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ULTRASONIC CALLS AND COMMUNICATIONS IN RODENTS

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The first report of high frequency calls from rodents came in 1948 (Schleidt, 1948), and was followed in 1956 by the now classic paper of Zippelius and Schleidt describing ultrasonic calling by the young of three species of rodents. The study of rodent ultrasound then appears to have lain dormant until about 1963 when Noirot suggested that the findings of Zippelius and Schleidt could account for many of her observations on maternal behaviour in non-lactating laboratory mice, Mus musculus (see Noirot, 1972). Noirot's subsequent studies on ultrasound in rodents marked the beginning of a rapid expansion of interest in the subject and it is now known that many species of rodent emit such calls and in a variety of situations. The year 1984 then represents approximately 21 years since the early studies of Noirot and it would appear to be a good time to review the present position of our knowledge of rodent ultrasound.

Ever since the calls were first detected it has been suggested that ultrasounds are used for communication in rodents. In any system of communication, a sender transmits a signal to a receiver. According to the semiotic theory of animal communcation, the signal or message carries information on the state of the sender, the receiver can detect the signal and the way in which it responds to it determines the meaning of the signal (see Adler & Anisko, 1979). Most of the studies of rodent ultrasound are concerned with various aspects of such communication. Many studies deal with signal emission; with the physical characteristics of the calls emitted at various ages or in different situations, or with the causal factors affecting ultrasound emission, that is with attempting to determine if particular calls are associated with a particular state of the sender. Other studies are concerned with signal reception; with auditory sensitivity and with the effect of particular calls, or the lack of them, on the behaviour of potential recipients in certain situations. This paper attempts to review briefly examples of the developments in each of these areas and to point to new areas of study. For brevity, review or most recent articles are cited whenever possible.

Ultrasonic calling by rodents. Ultrasonic calls have been detected from infants of over 60 species and from adults of over 30 species of rodents all, with one exception, from five subfamilies of the Family Muridae (rats, mice, hamsters and gerbils). There has been one report of ultrasonic calls from within the Family Gliridae (dormice). There appear to have been no adequate studies on other rodent families and the brief studies on the Families Caviidae, Ctenomidae and Dasyproctidae revealed only a few detectable calls in the latter (Sewell, 1969).

The ultrasonic calls of newborn rodents are typically between 2 and 200 ms in duration, 20–150 kHz in frequency and show little frequency change over their length. There appears to be no clear distinction between the calls of different species although there are some differences in the calls of the various subfamilies and even of different strains (Smith & Sales; 1980, in prep.) Infants of the Subfamily Murinae (Old World rats and mice) generally emit purely ultrasonic calls with a single frequency component (Sales & Smith, 1978), although lower frequency calls and more complex frequency patterns are occasionally found (Price, pers. comm.) In the Subfamily Microtinae (voles) the calls either consist of a single frequency component or have two to three harmonic components and often show instantaneous changes in frequency. In the other three subfamilies, the Hesperomyinae (New World rats and mice), Cricetinae (hamsters) and Gerbillinae (gerbils), a variety of frequency patterns are found including both narrowband sounds with a single frequency component or a narrow band of unstructured noise and wide bandcalls with many harmonic components or with unstructured components which in both cases may extend well below 20 kHz, although most of the energy is often in the ultrasonic range (Smith & Sales, in prep.) The frequency patterns, rates of calling and sound pressure levels of the calls all show changes with the age of the young (Smith & Sales, 1980). The calls recorded from hazel dormice, Muscardinus avellanarius, consist of one or more frequency components, generally between 16.8 and 25k4 kHz (range 8-40 kHz) and show frequency changes within single calls (Schupbach, 1974).

The emission of ultrasonic calls by infants is stimulated by changes in the physical state or environment of the pups. Several authors have shown that calling is related to a decrease in body temperature, as occurs when pups are removed from the nest. Calling responses are greatest when pups are most susceptible to cold and not able to maintain their body temperature and they decrease as homoiothermy develops (see Sales & Pye, 1974). Lack of familiar olfactory stimuli promotes calling in some species such as rats Rattus norvegicus (Oswalt & Meier, 1975), but not in others such as laboratory mice (Geyer, 1979), while the presence of unfamiliar olfactory stimuli have varying effects depending on the stimulus (e.g. Conely & Bell, 1978; Lyons & Banks, 1982). Lack of tactile stimuli from mother or siblings also affects calling and Hofer and Shair (1978) have pointed out that isolation involves changes in all of these stimuli. Positive tactile stimuli, such as handling by the experimenter or the mother affects calling in complex ways depending on the age and the species of the pups and calling rates may increase or decrease when compared to those of non-handled pups. In some species the structure of the calls is also affected by handling (Smith & Sales, 1980). Pups calls relatively little in the nest (Sales & Skinner, 1979), so the emission of calls appears to signal some form of disturbance, such as may be experienced by pups that had strayed or been removed from the nest or were being roughly treated.

Adult calls can be associated with different situations and to a certain extent the acoustic characteristics of the calls vary with the situation as well as showing some interspecific differences, although most of the calls are of a single frequency or narrow frequency band only. Ultrasounds have been detected during sexual behaviour in all 15 species of murid rodents studied so far. In general, the calls are associated with precopulatory behaviour of the male, but in some species such as rats, golden hamsters, Mesocricetus auratus, and collared lemmings, Dicrostonyx groenlandicus; the females also call (Brooks & Banks, 1973; Barfield et al., 1979; Floody, 1979). Precopulatory calls often show some degree of fairly rapid frequency change (Stoddart & Sales, in prep). In mice; rats; Mongolian gerbils, Meriones unguiculatus; woodmice, Apodemus sylvaticus; and golden hamsters, the calls can be elicited by female odour alone and by male odour in the case of female rats, hamsters and woodmice (Barfield et al., 1979; Floody, 1979; Thiessen & Kittrell, 1979; Cyger & Schenk, 1980;

Whitney & Nyby, 1983). Calling depends on adequate levels of the appropriate sex hormones in the caller and often also in the stimulus male or female (Barfield et al., 1979; Floody, 1979; Gyger & Schenk, 1980; Holman & Hutchinson, 1980). But in mice the potency of female urine to elicit calling from males depends on the olfactory experience of the male during his first sexual encounter with a female (Maggio et al., 1983) rather than on female sex hormones (Whitney & Nyby, 1983). The precopulatory calls therefore appear to reflect a state of sexual arousal in the caller. It may be significant that in golden hamsters and collared lemmings the females are solitary and very aggressive when not in oestrous. Their calls may therefore signal a temporary lack of aggression and willingness to mate.

Postcopulatory calls have so far been recorded regularly from only three species, laboratory rats (Barfield et al., 1979); roof rats, Rattus rattus, (Estep et al., 1978) and Mongolian gerbils (Holman, 1980). The calls are often much longer in duration (up to 3s) and lower in frequency (22-28 kHz in rats) than precopulatory calls and they show little or no frequency change over their length. In rats these calls, often called '22 kHz calls', are associated with a refractory state of the male and his temporary inability to mate, and they appear to indicate a state of social withdrawal (Barfield et al., 1979; Adler & Anisko, 1979).

The association of ultrasound emission with aggressive behaviour is not so widespread as its association with mating; so far it has been reported in only 15 out of 23 species studied (Stoddart & Sales, in prep). The calls are generally short and those produced during aggressive acts in rats may show small changes in frequency (Sales & Pye, 1974). In some species including rats and woodmice, the calls appear to be associated with the actions or movements of the more aggressive animal and it has been suggested that they are emitted by this animal (Sales & Pye, 1974; Hoffmeyer & Sales, 1977). However, this could not be confirmed in a recent study involving devocalised rats (Takahashi et al., 1963) where such calls appeared to be emitted by the intruder rather than the more aggressive resident. The possible message of these calls is therefore not clear.

In some Rattus species, defeated animals emit calls of relatively long duration (up to 3 s) and low frequency (between 22 and 28 kHz in R.norvegicus)(Sales & Pye, 1974; Watts, 1980). These 'long' calls are apparently identical to the post-ejaculatory calls of rats. They are produced more readily after experience of a previous attack and can be elicited from defeated animals by olfactory, but not auditory, cues from dominant animals (Corigan & Flannelly, 1979). Similar 'long' calls have been detected from undisturbed female rats (Francis, 1977) and from lactating females, particularly after disturbance including removal of the litter (Price, pers. comm). Removal of the litter elicits calling by the female in a number of other species (Smith & Sales, 1980), but the response is erratic and the exact causal factors have not been elucidated. Other situations in which ultrasound emission has been recorded include exploratory behaviour in woodmice and during social contact behaviour in yellow necked mice, Apodemus flavicollis,(Hoffmeyer & Sales, 1977; Schenk, 1978). Ultrasounds have also been detected during discrimination of a barrier by blinded rats (Chase, 1979).

There is evidence that all these calls are produced in the larynx, but the purely ultrasonic calls may be produced by a different mechanism to that of the lower frequency, broader bandwidth calls (Roberts, 1975). The brain pathways controlling ultrasound emission have been investigated in hamsters and rats and include the mesencephalic central gray area in hamsters (Floody, 1979) and neurones in the thalamus and medulla in rats (see Yajima et al., 1982).

Ultrasound reception. Sensitivity to high frequency sounds has been reported from a variety of murid rodents by several authors (see Brown & Pye, 1975; Movchan, 1978). But many rodents are especially sensitive to ultrasonic frequencies, and several physiological and behavioural studies have demonstrated a peak of sensitivity to ultrasonic frequencies, often at orjust below the frequencies they emit, as well as a lower frequency peak below 20 kHz (Brown & Pye, 1975; Ehret, 1977; Thompson, 1979). However, there appears to be no particular high level of frequency resolution or discrimination associated with these higher frequency peaks of sensitivity at least in the mouse. Behavioural studies have shown that in mice 'just noticeable differences' in frequency that can be discriminated and critical bandwidths (that are associated with the ability to resolve simultaneous tones) increase with increasing frequency particularly above 15 kHz (Ehret, 1977).

The structure of rodent ears in relation to high frequency hearing has so far received little attention and has been studied in detail only in mice. The ossicles are small and light, and in some species the malleus is attached to the wall of the auditory bulla by a pronounced phlange. In mice the ossicular chain shows two axes of rotation, one during low frequency stimulation and the other perpendicular to the first, during high frequency vibration (Saunders & Summers, 1980). All of these features would appear to enhance high frequency hearing. However, Saunders and Summers (1982) found that the velocity of vibration of the ossicular chain could account for the lower frequency peak of sensitivity at 15 kHz in mice, and Ehret and Frankenreiter (1977) found that the pattern of hair cells in the cochlea of mice and their innervation could be also related to the 15 kHz peak, but in neither study were any features reported that could account for the higher frequency peak at 50 kHz. Clearly, more studies are needed to determine how this higher frequency peak is achieved in mice and in other rodents.

The effects of ultrasonic calls on behaviour. In recent years there have been an increasing number of studies which attempt to determine the 'meaning' of particular calls and so their role in communication. But this is not an easy area to study; the calls, or models of them, must be recorded and/or replayed as faithfully as possible and subtle changes in behaviour may have to be assessed. Rodents use several sensory modalities during communication, particularly olfactory and tactile senses, so it is perhaps not surprising that the efects of calls alone are difficult to assess.

The effect of infant calls or of models, on adults, particularly lactating females is often to elicit an orientation response in rats or the searching and retrieving response in mice and woodmice, and this would probably result in stray pups being restored to the nest (Smith & Sales, 1980). Ehret and Haack (1982) have shown that lactating female mice respond preferentially to calls consisting of a narrow band of sound within the ultrasonic range. Critical bandwidths for recognition of infant calls correlated well with the critical bandwidths determined in other tests, and Ehret and Haack suggested that the discrimination of ultrasonic mouse pup calls from other calls and their recognition is probably directly related to the critical band analysis of the auditory system. The efects of calls on other behaviour patterns has not been rigorously studied. There is some evidence that calls do affect nest building (e.g. Elwood, 1979) but more studies are needed to confirm this and other possible efects on behaviour (Noirot, 1972).

The precopulatory calls of male rodents have been shown to affect several aspects of female behaviour; they attract females to the source of the calls in rats, hamsters and mice and in hamsters calling by either sex increases calling by the opposite sex (Barfield et al., 1979; Floody, 1979; Pomerantz, 1983). Calling also enhances proceptive behaviour (earwiggling and darting) in female rats and receptive behaviour (lordosis) in rats and hamsters (Barfield et al., 1979; Floody, 1979). Clearly the calls stimulate sexual responses in potential partners and so could enhance mating success. The effects of postcopulatory calls is not so clear. They may serve to keep the female away from the male, so preventing another copulation during sperm transport; they may also serve to keep the male in contact with the female so that mating can resume when the vocalizations cease, or the calls may inhibit aggressive behaviour of other males in the group towards the refractory male (Barfield et al., 1979; Adler & Anisko, 1979).

The effects of the short calls emitted during aggression have received little atention so far. Thiessen and Kittrell (1979) reported an inverse relation between aggression and ultrasound emission in Mongolian gerbils and suggested that high levels of calling may inhibit fighting. However, in rats muting residents had no effects on the behaviour of intruders (Takahashi et al., 1983) and so the possibility that these calls affect the behaviour of opponents remains an open question.

The suggestion that 'long' calls from submissive rats inhibits aggression(Sales & Pye, 1974) has received some support from Lore and his colleagues (1976) who found that a lack of aggression towards previously attacked intruders was associated with shorter latencies to emit these calls during a second encounter. However, Thomas and his coworkers (1983) could find no evidence for this view. They reported that deafening residents had no detectable effect on their aggressive behaviour towards intruders. More recently, Sales (in prep) has found that prior exposure of individual resident male rats to replayed 'long' calls decreased the number of animals showing aggressive behaviour in later encounters with an intruder, when compared to animals exposed to the replay of blank tape or of artificial 38 kHz calls. Within the animals showing aggression, the latency to aggression was significantly increased in those exposed to 'long' calls but there was no significant effect on other measures of aggression or on the emission of short or long calls. These results indicate that long calls do have some effect on aggression although the effect here is not dramatic.

Ultrasound transmission. All the studies on rodent ultrasonic communication so far have been carried out in the laboratory. Indeed there appears to be no record of the detection of ultrasounds from undisturbed animals in the wild. To understand the possible use of ultrasound in rodent communication in the wild, it is necessary to know if, when and especially where, the calls are emitted and how well they are transmitted through the relevant environment. Ultrasound transmission near the ground has been studied only briefly. High frequencies are absorbed rapidly in air, so would not travel far, but Smith (1979) found that there was little excess attenuation of ultrasounds near the floor of a wood. In grass and wheat, however, she found that sounds above 20 kHz were rapidly attenuated so in such environments ultrasounds could only be used over extremely short distances. It is possible that much ultrasonic communication occurs in burrows, and Smith has suggested that these may act as wave guides to ultrasounds and so reduce the effect of high atmospheric attenuation. Indeed, Thiessen and Kittrell (1977) reported that gerbil calls were not measurably attenuated over 1.22 m in an artificial burrow system.

New areas of study. As the calls of infant rodents are emitted fairly reliably and can be readily quantified, they are becoming used as a bioassay in pharmacological studies. So far they have been monitored in the assessment of neurotoxins on the development of emotional behaviour (Hard *et al.*, 1982) and of alcohol consumption by mother rats on the development of offspring (Adams, 1979). It seems that ultrasound emission by infants could be a useful assay in several aspects of behavioural teratology (Cuomo and Cagiano, pers. comm).

The use of ultrasound in commercial rodent deterrents appears to have developed independently of the knowledge of the emission of ultrasound by the rodents themselves. The deterrents generally generate signals of around 18-30 kHz at high intensity and are claimed to interrupt reproduction and feeding and to clear premises of infestation within weeks. There have been only a few published studies of the effectiveness of such devices and these are less encouraging (e.g. Meehan, 1976). The increasing understanding of the role of ultrasound in rodent communication should allow more effective investigations into the possible role of ultrasound in rodent control. Initial studies in this area are being carried out by the author.

Conclusions. Over the past 21 years the study of rodent ultrasound has developed from purely descriptive studies of a little known phenomenon into an expanding field involving many disciplines. While the study of ultrasound is exciting, partly because of its relative novelty, it is important to remember that ultrasonic calls are only part of the vocal repertoire of a species (Watts, 1980) and that sound is only part of the total stimulus environment of an animal. Future studies must then attempt not only to extend our knowledge of ultrasonic calling itself but also to determine its interactions with other sensory modalities and physiological systems in order to determine the exact role of ultrasound in the lives of rodents.

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