



## Categorical perception of mouse-pup ultrasounds in the temporal domain

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(Received 23 November 1990; initial acceptance 26 February 1991;  
final acceptance 11 July 1991; M.S. number: 3694)

**Abstract.** Mouse-pup ultrasounds emitted from outside the nest area are releasers of maternal pup searching and retrieving behaviour. House mouse, *Mus domesticus*, mothers were tested in a situation with two alternative choices for their unconditioned preference of 50 kHz tone bursts of various durations (models of mouse-pup ultrasounds). Categorical perception in the temporal domain was established by labelling and discrimination tests. Two categories occurred: one of non-preferred short-duration tones (25 ms and shorter) and the other of preferred long-duration tones (30 ms and longer) with a sharp boundary between 25 and 30 ms. Stimuli from the two categories were discriminated, however, only if they differed in duration by at least 20–25 ms, which may be the threshold of duration discrimination. The discussion concentrates on the biological significance of categorical perception of communication sounds and possible mechanisms of boundary formation.

Animals communicating with various species-specific sounds must recognize their distinct acoustic structures; that is, they have to differentiate between the important or characteristic 'key-stimulus' patterns of these sounds in order to generate a biologically significant adaptive response in a given behavioural context. The problem of sound-pattern recognition is a general one for a wide variety of species (from insects to humans) using sound for communication purposes. Thus we may expect and actually find many strategies in the auditory and perceptual systems and in the behaviour patterns of species that contribute to optimizing the discrimination of sound-pattern and extraction of the message. One such strategy is categorical perception, a standard term in human psychophysics and cognitive psychology (Harnad 1987). In an auditory test of categorical perception, for example, a single acoustic parameter of a sound signal is varied on a continuous scale while the listener indicates the perceived quality of the sounds. If the listener labels or identifies the sounds as belonging to separate perceptual classes or categories and if sounds with the same labels are poorly discriminated but sounds with different labels are well discriminated in discrimination tests, then a categorical perception along the continuum of the varied sound parameter is established (compare Liberman et al. 1957; Ehret 1987a; Harnad 1987). Thus, the criterion for categorical perception to occur is that both labelling (identification) and

discrimination tests reveal categorization of sounds differing continuously in a single sound parameter.

Categorical perception of sounds has been found, for example, in the frequency domain for musical pitch and in the time domain for speech-phoneme recognition. The perceptual differences between a number of phonemes composed of stop consonants and a vowel depend on the length of the interval between the articulation of the stop-consonant and the beginning of the vowel (voice-onset-time). The formation of category boundaries in the continuum of voice-onset-times, however, is a characteristic of speech phoneme discrimination not only by humans but also by animals such as budgerigars, *Melopsittacus undulatus*, chinchillas, *Chinchilla laniger*, and rhesus monkeys, *Macaca mulatta*. Interestingly, boundaries on the /ba-/pa/ continuum of voice-onset-times are very similar for humans (about 27 ms; Pisoni & Lazarus 1974; Kuhl & Miller 1978), chinchillas (23 ms; Kuhl & Miller 1978) and rhesus monkeys (31 ms; Waters & Willson 1976), which is also the case for the /da-/ta/ continuum (budgerigars: 35 ms; Dooling 1989; humans 35 ms, chinchillas 33 ms; Kuhl & Miller 1975, 1978; Kuhl 1981). Thus, birds and mammals can categorize complex sounds in the time domain and perform very similarly to humans if the sound is speech. Obviously, mammalian auditory systems and sound processing strategies carry adaptations as mechanisms not only to differentiate

but also to classify sounds on the basis of certain acoustic features.

An evolutionary perspective on categorical perception is supported by data on species-specific communication sounds that may be perceived categorically in a certain sound dimension by the respective animals (reviews in Ehret 1987a; Snowdon 1987). Labelling functions with relatively sharp category boundaries have been shown for responses to (1) syllable repetition rate of calling songs of field crickets, *Gryllin campestris* (Thorson et al. 1982), (2) carrier frequency of calling songs of Australian crickets, *Teleogryllus oceanicus* (Moiseff et al. 1978), (3) pulse number in mating calls of green treefrogs, *Hyla cinerea* (Gerhardt 1978a, b), (4) sound pressure level of a 500 Hz component in a mating call of bullfrogs, *Rana catesbeiana* (Capranica 1966), (5) frequency bandwidths of mouse-pup ultrasounds (Ehret & Haack 1981, 1982; Ehret 1987a), (6) duration of contact trills of pygmy marmosets, *Cebuella pygmaea* (Snowdon & Pola 1978; Snowdon 1987) and (7) frequency modulation of the coo calls of Japanese macaques, *Macaca fuscata* (May et al. 1989). Discrimination functions confirming categorical perception by across-boundary discrimination and within-category non-discrimination were obtained only for the bandwidth dimension of mouse-pup ultrasounds. Since categorical perception can be assessed only if both labelling and discrimination tests indicate the presence of boundaries at the same location of a continuously variable parameter, categorical perception of species-specific calls needs to be substantiated by more examples as an important mechanism of communication call perception and recognition in animals.

The present experiments are designed to contribute more data to the previously measured labelling functions of duration perception of mouse-pup ultrasounds (Ehret & Haack 1982; Ehret 1987a) and to add discrimination tests which are critical for the assessment of categorical perception. If a stable category boundary is confirmed close to a sound duration of 25 ms, as the preliminary labelling tests suggest, it will be important to discuss this value with regard to the biological significance of communication-sound categorization, and mechanisms that may set such boundaries.

## MATERIALS AND METHODS

Experiments were conducted with the same methods as described in Ehret & Haack (1982). Ultrasound-

**Table I.** Responses to synthesized ultrasonic pup calls of various durations

Stimulus alternatives	Number of responses	<i>P</i> *
†100 (10) ms:20 (5) ms	38:16	0.004
†100 (10) ms:25 (5) ms	38:16	0.004
†100 (10) ms:30 (5) ms	31:23	0.342
†100 (10) ms:40 (5) ms	30:24	0.496
85 (2.5) ms:10 (2.5) ms	38:16	0.004
85 (2.5) ms:20 (2.5) ms	35:18	0.028
85 (2.5) ms:25 (2.5) ms	36:18	0.020
85 (2.5) ms:50 (2.5) ms	27:24	0.779
105 (2.5) ms:15 (2.5) ms	36:18	0.020
105 (2.5) ms:25 (2.5) ms	33:17	0.034
105 (2.5) ms:35 (2.5) ms	26:24	0.888
105 (2.5) ms:45 (2.5) ms	27:23	0.670

The standard calls (preferred releasers of pup searching behaviour) are indicated first. They have longer durations than the comparison calls of which the label 'preferred' or 'non-preferred' is tested. The durations include the rise and fall times (indicated in parentheses) of the tone bursts. \*Binomial test, two-tailed.

†Values measured previously (Ehret & Haack 1982).

released pup-searching behaviour served as an indicator of stimulus preference. Female house mice (outbred strain NMRI, aged 3–5 months) with litters 2–6 days old were used. Tests were run under dim red light in a sound-proof and anechoic room. At a minimum of 6 h before testing, a female with her own litter was placed in the central nest depression of a running board (length: 110 cm; width: 8 cm) suspended between two ultrasonic speakers (distance of speaker from nest = 65 cm). One speaker emitted one stimulus alternative (A or B) which, together with the other alternative from the other speaker, formed a single series of equally spaced alternating stimuli (e.g. A, B, A, B . . .) at a rate of 3 per s. Stimuli were 50 kHz tone-bursts (average sound pressure level in the nest = 75 dB re. 20 µPa) with 2.5 ms rise and 2.5 ms fall times and various durations as critical parameters (see Tables I, II). In the previous tests (Ehret & Haack 1982; Ehret 1987b) tone bursts of 40, 50 or 60 kHz and 80 ms duration (+10 ms rise and 10 ms fall time) were used as standard stimuli. These stimuli elicited the same phonotactic behaviour as natural ultrasounds when tested against other stimuli in a test with two alternative choices (Ehret & Haack 1982; Ehret 1987b). Lactating females accepted these standard tone-bursts as relevant models of pup

**Table II.** Discrimination tests with stimulus alternatives of various durations (2.5 ms rise and 2.5 ms fall times included) taken from the two categories established by the labelling tests (see Fig. 1, Table I)

Stimulus alternatives	Number of responses	<i>P</i> *
Within-category comparisons		
20 ms:10 ms	23:31	0.342
25 ms:10 ms	22:32	0.221
25 ms:15 ms	30:24	0.496
55 ms:35 ms	21:29	0.322
Across-boundary comparisons		
30 ms:10 ms	29:23	0.488
35 ms:10 ms	33:17	0.034
35 ms:15 ms	33:18	0.050
35 ms:20 ms	24:26	0.888
35 ms:25 ms	29:23	0.488
45 ms:25 ms	25:25	1.000
45 ms:20 ms	36:16	0.008
55 ms:25 ms	33:18	0.050

\*Binomial test, two-tailed.

ultrasounds. The stimuli to be labelled same or different compared to the standard were of the same frequency but differed in duration and rise and fall times of the bursts. To reduce variables, all stimuli employed in labelling and discrimination tests of the present study had the same rise and fall times (2.5 ms) and differed only in duration which is the critical variable of the present tests of categorical perception.

I started a test by letting the female carry four pups of her own litter distributed on the running board (two on each side of the nest) back to the nest. After she had retrieved the pups and settled again in the nest (usually within 5 min), the two speakers were switched on simultaneously. The female indicated her preference for one of the stimulus alternatives by leaving the nest within 10 min (criterion) and moving at least 30 cm (criterion) towards one of the speakers. As soon as she had reached the 30-cm mark, the speakers were switched off. After the female had moved back to the nest and remained there for at least 30 s, the speakers were switched on for the second run. A maximum of six runs, with stimulus alternatives assigned randomly to the speakers, were sampled in a test. Each female was used in two tests with different stimulus alternatives on different days.

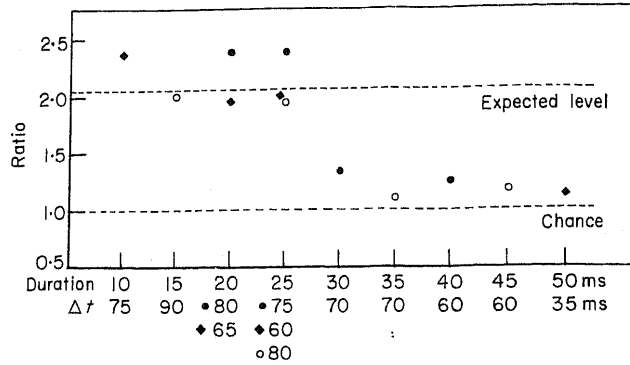
Several females did not respond six times in a test because they started nursing their pups and stayed

in the nest for more than 10 min after stimulus onset. I did not disturb or force the animals in any way and thus collected fewer than six decisions from a number of females. Since I generally allowed six runs per female and aimed at a total of 50 runs per stimulus alternative, the number of runs at each stimulus alternative varied between 50 and 54, and involved 9–12 females.

The statistical significance of stimulus preference in this test with two alternative choices was assessed with a two-tailed binomial test. To be able to use the binomial test, all responses to be compared must be independent events. Haack and I have shown before for a large sample of 215 female mice (Ehret & Haack 1984; Haack 1985) that the six consecutive runs of a given female in response to synthesized pup-ultrasounds can be regarded as independent of each other under the experimental setting and conditions and with the strain of mice used in the previous and present tests. This justifies the application of the binomial test to the present data set (despite multiple tests of every animal) and thus led to a reduction of the number of experimental animals ( $N=112$ ). If I had allowed only one run per female in a test with other conditions unchanged, 500 animals would have been necessary to complete the 20 stimulus discriminations of the present measurements.

## RESULTS

Labelling tests were done with the stimulus alternatives listed in Table I. Consistently, tone bursts longer than 25 ms (rise and fall times included) were not labelled as different from the standard tone bursts with standard durations (85, 100 or 105 ms rise and fall times included). When the comparison tones were 25 ms or shorter the standard bursts were significantly preferred, e.g. the females directed their search for pups significantly more often towards the speaker emitting the longer signals. The sharp boundary of labelling tone-durations of 25 ms and shorter as different from the standard and those of 30 ms or longer as same as the standard is illustrated in Fig. 1. Tone bursts of 25 ms and shorter all led to response ratios close to an expected level of discrimination previously obtained in tests of natural ultrasounds versus a neutral non-preferred stimulus (20 kHz tone-bursts of 100 ms duration, Ehret & Haack 1981, 1982). An increase of only 5 ms duration (from 25 to 30 ms)



**Figure 1.** Labelling of synthesized ultrasounds of various short durations (10, 15, 20... 45, 50 ms; rise and fall times included) against preferred standard tone bursts of long-durations (85 ms =  $\blacklozenge$ , 100 ms =  $\bullet$ , 105 ms =  $\circ$ ; rise and fall times included). The ratio is the number of responses to the long stimulus divided by that to the short stimulus (see Table I). The chance level indicates that the stimulus alternatives (long versus short) are labelled 'same'; the expected level shows the ratio if natural ultrasounds are compared with a non-preferred stimulus. The duration differences,  $\Delta t$ , between the stimulus alternatives are also indicated.

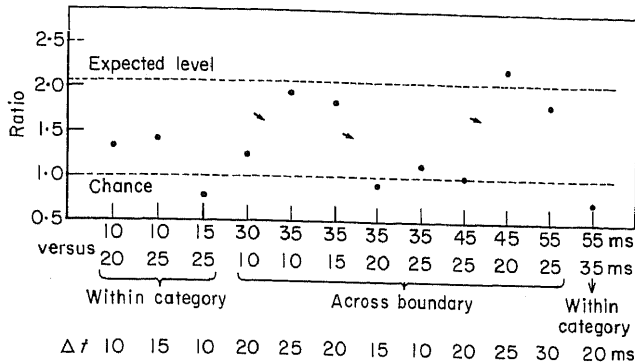
changed a non-preferred stimulus to one chosen as much as the standard (chance level of discrimination). Thus the labelling tests divide up into two categories: the first category includes all stimulus pairs that are well discriminated, the second category includes stimulus pairs that are not discriminated.

Duration differences ( $\Delta t$ -values) between the test stimuli overlapped in the two categories on the duration continuum (Fig. 1). Thus, the boundary between 25 and 35 ms tone duration was established by duration discrimination and not on the basis of perception of the difference in tone duration ( $\Delta t$ ) itself.

If the formation of two perceptual categories in the duration continuum illustrated in Fig. 1 is evidence for categorical perception, then discrimination tests should reveal within-category non-discrimination and across-boundary discrimination. To test this, the stimulus alternatives listed in Table II were offered and the choice behaviour of the mice observed. The data (Table II and Fig. 2) indicate that the criterion of within-category non-discrimination is fulfilled in all cases. Response numbers vary at about chance level. The results of across-boundary discriminations, however, are not coherent in that in some cases the longer stimulus is preferred over the shorter one as is expected, while in others a significant preference does not occur. In all across-boundary non-discriminations the

durations of the stimulus alternatives differed by only 20 ms or less, while in all across-boundary discriminations the durations of the stimulus alternatives differed by 20 ms or more. Obviously, a  $\Delta t$  of 20–25 ms is a critical duration difference beyond which a further reduction prevents any tone-duration discrimination irrespective of the categories the sounds are taken from. This is evidence that a 20 ms duration difference may be the absolute threshold of discrimination of tone duration for mice in these tests. Tones from the two categories that differed by only 10 or 15 ms were not discriminated. There was only one case out of three of an across-boundary discrimination with a 20 ms duration difference between the tones (35 ms versus 15 ms). In this case, the 20 ms difference of tone duration was distributed symmetrically on each side of the category boundary close to 25 ms. In the other two cases (30 ms versus 10 ms and 45 ms versus 25 ms) the duration of one stimulus alternative was very close to the category boundary which may have prevented discrimination of a 20 ms difference.

Thus, the data demonstrate clear evidence of categorical perception in the temporal domain by house mice as long as the mice are not forced to make across-boundary comparisons beyond their absolute threshold of duration discrimination which occurred at about 20–25 ms in these tests of natural unconditioned response behaviour.



**Figure 2.** Discrimination ratios for stimuli of different durations labelled 'same' (within-category) or 'different' (across-boundary) in the labelling tests (Table I, Fig. 1). Stimulus alternatives are indicated (e.g. 10 versus 20 ms) and the ratios of the response numbers plotted (chance and expected levels as in Fig. 1). Arrows point to shifts of the duration difference between the stimulus alternatives critical for the assessment of across-boundary discriminations.

## DISCUSSION

The present labelling and discrimination tests yield the first demonstration of categorical perception of species-specific communication sounds in the temporal domain by a non-human animal. Female house mice divide the duration continuum of pup ultrasounds into two categories. Sounds longer than 25 ms belong to the category of relevant stimuli for a phonotactic approach towards the sender. Sounds of 25 ms and shorter may also elicit a run towards the sound source; however, if tested in a choice situation with sounds of the long-duration category as an alternative, the short sounds are significantly less preferred than the longer ones. Interestingly, the durations of natural ultrasounds of mouse pups vary between about 30 ms and 120 ms (Ehret 1975; Sales & Smith 1978). That is, despite the large variability of natural stimuli, virtually all natural ultrasounds are within the preferred long-duration category. Haack and I have shown before (Ehret & Haack 1981, 1982; Ehret 1987a) that female house mice categorize pup ultrasounds in the spectral domain (boundaries at a minimum frequency and a maximum frequency bandwidth). As with the present duration perception, the category boundaries are such that virtually all natural ultrasound spectra fall into the category of preferred releasers of the phonotactic approach. Thus, as far as I know, house mice are the only non-human animals for which categorical perception of communication calls has been shown in two sound dimensions: duration and spectral composition. The places of the category boundary on the respective sound dimensions are in both cases optimally

sited to allow discrimination between relevant and irrelevant sounds as key-stimuli for the release of a certain maternal behaviour. The close matching of the acoustic structure of ultrasounds and categorical perception as a mechanism to optimize an adaptive response behaviour or 'recognition' of the ultrasounds is evident.

The formation of category boundaries of perception at the natural acoustic boundaries of production of ultrasounds with regard to sound duration and frequency parameters shows that the mouse can use the whole natural physical range of ultrasounds in the duration and frequency domain for call recognition. This ensures that the variability of structure among the ultrasounds of individual mouse pups of a litter and among the pups of various ages is ignored by the mother who responds to a call type standardized by her perceptual mechanisms. At the same time, the category boundaries of perception set the limits beyond which an increase in variability or a shift in ultrasound structure in the course of further evolution becomes unlikely because sounds outside these limits would have a low probability of releasing a biologically significant response. Further, the category boundaries of ultrasound perception in the duration and frequency domain ensure that pup ultrasounds cannot be confused with (1) very short smacking and cracking sounds of pups (duration and frequency boundaries relevant), (2) wriggling, postpartum and rough-handling sounds of pups (Haack et al. 1983) and (3) distress and defensive calls of adult mice (frequency boundary relevant; Ehret 1975; Whitney & Nyby 1983). The only overlap in both the duration and frequency domain is with

ultrasounds of adult mice that are emitted mainly during social investigation and mating. Since in such behavioural contexts ultrasounds are produced by an adult animal in close physical contact with the receiver of the sounds, the behavioural setting is very different from that of perceiving pup ultrasounds from outside the nest. Thus, the perception of the behavioural context together with ultrasounds may help to guide the behaviour of the receiver to an adaptive response. In conclusion, the discussed category boundaries of ultrasound perception lead to a clear discrimination of ultrasounds and their message from all other sound of the mouse repertoire and from very many environmental sounds such as clicks, noise bursts, low-frequency and broad-band sounds. As I have argued before (Ehret 1987a), categorical perception is ideal to enhance on the perceptual side the acoustic contrast between different sounds of a repertoire, to reduce the influence of background noise on the perception process and to ensure biologically significant responses to sounds of importance. Hence, the renunciation of discrimination possibilities by mice and other animals using categorical perception in sound recognition does not mean that these animals give away useful information present in their auditory systems. On the contrary, the biologically useless individual and inter-individual variability, with regard to sound parameters perceived categorically, is disregarded so that the perception of the main message, which in the case of pup ultrasounds is 'a pup needs help', is improved. Finally, the occurrence of categorical perception may indicate that the perceptual and recognition system of an animal is tuned to detect discrete types of message (i.e. call types) and not to evaluate continuous motivational levels of the sender that are reflected in continuous variations of sound parameters.

Mechanisms of boundary formation for categorical perception are still obscure. From experiments on ultrasound perception in the spectral domain (Ehret & Haack 1982, 1984) and on the spectral resolution in the auditory system (critical band mechanism: Ehret 1976; Ehret & Merzenich 1985, 1988) I have previously suggested that boundaries of categorical perception may be set by sensory mechanisms, and recognition of the category label would be part of higher innate releasing mechanisms or cognitive processes (Ehret 1987a). This conclusion from ultrasound perception in the spectral domain is supported by the present data. The cat-

egory boundary on the duration continuum (25–30 ms) occurs very close to the estimated absolute threshold of duration discrimination (20–25 ms) both determined by an unconditioned behaviour in the same natural communication situation. The boundary close to 25 ms seems to be established on the basis of a natural time constant of the auditory system that is responsible for the duration discrimination threshold of 20–25 ms. A threshold of perception or time constant of about 20 ms has been observed in various psychophysical measurements in humans. Examples are the studies of Summerfield (1982) on the perception of temporal order of sound stimuli, Stevens & Klatt (1974) on the detection of a gap between a noisy sound onset and a buzz-like stimulus continuation, Penner (1975) on the perception of a temporal gap in noise, Pisoni (1977) on the perception of a two-frequency tone with onset-differences between the two frequencies, de Boer (1985) on the detection of amplitude modulation as a function of modulation frequency, and Madler & Pöppel (1987) on periods of neural oscillations in networks of the brain. This evidence and the present work suggest that the mammalian auditory system has a time constant or a threshold of perception in the time domain close to 20 ms. That is, whenever a time difference is introduced as a critical variable in a psychoacoustical test, the change of the perceived stimulus quality should occur close to a 20 ms difference. In addition to the above mentioned data, studies on the perception of voice-onset-time of speech phonemes in animals, including humans, are in harmony with the suggestion of a basic 20–25 ms time constant. The shortest boundary on the continuum of voice-onset-times occurs with the /ba-/pa/ discrimination at about 27 ms in humans and 23 ms in chinchillas (Pisoni & Lazarus 1974; Kuhl & Miller 1978). The boundaries for other phoneme discriminations on the basis of voice-onset-times are set at longer voice-onset-times and thus require additional, perhaps higher, mechanisms of learning and cognitive strategies.

The present data on the categorical perception of mouse ultrasounds in the time domain and the previous ones in the spectral domain (Ehret & Haack 1981, 1982; Ehret 1987a) support the view that processing mechanisms and limits of the auditory system serve as guidelines for the perceptual differentiation between communication calls and between communication sounds and other sounds. Mice may still be on this rather basic level when

they respond innately to the calls of conspecifics which are also produced innately (Rottberger 1980). In humans with our highly differentiated and well learned speech, natural boundaries on various sound dimensions (spectral composition, duration, etc.) could guide a rapid acquisition of further learned perceptual boundaries on these dimensions by providing examples for learning what sound features are important so that selective attention may be directed to these features (see Ehret 1987a; Kuhl 1987).

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