J Comp Physiol (1982) 148:245–251

Journal
of Comparative
Physiology · A

# Ultrasound Recognition in House Mice: Key-Stimulus Configuration and Recognition Mechanism

Günter Ehret and Bernd Haack
Fakultät für Biologie, Universität Konstanz, Postfach 5560, D-7750 Konstanz, Federal Republic of Germany

Accepted May 9, 1982

**Summary.** 1. We determined the ability of lactating female house mice (*Mus musculus*, strain NMRI) to recognize natural ultrasonic calls (USC) of their pups or synthesized USC models. Recognition was shown by the mice preferentially responding to these sounds in the presence of an alternative sound signal.

2. Preferred USC models had total durations (flat top + rise and fall times) between 30 and 270 ms. Shorter and longer ones were not preferentially responded to. Response to USC models with major frequency components above 40 kHz was the same as that to natural ultrasonic calls of mouse pups.

3. The key-stimulus configuration for recognition of mouse pup ultrasound in the frequency domain can be characterized as pulses of sound energy in a narrow frequency band in the ultrasonic range with significantly less energy in adjacent frequency bands. The decisive units for call recognition are frequency bandwidths which are almost identical in width with the critical bands of hearing, a measure of frequency resolution in the auditory system. The critical frequency bands for the recognition of USC models have a bandwidth of 22.5 kHz at a center frequency near 50 kHz (the critical band of hearing is 22 kHz wide), and 15 kHz at a center frequency near 40 kHz (the critical band of hearing is 18 kHz wide). We conclude that the discrimination of ultrasonic mouse pup calls from other mouse calls and their recognition is most probably directly related to the critical band analysis in the auditory system.

## Introduction

Pure ultrasonic calls are probably the most important and certainly the best studied calls in the sound communication systems of the house mouse and of other murid rodents. Pure ultrasounds are produced in sexual encounters between adult mice (Sewell 1968; Sales 1972; Whitney et al. 1973) as well as by mouse pups when they lose contact with their littermates, become cold or distressed (Okon 1972; Noirot 1972; Sales and Smith 1978; Haack et al. 1982). In the latter case the parents (in the first place the mother) respond with such brood-caring behavior as searching for a lost pup, retrieving it back to the nest and grooming and feeding it. The function of the ultrasound seems twofold, a) to release maternal behavior, and b) to serve as an indicator of the pup's location.

Since the vocal repertoire of the house mouse consists of at least 6 structurally different call types of which 4 are known to be used in intraspecific communication (Haack et al. 1982; Whitney and Nyby 1982), the question arises as to which characteristics are essential for recognition of ultrasonic calls and for discrimination of these sounds from other mouse calls and from environmental background noise.

Mouse pup ultrasounds (Fig. 1) are pure tone whistles usually between about 40 and 80 kHz with frequency modulations and jumps, and variations in intensity and duration. We would expect the boundaries for call recognition to be wide enough to cover the normal range of variability of these calls but narrow enough for discrimination against other mouse pup calls.

In the present paper we investigate and discuss a) the frequency range in which USC recognition

---

*Abbreviations: SPL* sound pressure level; *USC* ultrasonic call

0340-7594/82/0148/0245/$01.40

occurs, i.e. in which USC are preferentially responded to, b) the influence of disturbing sound on the recognition process, c) the boundaries in the time domain within which response preference to USC models occurs, and d) a physiological mechanism possibly underlying recognition in the frequency domain.

## Materials and Methods

The response used to obtain the results described in this paper was maternal pup searching behavior, which was indicated by a female moving towards one of two loudspeakers, each of which emitted a different signal. Responses were obtained from 215 lactating house mice (*Mus musculus*, strain NMRI). Only females aged 3–5 months and with litters less than 7 days old were used. Each female responded at most 6 times to a given stimulus configuration, and to no more than two different configurations presented on different days.

*Equipment.* We tested the response to 3 basically different stimuli: pulses of pure tones, pulses of bandpassed white noise (see Fig. 1) and pulses of bandpassed white noise with a pure tone added. The tones and noise were generated by function generators (Wavetek, 130 and 132), passed through electronic switches and adders, attenuators (Hewlett-Packard 350D) and amplifiers (Hewlett-Packard, 466A and Exact 170) before going to the speakers. In addition, the noise was passed through two digital bandpass filters in series (Krohn-Hite, 3323 and Rockland, 852) to be shaped into bands with 96 dB/octave initial slopes. In tests where frequency was the variable temporal patterns of the synthesized stimuli were the same as in averaged natural call series (80 ms duration, 10 ms rise and fall times, 3 calls/s). Two identical electrostatic loudspeakers after Machmerth et al. (1975) with flat ±1 dB response characteristics between 15 and 100 kHz were used. Each speaker (a or b) emitted one stimulus alternative (A or B) in such a way that the experimental animal heard a series of alternating stimuli (e.g. $A_a$, $B_b$, $A_a$, $B_b$...).

*Testing Procedures.* All tests were done under dim red light in a sound-proof and anechoic room. At least 6 h before testing began, a female with her litter was placed in a nest depression in the middle of a running board (length 110 cm, width 8 cm) in the anechoic room. The two ultrasonic speakers were 65 cm from the nest depression one at each end of the running board and mounted independently of it.

Unless otherwise stated the intensity of all sound stimuli used was $75 \pm 2$ dB SPL (re. 20 µPa) at the nest depression. At the start of each test the female was motivated by letting her carry 4–6 pups, randomly distributed on the running board, back to the nest. By motivating we kept the maternal responsiveness at a high level, in order to reduce motivational variability among animals and to complete the tests in a reasonable time. For example, sleeping, feeding, and self-grooming females do not readily respond to pup USC (Haack and Ehret, in preparation). After a female had retrieved the pups and was settled once more in the nest, the speakers were switched on simultaneously. The speakers were switched off immediately after the female had responded by moving out from the nest at least 30 cm towards one of the speakers (criterion for a positive response). Sometimes a female moved out from the nest in one direction but changed her mind before the 30 cm mark, moved back through the nest in the other direction and reached the criterion there. When the female was settled back in the nest again for at least 30 s, the speakers were switched on for the second run; this procedure was repeated until a maximum of 6 trials were completed. In this series of 6 trials the stimulus alternatives were assigned randomly to the two speakers. Often females had to be re-motivated before 6 tests were finished. Otherwise they did not respond within a 10 min time limit which we used.

Occasionally females became very nervous and continued running back and forth the running board for more than 10 min after the end of a trial. They were excluded from further testing, as were females which continued nursing their pups more than 10 min. Thus we collected fewer than 6 trials from a number of females in a particular test. Since we generally allowed 6 trials per female and aimed for a total number of 50 trials per stimulus configuration, the total number of responses to each stimulus configuration varied between 50 and 54.

**Table 1.** A: Responses of lactating female house mice to natural ultrasounds (natural USC) and to a 20 kHz tone stimulus. B: Responses to pure tone call models compared with the 20 kHz tone stimulus. C: Responses to call models consisting of bands of white noise centered around near 50 kHz compared with the 20 kHz tone stimulus. The probabilities of the response distributions are calculated from a two-tailed binomial test. NS = not significant

| | Stimulus alternatives | Number of responses | Probability |
|---|---|---|---|
| A: | Natural | | |
| B: | 60 kHz : 20 kHz | 34 : 16 | 0.016 |
| | 40 kHz : 20 kHz | 34 : 16 | 0.016 |
| | 35 kHz : 20 kHz | 21 : 30 | 0.263 NS |
| C: | 42.5–60 kHz : 20 kHz | 37 : 14 | 0.002 |
| | 40 –60 kHz : 20 kHz | 35 : 17 | 0.018 |
| | 37.5–60 kHz : 20 kHz | 36 : 15 | 0.005 |
| | 36 –60 kHz : 20 kHz | 25 : 25 | 1.0 NS |
| | 35 –60 kHz : 20 kHz | 28 : 22 | 0.478 NS |
| | 30 –60 kHz : 20 kHz | 31 : 21 | 0.212 NS |

*Statistical Tests.* A two-tailed binomial test was used to calculate the probability of occurrence of the observed response distribution and a $\chi^2$-test was used to estimate the differences between observed response distributions.

## Results

### *Test 1*

We compared the responses to natural mouse pup USC with that to 20 kHz tone pulses, a stimulus which does not occur in the mouse vocal repertoire, but which is clearly audible (Ehret 1974). A rather homogeneous (with respect to intensity, call duration and inter-call intervals) series of mouse pup calls was prepared on a tape loop and played back from a high-speed tape recorder (Philips, Analog 7).

As shown in Table 1 A there were 35 responses to the natural USC and 17 to the 20 kHz stimulus. This distribution indicates a significant preference for the natural USC. This test demonstrates, there-

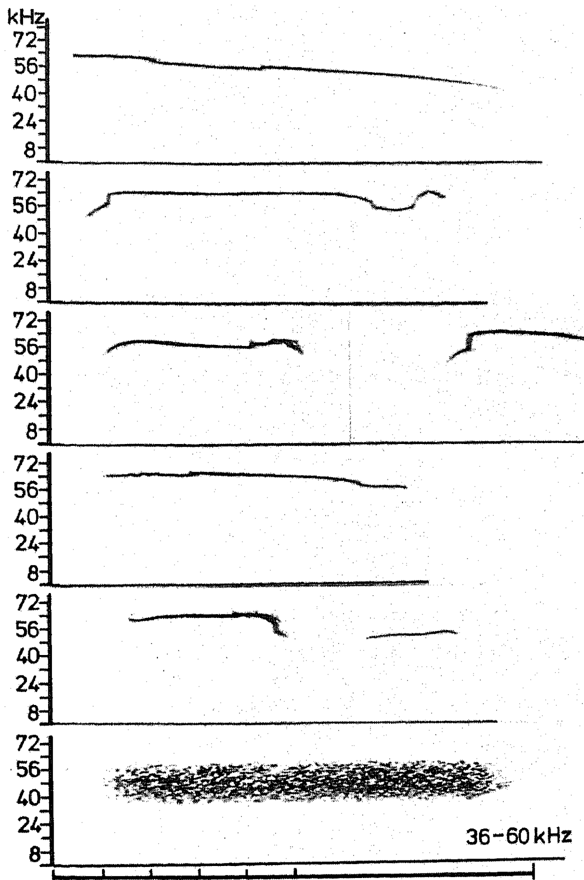

**Fig. 1.** Sonagrams of natural mouse pup ultrasounds giving an impression of the range of variability in frequency, intensity and duration. At the bottom is a sonagram of a pulse of a bandpassed white noise used as one of the call models in the choice tests

fore, that lactating female house mice prefer natural ultrasonic calls of pups to tone pulses falling in the middle part of their hearing range.

### *Test 2*

In this test we replaced the natural ultrasound by 60, 40 and 35 kHz pure tone pulses to determine whether pure tones without variations in frequency, intensity and duration were preferred as models of ultrasonic pup calls.

Table 1 B shows that 60 and 40 kHz tone pulses were preferred to the 20 kHz stimulus however, the 35 kHz tone pulses were not. It is evident that pulses of pure tones in the high ultrasonic range (40 and 60 kHz) are treated like natural pup ultrasound (see Fig.1) whereas tone pulses at the lower frequency (35 kHz) are not.

### *Test 3*

In this test we replaced the natural ultrasound by pulses of white noise of different bandwidths centered around near 50 kHz to determine whether or not the pure tone characteristic in the natural USC (Fig. 1) is a necessary prerequisite for ultrasound recognition.

The results in Table 1C show that the three narrowest noise bands used (17.5, 20, 22.5 kHz wide) were preferable to the 20 kHz stimulus. Again the probability of this preference is very similar to that for the natural USC. Changing the lower cutoff frequency of the noise band from 37.5 to 36 kHz, which is an increase of only 1.5 kHz in noise bandwidth, shows that the females are unable to discriminate between the two stimuli, and they respond due to the high arousal level to both of them equally. The same was true for still broader noise bandwidths (35–60 kHz and 30–60 kHz). Statistically, the response distribution to the 37.5–60 kHz noise band vs. 20 kHz is significantly different from that to the 36–60 kHz noise band vs. 20 kHz ($P < 0.04$). Comparison of the sum of the responses to the three narrow noise bands vs. 20 kHz with the sum of the responses to the three broader noise bands vs. 20 kHz shows that the narrower noise bands are significantly preferred ($P < 0.01$).

From these tests we can conclude that pure tone quality is not a necessary feature of USC models for eliciting preferential responses and thus for demonstrating recognition as pup ultrasound. However, the preferential response to a noise bandwidth centered near 50 kHz is restricted to those with a lower cutoff frequency above 37 kHz.

### *Test 4*

Test 2 and 3 taken together suggest a lower frequency limit for discrimination of preferable and non-preferable USC models near 37 kHz. To investigate further whether the lower frequency cutoff or the bandwidth limit of the stimulus is the decisive factor for this discrimination, we tested a) a series of noise bands centered around a lower mid-frequency (about 40 kHz), and b) a series of stimuli in which a noise band (40–60 kHz), which in test 3 was shown to be a preferred USC model, was combined with pure tones of different frequencies.

The results of both tests are shown in Table 2A. A 15 kHz wide noise band with a lower cutoff at 35 kHz was clearly preferred to the 20 kHz tone. This preference does not extend to wider noise bands with lower frequency cutoffs.

**Table 2.** A: Responses to call models consisting of noise bands centered around near 40 kHz, and of noise bands combined with pure tones of different frequencies, compared with the 20 kHz stimulus. B: Responses to call models consisting of combined stimuli (40–60 kHz noise band plus 35 kHz tone) in which the intensity of the 35 kHz component was varied, compared with the 20 kHz tone stimulus. SPLs of all stimulus components had intensities of 75 dB unless otherwise stated. NS = not significant

| Stimulus alternatives | Number of responses | Probability |
|---|---|---|
| A: 35 –50 kHz:20 kHz | 34:17 | 0.025 |
| 33.5–50 kHz:20 kHz | 29:21 | 0.322 NS |
| 30 –50 kHz:20 kHz | 28:23 | 0.575 NS |
| 25 –55 kHz:20 kHz | 24:26 | 0.888 NS |
| 40–60 kHz+25 kHz:20 kHz | 34:16 | 0.016 |
| 40–60 kHz+30 kHz:20 kHz | 36:18 | 0.021 |
| 40–60 kHz+35 kHz:20 kHz | 29:22 | 0.401 NS |
| B: 40–60 kHz+35 kHz:20 kHz (75 dB) | 29:22 | 0.401 NS |
| 40–60 kHz+35 kHz:20 kHz (65 dB) | 30:24 | 0.496 NS |
| 40–60 kHz+35 kHz:20 kHz (55 dB) | 38:16 | 0.004 |

Thus it is clear that sounds with energy below 37 kHz can be a preferred USC model. This was confirmed by the tests with the combined stimuli (Table 2A). Addition of energy at 25 or 30 kHz with intensity equal to that of the noise band did not change the preference of the females for the combined stimulus, indicating that the noise component was still attractive. If, however, energy at 35 kHz was added, the preference disappeared.

These results demonstrate that pup ultrasound recognition is possible in the presence of lower frequency energy, so long as the additional energy is separated from the USC model by a certain minimum amount of frequency.

### *Test 5*

To determine at what intensity, relative to the noise band, the disturbing effect of the 35 kHz tone becomes significant, we tested combined stimuli in which the noise intensity was 75 dB SPL and that of the 35 kHz tone either 65 or 55 dB.

As shown in Table 2B a 35 kHz tone at 65 dB is just as effective as a 75 dB tone in eliminating the preference for the noise band. If the SPL of the 35 kHz tone is decreased to 55 dB, however, the preference for the noise band re-appears, i.e. the 35 kHz tone no longer influences the perception of the noise band as a preferred USC model.

**Table 3.** Response distributions to different call models. A: Two preferred or two non-preferred call models; B: One preferred and one non-preferred call model. NS = not significant

| Stimulus alternatives | Number of responses | Probability |
|---|---|---|
| A: Natural USC:40–60 kHz | 22:29 | 0.401 NS |
| 40–60 kHz: 35–50 kHz | 26:24 | 0.888 NS |
| 40–60 kHz+25 kHz:40–60 kHz | 26:26 | 1.0 NS |
| 42.5–60 kHz:37.5–60 kHz | 27:25 | 0.890 NS |
| 36 –60 kHz:30–60 kHz | 27:24 | 0.779 NS |
| 33.5–50 kHz:25–55 kHz | 32:19 | 0.093 NS |
| B: 37.5–60 kHz:35–60 kHz | 40:14 | 0.0007 |
| 40 –60 kHz:35–60 kHz | 33:18 | 0.05 |
| 42.5–60 kHz:30–60 kHz | 37:16 | 0.006 |
| 35 –50 kHz:25–55 kHz | 36:18 | 0.021 |
| 40–60 kHz+35 kHz:40–60 kHz (75 dB) | 20:32 | 0.127 NS |
| 40–60 kHz+35 kHz:40–60 kHz (85 dB) | 18:36 | 0.021 |

### *Test 6*

So far we found synthetic stimuli which, like the natural USC, are discriminated and preferred to 20 kHz tone pulses, and others which are not discriminated and preferentially responded to. Our next question was whether females discriminate a) among preferred USC models, and b) between preferred and non-preferred models.

The results are shown in Table 3. Females showed no significant difference in their response to natural USC and to the 40–60 kHz noise band (which was shown in test 3 to be a preferred USC model). They also did not discriminate between a noise band of 40–60 kHz and one of 35–50 kHz and a combined stimulus of 40–60 kHz+25 kHz. There was no difference in the response to two other, formerly preferred, noise bands (42.5–60 kHz and 37.5–60 kHz) nor to formerly non-preferred noise bands (36–60 kHz and 30–60 kHz, and 33.5–50 kHz and 25–55 kHz).

These results show that the females do not discriminate among stimuli within the class of preferred and within the class of non-preferred ultrasonic call models. However, discrimination between formerly preferred and non-preferred stimuli was found in all cases except when a 40–60 kHz noise band was tested against 40–60 kHz noise + 35 kHz at the same intensity (75 dB). When the SPL of the 35 kHz tone was increased to 85 dB the expected preference for the 40–60 kHz noise band alone re-appeared. Thus females obviously discriminate between preferred and non-preferred USC models. The outcome of test 6 therefore confirms the classification of the model calls in the

**Table 4.** Responses to call models with different temporal structure. The standard call was a series of 60 kHz tone pulses with 80 ms duration + 10 ms rise and fall times and a repetition rate of 3 calls/s. This stimulus was found in test 2 to be a preferred ultrasound model. Rise and fall times are given in brackets behind the durations. NS = not significant

| Stimulus alternatives | Number of responses | Probability |
|---|---|---|
| 80 (+10) ms: 10 (+ 5) ms | 38:16 | 0.004 |
| 80 (+10) ms: 15 (+ 5) ms | 38:16 | 0.004 |
| 80 (+10) ms: 20 (+ 5) ms | 31:23 | 0.342 NS |
| 80 (+10) ms: 30 (+ 5) ms | 30:24 | 0.496 NS |
| 80 (+10) ms: 200 (+ 10) ms | 26:28 | 0.892 NS |
| 80 (+10) ms: 250 (+ 10) ms | 31:23 | 0.342 NS |
| 80 (+10) ms: 275 (+ 10) ms | 36:18 | 0.021 |
| 80 (+10) ms: 300 (+ 10) ms | 38:16 | 0.004 |
| 80 (+10) ms: 50 (+100) ms | 31:23 | 0.342 NS |
| 80 (+10) ms: 80 (+ 50) ms | 29:25 | 0.631 NS |

previous tests. Identification of the preferred class of stimuli (tests 1–5) and discrimination between preferred and non-preferred classes of stimuli but non-discrimination of stimuli from within each class fulfils the conditions for a categorical perception of mouse pup ultrasounds by the females (Ehret and Haack 1981).

### *Test 7*

In this test we investigated recognition in the time domain by varying the stimulus duration and its rise and fall time while keeping the frequency constant. The stimuli were series of 60 kHz tone pulses at 75 dB SPL; the duration and/or the rise and fall times of the pulses were systematically varied. The standard against which the females had to discriminate had a duration of 80 ms and rise and fall times of 10 ms. We know from test 2 that this stimulus is a preferred USC model. In tests with signal durations (including rise and fall times) shorter than 150 ms, inter-pulse intervals were adjusted so that a repetition rate of 3 pulses/s resulted; when the total signal duration was longer than 150 ms the inter-pulse interval was always set at 150 ms.

As shown in Table 4 the females did not discriminate for or against the standard when test signal durations were longer than 20 ms and shorter than 270 ms. Within that range of total signal durations rise and fall times of 5, 10, 20, and 100 ms did not alter the response distribution significantly. Clear preference for the standard occurred when the stimulus alternatives had very short (10 or 15 ms with 5 ms rise and fall times) or very long (>275 ms) durations.

Thus the time window for USC recognition is very broad extending from 20–270 ms. Recognition is also insensitive to variations in repetition rate within the tested range.

## Discussion

### *Key-Stimulus Configuration for Ultrasound Perception*

One important conclusion from the tests just described is that neither the variations in frequency, intensity and duration nor the pure tone characteristics which are features of the natural USC produced by mouse pups are necessary for recognition of these sounds by lactating females, since they respond to pulses of pure tones and of narrow band white noise in the ultrasonic range with very similar probabilities as to natural USC. Relative high response levels were measured to the 20 kHz tone and to other non-preferred signals. This responsiveness to sound which has not the key-stimulus configuration for recognition can be explained by the motivation for searching pups, which, for reasons mentioned in Materials and Methods, was kept high in the present tests. Since it is generally accepted that the specificity and selectivity of response behavior decreases with increasing motivational level, we would expect even higher preference rates for the preferred USC models than found in the present study, if less motivated mice were used. Motivational effects will be discussed in a further study (Haack and Ehret, in preparation).

Smith (1976) investigated the responses of female mice to USC models in a differently designed choice test. Only 5 stimuli were used. The results are comparable with the present ones in that a constant frequency tone of 65 kHz with a downsweep to 45 kHz was preferred over a 55 kHz tone with a downsweep to 35 kHz, and a 80 ms 65 kHz tone was preferred over a 15 ms tone of 65 kHz. With the present results, however, we can define the key-stimulus configuration for recognition of mouse pup USC more precisely. The tests with noise bands indicate the existence of a bandwidth effect. The widest noise band centered near 50 kHz that was accepted as a preferred USC model was 22.5 kHz and had a low frequency cutoff at 37.5 kHz. Around a mid-frequency of near 40 kHz the widest preferred noise band was only 15 kHz and had a lower cutoff at 35 kHz. Since this 15 kHz band contained energy between 37.5 and 35 kHz, which impaired the preferential response to the bands centered near 50 kHz, the limitation for recognition in this case can only be exceeding a bandwidth limit. This critical bandwidth is 22.5 kHz at a center frequency near 50 kHz and 15 kHz at a center frequency near 40 kHz. Sound energy adjacent to the decisive frequency bands disturbs the recognition process (tests 3 and 4). If the additional energy, however, is far enough removed in frequency from these critical frequency bands (test 4) or if its intensity is sufficiently low relative to that of the noise band (test 5) recognition is not affected.

Therefore the condition necessary for recognition of ultrasonic mouse pup calls in the frequency domain is sound energy in a narrow frequency band in the ultrasonic range and significantly less energy in an adjacent frequency band. Low frequency sounds which are heard simultaneously with USC models do not affect the recognition process. The absolute bandwidth for recognition depends on and decreases with its center frequency which probably should not be below 40 kHz (test 2). The upper frequency boundary has not been determined because the auditory thresholds of the mouse increase rapidly above 60 kHz (Markl and Ehret 1973; Ehret 1974) so that the perceptability of sound will be considerably reduced by the absolute sensitivity of the auditory system in that frequency range.

The constraints on sound stimuli for them to be recognized as mouse pup ultrasonic calls are such that no other calls of the mouse vocal repertoire (Ehret 1975; Haack et al. 1982; Whitney and Nyby 1982) can be confused with pup USC, except the ultrasonic calls of adult mice which are produced by both males and females in sexual encounters and by females when they are totally confused. These sounds occur in behavioral contexts very different from that in which pup ultrasound is produced, so that the appropriate response to ultrasound can be adjusted by recognizing the behavioral context together with the sounds.

### *Perception Mechanism*

The frequency domain measurements have shown that pulses of white noise up to certain bandwidths are recognized just as natural mouse pup ultrasound. Such narrow bandwidth sounds are preferred to wider bandwidth sounds. The mechanism responsible for this discrimination must have information about the sound energy distribution over frequency, in order to set up the critical frequency window. At the same time it should ignore variations in temporal parameters as long as their values fall within the permitted range of durations and rise and fall times. One mechanism satisfying these conditions is the "critical band" mechanism of the auditory system. Critical bands of hearing have been defined as a behavioral measure of frequency resolution by the ear and have been found to play a major role in many auditory perception tasks in man (reviews in Fletcher 1940; Zwicker and Feldtkeller 1967; Scharf 1970; Roederer 1975). To perform a critical band analysis of a sound spectrum an animal resolves the spectrum, with the aid of an array of independent bandpass filters, into "packages" of spectral energy each of which is processed and perceived separately. A comparison of the outputs of the critical band filters allows a reconstruction of the original sound spectrum within the limits of frequency resolution of the ear.

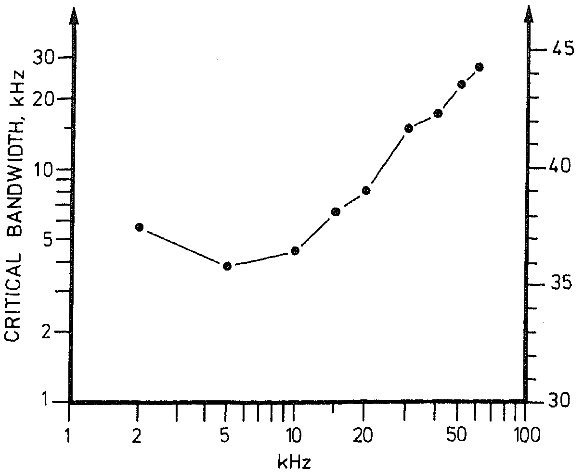

**Fig. 2.** Relation between the critical bandwidths of hearing for the house mouse and the mid-frequencies of these bands. Ordinates: critical bandwidth in kHz and in dB; abscissa: mid-frequencies in kHz. (Data taken from Ehret 1976)

Figure 2 shows a plot of critical bandwidths of hearing against center frequency of the bands for the mouse (Ehret 1976). The critical bandwidth is 22 kHz at 50 kHz center frequency and 18 kHz at 40 kHz center frequency. A comparison of the critical bandwidths of hearing with the critical bandwidths of ultrasound recognition shows that the values are very close: at 50 kHz mid-frequency 22 vs. 22.5 kHz, and at 40 kHz mid-frequency 18 vs. 15 kHz. We can conclude from this excellent agreement between frequency resolution of hearing – the critical band analysis of sound – and of the bandwidths of the preferred USC models that the critical band mechanism in the auditory system is most likely the basis for ultrasonic call recognition in the frequency domain.

This conclusion is also supported by the results of the tests with tone-noise stimuli. In tests 4 and 5 we found that a pure tone the frequency of which was considerably lower (25 and 30 kHz) than the preferred noise band (40–60 kHz) did not disturb call recognition, whereas the 35 kHz tone, which is closer in frequency to the noise band, did. The critical band of hearing around a mid-frequency of 25 kHz is 12 kHz, around a mid-frequency of 30 kHz is 15.5 kHz and around a mid-frequency of 35 kHz is 17 kHz (Fig. 2). Thus critical bands at 25 and 30 kHz mid-frequency do not overlap with the critical band around 50 kHz mid-frequency, within which the noise band was situated; the critical band at 35 kHz mid-frequency, however, extends to 43.5 kHz which is within the noise band. Overlap of critical bands around energy centers in the ultrasonic range apparently abolishes USC recognition, while non-overlap makes recognition possible. We would predict that energy peaks in a sound spectrum containing mouse pup ultrasound have to be separated by at least one critical band (calculated from the higher frequency peak) in order to allow response behavior to the pup calls. This prediction includes that spectral peaks which are separated my more than one critical band do not influence the perception of each other so that pup call recognition should not be influenced by low frequency sounds. This is what we actually found.

Two further properties of critical bands of hearing are of interest. Except very near the absolute threshold of hearing and at very high intensities critical bands are intensity independent (Scharf 1970; Scharf and Meiselman 1977), i.e. frequency resolution does not change with intensity over a considerable range. Thus we have a recognition mechanism which is rather independent of the absolute intensity of the calls. This is important when we consider that female mice must respond to the calls of pups which are different distances away or which are hidden behind sound absorbing objects. Finally the critical bandwidths of hearing do not depend on sound duration or on rise and fall times which means that the temporal variations in the natural calls do not influence processing and recognition in the frequency domain.

In conclusion, the critical band-related mechanism for recognition of ultrasonic calls of mouse pups by their mothers is an efficient strategy for sound evaluation. A model involving critical band processing in the brain has been proposed by Ehret (1982).

*Acknowledgements.* This study was supported by the Deutsche Forschungsgemeinschaft, Eh 53/1–5 and Ma 374/12. We thank Dr. H. Markl and A.J.M. Moffat for discussions and comments on the manuscript.

## References

Ehret G (1974) Age-dependent hearing loss in normal hearing mice. Naturwissenschaften 61:506

Ehret G (1975) Schallsignale der Hausmaus (*Mus musculus*). Behaviour 52:38–56

Ehret G (1976) Critical bands and filter characteristics in the ear of the house mouse (*Mus musculus*). Biol Cybern 24:35–42

Ehret G (1982) Auditory processing and perception of ultrasounds in house mice. In: Ewert JP, Capranica RR, Ingle DJ (eds) Advances in vertebrate neuroethology. Plenum Press, New York London (in press)

Ehret G, Haack B (1981) Categorical perception of mouse pup ultrasound by lactating females. Naturwissenschaften 68:208

Fletcher H (1940) Auditory patterns. Rev Mod Phys 12:47–65

Haack B, Markl H, Ehret G (1982) Sound communication between parents and offspring. In: Willott JF (ed) Auditory psychobiology of the mouse. Thomas, Springfield (in press)

Machmerth H, Theiss D, Schnitzler HU (1975) Konstruktion eines Luftschallgebers mit konstantem Frequenzgang im Bereich von 15 kHz bis 130 kHz. Acustica 34:81–85

Markl H, Ehret G (1973) Die Hörschwelle der Maus (*Mus musculus*). Eine kritische Wertung der Methoden zur Bestimmung der Hörschwelle eines Säugetiers. Z Tierpsychol 33:274–286

Noirot E (1972) Ultrasounds and maternal behavior in small rodents. Dev Psychobiol 5:371–387

Okon EE (1972) Factors affecting ultrasound production in infant rodents. J Zool 168:139–148

Roederer JG (1975) Introduction to the physics and psychophysics of music. Springer, Berlin Heidelberg New York

Sales GD (1972) Ultrasound and mating behaviour in rodents with some observations on other behavioral situations. J Zool 168:149–164

Sales GD, Smith JC (1978) Comparative studies of the ultrasonic calls of infant murid rodents. Dev Psychobiol 11:595–619

Scharf B (1970) Critical bands. In: Tobias JV (ed) Foundations of modern auditory theory, vol 1. Academic Press, New York, pp 159–202

Scharf B, Meiselman CH (1977) Critical bandwidth at high intensities. In: Evans EF, Wilson JP (eds) Psychophysics and physiology of hearing. Academic Press, New York, London, pp 221–232

Sewell GD (1968) Ultrasounds in rodents. Nature 217:682–683

Smith JC (1976) Responses of adult mice to models of infant calls. J Comp Physiol Psychol 90:1105–1115

Whitney G, Nyby J (1982) Sound communication among adults. In: Willott JF (ed) Auditory psychobiology of the mouse. Thomas, Springfield (in press)

Whitney G, Coble JR, Stockton MD, Tilson EF (1973) Ultrasonic emissions: Do they facilitate courtship in mice? J Comp Physiol Psychol 84:445–452

Zwicker E, Feldtkeller R (1967) Das Ohr als Nachrichtenempfänger. Hirzel, Stuttgart