AUDITORY PROCESSING AND PERCEPTION OF ULTRASOUNDS

IN HOUSE MICE

Günter Ehret

Fakultät für Biologie
Universität Konstanz
D-7750 Konstanz, F. R. of Germany

Housemice have a vocal repertoire of 8 different call types, at least 4 of these are used in intraspecific communication (Ehret, 1975; Haack et al., 1982; Whitney and Nyby, 1982). There is always interindividual variability among calls of one type; therefore, the receiver of the calls must generalize across this variability in order to identify a call type, and to discriminate a particular call from others and from the acoustic background. The present paper deals with ultrasound perception by house mice. This example of call perception clearly demonstrates the abilities of the animals to generalize, to identify and to discriminate species-specific calls. The key-stimulus configuration in the frequency domain for ultrasound perception is described and then the physiological basis for why and how the mouse is able to perceive the ultrasonic calls is discussed.

Key-Stimulus Configuration. Fig.1 shows sonagrams of the ultrasonic calls emitted by a mouse pup when distressed or isolated from the nest. The range of variability in the calls of an individual pup (Fig.1) is about as great as the range of interindividual variability of the calls of pups of a given age. The receivers of these calls are the mothers, who respond with such maternal behavior as searching for a lost pup, retrieving it to the nest, licking, warming and lactating it. When adult females recognize such calls and discriminate them from other sounds, they do so by generalizing across frequency and intensity variations, frequency sweeps, and call durations. In a series of choice experiments, Ehret and Haack (1981) and Ehret and Haack (in prep.) investigated the preference of lactating female mice for synthesized model calls such as bursts of pure tones or of narrow band white noise (see sonagram in Fig.1). Females placed in the central nest area of a running board had the choice of moving to the right or to the left toward one of two speakers each emitting a different sound alternative.

Table 1 shows the results. Playbacks of natural ultrasonic calls were clearly preferred to a 20kHz tone stimulus of equal sound pressure level which served as a neutral stimulus (not occurring in

Fig.1. Sonograms of ultrasonic calls of a mouse pup and of a narrow band noise used as a call model.

the mouse' vocal repertoire) and which was even better audible to the mouse than the ultrasound (Ehret, 1974). Call models, either pure tones of 60 and 40kHz or noise bands of 17.5, 20, and 22.5kHz bandwidth centered at approx. 50kHz were all about equally preferable. If the noise bandwidth was increased to 24, 25, or 30kHz, the preference for the ultrasound model disappeared. We tested a similar sequence of noise bands centered at about 40kHz and in this case only a noise band of 15kHz width was preferred; bandwidths of 16.5, 20 and 30kHz were not. Finally, 3 combined stimuli were tested: a narrow noise band (40-60kHz) which we know was preferred as a call model plus a 25, 30, or 35kHz tone of SPL equal to that of the noise band (75dB). The response distribution shows (Table 1) that the 25 and 30kHz tones did not change the preference for the noise band; the 35kHz tone, however, which is closer to the noise band, did.

These results demonstrate that neither frequency nor intensity variations nor the pure tone characteristics of the natural calls

Table 1. Responses of lactating house mice in tests where they had to identify natural ultrasonic calls (natural USC) and synthesized model calls (tones and noise bands) against a neutral 20kHz stimulus. Data were analyzed with a two-tailed binominal test and the probability of the response distribution is indicated. NS = not significant.

Stimulus alternatives		No. of responses	Probability
natural USC	: 20 kHz	35 : 17	0.018
60 kHz	: 20 kHz	34 : 16	0.016
40 kHz	: 20 kHz	34 : 16	0.016
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
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	0.011
40 -60 kHz+35 kHz	: 20 kHz	29 : 22	0.401 NS
natural USC	: 40-60 kHz	22 : 29	0.401 NS

are necessary for ultrasound perception and response release in lactating females. Bursts of pure tones and of narrow band noise are responded to equally well. In a discrimination test, natural ultrasound and a narrow noise band were not differentiated (Table 1). We found that the females do not discriminate among relevant ultrasound models but they do discriminate between narrow and broadband noises and they do this in a categorical fashion (Ehret and Haack, 1981). Thus, the conditions necessary for the perception and recognition of ultrasonic mouse pup calls in the frequency domain are sound energy in a narrow frequency band in the ultrasonic range and significantly less energy in adjacent frequency bands. The bandwidths over which mice generalize are 22.5kHz at about 50kHz mid-frequency and 15kHz at a mid-frequency of about 40kHz. Such a system is a highly effective receiver for a call with the variabilities of parameters shown in Fig.1.

Physiology of Perception and Discrimination. The choice tests have shown that ultrasound perception depends on the resolution of a sound spectrum into frequency bands. A behavioral measure of frequency resolution in the auditory system is the critical band (Fletcher, 1940; Scharf, 1970; Ehret, 1976). Critical bands are frequency filters which have been found to play a role in many auditory perception tasks in man. A critical band analysis of a sound spectrum means that an animal resolves the spectrum with the aid of a frequency screen the mesh-size of which is the critical bandwidth. A plot of the critical bandwidth against center frequency of the bandwidth for the mouse (Ehret, 1976) shows that at 50kHz center frequency the critical band of hearing is 22kHz which is almost identical with the widest bandwidth of acceptable ultrasound models (22.5kHz). At 40kHz the critical band of hearing is 18kHz, which compares well with the 15kHz found in the behavioral experiments. We can conclude from this excellent agreement between frequency resolution of hearing - the critical bandwidth - and the bandwidths of the preferred ultrasound models that the critical band mechanism in the auditory system of the mouse is involved in ultrasound perception and recognition.

In search of the critical band mechanism we recorded from single units in the auditory nerve, ventral cochlear nucleus and inferior colliculus of the adult mouse (Ehret and Moffat, in prep.) and determined their filtering properties with the same tone-noise stimuli used in the psychophysical tests. Fig.2 shows the frequency dependence of critical bandwidths of auditory nerve and cochlear nucleus units plotted as the means for all neurons with best frequencies around the center frequencies (abscissa) indicated. Behavioral means and standard deviations are also shown. It is evident that critical bands in single units in the auditory nerve and cochlear nucleus exist and, therefore, the basis for the critical band mechanism is in the cochlea. The shape of the curves and the absolute values, however, are somewhat different from the behavioral bandwidths; therefore, further processing in the brain toward the psychophysical filter bands must occur. In the colliculus, neurons show a variety of different response patterns to our stimulus configuration. Preliminary results suggest that the critical bands of one group of neurons, those which are excited by continuous noise, follow the behavioral curve. However, our data also indicate that at the midbrain level all units may be involved in processing critical band information. In addition, not all properties of the behavioral critical bands are obvious at the colliculus level suggesting that still further processing is necessary.

A Model of Critical Band Related Sound Perception. The descriptive model shown in Fig.3 is based on the psychophysics of critical bands, on data for ultrasound perception by the mouse and on the physiology of critical bands at the level of single units. The

Fig.2. A comparison of neural and behavioral critical bands (measured as critical ratio bands). Filled circles: behavioral means with standard deviations. Filled and open squares: Mean critical ratio bands from single units in the auditory nerve and cochlear nucleus (lower curves determined from the total response to a tone burst in noise; upper curves from the latency to the tone onset).

instantaneous sound spectrum shown (Fig.3) mimics the situation where the mouse recognized a narrow noise band around 50kHz as an effective ultrasound model in the presence of a pure tone at 25kHz (Table 1). There may also be some low-frequency background noise.

Within the cochlea the spectrum is divided among tonotopically arranged frequency channels. One column represents the total excitatory output of a number of neurons with characteristic frequencies within one critical band. The psychophysical critical bandwidth can be defined at a higher brain level as the frequency band over which the excitation of many units is integrated. After comparison of the integrated excitation distribution with a template (which, for ultrasound perception in mice is equal to excitation in a critical band in the ultrasonic range and significantly less excitation in neighbouring critical bands, with excitation in the low-frequency range being irrelevant for perception) and after the influences of other factors a response may occur. This simple model works for time invariant signals. If it is applied to time varying sounds the template should have also a temporal dimension. This model brings the important steps of

Fig.3. Model of processing and detection of sound in critical bands in the auditory system (for explanation see text).

ultrasound perception and recognition within critical bands into a logical sequence. It shows that the perception process generalizes over interindividual variations in frequency and intensity and ignores the presence of low-frequency sound which is of advantage for identification of the call type "ultrasound".

Acknowledgement: This work is supported by the Deutsche Forschungsgemeinschaft, Eh 53/1-6.

REFERENCES

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

Ehret,G.,1975, Schallsignale der Hausmaus. Behaviour, 52:38-56.

Ehret,G.,1976, Critical bands and filter characteristics in the ear of the house mouse. Biol. Cybernetics, 24:35-42.

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

Fletcher,H.,1940, Auditory patterns. Rev. Modern Phys., 12:47-65.

Haack,B., Markl,H., and Ehret,G.,1982, Sound communication between parents and offspring, in "Auditory Psychobiology of the Mouse", J.F.Willot, ed., Charles C.Thomas, Springfield.

Scharf,B.,1970, Critical bands, in "Foundations of Modern Auditory Theory" Vol.I, J.V.Tobias, ed., Academic Press, New York.

Whitney,G., and Nyby,J.,1982, Sound communication among adults, in "Auditory Psychobiology of the Mouse", J.F.Willot, ed., Charles C.Thomas, Springfield.