Audition in vampire bats, *Desmodus rotundus*

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Summary. 1. Within the tonotopic organization of the inferior colliculus two frequency ranges are well represented: a frequency range within that of the echolocation signals from 50 to 100 kHz, and a frequency band below that of the echolocation sounds, from 10 to 35 kHz. The frequency range between these two bands, from about 40 to 50 kHz is distinctly underrepresented (Fig. 3B).

2. Units with BFs in the lower frequency range (10–25 kHz) were most sensitive with thresholds of −5 to −11 dB SPL, and units with BFs within the frequency range of the echolocation signals had minimal thresholds around 0 dB SPL (Fig. 1).

3. In the medial part of the rostral inferior colliculus units were encountered which preferentially or exclusively responded to noise stimuli. – Seven neurons were found which were only excited by human breathing noises and not by pure tones, frequency modulated signals or various noise bands. These neurons were considered as a subspeciality of the larger sample of noise-sensitive neurons. – The maximal auditory sensitivity in the frequency range below that of echolocation, and the conspicuous existence of noise and breathing-noise sensitive units in the inferior colliculus are discussed in context with the foraging behavior of vampire bats.

Key words: Hearing – Chiroptera – *Desmodus* Inferior colliculus – Tonotopy

Introduction

Among mammals, echolocating bats are the order that exploits the widest variety of food resources. Bats capture flying insects, arthropods living on vegetation, insects and fishes at the surface of water, ground-dwelling

Abbreviations: BF Best frequency; *IC* inferior colliculus

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small vertebrates, and also fruits, nectar and pollen. The most specialized of all mammals are the echolocating vampire bats of the neotropics which exclusively subsist on blood from mammals and birds (review see Schmidt 1978; Greenhall and Schmidt 1988).

Studies on audition of echolocating bats have demonstrated that the auditory system is intricately adapted to the specific requirements of species-specific acoustic foraging strategies (review see Neuweiler 1990). For instance, rhinolophids, hipposiderids and *Pteronotus parnelli*, which pursue flying insects in or around dense vegetation, have evolved a sophisticated cochlear fovea and neuronal specializations which allow the selective detection of wing-beating targets among echo-clutter (echo-glint detection, Schnitzler et al. 1983). In these bats the tonotopic organization of the ascending auditory pathway is heavily biased in favor of the species-specific and even individual, specific narrow frequency band used for glint detection in echolocation.

Other bat species have other specific types of auditory adaptations. For example, *Plecotus auritus*, *Megaderma lyra* and *Macroderma gigas* forage on prey living on substrates and their auditory systems are extremely sensitive (up to −27 dB SPL) to a frequency range (15–25 kHz) just below that of their echolocation signals (review see Neuweiler 1990). The Indian false vampire *Megaderma lyra*, has a hunting style similar to that of owls (Payne 1971) in that they can precisely locate and attack a source of noise in a familiar room in complete darkness (Fiedler 1979). In contrast, the false vampire does not detect prey which does not generate noise (Marimuthu and Neuweiler 1987). The auditory system is specifically adapted for detecting faint noises; these adaptations include unusually large pinnae, and auditory neurons in the lateral and central part of the inferior colliculus (IC) which specifically respond to faint noises and react poorly to other types of auditory stimuli (Rübsamen et al. 1988).

Megaderma lyra differs from horseshoe bats, in that frequencies below the band used for echolocation occupy more neural space in the inferior colliculus than do the

frequencies of the echo signals. Thus, the auditory system of *Megaderma lyra* appears to be differentiated for passive acoustical prey detection in addition to echolocation.

Vampire bats depend on a nightly blood meal, and therefore have to detect and locate their prey. In a natural tropical habitat without anthropogenic blood sources such as farm stock living on pastures, the vampire's prey usually rest under cover. It is unlikely that echolocation would be of much help for detecting mammals under cover. However, if vampire bats had such extreme auditory sensitivity for faint noises as has been demonstrated in false vampires, they might be able to detect the sources for a blood meal by noises generated by the prey. Since the false vampires of the Old World and the vampires of the New World are unrelated families, possible convergent auditory adaptations would demonstrate the adaptive power of the mammalian auditory system to external evolutionary pressure.

In a first investigation of specific auditory capacities in the vampire bat, *Desmodus rotundus*, we looked for frequency ranges of behavioral significance as seen by overpresentation of certain frequency bands within the tonotopic organization of the IC, and we also searched for neurons that were specifically sensitive to noise.

Material and methods

The animals used in these experiments were 9 adult male *Desmodus rotundus* which were born and brought up in the vampire colony of the Zoological Institute, University of Bonn.

Surgery and electrophysiological methods were the same as described by Pollak and Schuller (1981) and by Rübsamen et al. (1988). Briefly, surgery was performed under halothane anesthesia (dosage 1.5 vol%). The head was fixed in a head holder by a metal bolt glued to the frontal skull, and a hole (1 mm $\varnothing$) was drilled into the bone covering the inferior colliculus. This opening for electrode penetrations was filled with paraffin oil and the wound margins were treated with a local anesthetic (novocain).

Recordings in awake specimens started one day after surgery and continued over 2–3 consecutive days. Recording was through glass micropipettes, filled with 3 M KCl and a resistance of 1–2 MΩ for multi-unit, and 4–8 MΩ for single-unit recordings. The electrodes were advanced dorsoventrally through the inferior colliculus. The last track of a series of parallel penetrations was marked with two iontophoretic HRP-injections (1 μA, 2.5 min) at different depths. The stereotaxic coordinates of the penetrations were reconstructed according to histological data from parasagittal and frontal sections of the brains.

BFs and thresholds were determined audiovisually, and PST histograms (32 sweeps, bin width 1 ms) were sampled with a computer (PDP11/40).

The acoustical search stimuli consisted of pure tones (3.5 ms duration, incl. 0.5 ms rise/fall time) and bandpassed noise (80 ms, 0.5 ms rise/fall time). In some cases frequency modulated downward sweeps and harmonic signals were presented. The loudspeakers, a condenser loudspeaker for frequencies from 15 to 120 kHz and a dynamic one for frequencies below 15 kHz, were mounted on a hoop and placed in front of the contralateral ear. The position of the ultrasonic loudspeaker was adjusted in azimuth and elevation for the best neuronal response (Schlegel et al. 1988). The frequency characteristics of the speakers were calibrated by a 1/4″ and a 1/8″ B&K condenser microphone (models 4135/4138). Stimulus intensity is expressed in dB SPL (re 20 μPa).

Results

Audiogram and tuning

In 62 penetrations in the IC, BFs and thresholds of multi-units were recorded every 50 μm in 3 bats, and every 100 μm in 6 bats. The BFs ranged from 800 Hz to about 110 kHz (Fig. 1). The lowest thresholds of −5 to −11 dB SPL were found for BFs between 10 and 25 kHz, i.e. below the frequency range of the echolocation sounds. Within the frequency range from 50–95 kHz, units were less sensitive and only reached minimal values slightly above 0 dB SPL. Minimal thresholds rapidly increased for BFs below 10 kHz and above 96 kHz. At BFs of 2 and 100 kHz lowest thresholds range between 20 and 30 dB SPL.

Pure tone thresholds were determined for 132 single units. The data confirm the results of the multi-unit recordings: the most sensitive units have BFs around 20 kHz, and for BFs in the ultrasonic range thresholds are above 0 dB SPL. The lowest BF was found at 700 Hz (thresholds 68 dB SPL).

Figure 2 demonstrates some typical tuning curves of single units. Most units were rather narrowly tuned, and some of them had upper thresholds. A few neurons responded to a wide range of frequencies, for instance one neuron with a BF of 65 kHz responded 10 dB above threshold to pure tones from 11 to 93 kHz.

Most Q_{10dB}-values were below 15. Only in the frequency range of the second harmonic of echolocation calls (45–70 kHz) were 5 units found with Q_{10dB}-values above 15 (the highest Q_{10dB}-value was 77 at 54 kHz).
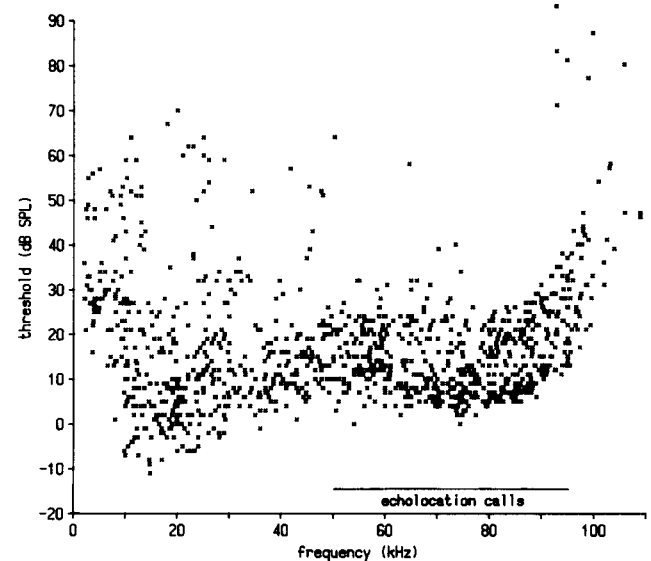

Fig. 1. Neural audiogram of *Desmodus rotundus*, obtained by multi-unit thresholds in the IC (each dot signifies a threshold value as a function of the respective BF at a given electrode position). The frequency range of the echolocation calls is indicated
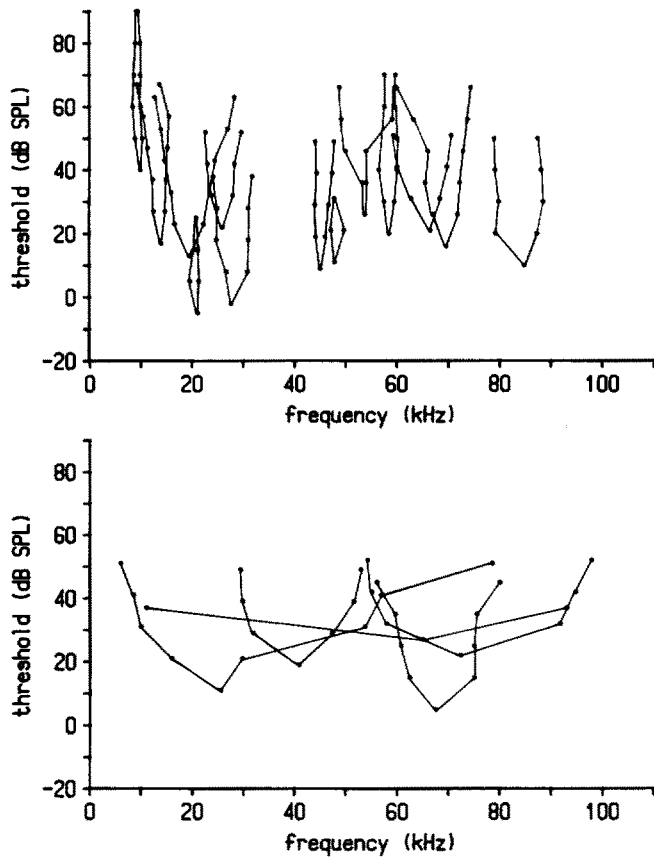
Fig. 2. Some representative tuning curves of single units (above: narrow-band units; below: broad-band units)

Tonotopy

The IC in *Desmodus rotundus* is covered by the cerebellum dorsally and extends about 3100 μm in dorsoventral, 2800 μm in lateromedial, and 1400 μm in caudofrontal direction. The tonotopy of the IC was derived from 55 electrode penetrations, of which 13 were marked by HRP. Figure 3A shows the location of these penetrations through the IC.

The general tonotopic arrangement of the IC in *Desmodus rotundus* follows the typical mammalian pattern, i.e. low frequencies are represented dorsally, and higher frequencies in progressively more ventral parts. In the posterior and medial parts of the IC the isofrequency contours follow the curved surface of the IC and fall off from the medial to the lateral margin (Fig. 3B). In the rostral part of the IC the isofrequency contours also descend medially from the top of the IC.

Two frequency ranges are well represented within the IC: frequencies from the lower limit of sensitivity to about 35 kHz in the dorsal third, and the frequencies from about 60 to 100 kHz in the ventral half of the IC. This latter, high frequency range does not extend to the lateral margin in the caudal third of the IC. Units with BFs between about 40 and 50 kHz form a relatively thin slab sandwiched between the low and high frequency representations (Fig. 3B).

Noise-sensitive units

During the multi-unit recordings single units were occasionally encountered that vigorously responded to the
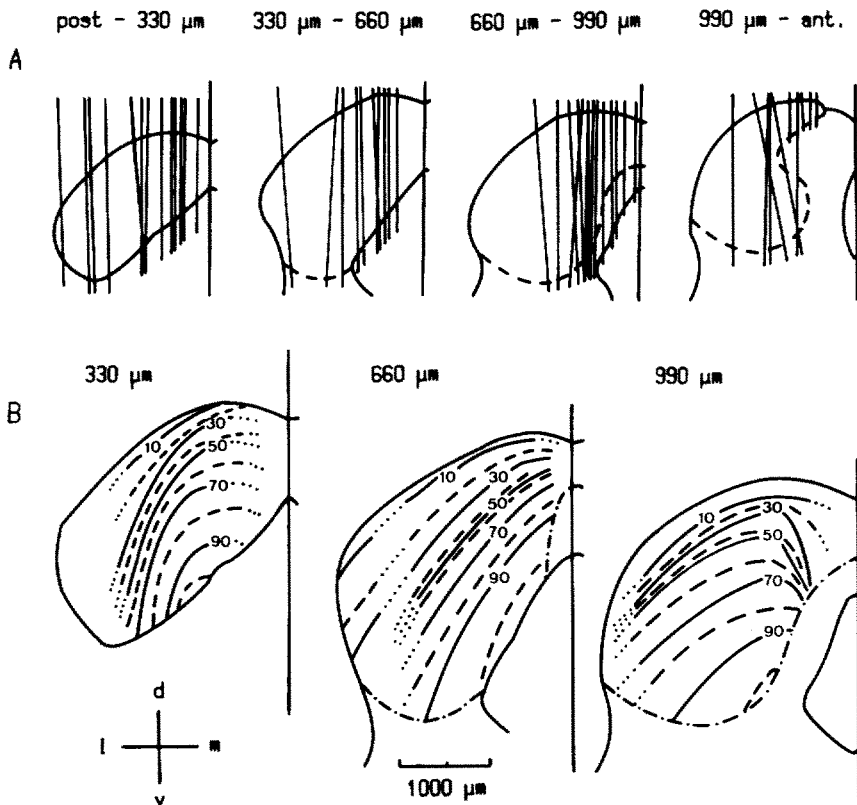

Fig. 3A. Projection of the electrode penetrations (n = 46), considered for establishing the tonotopy, onto 4 transverse sections of the IC (combined from 9 bats). The figures indicate the collicular range of the penetrations (9 additional penetrations in the medial area are not drawn).
B Reconstruction of tonotopy in 3 transverse sections of the IC in *D. rotundus* (left: caudal, right: rostral). The measurements above the drawings give the distance of the sections from the posterior margin; numbers inside the drawing delineate the particular iso-freqency layer (*d:* dorsal, *v:* ventral, *l:* lateral, *m:* medial)
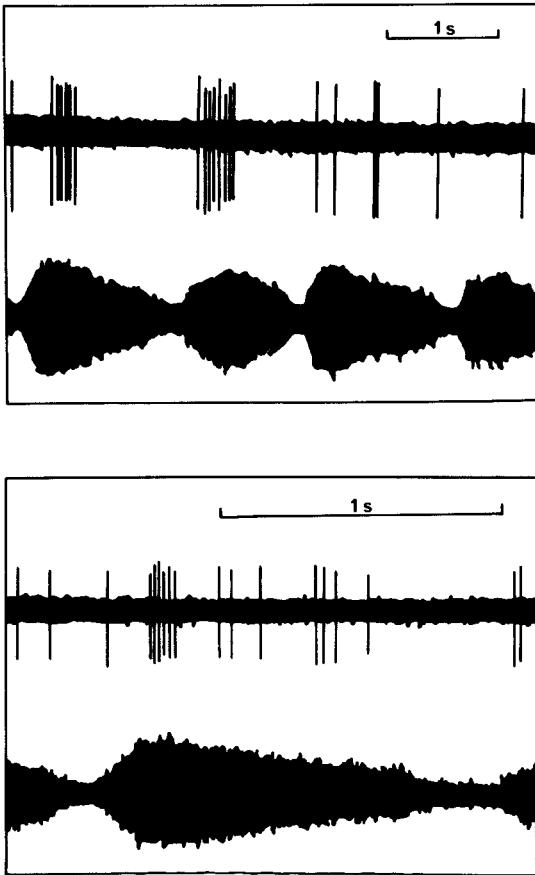
Fig. 4. Response of 2 noise-sensitive units to the playback of human respiration (intensity of noise at the head position of the bat: 30 dB SPL RMS; horizontal bar: 1 s)

Fig. 5A. Noise-thresholds (center-frequency) of IC units ($n = 32$) *sensitive* to human respiration sounds. B Noise thresholds of single units ($n = 59$) *not responding* to human respiration sounds (circles: bandpassed noise ± 10 kHz, triangles: ± 5 kHz, squares: ± 2 kHz)

faint breathing noise of the experimenters. Spike bursts locked to the breathing rhythm were also elicited when the person was 6 m away from the open recording chamber which housed the bat. Therefore, in 5 specimens of *Desmodus rotundus* we systematically searched for such units.

Single units sensitive to breathing noise were only found in the dorsal region of the IC where BFs between 10 and 30 kHz are represented. They were most abundant in the medial part of the rostral IC where the isofrequency slabs descend ventrally, and none were encountered in the lateral areas.

Forty-six neurons were recorded which responded to human breathing noise. Seven of these units were stimulated by tape-recorded breathing noises and their responses were audiovisually assessed (Fig. 4). Another 7 units of the total sample only responded to the breathing noise and were not excited by pure tones, FM sweeps or various noise bands.

Most units ($n = 32$) sensitive to breathing noise also vigorously reacted to faint bandpass filtered noise in the frequency range below 30 kHz, and most of them ($n = 28$) also responded to more intense pure tones. Thresholds were measured for noise signals with a bandwidth of
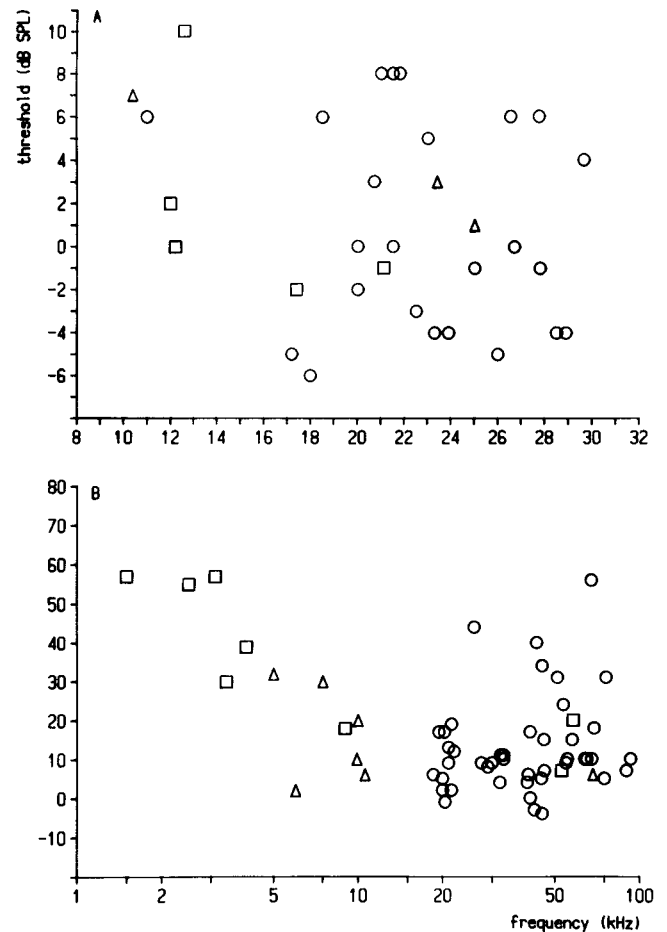
± 10 kHz, and the center frequency was adjusted to the minimal threshold. As shown in Fig. 5, all units sensitive to breathing noise had minimal noise thresholds for center frequencies between 10 and 30 kHz. Noise thresholds were low and ranged from + 10 to − 6 dB SPL. Eight units were more sensitive to narrower noise bands of ± 5 and ± 2 kHz (Fig. 5A). Thresholds to pure tones at BF-frequency exceeded those to noise by from 10 to more than 40 dB (Fig. 6). Whereas there seemed to be no habituation to the breathing noise in any of the breathing sensitive neurons, some of them habituated rapidly when stimulated with band passed noise.

In 25 units sensitive to breathing noise, 3 different response patterns were recorded by PST-histograms. Fifteen units showed phasic and phasic-tonic responses during noise stimulation, and the spike rate increased monotonically with noise intensity (Fig. 7). In six units an additional strong off-response appeared when the noise intensity increased (Fig. 8). Interestingly, the magnitude of the off-response increased with stimulus duration, e.g. in one unit a 5 ms noise pulse elicited one off-burst, and a 80 ms noise pulse three off-bursts (Fig. 8C).

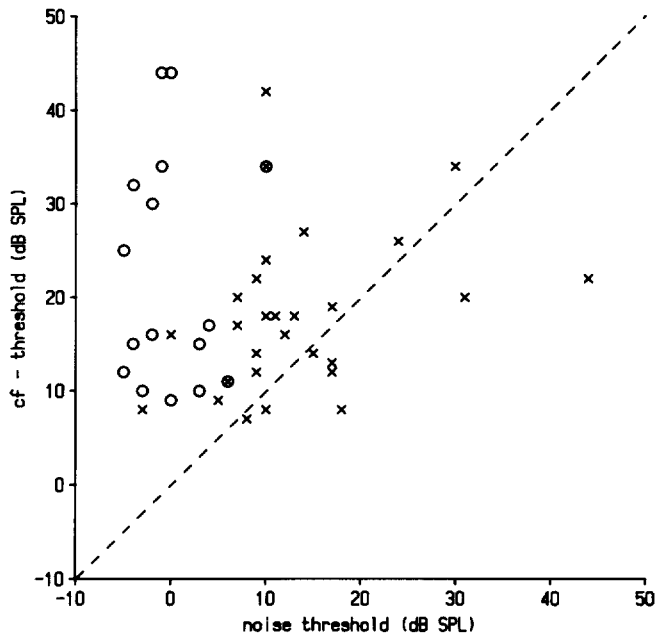Four units were excited only within a narrow inten-

Fig. 6. Correlation between pure tone threshold and noise threshold in units responding to faint human respiration sounds (circles, $n = 16$) and units not responding to this stimulus (crosses, $n = 28$). The 45°-line indicates threshold values equal for pure tone and noise stimuli
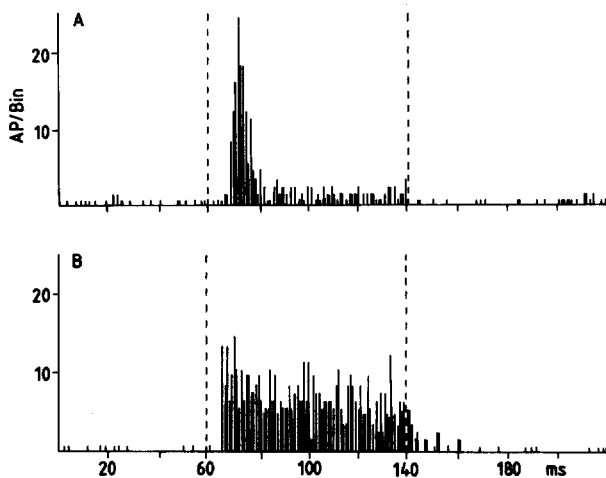

Fig. 7A, B. PST-histogram (bin width 1 ms) of noise-unit type I. Stimulus: bandpassed noise 26.7 ± 10 kHz (threshold value 0 dB SPL); A 10 dB above threshold, B 40 dB above threshold

Fig. 8A–C. Noise-unit type II. Stimulus: bandpassed noise 22.5 ± 10 kHz (threshold value –3 dB SPL); A 4 dB above threshold, B 20 dB above threshold. C Bursting off-response of noise-unit type II to intense stimulation (bandpassed noise 21.8 ± 10 kHz, 50 dB above threshold; threshold value 8 dB SPL)

sity range and had distinct upper thresholds. In three spontaneously active neurons excitation was only recorded in the threshold range, and activity was totally inhibited by noise stimuli 20 dB above threshold (Fig. 9A, B). One non-spontaneously active unit responded only in the intensity range between 4 and 19 dB SPL (Fig. 9C, D). Since these specialists for faint noises were difficult to detect, we suspect that this category may be represented in the rostro-medial IC in larger numbers than indicated by our sample.

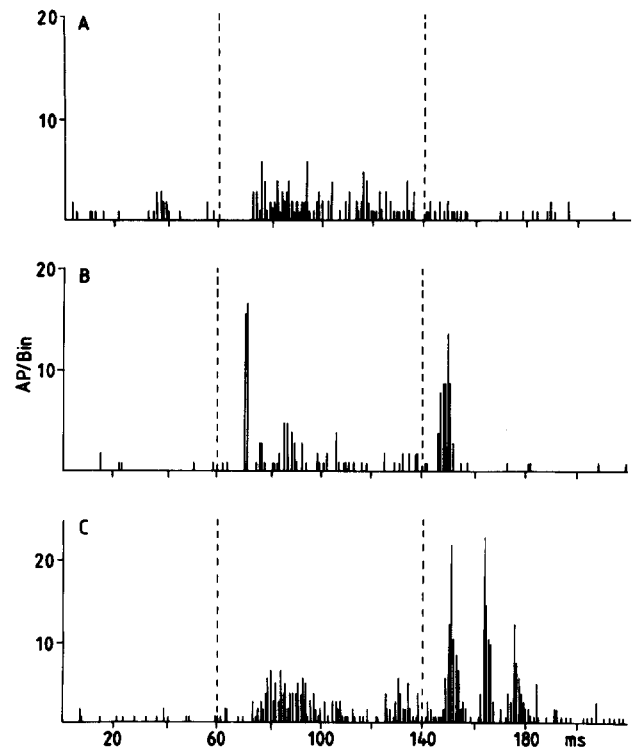In various parts of the IC we additionally recorded 59 units which were sensitive to bandpass filtered noise but did not react to breathing noise. Thresholds ranged between 0 and 55 dB SPL, and thus were considerably higher than those of units sensitive to breathing noise (Fig. 5B). Most of the units in this category were less sensitive to pure tones, but there was not as great a range of threshold differences as in units responding to breathing noise (Fig. 6). The BFs ranged from 1.5 to 100 kHz. Thus, in the range of BFs from 10 to 30 kHz we found noise sensitive units which responded to breathing noise, and others which did not. Therefore, we conclude that sensitivity to breathing noise may be more specific than sensitivity to noise in general within the frequency band of 10 to 30 kHz.

Discussion

The most interesting result of this study is the detection of IC neurons which are sensitive to breathing noises. These units belong to a class of neurons, found in the dorsomedial part of the IC, which are highly sensitive to noise bands in the frequency range below that of the echolocation signals emitted by *Desmodus rotundus*. A few of these units vigorously responded to breathing noises but not to noise signals of various center frequencies and bandwidths. We therefore suspect that these units are optimally activated by some as yet undefined stimulus parameters of breathing noise. The data suggest that some of the breathing-sensitive units are optimally
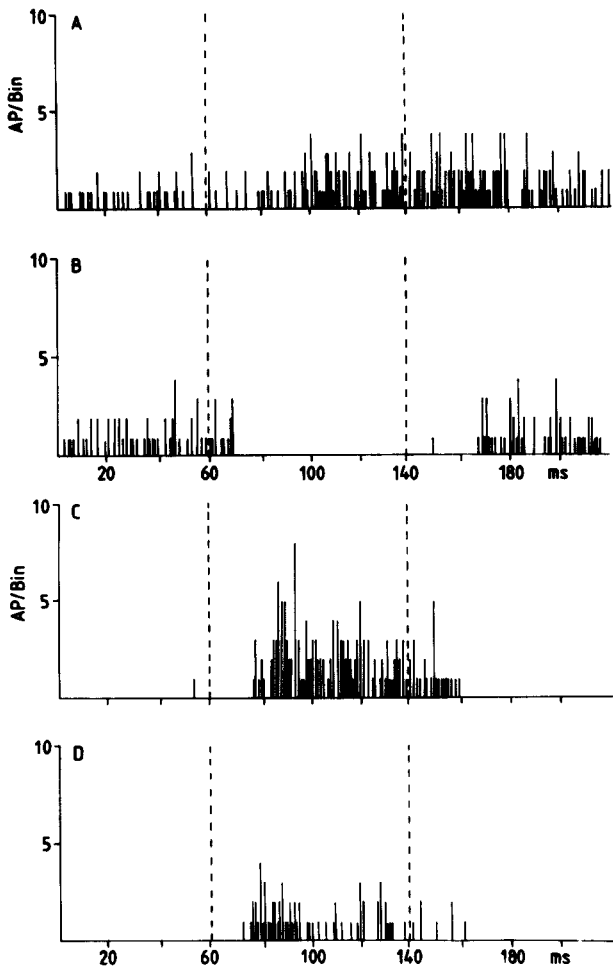
Fig. 9A–D. Noise-unit type III (spontaneously active neuron). Stimulus: bandpassed noise 21.5 ± 10 kHz; **A** threshold intensity (8 dB SPL), **B** 20 dB above threshold. **C/D** Noise-unit type III (not spontaneously active). Stimulus: bandpassed noise 29 ± 10 kHz (threshold value 4 dB SPL); **C** 5 dB above threshold, **D** 10 dB above threshold

activated by stimuli of long durations, however, the sample is still to small to make any definitive conclusion, and the units could not be held for a long enough time in order to investigate systematically the effect of all possible stimulus parameters.

In previous studies of the ascending auditory pathway, noise stimuli have mainly been used to evaluate signal/noise ratios or for system analysis in terms of information theory (e.g. Møller 1982). Evans and Whitfield (1964) were among the first who considered noise pulses as a class of natural auditory stimuli: In the auditory cortex of cats 27% of 125 units, they studied, responded only to clicks and odd sounds such as jangling of keys. Such units habituated easily. Specificity for odd sounds was considered to be a cortical feature not to be expected in subcortical nuclei. However, Suga (1969) recorded 3 noise-specific units among 250 neurons of the IC in two echolocating bat species. Since noise sensitivity did not make much sense in the context of echolocation,

little attention has been paid to this early discovery. In the false vampire bat, *Megaderma lyra*, Rübsamen et al. (1988) described IC neurons which were extremely sensitive to faint noises and odd sounds such as brushing of the experimenter's beard or clothing. *Megaderma lyra* is known to detect ground-dwelling prey (e.g. frogs, mice) by passive detection of rustling noises and not by echolocation (Fiedler 1979; Marimuthu and Neuweiler 1987). Therefore, such units sensitive to faint noises may be interpreted as an adaptation to the auditory detection of concealed prey (Neuweiler 1990). It is tempting to interpret the IC units sensitive to breathing noises as a specific adaptation for the detection of resting mammals by vampire bats. However, since virtually nothing is known about how vampire bats search for and find wild prey or live-stock (Schmidt 1988), such speculations are premature. Our results suggest that prey-generated noises should be included in the list of possible clues vampire bats might use for prey detection and location.

This suggestion is corroborated by the audiogram and the IC tonotopy described in this study. The vampire bat is most sensitive in the frequency range between 10 and 20 kHz, with thresholds around −10 dB SPL. This is clearly below the frequency band used for echolocation, even if one includes the faint fundamental. *Desmodus rotundus* emits brief frequency modulated and multiharmonic echolocation signals of 0.4 to 1.4 ms duration. The main energy of the sound is in the frequency range of the second and the third harmonic which sweep from about 75 to 45 kHz, respectively, from about 100 to 65 kHz. The fundamental that sweeps from about 35 to 25 kHz seems to be present during flight, but is 20 to 25 dB less intense than the other harmonics (Joermann and Schmidt 1981).

The neuronal audiogram derived from the IC recordings in awake specimens described here is distinctly different from the ones recorded by cochlear microphonic potentials in anesthetized vampire bats (Vernon and Peterson 1966). In the latter study, the lowest thresholds occurred at 50–60 kHz and increased monotonically by nearly 1 dB/1 kHz for lower frequencies. This discrepancy may be explained by the effects of anesthesia. In 16 species of echolocating bats in which audiograms have been recorded under anesthesia thresholds are generally high with a minimum in the frequency range of the emitted echolocation sounds. However, in 24 different species recorded under awake conditions, the audiograms uniformly have much lower thresholds and all species are most sensitive in the low frequency range between 12 and 25 kHz, and usually less sensitive by a few dB up to 20 dB in the ultrasonic frequency range of their echolocation signals (Neuweiler 1990). Obviously, the vampire bat may be added as the 25th species to this list. These uniform data from many different species and from various labs indicate that it is common for bats to be highly sensitive to lower frequencies which are prominent in the power spectra of all sorts of noises generated by animals. Therefore, all echolocating bats may sensitively listen to such noises and be attracted to or repelled from locations from which such noises emanate. The vampire bats (this study) and the false vampires (Rübsamen et al. 1988; Guppy and Coles 1988) might

simply be outstanding examples of a general auditory sensitivity to faint noises in all bats. For instance, the insectivorous bat *Antrozous pallidus* mainly detects its prey by sound of its flight and other movement and not by echolocation (Bell 1982). Other echolocating bats are attracted to insect aggregations by their humming flight noises (Buchler and Childs 1981).

In vampire bats, high sensitivity to lower frequencies coincides with a good representation of frequencies up to 35 kHz in the dorsal and lateral parts of the IC. However, frequencies from about 50 to 100 kHz are equally well represented in the ventral half of the IC. Only the representation of the frequency band in between these two large portions, from 40 to about 50 kHz, is squeezed into a thin sheet. The same sort of underrepresentation has been observed in *Hipposideros ·speoris*. This bat emits echolocation signals within the frequency range of 110 and 140 kHz, and the frequency band from 110 to 75 kHz is compressed into a thin sheet within the tonotopy of the IC (Rübsamen et al. 1988). In the horseshoe bat *Rhinolophus rouxi,* which emits sounds from about 65 to 78 kHz, the frequencies of 60 to 40 kHz are poorly represented (unpubl. data). Thus, it appears that in several bat species the transitional area between echolocation and passive listening is poorly represented in the tonotopy of the ascending auditory pathway.

The results from various species of bats suggest that a detailed comparative study of tonotopy will disclose those frequency bands which are behaviorally significant. This is especially obvious in the tonotopy of horseshoe bats and hipposiderids which is focused not only on the species-specific frequency band of echolocation, but also precisely on the frequency of a given individual. In the vampire bat the specific tonotopy suggests that not only echolocation signals, but also auditory events at low frequencies are highly significant.

Scanning through the literature on audition in mammals quickly discloses that the general rule of a logarithmic frequency representation is modified in most cases by overrepresentations of specific frequency bands. In mice the largest percent volume of the IC is occupied by neurons with BFs between 15 and 35 kHz (Stiebler and Ehret 1985). In cats the frequency range from 5 to 30 kHz is overrepresented in the IC (Rockel and Jones 1973), and in the rabbit low frequencies up to 6 kHz occupy the dorsal half of the IC (Aitkin el al. 1972). In the marsupial *Dasyurus hallucatus* an overrepresentation from 10 to 40 kHz coincides with lowest thresholds of −10 dB SPL in the same frequency range (Aitkin et al. 1986). Apparently overrepresentation of specific frequency bands is not just a specialization restricted to echolocating bats, but is rather the rule in mammals.

Noise sensitive neurons may be specific adaptations for species which have to detect and locate prey acoustically; our results suggest that vampire bats belong into this category of mammals.

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