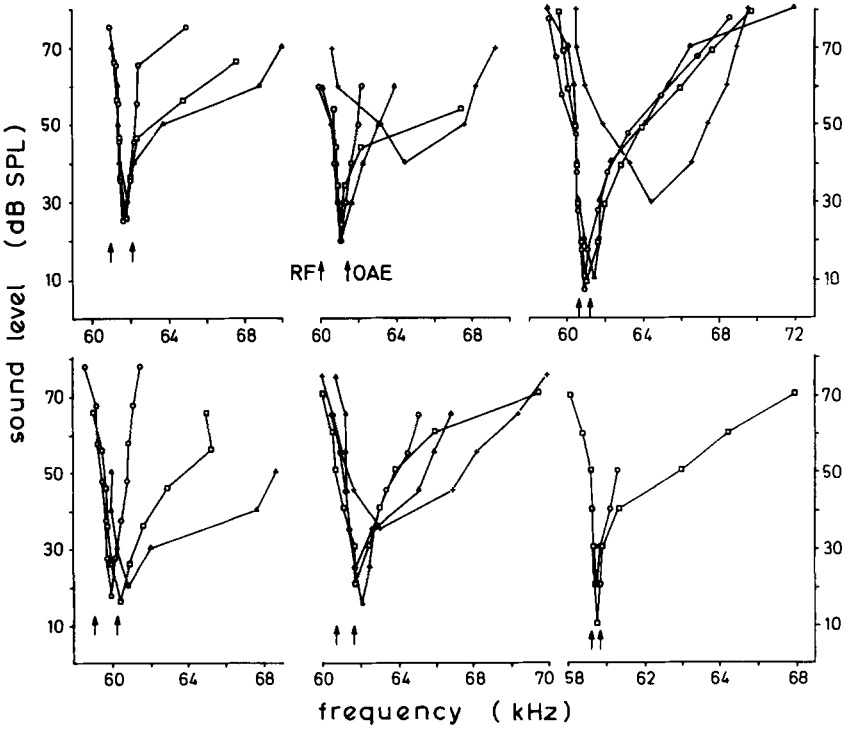

Fig. 9. Examples of symmetrical tuning curves and tuning curves with shallow high frequency slopes in six animals

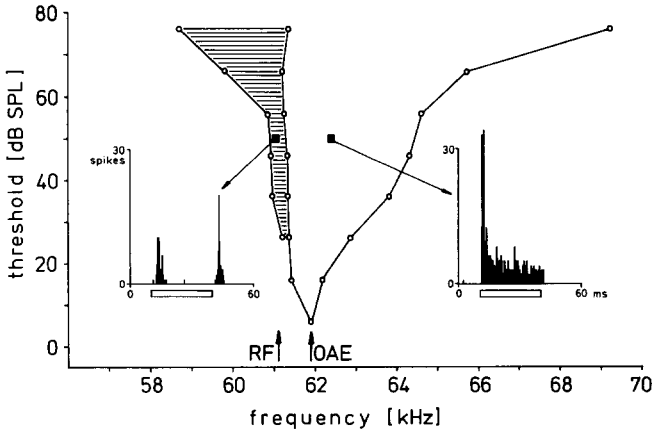

Fig. 10. Tuning curve and post stimulus time (PST) histograms from a neuron with on-off response properties: around the bat's resting frequency (RF), the neuron only responds to the stimulus onset and offset (hatched area of the tuning curve) whereas at higher frequencies the off response diappears and tonic activity during the stimulus occurs. PST-histograms were constructed from 40 stimulus presentations with bin width of 200 μsec

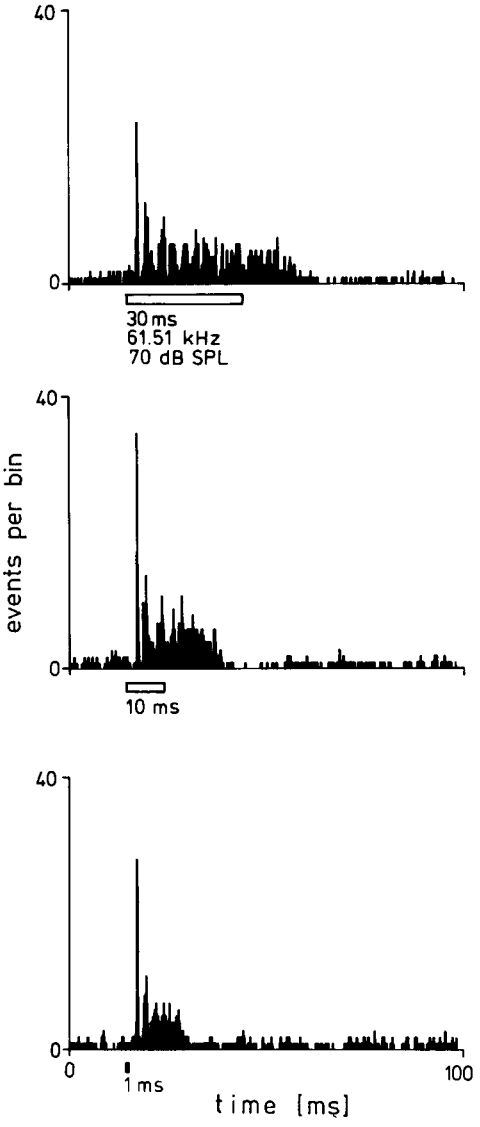

Fig. 11. Response pattern of a neuron tuned to 61.87 kHz (OAE-frequency: 61.85 kHz) over 3 different stimulus durations. Note the long lasting discharge activity after the end of each stimulus. The duration of this after-discharge is nearly independent of stimulus duration

Their thresholds were about 10 dB above the thresholds of the most sensitive units which had best frequencies between 61.85 and 62.9 kHz (Fig. 7). The best frequencies of the most sensitive neurons coincided exactly with the OAE-frequency (61.90 kHz) or were slightly higher. The resting frequency (61.4 kHz) was located at the low frequency slope of the minimum of the hearing curve whose contour is given by the distribution of best frequencies. The resting frequency lay within the range of best frequencies of the most sharply tuned neurons.

A similar situation exists in the CF_3-frequency range: The most sharply tuned units had best frequencies between 90.7–91.6 kHz whereas the most sensitive units lay above between 93 and 97 kHz (Fig. 6).

As reported for units in the anteroventral cochlear nucleus of other mammals, the tuning curves in the anteroventral CN of *Pteronotus* are either symmetrical or asymmetrical with a steep high frequency slope (Fig. 8, upper part). In addition to these types, units with best frequencies in the CF_2- and CF_3-frequency range exhibit tuning curves that were asymmetric in the reverse direction, i.e. they had a steep slope towards lower frequencies and a shallows slope towards higher frequencies. Figure 8 (lower part) illustrates that very narrow symmetrical tuning curves similar to those reported in detail by Suga and Jen (1977) were found for best frequencies within the range of highest $Q_{10\,dB}$ values between 61.0 and 61.8 kHz whereas at higher frequencies between 61.85 and 64 kHz the tuning curves had shallower high frequency slopes. Figure 9 shows examples of both types of tuning curves measured in 6 animals. Neurons with a BF of about 61.90 kHz (OAE-frequency) were often relatively sharply tuned near the threshold ($Q_{10\,dB}$ values between 50 and 200) but at higher intensities the tuning curve widened towards high frequencies (Figs. 8, 9, 11).

Specialized temporal response patterns of neurons tuned to the 60 kHz range

The temporal response patterns of single units in the anteroventral cochlear nucleus are similar to other mammals as shown by Kössl and Vater (1990). Systematic frequency dependent changes in temporal response patterns within the excitatory tuning area occurred in neurons with BFs close to the range of the 2nd harmonic CF-component of the orientation calls. There is a narrow frequency range close to 60 kHz where the temporal response patterns of single units show distinct on and off responses as reported in detail by Suga et al. (1975). Figure 10 demonstrates that the primary like response pattern (see below) of a single unit abruptly changed into an on-off type of response when the stimulus fre-

quency was decreased beyond 61.4 kHz. In 4 individual bats the relation to the on-off range to resting frequency and OAE was studied thoroughly (27 units). In all cases the on-off range was centered at about the resting frequency and nearly independent of the stimulus intensity a relatively sudden change from on-off to primary like responses occurred about 200 Hz above the resting frequency (Fig. 10). The low frequency boundary of the on-off range decreased from about 60.8 kHz at 30 dB SPL to 58 kHz at 80 dB SPL.

A second type of specialized response pattern in units with a best frequency close to the OAE frequency is characterized by long lasting excitation after the end of the stimulus (19 units). This excitation maximally lasted for about 10 to 15 ms and was nearly independent of the stimulus duration (Fig. 11, best frequency of 61.87 kHz). The on-off area ranged from 60.5 to 61.3 kHz (comprising the resting frequency of 61.1 kHz) at 40 dB above threshold, while the area of the long lasting excitation was at slightly higher frequencies, ranging from 61.3 to 62.0 kHz (comprising the OAE-frequency of 61.85 kHz). These after-discharges could be a direct neuronal correlate of the pronounced oscillatory phenomena in CM and OAE after the offset of a tone at the OAE frequency (Kössl and Vater 1985a). Support for this idea comes from the fact that the neuron in Fig. 11 shows chopper activity at the begin of the tone evoked response. CM-measurements show strong beats in the response if the stimulus frequency and the frequency of resonance oscillations do not exactly coincide and interferences between both occur (Suga and Jen 1977) with the beat frequency corresponding to the difference between the two frequencies. In the neuron in Fig. 11, six conspicuous response peaks occur within the first 17 ms of the response duration. This corresponds to a chopping frequency of 353 Hz which closely matches the difference of 340 Hz between stimulus frequency and OAE frequency.

Discussion

Cochlear resonance is related to otoacoustic emissions and could be produced by reflections in the cochlea

Evoked OAE in the cochlea of *Pteronotus* are characterized by a sharp tuning and high intensity. After short tone stimuli the OAE show a distinct and slow temporal decay (Kössl and Vater 1985a) comparable to CM-oscillations at the same frequency which first suggested the existence of resonance mechanisms in the cochlea of *Pteronotus* (Suga et al. 1975; Suga and Jen 1977). The maximum amplitude of the CM occurs at the OAE frequency. In the following this frequency will be referred to as 'resonance frequency'. CMs, as the extracellular correlate of the receptor potentials of the outer hair cells (Davis 1965; Dallos 1981; Russell 1983), are expected to be directly induced by the mechanical events leading to the emission of OAE. Other evidence for the close relation between CMs and OAE is their identical masking and saturation behaviour.

The generation of the resonance oscillations responsible for the OAE and the pronounced maximum of CM amplitude appears to involve cochlear structures located basal to the cochlear place that represents the OAE frequency. This is indicated by the high susceptibility of OAE and CM to pure tone maskers of frequencies between 62 and 70 kHz, both in forward masking (Kössl and Vater 1985a) and simultaneous masking procedures (Fig. 2). As discussed in Kössl and Vater (1985a), mechanisms that generate the OAE in *Pteronotus* can include active processes dependent on metabolic energy as well as passive reflections at discontinuities in cochlear structure that cause a local change in acoustic impedance. The present discussion will focus on passive mechanical mechanisms. Reflected mechanical waves would reverberate between the morphological discontinuity and the oval window. Possible reflection zones are probably provided by sharp discontinuities in the thickness of the basilar membrane and the diameter of the scala vestibuli located in the basal turn of the cochlea at frequency loci between 60 and 70 kHz (Henson et al. 1977; Kössl and Vater 1985b). A similar mechanism has been proposed for the horseshoe bat cochlea (Duifhuis and Vater 1985).

Relation between otoacoustic emissions and high sensitivity and sharp tuning

The best frequencies of the most sensitive single units in the 60 kHz range correlate with the frequency of the OAE. This implies that phenomena leading to OAE improve cochlear sensitivity to certain frequencies. A similar correlation was found between the frequencies of human OAE and local minima in the auditory threshold (Zwicker and Schloth 1984). Around such local threshold minima the human capability of frequency differentiation is increased (Thomas 1975; Kemp 1979) which could ensue from a locally increased sharpness of tuning in the cochlea. In *Pteronotus* the most sharply tuned neurons have best frequencies close to, but not exactly at the OAE frequency. Such neurons with $Q_{10\,dB}$ values above 200 have best frequencies about 300 Hz below the resonance frequency and are about 10 dB less sensitive than the neurons with the lowest thresholds. The steep slopes of their tuning curves could be created by wave cancellations between resonance oscillations and the input stimulus if both are out of phase. Measurements of CMs (Henson et al. 1985) show that around 61 kHz there are phase shifts of 220° per 450 Hz. Optimal extinctions should occur at a phase difference of 180° which corresponds to 360 Hz. This value roughly fits the 300 Hz difference between resonance and sharpest tuning.

A difference between the frequency range of sharpest tuning and the range of highest sensitivity was not only seen in neurons responding to the dominant second harmonic of the echolocation call around 60 kHz but also for neurons with BFs in the range of the third harmonic at about 90 kHz. Furthermore, there are significant

threshold maxima of single units at about 2–4 kHz below the most sensitive frequency band in both frequency ranges. This is in agreement with Suga and Jen (1977) who also found very insensitive single units in a narrow frequency band below 60 kHz. The similarities between the 60 and 90 kHz regions are astonishing since there are no cochlear specializations, visible by light microscopy, reported so far for the very basal representation place of 90 kHz. Further evidence for similar processing of different CF-harmonics is provided by the N1-off thresholds which show distinct minima not only at 60 kHz but also at 30 and 90 kHz (Fig. 3; Pollak et al. 1979). These correlations might indicate that the adaptations for specialized processing of the 60 kHz range also affect cochlear places representing harmonic frequencies. This implies that resonance oscillations should spread along the cochlea. For the 90 kHz place this should be facilitated by the retrograde propagation of waves involved in the production of OAE. Alternatively, the sharp tuning at other harmonics might be produced by different mechanisms as suggested by Pollak et al. (1979). Pollak et al. (1979) showed that sharp tuning and high sensitivity in the N1 audiogram at 60 kHz is eliminated by exposure to 60 kHz tones of 90–100 dB SPL without affecting the sharp tuning at 30 and 90 kHz. These data do not necessarily contradict our interpretation. Assuming that acoustic overstimulation mainly impairs hair cells (Saunders et al. 1985) at the place of representation of 60 kHz, the sharpness of cochlear potentials at the same frequency should deteriorate even though the mainly passive resonance which is located prior to the level of the hair cells is still intact. Consequently there will still be sharp tuning of receptor potentials in cochlear regions where there are unimpaired hair cells (30 and 90 kHz).

Are on-off responses of N1 and single units related to mechanical cancellations in the cochlea?

The resonance frequency is always above the resting frequency. The difference between both frequencies largely varies among individual bats and in the present study amounted to 880 ± 400 Hz comparable to 700 ± 312 Hz found by Kössl and Vater (1985a). CM data versus recordings in the inferior colliculus show the same trend, even if the difference is smaller (Henson et al. 1982: 200 Hz; Henson et al. 1988: 60–540 Hz).

In relation to the resonance frequency the threshold minimum of the N1-on potential is shifted towards higher frequencies. This shift amounts about 2 kHz and was explained by Suga and Jen (1977) to be due to the resonance in CM-potentials which will cause a less steep onset of the response and thus a less tight synchronization of the first spikes of auditory nerve fibers tuned to the resonance frequency. Thereby the threshold of the compound action potential will be locally elevated and the threshold minimum shifts in relation to the most sensitive frequency range of auditory nerve fibers. The N1-off minimum was located about 500 Hz below the resonance frequency close to the resting frequency, and matches the frequency range of on-off responses seen in neurons of the cochlear nucleus. This leads to the conclusion that the N1-off minimum most probably reflects the true frequency range of off-events in single auditory nerve fibers. On-off phenomena could be produced in the cochlea by mechanical cancellations which are restricted to a narrow frequency range. Shortly after the onset of the stimulus cancellations would suppress tonic activity, whereas after the end of stimulus, release of suppression would produce an offset response. In the cochlea of *Pteronotus* the tectorial membrane is locally enlarged in the second half turn where the 60 kHz range is represented (Henson and Henson 1989). In particular at a basilar membrane position slightly apical to the representation of the resting frequency where the on-off frequency range is represented, the cross-sectional area of the tectorial membrane is maximal and about twice as large as in other regions of the cochlea (compare tectorial membrane data of Henson and Henson 1989 with the frequency map of Kössl and Vater 1985b). This opens the question if a local increase of the inertness of the tectorial membrane is involved in the mechanical suppression as observed in on-off neuronal response patterns.

Relation between the shape of neuronal tuning curves and cochlear specializations

The tuning curves of neurons with BFs at or slightly above the resonance frequency are opened to the high frequency side. This is just the reverse of the normal type of tuning curve seen in other mammals and in the other frequency regions of *Pteronotus*. Similar to Suga and Jen (1977) we found symmetrical tuning curves for the most sharply tuned neurons below the resonance frequency. Neurons opened at the high frequency side were not described in detail by Suga and Jen (1977), they only show one tuning curve of this kind but their sample of neurons was focused on the 500 Hz wide range of sharpest tuning. Assuming that the sensitivity to higher frequencies does not result from convergence of auditory nerve fibers carrying different BFs onto single neurons in the cochlear nucleus, the tuning curves which are open at the high frequency end must be derived from cochlear properties. Two factors could be involved in their generation: (I) Wave cancellations slightly below the resonance frequency could be responsible for a steep low frequency slope. (II) In the cochlea there are morphological specializations located basal to the site where the frequency of resonance is represented. These could participate in the generation of the otoacoustic emissions or their amplification as discussed above. In particular, pronounced thickening of the basilar membrane at the site between 62 and 70 kHz could provide an increased longitudinal coupling and a discontinuity in cochlear impedance (Kössl and Vater 1985a). The possible increase in longitudinal coupling could contribute to the relatively high sensitivity for the frequencies above the reso-

nance frequency and the opening of the tuning curves at the high frequency end.

In the cortex of *Pteronotus* tuning curves opened towards the high frequency end have not been described (Suga et al. 1978, 1979). Tuning curves of neurons with best frequencies above the resting frequency are only slightly asymmetrical in the inferior colliculus (Bodenhamer and Pollak 1983). In the lateral lemniscus of *Rhinolophus rouxi*, a bat which also possesses specializations of the basilar membrane (Vater et al. 1985), tuning curves of high frequency neurons are distinctly opened at the high frequency end (Metzner and Radtke-Schuller 1987). This supports the suggestion of Suga and Tsuzuki (1985) that within the various levels of the ascending auditory pathway an increasing neuronal inhibition progressively narrows the upper part of the tuning curves while the tip of the tuning curves remains constant.

Acknowledgements. We thank G. Neuweiler and E. Covey for critically reading earlier versions of the manuscript and H. Tscharntke and M. Pötke for photographic work. This work was supported by SFB 204.

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