CHAPTER 3.3

Rat ultrasonic vocalization: short-range communication

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Abstract: Rodents are subjected to a significant environmental pressure as prey for a large number of carnivore predators. Ultrasonic vocalization is one of the defensive adaptations which minimize the chances of being detected by a predator. Two mechanisms of ultrasound production in the larynx are discussed, with a whistle mechanism being the most probable one. Physical features of ultrasounds, such as greater directionality, greater attenuation, greater scattering, decreased localizability than vocalizations audible to humans and suitability for communication in underground burrows, make ultrasound a superior alternative to sonic vocalization for short-range communication, particularly in emergencies.

Keywords: defensive adaptation; ultrasonic vocalization; evolution of ultrasound calls; conspecific communication; alarm calls; whistle mechanism; rodents; rat

I. Introduction

The vast majority of rodents are prey for numerous carnivores belonging to different groups of vertebrates (Lack, 1946; Ryszkowski et al., 1973; Andersson and Erlinge, 1977). Many species of predators have specialized in hunting and killing rodents, and rely on them as their main source of food (e.g., owls, buzzards, weasels, wildcats and some species of snakes). They are referred to as specialists. Probably the most effective predators within this group are birds of prey which, after depleting the local population of rodents, will undertake migrations in search of their prey in other areas. Weasels represent one of the most specialized hunter species and their slender and elongated body allows them to capture prey in burrows and hidden nesting chambers. Thus, rodents are not only endangered in open spaces, but the safety of their nest areas may also be ineffective against this predator and as a result adult rodents of both sexes, their young and infants are all subject to predation.

The other category of rodent predators, termed generalists, may consume a large range of different foods, but they will feed on small rodents when these are available (Andersson and Erlinge, 1977). Foxes, martens, polecats, domestic cats, badgers and hawks are examples of these generalists. All the predators together have a powerful impact on populations of small rodents. Some recent studies reported predators having up to 95% predation impact on rodent population as studied within a three year period in the wild (Jędrzejewski and Jędrzejewska, 2007). It is not surprising that predators are believed to be one of the main factors influencing not only population dynamics, but also behavior and evolution of rodent species (Sundell, 2006).

As in most other rodent species, the position of rats in the food chain and the constant environmental pressure shaped rat evolution for millions of years, and resulted in various antipredator adaptations. This chapter is focused on one of the most complex adaptations, ultrasonic communication among rats, and particularly on ultrasonic alarm calls, which cannot be heard by many (reptiles and birds) but not all predators, and provide warning to the entire social group.

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Alarm calls probably significantly contribute to survival of the rat colony.

II. Development of ultrasonic vocalization in rats

For the purpose of this chapter, "ultrasonic" will be taken to mean frequencies above 20 kHz, and calls of lower frequency will be called "sonic." While these words derive from human hearing, they may also apply to some extent to the hearing of rodent predators. Although the evolution of vocalization and auditory communication in vertebrates has a long phylogenetic history stemming from fish (Bass et al., 2008; Margoliash and Hale, 2008), ultrasonic calling in rats, as a defensive adaptation, seems to be a relatively recent development in evolution. Mammalian radiation began about 65 million years ago (Easteal, 1999). The myomorph rodents (suborder Myomorpha, which includes Muroidea, to which the rat belongs) are a group of mammals particularly rich in species, with about 40 million years of phylogenetic history (Catzeflis et al., 1992). Since the genera of the mouse (*Mus*) and rat (*Rattus*) have emerged as separate groups, probably about 16–23 million years ago (Catzeflis et al., 1992; Springer et al., 2003), and both these groups use ultrasound for communication, the mechanisms for ultrasonic calling would appear to have arisen between 20 and 40 million years ago. One of the prerequisites for ultrasonic communication was development of auditory sensitivity reaching far into the ultrasonic frequency spectrum. This sensitivity would be stimulated by a nocturnal life style, when the visual system is unhelpful in avoiding night predators (e.g., owls).

As suggested by Newman and by Hofer (see Newman, Chapter 2.2 and Hofer, Chapter 2.3 in this volume), ultrasonic vocalization probably appeared first in mother–infant interactions. Altricial rat infants rely entirely on maternal help for survival, and calling mother (e.g., after falling out of the nest, which, based on laboratory observations, may happen relatively frequently and is a life-threatening event) was probably a necessary development. The ultrasonic nature of infant vocalizations may arise from increased air pressure in the thorax, together with constricted vocal folds, both of which evolved in the respiratory system in response to cold (outside of the nest, see Hofer, Chapter 2.3 in this volume). Air escaping through a very small orifice of initially closed vocal folds (laryngeal breaking) could create high-pitched ultrasonic sound (see Section III). Rat pups maintain this way of sound production for about the first 20 days of their life, up to weaning. During that time, young rats demonstrate an extremely rich repertoire of different calls, with sound components reaching from audible to humans to high ultrasonic frequencies. In a sonographic study, 10–17 day old rat pups emitted almost all their calls as frequency modulated vocalizations with minimum frequency as low as 1.9 kHz and maximum frequency as high as 125 kHz (Brudzynski et al., 1999). This variety of vocalizations indicates that pups use different forms of vocalizations, and can readily make the functional transition from sonic to ultrasonic calls, which happens sometimes even within a single-frequency sweep beginning as an audible sound and ending in a high ultrasonic range of frequencies. Since rat pups are born at a very immature state, the early developmental stages right after their birth may represent a brief recapitulation of the evolutionary history and developmental pattern of the mechanisms needed for communication with ultrasonic vocalization, in an analogous way to the biogenetic law of Haeckel, which applies to embryogenesis. Adaptive advantages of vocalization in the ultrasonic range will be discussed later in this chapter.

The infantile pattern of vocalization in the rat (isolation calls) changes abruptly at weaning into the adult forms of vocalization. Adult rats have two forms of vocalization: an audible (to humans) or sonic form of calls with fundamental frequency between 2–4 kHz and rich harmonic components (Nitschke, 1982); and an ultrasonic form with much higher frequency, 20–70 kHz, and possibly as high as 100 kHz. Recent behavioral studies have shown that these sonic calls (squeals) may be used by rats in direct confrontation with a predator as a short-distance warning signal directed to the predator (Litvin et al., 2007), but would also be detectable over a larger area by conspecifics. These defensive threat vocalizations (heterospecific communication) increase with predator proximity, and they are thought to inform the predator that the targeted rat is ready for a defensive attack (Litvin et al., 2007). On the other hand, the ultrasonic calls are well-suited for communication at short distances and exclusively for communication with conspecifics within the social group.

There are then two major questions to be answered: what is the mechanism used for producing these ultrasonic calls, and why are they favored for short-range conspecific communication? Here we mostly confine our attention to laboratory Norway rats, since these have been most often studied, and attempt to arrive at conclusions that apply more generally to rodent species.

III. Ultrasound production

III.A. The whistle mechanism

The vocal anatomy of rodents, as shown in Fig. 1, is similar to that of other mammals and consists of a pair of vocal folds at the top of the trachea. During the production of most audible sounds the folds vibrate together under the influence of raised lung pressure, and thereby create a pulsating airflow into the upper vocal tract, the frequency of vibration being determined by the mass and tension of the vocal folds (see Berke and Long, Chapter 10.1 in this volume). Because the vocal folds close once in each vibration, their valve behavior is nonlinear and the airflow consists of a fundamental frequency together with a relatively strong admixture of many harmonic components. The acoustic influence of this flow is modified by resonances of the upper vocal tract to produce emphasized frequency bands, or vocal formants, like those distinguishing different vowel sounds in human speech. The object of this usual vocalization appears to be conspecific communication at large distances, and the fundamental frequency is related to animal size as discussed in Chapter 3.1 and is typically in the range 2–4 kHz for rats with body mass around 250 g.

There is, however, much uncertainty about the way in which ultrasonic calls are produced. For rats of this size the frequency range for conspecific alarm calls is typically 20 to 30 kHz (see Fig. 2), and the sound consists of a nearly pure tone with very little acoustic power in higher harmonics (Roberts, 1975a; Brudzynski and Holland, 2005). A functioning larynx is essential for this to occur, as indicated by laryngeal denervation studies (Roberts, 1975b; Nunez et al., 1985). These and other observations have led to the speculation that the tones are actually produced by some sort of whistle mechanism in the vocal tract, rather than by vibration of the vocal folds.

Roberts (1975a) has provided support for this hypothesis by simulating the rat calls using a "bird whistle" device in which air is blown through two aligned circular holes in two parallel plates separated

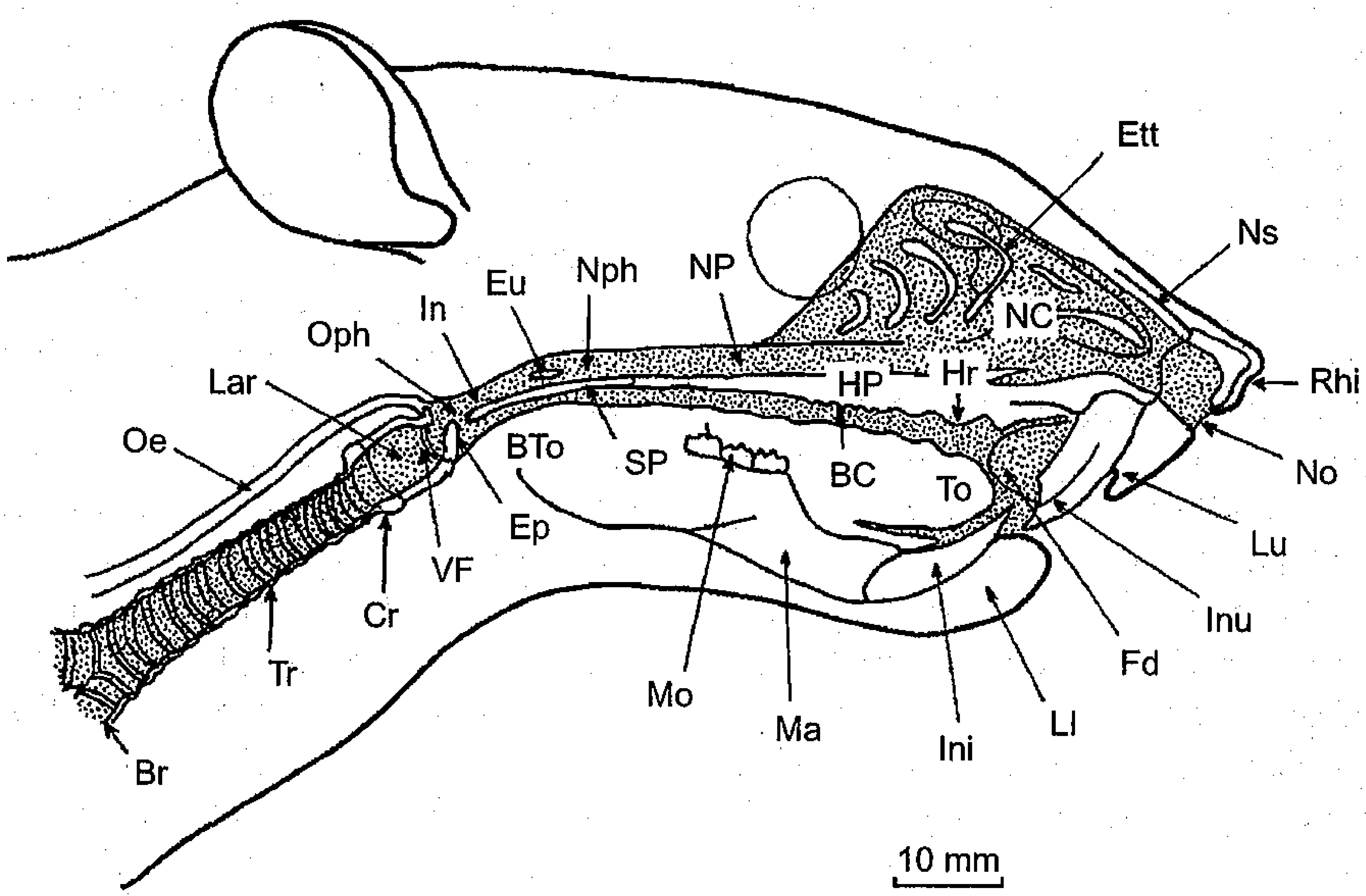

Fig. 1. The cross-section of the upper respiratory tract (stippled) with outlines of selected head and neck structures of an adult male Wistar rat, 300 g body weight. Abbreviations: Bc: buccal (oral) cavity; Br: bronchus; BTo: base of the tongue; Cr: cricoid cartilage of the larynx; Ep: epiglottis; Ett: ethmoid bones and nasal turbinates; Eu: opening into eustachian tube; Fd: fold of skin covering diastema; HP: hard palate; Hr: hard palate rugae; In: opening of internal nostrils (choana); Ini: lower jaw incisor; Inu: upper jaw incisor; Lar: larynx; Ll: lower lip; Lu: upper lip; Ma: lower fragment of the mandible; Mo: three molar teeth in the lower jaw (the upper ones are omitted); NC: nasal cavity; No: external nostrils; NP: nasal passage; Nph: nasopharynx (above soft plate); Ns: nasal bones of the skull (fragment); Oe: esophagus; Oph: oropharynx (behind the soft palate); Rhi: rhinarium; SP: soft palate; To: rostral part of the tongue; Tr: trachea; VF: vocal folds. For other anatomical details omitted in this diagram, see Rowett (1960) and Wells (1964).

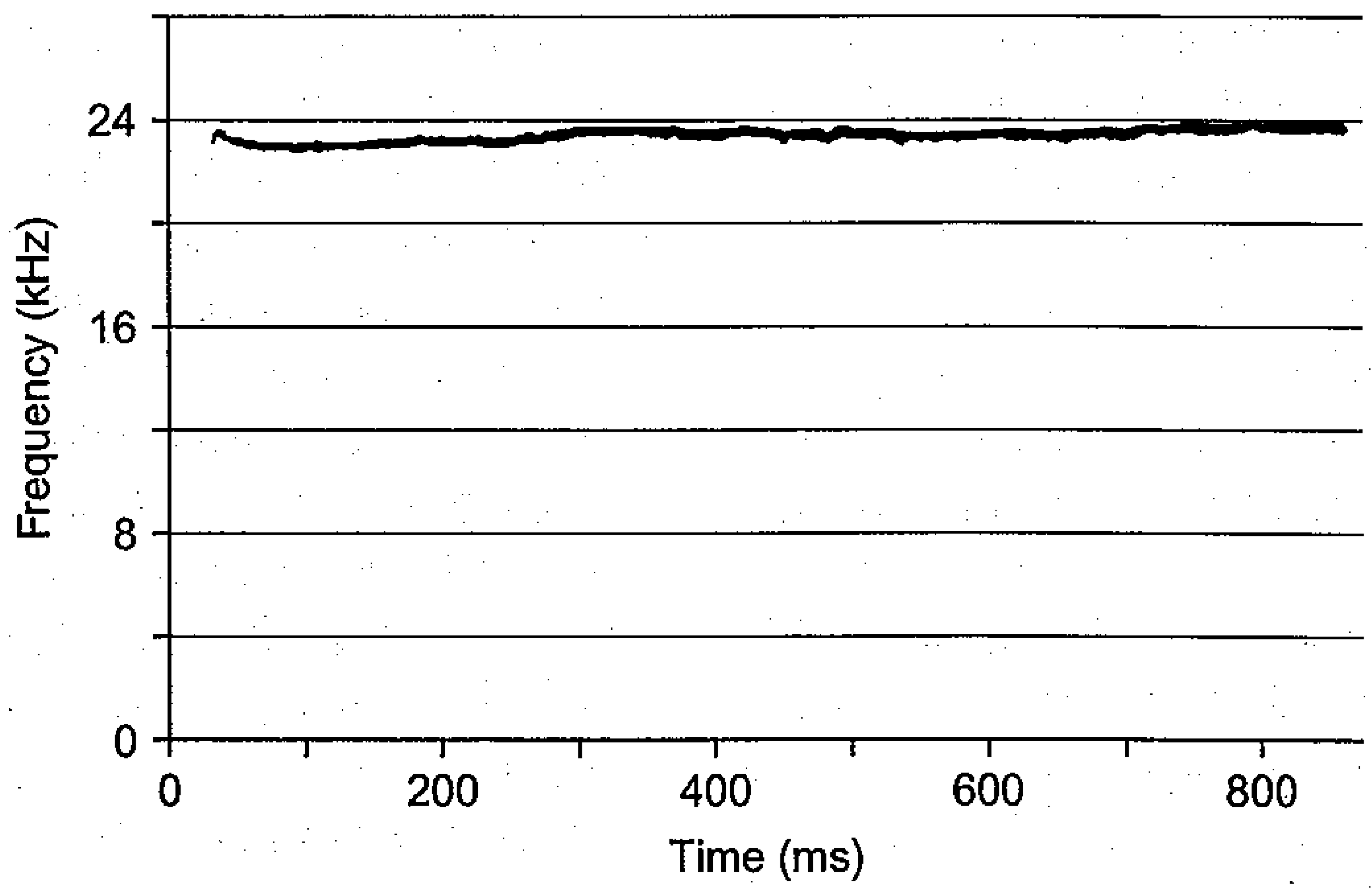

Fig. 2. A sonogram of a single typical alarm call emitted by an adult Wistar rat. Peak frequency of this call is 22.7 kHz.

by about 1.5 mm and sealed with a Perspex ring. The blowing pressures used were said to be "within the physiological range," although no details were given. This whistle could be made to produce sounds in the frequency range 20 to 80 kHz that closely resembled the vocalizations of rodents in both frequency and temporal pattern.

If this hypothesis is correct, then the one thing that remains to be identified is the anatomical structure responsible for the sound production mechanism. Studies on rats in which either the mouth or the nose were blocked during vocalization (Roberts, 1975b) established that the source of the sound was below the junction between the nasal cavities and the buccal cavity, and the opening of larynx (i.e., in the oropharynx; see Fig. 1). The vocal folds provide one of the two required apertures, and the evidence for that was provided by a direct observation of vocal folds during production of ultrasounds (Sanders et al., 2001). Sanders and colleagues reported that vocal folds were tightly opposed during emission of ultrasounds in a rat and an opening of 1–2 mm in diameter was observed in the back of the folds (dorsal direction). It was also noticed that the vocal cords did not vibrate during production of ultrasounds. Thus, the question remains: where is the other opening of the "whistle" located?

It is conceivable that the other opening of the whistle is created in the oropharynx, which is roughly 3–4 mm in diameter (these dimensions may change depending on the position of the soft structures around them). The space of the oropharynx is surrounded by movable elements (see Fig. 1), such as the epiglottis, the end of the soft palate around the internal nostrils, and the muscular base of the tongue. It is possible that the base of the tongue may push up against the tip of the soft palate while shaped in a form of a trough. This would create a second small opening between the tongue and soft palate. The second opening would be leading to the mouth cavity (or predominantly to the mouth), which could explain Roberts' observations that rat ultrasounds are emitted mainly through the mouth (Roberts, 1975b).

The other possibility is that the epiglottis could be stabilized in a semi-closed position, in this way creating the second opening above the vocal folds at the epiglottal level of the larynx. The rodent epiglottis is reinforced by an epiglotic cartilage joined with the thyroid cartilage and probably could be rigidly stabilized (Roberts, 1975c). The distance between these two openings would then be about 1–1.5 mm. This arrangement would explain why Sanders et al. (2001) have observed the opening in the vocal folds toward the dorsal side of folds. In this way, the two openings (in vocal folds and between the epiglottis and the top of the larynx) would be aligned. These mechanisms would be almost identical as to the location, size of the openings and the distance between them, to that found in Roberts' (1975a) simulation experiment. The option that two openings could be created by vocal folds (inferior folds), and superior folds (false folds) is unlikely, because false folds are not well-described in the rat and their distance from inferior folds would be too small.

It is helpful to have a general understanding of the operation of such a device (Chanaud, 1970; Wilson et al., 1971; Fletcher, 1992; Fletcher and Rossing, 1998). Air from the lungs forms a jet that emerges from the first aperture and is aligned so that it passes out through the second aperture. Such jets are, however, subject to instabilities and the one of interest here is often referred to as a "varicose," with the diameter of the jet varying. If the jet is too wide to pass through the exit aperture, this causes an increase in the pressure in the enclosed region between the apertures which, in turn, influences the diameter of the jet emerging from the entry aperture. If the propagation delay of the wave along the jet between the apertures is such that there is about one wavelength along the jet between them, this causes a reinforcement of the wave and the oscillating flow from the exit aperture generates a sound wave at that frequency.

If the lung pressure is p, then the speed of the jet is $v = (2p/\rho)^{1/2}$, where ρ is the density of air, and the speed of the varicose wave varies from v if the wavelength is long compared with the jet diameter, down to $v/2$ if the wavelength is less than the jet diameter (Fletcher and Rossing, 1998). Inserting some figures, we might take the lung pressure p to be about 1 kPa (10 cm water pressure) and, since $\rho \approx 1.2\,\text{kg/m}^3$ this gives a jet speed of about 40 m/s, and so a wave speed of 20–40 m/s. If the distance between the apertures is about 1 mm, then the frequency of the oscillating airflow emerging from the exit will be 20–40 kHz, which accords well with what is observed and with the mechanism proposed above.

There are two ways in which the frequency of the sound could be controlled: either by changing the lung pressure or by changing the distance between the two apertures, both of which seem possible. Further support for this whistle mechanism comes from studies by Roberts (1975a), who recorded the effect on the frequency of the ultrasonic calls of young rats when air was replaced by a heliox (He–O_2 mixture). The frequency of the calls was found to increase in proportion to the increase in sound speed, and thus $1/\rho^{1/2}$ as expected for a whistle-generated sound, since there must be about one wavelength of the disturbance along the jet.

III.B. Frequency-shift mechanism

While this whistle mechanism is plausible, no direct evidence of a suitable opening structure above the larynx has been observed, so alternatives must be considered. The obvious one is something analogous to the human singing of counter-tenors, who have two clearly defined vocal ranges, a low-frequency one about 100–300 Hz for normal speech, and a high-frequency range about 400–1,000 Hz for singing – a frequency difference of about a factor of three between the two registers, which is similar to that in some rats. Something similar is heard in the voices of male children reaching puberty, where there can be uncontrolled jumps between the two registers. Men and women in some cultures can also produce "yodels" in which there are sudden jumps between two registers quite widely separated in frequency. The physiological difference relates to the way in which the vocal folds vibrate, the low registers involving vibration of the whole fold while the high register operates with vibration confined to a soft surface layer (see Finck and Lejeune, Chapter 10.2 in this volume). In some versions of the high-register technique the vocal folds do not touch each other during their vibration, with the result that the airflow is much more nearly sinusoidal and the resulting sound has only very weak upper harmonics. It has not yet been established whether something similar might occur in rodents. The frequency-shift evidence of Roberts (1975a), however, would support either the simple jet mechanism or a mechanism involving excitation of a cavity resonance by a jet, as in some musical wind instruments, but not a mechanism relying solely on vocal fold vibrations, the frequency of which is determined by the mass and elasticity of the vibrating structures and is affected very little by the properties of the surrounding atmosphere.

III.C. Acoustic power of ultrasonic calls

There is very little information in the literature about the acoustic power typically produced by rodents during their ultrasonic calls. Roberts (1975a), however, gives a value for sound pressure level of up to 100 dB re 20 μPa at a distance of 10 cm for the loudest calls of the rodents he studied. This figure is equivalent to 80 dB at 1 m, which would be about 1 mW of sound power if the signal were to spread uniformly over a sphere. As will be discussed later, however, the ultrasonic signal is quite directional once the sound wavelength becomes comparable with the mouth diameter, so that the actual radiated sound power is probably closer to 0.1 mW. For a typical young adult rat the body mass is about 200 g, so that this corresponds to about 0.5 mW/kg. This sound production level per unit of body mass is comparable with that of birds, but much greater than that of larger mammals.

A study of auditory sensitivity in rodents (Brown, 1973) has shown that the *Mus musculus* species shows a main peak in cochlear microphonic output at about 15 kHz and a subsidiary peak at about 50 kHz. This corresponds roughly to hearing sensitivity as shown by behavioral studies, and indicates that these rodents and presumably most other murid rodents have evolved hearing abilities tuned to both their sonic vocalizations, and also to their ultrasonic calls. A study of audibility in rats using operant conditioning provided similar results of audibility within the frequency range from 10 to 50 kHz with the band of greatest auditory sensitivity being approximately one octave in width and located around 40 kHz (Gourevitch and Hack, 1966). Bats, unsurprisingly, show similarly tuned hearing abilities.

IV. Ultrasonic vocalization as adaptation for a short-range communication

The cost of a complex laryngeal control during emission of ultrasounds, the need for significantly prolonged exhalations and increased lung pressure during production of alarm calls, as well as the use of ultrasonic vocalizations for rat communication in both appetitive and aversive behavioral situations (Brudzynski, 2007) indicate a significant adaptive value of high sound frequency in minimizing chances of being detected by potential predators. As compared to sonic vocalization, these features could be summarized as directionality, increased attenuation, deflection and scattering, and decreased localizability of the source. Most of these features are important for the role of ultrasonic vocalization as a short-range communication system.

IV.A. Directionality

One advantage of using ultrasounds for communication is their directionality. Thus, rats may have, to some extent, control over emitting their vocalizations in a desired general direction of conspecific recipients and away from the suspected or real location of a predator.

Biological ultrasound behaves rather differently in the environment from the sounds audible to humans, because the wavelengths involved (typically in the range 5–15 mm) are small compared with physical features of the immediate surroundings. This is apparent in the directionality of the sound emitted from the rodent mouth. Even if for simplicity we take the animal mouth to be a circular aperture of radius a, which is set in a sphere representing the animal's head, then the analysis is still very complicated (Morse, 1981). A more drastic approximation, in which the mouth is set in a rigid plane as though the animal were against a tree or a bank, is more readily soluble and leads to the conclusion that the radiated sound is concentrated in a beam with an angular half-width equal to about 20 λ/a degrees, where λ is the sound wavelength and the beam width is taken to be that beyond which its intensity has declined by more than about 10 dB. For a rodent with external mouth diameter of 10 mm, this gives a half-width of about 50° at 20 kHz and 20° at 70 kHz.

IV.B. Attenuation and scattering

As discussed in Chapter 3.1 in this volume, the attenuation of sound due to atmospheric absorption is greater at high frequencies than at low frequencies, the attenuation coefficient increasing about as frequency to the power 1.5 in an open environment. This could be an incentive to use ultrasound for conspecific short-range communication, as atmospheric attenuation has little effect at close range. The directionality of ultrasound is also an advantage, since the rat's head can be turned away from the predator and towards other members of its community.

More important than attenuation is probably the effect of scattering of the sound from surrounding obstacles in the environment, such as rocks and large, leafy plants, which obscure information about the location of its source. This scattering becomes extreme when the scattering objects are larger in size than the sound wavelength, which in this case is typically about 1 cm, and of course varies with the number of scattering objects involved.

The use of a simple ultrasonic cry with fixed frequency and duration certainly limits the amount of information it can convey, although sometimes the duration and frequency are varied. This limitation is probably not of great importance, however, since only a small amount of information needs to be encoded in an alarm call.

IV.C. Localizability of the vocalizing rat

The ultrasonic alarm vocalizations produced by rats are generally of a very simple form, as shown in Fig. 2, and consist of a repetitive series of approximately fixed-frequency pulses each lasting for about 1 second, and typically arranged in groups of 3 to 5 calls (Brudzynski and Holland, 2005), although shorter pulses of 30–60 ms duration can be generated by rats and are observed in some species (Sewell, 1967). As noted before, these tones have very little harmonic development. The call frequency is very nearly constant, except for an initial adjustment in which the frequency of the first call in the sequence may begin a little higher and then fall to the dominant frequency within the series.

Since the biological role of these vocalizations is largely that of alarm calls, the objective would be to distribute the signal strongly over a local area without giving too many clues as to its place of origin. Multiple local reflections would help to achieve this aim as though the source is in the sonic analog of a hall of mirrors. It is also observed that most of the calls begin and end in a gradual way, and the rat maintains an almost constant frequency during the entire call. These acoustic features make localization of sound source even more difficult.

IV.D. Underground communication

It is well-justified from an acoustical point of view that vocalizations in the ultrasonic range of frequencies represent an effective adaptation in rats, minimizing the danger of being detected and attacked by predators. It seems, however, that rats safely hidden in underground burrows would not need to communicate in the ultrasonic range and could return to the regular mammalian sonic range. This could even extend the range of communication within the tunnels. Rats, however, appear not to do that and keep the ultrasonic form of communicating underground.

Rodents spend much of their time in underground burrows, and it is relevant to examine the transmission of sound and ultrasound through such environments. Although there is the normal attenuation due to molecular losses in the air, the attenuation underground is primarily due to losses to the burrow walls (Fletcher, 1992). This causes the sound intensity to decrease with distance x along the burrow as $\exp(-2\alpha x)$, and the attenuation coefficient α at frequency f in a smooth-walled pipe of radius r is approximately $3 \times 10^{-5} f^{1/2}/r$. For a rough-walled burrow, the attenuation will be greater by a large factor. The rate of increase of attenuation with frequency in a burrow is, thus, much less than for sound in the open air where attenuation varies about as $f^{3/2}$, and of course there is no extra effect of spherical spreading of the sound. It is therefore advantageous for rodents to use high frequencies for communication within a burrow, since they can produce these with greater source power than low frequencies (see Fletcher, Chapter 3.1 in this volume). Because of their higher information content, however, rapidly varying sonic vocalizations may be preferred for other communication.

V. Conclusions

The position of rodents in the food chain created a substantial environmental pressure on them. Rodents developed vocal communication in the ultrasonic range of frequencies as part of their antipredator adaptations. Particularly, ultrasonic alarm calls appeared to be an effective social defensive behavior. Physical features of ultrasounds and acoustic features of rat vocalizations provide congruent evidence that the ultrasonic form of vocalization serves for short-range communication. Ultrasonic calls have probably evolved to facilitate conspecific communication on the one hand, and to minimize chances of being detected by predators, on the other. Ultrasonic vocalizations, which may perhaps be produced with greater acoustic power than lower-frequency sonic vocalizations, are suitable for communication both inside and outside the burrows when only simple information such as an alarm call needs to be conveyed.

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