Communication of Adult Rats by Ultrasonic Vocalization: Biological, Sociobiological, and Neuroscience Approaches

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Abstract

Rats have developed antipredator defensive adaptations to protect themselves from the large number of animals that prey on them. One such adaptation is the ability to communicate by ultrasonic vocalization, which decreases the likelihood of detection by a predator. Almost all rat vocalizations are inaudible to the human ear as well, so laboratory studies of ultrasonic vocalization require specialized electronic equipment. The most popular of these is the “bat detector,” which lowers ultrasonic frequency to a humanly audible frequency. Adult rats emit two types of ultrasonic calls: alarm (22 kHz) calls, in aversive and dangerous situations, and appetitive (50 kHz) calls, in appetitive or “friendly” (i.e., nonaggressive) behavioral situations. These two types of calls differ in all acoustic parameters, and their initiation depends on activity in different ascending tegmental pathways to the forebrain: 22 kHz calls require activity in the cholinergic system, and 50 kHz calls in the mesolimbic dopaminergic system. The release of acetylcholine in the diencephalon and forebrain is associated with the emission of 22 kHz vocalizations, and the release of dopamine in the nucleus accumbens with 50 kHz calls. Thus the two calls are reliable predictors of increased cholinergic or dopaminergic activity in the brain. The calls serve as indices of the rat’s state, including its affective state, induced by activity of one or the other neurochemical system.

Key Words: alarm calls; cholinergic system; defensive behavior; dopaminergic system; ultrasonic vocalization; warning calls; 22 kHz calls; 50 kHz calls

Introduction

There is growing research interest in vocal communication in rats. Unlike many other rodent species, rats are highly social animals (Barnett 1967; Blanchard and Blanchard 1980; Lore and Flannelly 1977; Nyby and Whitney 1978) and vocal communication is a regular feature of their social interactions. It is an intriguing phenomenon that rats and other rodents have developed communication in the ultrasonic range of sound frequencies. Although researchers have known since the early 1960s, when bat detectors became commercially available, that rats could emit and hear ultrasounds, studies of their ultrasonic communication were hampered for at least a decade by technical difficulties in recording and analyzing the ultrasonic signals.

Like other mammals, rats produce sound through the larynx. But unlike most other mammalian species, rodents can use their larynx in two modes of functioning. The first, common to most other species, causes vibrations of vocal folds and produces audible sound (squeals) of 2-4 kHz (Nitschke 1982). These calls express both physical pain or discomfort—acute, approaching, or anticipated—and the affective dimension of pain or anticipated pain (Borszcz 2006). Rats use similar audible vocalizations, sometimes not distinguishable from pain calls, against predators. These signals not only indicate a potentially painful encounter but also serve to intimitate or stop the advance of a predator, warning the approaching animal that the rat is ready for an active defense (Litvin et al. 2007). The intensity of the call is dependent on the proximity of the predator and independent of the proximity of other conspecifics (Litvin et al. 2007). Rats may also direct these vocalizations at humans in anticipation of, or when experiencing, physically unpleasant treatment or rough handling.

The second mode of larynx function in the rat is in the emission of ultrasounds. For these sounds, the larynx is stabilized and used as a whistle with a very small orifice created by the vocal cords (Sanders et al. 2001), which are tightly constricted and cannot vibrate (Nyby 2001). Animals build up considerable abdominal pressure and push air through the orifice. It is possible sometimes to observe this so-called “pressure breathing” (Fokkema et al. 1986) with deep inhalations and prolonged exhalations associated with the production of long and loud alarm calls. The vibrating air column produces the ultrasonic sound on the same principle as a human whistle does, except that the small size of the rat’s respiratory tract creates sound in the ultrasonic range of frequencies. In this mode of vocalization, rats usually emit pure sounds of a constant or variable frequency with few or no overtones.

Rats use the ultrasonic call in a variety of social situations that include both aversive and appetitive encounters. Ultrasonic acoustics and vocalizations are very natural for...
rants and they emit these sounds from birth, although their hearing develops at a slower rate (studies have reported the onset of rat pup auditory function on postnatal day 12-14; Freeman et al. 1999a,b; Geal-Dor et al. 1993). Rat pups emit early ultrasonic “isolation calls” when separated from their littermates or when they fall out and lose contact with the nest. The isolation calls change only slightly in their acoustic structure until the pups reach about 21 days of age, when a more abrupt transformation occurs (Brudzynski 2006) and the juvenile rats soon begin to emit calls similar to the 22 kHz and 50 kHz types of adult ultrasonic vocalization.

But why have rats, and rodents in general, developed vocalization in the ultrasonic range of frequencies?

**Biological Causes of the Development of Ultrasonic Communication**

An impressively large number of species—mammals, birds, and reptiles—feed on rodents, many of them almost exclusively. In addition, other vertebrate species may eat rodents occasionally or kill them during encounters without eating them. This environmental pressure forced rats to develop, in the process of natural selection, anatomical, physiological, and behavioral adaptations enabling their individual and species survival; such adaptations, which represent behavioral adjustments to minimize bodily harm and/or death, are termed defensive responses (McFarland 1987). Taking into consideration the position of rats in the food chain, researchers hypothesized that the rich repertoire of rat defensive responses, including ultrasonic vocalization, developed primarily as an antipredator behavior, and to a lesser degree as a result of interactions between individuals within the species (Blanchard and Blanchard 1988, 1989, 1990; Blanchard et al. 1990).

Communication in the ultrasonic range of frequencies (above 20 kHz) has a significant advantage over communication by sonic signals (below 20 kHz): many predators, although not all, cannot hear ultrasounds (e.g., birds of prey). Moreover, ultrasonic vocalizations are propagated more directionally than audible sound, they are difficult to detect and localize, and they dissipate easily in environmental obstacles and weather conditions (e.g., wind, rain, fog). Finally, predators on the ground or in the air cannot hear these calls when they are emitted in underground burrows.

Defensive behaviors may be primary or secondary in nature (Edmunds 1974) but all are specific to the individual—that is, only the animal demonstrating the behaviors benefits from them. Primary defensive behaviors decrease the chance of being noticed or found by a predator, whether the predator is nearby or not. They include thigmotaxy, when an animal avoids open spaces and remains or moves in contact with objects, or anachoresis, when the animal remains for a prolonged period of time in burrows or other hiding spaces, usually during the daytime (Edmunds 1974; McFarland 1987; Treit and Fundytus 1988). A secondary defensive behavior appears once the animal has noticed the presence of a predator (or other localized source of danger) and acts to avoid or eliminate the threat. This category includes many classic defensive behaviors such as immobility (freezing), avoidance, escape, threatening, or defensive attack (Edmunds 1974; McFarland 1987).

The evolution of social life in most species created new forms of defensive behavior. Animals living in groups do not need to be in a constant state of utmost vigilance and careful observation for the possible appearance of predators, since warning signals will likely arise from other group members that spot the predator first (Edmunds 1974). Thus the social group provides some security. Rats developed well-organized colonies with 22 kHz vocalizations that serve as alarm calls (Blanchard et al. 1991, 1992) and thus form a higher-order defensive system (Brudzynski and Holland 2005). The system depends on the fact that ultrasonic calls emitted by one individual alarm and activate the whole colony, thus the entire social group benefits from the behavior of one individual.

But communication in the ultrasonic range of sound frequencies only increases the chances of survival, it does not fully protect rats from predators. Indeed, the rat emitting alarm calls (usually the alpha or other dominant male; Blanchard et al. 1991) may do so even when the calls could attract the predator’s attention to the vocalizing rat. Therefore many other factors contribute to rodent survival, such as the location of a particular rodent on its territory, duration of residence in a colony, and age, as was recently shown for prairie dogs (Hoogland et al. 2006). Also, the animal’s involvement in a particular type of activity, or its preoccupation with important biological functions such as sexual behavior or fighting in males, or pregnancy in females, may further influence its susceptibility to capture by predators despite early warning signals (Hoogland et al. 2006).

**Detection of Ultrasounds**

**Equipment**

Because ultrasounds are (by definition) beyond the human hearing threshold, they require computerized electronic equipment to transform the frequency by lowering it to the human hearing range. The transformation is done by bat detectors, which were initially, as the term implies, designed and used to detect the ultrasonic signals of bats (Pierce and Griffin 1938). These instruments lower or divide the sound frequency by a given factor (usually 10 or 16 times); thus, for example, the bat detector would transform a frequency of 20,000 Hz to 2000 Hz or 1250 Hz, well within the range of human audibility.

Acoustic analysis of detected ultrasonic vocalizations requires their storage, for which several options are available: the divided signal can be recorded on a classical tape recorder, or digitized and stored on the computer drive as...
a divided frequency record, or the original signal can be digitized by the analyzing system. The most modern acoustic recording and analyzing systems do not require bat detectors, instead recording, digitizing, and saving the signals directly on the hard drive of a computer in the original, undivided form. This method of recording is more accurate, eliminating the distortions introduced by bat detectors during frequency division (Holland and Brudzynski 2004), but it requires more expensive equipment.

Acoustic analysis also requires the use of a sonograph or sonographic computer program, which uses digitized records to show the sound as it is emitted, displaying it in a sonogram, a graph showing the sound frequency on the y-axis and time on the x-axis, thus illustrating changes of sound over time. Sonographs can further generate spectrograms (also called power spectra), which show all individual sound frequencies (in kHz) and their relative power (in dB) on a separate graph.

Parameters

The acoustic outcome from the bat detector is not how the original call sounded because the instrument changes the frequency, but the output faithfully conveys other parameters that are useful to researchers’ efforts to characterize the calls. These parameters usually include the duration of ultrasonic signals (in ms), bandwidth (i.e., the difference between the call’s minimal and the maximal sound frequencies, in kHz), frequency modulation, and the overall sonographic pattern of the call (e.g., sweep, trill, step). Use of the spectrogram is necessary to calculate the original peak frequency of an individual call (its strongest frequency component, i.e., the one that had the highest amplitude and/or was the most abundant) by, first, identifying the peak frequency and then multiplying it by the frequency division of the bat detector. The basic acoustic parameters are illustrated in Figure 1.

In addition, the call rate (number of calls per time unit) is a useful parameter to determine the magnitude of calling. A series of individual calls is separated by breaks (intercall intervals) of about 100 ms apiece (although they may be much longer). The challenge is to determine how short these breaks might be, a difficult measure as rats sometimes emit fragmented calls. Fragmentation happens with long calls when the animal emits the call with a low air pressure and occasionally loses the sound, as a weak human whistle may be interrupted by too little airflow. The ability to recognize two sounds as either separate vocalizations or two fragments of one call comes only with experience. Call fragmentation also poses a significant problem in studies that depend on the use of automated vocalization counting devices, which count all sounds separated by a given time interval (including broken calls) as two or more separate calls, thus inflating the number of emitted calls.

Ultrasonic calls, and particularly the 22 kHz alarm calls, are usually emitted in series. Thus, another acoustic parameter describes the number of calls per series or the number of series and the interseries time interval.

Emission of 22 kHz Alarm Vocalizations

Circumstances

Rats emit the 22 kHz alarm call when facing danger, which includes any circumstance that causes significant anxiety in anticipation of an aversive, potentially harmful, or life-threatening situation (e.g., an aggressive opponent, predator, large mammal, loud noise). The animal may also emit such calls when it expects a known unpleasant stimulus without exact information about when it will happen (e.g., when an aversive stimulus appears in an unpredictable way or startles the animal). Classic examples are the presence of a predator (e.g., a cat at a distance that allows the rat to escape), detection of a predator’s odor (Blanchard et al. 2005), confrontation with a dominant and aggressive rat (Panksepp et al. 2004; Thomas et al. 1983), an encounter with an unfamiliar human (Blanchard et al. 1986; Brudzynski and Ociepa 1992), or even a light but unpredictable and sudden air puff (Brudzynski and Holland 2005; Knapp and Pohorecky 1995) or startling acoustic stimulus (Kaltwasser 1990, 1991).

Other circumstances in which rats emit 22 kHz vocalizations are dyadic encounters such as fights or sexual contact (Barfield and Geyer 1972; Barfield and Thomas 1986; Lore et al. 1976; Thomas et al. 1983). In these situations, only one
rat in the pair—for example, the losing rat during a fight—
emits the calls (Panksepp et al. 2004; Thomas et al. 1983),
which not only signal an aversive and potentially dangerous
situation for the loser but may also serve to appease the ag-
gressor so that it reduces or stops the attacks, although stud-
ies have not confirmed the latter (Thomas et al. 1983). In
sexual contacts, males emit 22 kHz calls toward the end of
the series of copulations, probably signalling either a change
from an appetitive to an aversive affective state and expres-
sion of the absolute refractory period (Bartfield and Geyer
1972) or cessation of contact with the female (Van der Poel
and Miczek 1991). Males may also emit such vocalizations
if they experience unsuccessful intromission while attempt-
ing to copulate (McIntosh et al. 1984) or if a female shows a
low level of lordosis and a high number of agonistic re-
sponses, making the sexual encounter difficult and aversive
(Brown 1979).

Social conditions and status may also influence the mag-
nitude (i.e., number and/or duration) of 22 kHz calls. Indi-
vividually reared rats emitted significantly fewer such calls in
response to a mild aversive stimulus than rats reared in pairs
(but tested individually) (Inagaki et al. 2005). Among rats
that remained in established pairs, the subordinate rats emit-
ted significantly more 22 kHz calls than the dominant ones
(Inagaki et al. 2005).

Although rats generally emit 22 kHz alarm calls in aver-
sive situations, the calls do not express direct pain. In fact, a
vocalizing rat subjected to acute pain ceases to make ultra-
sonic calls. One study reported the emission of similar au-
dible calls as a result of direct painful stimuli, and noted that
the acoustic structure of the calls was dependent on the in-
tensity of the nociceptive stimulus (Jourdan et al. 1995). The
same group more recently demonstrated that the 22 kHz
calls do not represent affective pain (Jourdan et al. 2002); the
calls signal anxiety caused by potential danger, not an actual
painful or nociceptive event. For example, highly aversive
foot shock associated with more intensive anxiety (unavoid-
able shock) caused more 22 kHz calls than the same foot
shock associated with less anxiety (avoidable shock; Kikusui
et al. 2003). Thus, the magnitude of the anxiety and not the
physical nature of the aversive stimulus is the driving force
for expression of alarm calls.

The biological role of these calls may be further illustrated
by the example of a rat threatened by a cat. If the intensity
of the danger is high enough (e.g., the cat is within striking
distance), the rat will either become silent or emit audible warn-
ing squeals (Blanchard et al. 1991; Litvin et al. 2007). If the
rat can escape, it will be silent until it reaches a safe place
(e.g., in or close to its burrow); then, when the immediate life-
threatening danger is over, it will emit the alarm calls. The 22
kHz vocalizations signal a proximate danger to the calling rat,
and the rats who hear the alarm call receive a message that
the individual emitting it is only in potential danger and still
has a chance to escape. The rats in the colony may therefore
not respond to the distant 22 kHz alarm call—unless they hear
an abrupt stop to an ongoing call, when they respond with
freezing and alert attention (Brudzynski and Chiu 1995).

Characteristics and Mechanisms

Rats’ alarm calls are long—a single call may last from 100
ms to well over 3000 ms (Figure 2A)—and the peak fre-
quency remains mostly within a narrow band of 20-23 kHz,
although some calls can reach 26 kHz or even 30 kHz (the
alarm calls of females may be shorter and of a slightly higher
sound frequency than those of males; Blanchard et al. 1992;
Haney and Miczek 1993). The vocalizing rats try to maintain
a constant sound frequency, so frequency modulation is al-
most absent and 22 kHz calls appear on a sonogram as
straight flat lines with a narrow bandwidth of 1-4 kHz. These
calls are emitted usually in short series of 2 to 7 calls. There
are also some short 22 kHz calls (less than 100 ms in dura-
tion), emitted almost exclusively after the long calls, but
their communicative role is unknown (Brudzynski et al.
1993; Brudzynski and Holland 2005).

All adult rats of different strains and ages know how to
reach the “alarming” frequency. How? There are undoub-
tedly some inborn mechanisms that enable them to do so.

Rats do not always begin their call at the right frequency,
so they “tune” the call down to the narrow band of 20-23
kHz. Thus the very first alarm call, or the first in a series of
calls, often has a mild downward frequency modulation (i.e.,
decreasing from a slightly higher to lower sound frequency;
the tuning is never upward). Once the call reaches the low
band, the frequency remains constant. This observation sug-
gests that rats attempt to emit their alarm calls at as low an
ultrasonic frequency as possible, reaching a common frequency

![Figure 2](https://academic.oup.com/ilarjournal/article-abstract/50/1/43/745096/50kHzcalls.png)

**Figure 2** Sonograms of typical 22 kHz (A) and 50 kHz (B) calls. During 2 s of recording, a rat emitted one 22 kHz call (A) and seven
50 kHz calls (B). The duration of the 22 kHz call is 1125 ms, while
the 50 kHz calls do not exceed 50 ms in duration. Average peak
frequency for the 22 kHz call is 23 kHz and peak frequencies of the
50 kHz calls are between 54.5 and 62.5 kHz. The sonogram in (B)
(modified) is from Brudzynski SM, Pniak A. 2002. Social contacts
and production of 50 kHz short ultrasonic calls in adult rats. J
Comp Psychol 116:73-82.
Rats also have innate mechanisms associated with their response to the alarm calls. In addition to the direct alarming properties of the calls, data suggest that an innate mechanism facilitates defensive responses to 22 kHz calls. Rats readily associate aversive and dangerous situations with 22 kHz alarm calls and retain this association in their memory for a significantly longer time than they do for events associated with other types of calls or ultrasonic stimuli (Endres et al. 2007).

Emission of 50 kHz Appetitive Vocalizations

Circumstances

Rats emit 50 kHz calls, sometimes termed social calls, in many situations that appear neutral to the human observer but that seem to be associated with a positive social function. The circumstances for such calls may be appetitive or neutral (i.e., nonaggressive, nonaversive, or “friendly”) behavioral situations such as sexual contacts and the expectation of such contact, other rewarding situations (e.g., anticipation of play), encounters with an anesthetized (immobile and therefore easily approachable) conspecific, meeting rats after a period of separation, or in the initial meeting of a resident-intruder pair (to signal nonaggression) (Bialy et al. 2000; Blanchard et al. 1993; Brudzynski and Pniak 2002; McGinnis and Vakulenko 2003; Takahashi et al. 1983). Juvenile rats emit the same type of call during homospecific (rough-and-tumble) play or heterospecific play with a human hand (“tickling”) (Burgdorf and Panksepp 2001; Knutson et al. 1998; Panksepp and Burgdorf 2000).1

Rats also emit large numbers of 50 kHz calls in anticipation of other rewarding situations—for example, conditioned place preference, a feeding session, rewarding brain stimulation, or receipt of a drug with rewarding properties (Burgdorf et al. 2000; Knutson et al. 1999). They also emit many such calls when they enter places frequently visited by other rats (even in the absence of those animals), demonstrating that the emission of these calls is associated with expecting and/or seeking social contacts (Brudzynski and Pniak 2002). More specifically, the number of calls is directly proportional to the number of rats that had previously visited the cage (Brudzynski and Pniak 2002). However, calling associated with direct social contact may decrease in the constant presence of familiar conspecifics; and social housing, as opposed to isolation, decreased the number of 50 kHz calls that juvenile rats emitted in response to heterospecific play (“tickling”; Burgdorf and Panksepp 2001). This result is the opposite of the effects of social housing on the emission of 22 kHz alarm calls.

Characteristics

Appetitive 50 kHz calls are very brief, approximately a hundredth of the duration of an alarm call, and their sound frequency is subjected to more modulation than alarm calls (Figure 2B). The average duration of a 50 kHz call is 30-40 ms, with a peak frequency of 45-55 kHz, although it may reach 70 kHz. The bandwidth of these calls is 5-7 kHz, broader than that of 22 kHz calls.

Researchers recently distinguished two major types of 50 kHz calls: constant frequency (flat) calls and frequency-modulated calls (step calls with trills; Burgdorf et al. 2007; Wöhr et al. 2008). Further experimental data indicate that rats emit one or the other type of call in dissimilar situations. Calls with the flat sound frequency seem to play a social coordinating function (Wöhr et al. 2008), to be associated with aggressive situations, or to indicate social ambivalence (Burgdorf et al. 2008), whereas the frequency-modulated calls (step calls or combined step-trill calls) are characteristic of reward situations and the expression of positive affect (Burgdorf et al. 2008). These calls may represent a vocal homologue or a preserved-in-evolution counterpart of human laughter (Panksepp and Burgdorf 2000)—the calls themselves are not laughter in the human sense, but rather are used by rats in a way that is somewhat analogous to human laughter.

Neurochemical Substrates for Emission of 22 kHz and 50 kHz Calls

Rats emit either 22 kHz or 50 kHz calls depending on the situation, and both the circumstances and pattern of the emission of these calls seem to be mutually exclusive (Brudzynski 2007). While 22 kHz calls are associated with aversive situations, behavioral inhibition, and breaking contacts among rats, 50 kHz calls are associated with appetitive situations, reward, behavioral activation, and approach (Brudzynski and Chiu 1995; Wöhr and Schwarting 2007). There are extremely rare, behaviorally ambiguous situations with brief bouts of emissions of both types of call, but rats cannot acoustically mix the 22 kHz and 50 kHz calls.

Furthermore, the acoustic parameters of the two calls are not overlapping and are often separated by a significant safety space that ensures other rats’ unambiguous recognition of the calls (Brudzynski 2007). It is likely that each call type signals a particular behavioral state and that the recipients of the calls recognize and understand them as conveying information about the state of the caller. Such understanding is crucial for the receiving rat to determine its own appropriate behavioral response (Brudzynski 2007).

But how does the rat brain initiate these two different and mutually exclusive types of ultrasonic vocalizations? Initiation is regulated by two ascending systems that originate in

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1 It is worth mentioning that most juvenile rats readily learn to play with humans as they play with their siblings—after just 2-3 repetitions most juvenile rats will follow a human hand and emit many 50 kHz calls (Burgdorf and Panksepp 2001; Burgdorf et al. 2005). Many rats in adulthood may still emit such calls in contact with a familiar human (Schwarting et al. 2007), although these contacts do not have the features of juvenile play.
the brain stem tegmentum: the cholinergic system and the mesolimbic dopaminergic system (Figure 3). In a broad sense, these two systems are part of the ascending brainstem reticular system, which evolved as an ancient generalized arousal system (Pribram 1971) and regulates the entire state of the organism (for further discussion of the state of the organism, see McCarley 1980 and Brudzynski 2007).

Activation of the rat’s ascending cholinergic system, which originates from the laterodorsal tegmental nucleus and travels to the basal forebrain and limbic areas (Figure 3, filled arrows), induces defensive behavior and intensive 22 kHz vocalization (Brudzynski and Barnabi 1996; Brudzynski 2001). Pharmacological activation of this system by cholinomimetics also induces 22 kHz alarm calls, while antagonism of the system by anticholinergic agents blocks or decreases the number of such calls (for details, see Brudzynski 2001).

On the other hand, activation of the rat’s ascending dopaminergic system, which originates from the ventral tegmental area and terminates in the nucleus accumbens and other basal forebrain structures (Figure 3, blank arrows), induces behavioral activation—increased locomotor activity, exploration, and an increase in the number of 50 kHz vocalizations (Brudzynski 2007; Burgdorf et al. 2001; Thompson et al. 2006). Systemic or intra-accumbens application of amphetamine significantly increases the number of 50 kHz calls.

Activity of the ascending cholinergic system induces a general negative state, defined as a response to “external or internal stimuli and/or situations (complex stimuli) that present threat or danger to the organism, cause or can cause physical damage or impairment, biological or sociobiological destabilization, and disruption of physiological functions and balances” (Brudzynski 2007, 262-263). The negative state of the organism includes not only adaptive changes in the somatic, autonomic, and endocrine systems but also a negative affective state (for a full discussion, see Brudzynski 2007).

Activity of the ascending dopaminergic system induces a general positive state, defined as a response to “stimuli and/or situations that minimize threat or danger to the organism, enhance its security, preserve physical and social integrity, improve, or can improve biological or sociobiological stability, maintain and stabilize physiological functions and

Figure 3 Two ascending tegmental systems responsible for the initiation of vocalization. The system originating from the laterodorsal tegmental nucleus (LDT) is cholinergic (filled arrows). Release of acetylcholine in the medial cholinceptive vocalization strip (stippled area) induces 22 kHz vocalization. Main targets of this system are anterior hypothalamus (AH), preoptic area (PO), bed nucleus of stria terminalis (BS), and lateral septum (LS). The system originating in the ventral tegmental area (VTA) is dopaminergic (blank arrows). Release of dopamine in the nucleus accumbens (NA) and neighboring areas (TU, olfactory tubercle) induces 50 kHz vocalization. The diagram (modified) is from Brudzynski SM. 2007. Ultrasonic calls of rats as indicator variables of negative or positive states: Acetylcholine-dopamine interaction and acoustic coding. Behav Brain Res 182:261-273.
balances” (Brudzynski 2007, 263). The positive state of the organism includes the relevant changes in the somatic, autonomic, and endocrine systems, as well as a positive affective state (for a full discussion, see Brudzynski 2007).

These observations and numerous experimental results led to the postulation that 22 kHz alarm calls and 50 kHz appetitive calls can predict the state of an organism and thus serve as reliable indices of the general (including the affective) state of the rat organism (Brudzynski 2007; Knutson et al. 2002 had already postulated the usefulness of the ultrasonic vocalization in assessing an animal’s affective state). Based on the evidence presented in this review, one may further postulate that rats’ 22 kHz and the 50 kHz calls are also reliable predictors of increased cholinergic or dopaminergic activity in the brain.

Conclusions

Rats are highly social animals that can emit audible sounds but communicate among themselves predominantly in the ultrasonic range of sound frequencies. Their ultrasonic vocalization evolved as a defensive behavior and an antipredator adaptation in particular.

Rats emit two basic types of ultrasonic calls: 22 kHz (alarm) calls and 50 kHz (appetitive or social) calls. Behavioral observations consistently indicate that a rat’s 22 kHz vocalizations signal aversive situations and a negative state, and 50 kHz calls signal appetitive situations and a positive state. The calls differ dramatically in their acoustic parameters and are easily distinguishable: the alarm calls (22 kHz) are long (from 100 to 3000 or more ms) and have a low sound frequency, whereas the appetitive calls (50 kHz) are short (30 to 40 ms) and have a twofold higher sound frequency.

The two call types are driven from the core limbic midbrain regions by two ascending projections: the activity of the ascending cholinergic system initiates alarm calls and the ascending dopaminergic system initiates appetitive calls. These two systems work in a mutually exclusive way, thus animals normally emit only one or the other type of call.

The underlying neurochemical mechanisms and consistency of acoustic parameters of these two different calls make them good indices of the rat’s general and affective state. The 22 kHz alarm calls inform about the rat’s anxiety and negative state, and the 50 kHz calls about its appetitive and positive state. Although the calls may be useful in assessments of a rat’s affective state, ultrasonic vocalization does not provide information about a rat’s physical or affective (the psychological dimension) pain.

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References


2The general state of an organism is a “sum of measurable values obtained from a (practically infinite) number of variables describing functions of the whole organism” (Brudzynski 2007, 262, based on Rosen 1970). Thus the state of the organism includes both the psychological (affective) dimension as well as the physiological correlates from subcellular to cognitive parameters.