

Review

Rat 22 kHz ultrasonic vocalizations as alarm cries

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Abstract

Rats incorporate circa 22 kHz ultrasonic alarm cries into their defense pattern in response to a predator threat. These calls are dependent on conspecific presence, show gender differences, and tend to be emitted from a place of relative safety. Rats emit sonic defensive threat vocalizations when approached by a potential threat. These are emitted regardless of conspecific presence, and increase as a function of threat proximity, eventually culminating in defensive attack at close distances. Ample data from field studies suggest a similar division of vocalizations into alarm or warning cries, and defensive threat vocalizations, although both are often subsumed under the rubric of “alarm cries”. A clear distinction between these types of calls is necessary for proper analysis of the evolutionary mechanisms responsible for the development and maintenance of each of them. Furthermore, the integration of data from field studies and laboratory experiments may prove useful in evaluation of the relationship between each type of cry and emotional (fear or anxiety-like) states in mammals.

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1. Introduction

Three classes of ultrasonic vocalizations (USVs) (inaudible to humans, >20 kHz) and one sonic vocalization (audible to humans, <20 kHz) have been described in the laboratory rat (*Rattus norvegicus*) [13,21]. As pups, rats emit short distress vocalizations that may reach a peak frequency of 40 kHz when isolated from the dam [23]. As adults, rats emit two distinct USVs; a high-pitched and short circa 50 kHz USV,

and a low-pitched and longer circa 22 kHz USV. The 50 kHz USV tends to be produced in non-aggressive conspecific social interactions [14]; during play [37]; and during the male ejaculatory period [46]. Sales and Pye have also reported such cries during fighting in male conspecifics [53].

Rats emit 22 kHz USVs in a variety of circumstances (for review see [20,53]). These include cries during the post-ejaculatory period [2,3], while engaging in intraspecific defensive/submissive postures as part of intermale social interactions [40,51,65], when exposed to a predator [8,11], when startled during opiate and cocaine withdrawal [27,48,69] and in a model of chronic pain [24]. Twenty-two kilohertz USVs

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have been suggested as a measure of affective shifts in rats [5,19,38] and have been used in a variety of both conditioned and unconditioned models of anxiety [22,39,47,49,54,68].

Sonic vocalization occurs in wild *R. norvegicus* as part of a defensive threat response to an oncoming predator, appearing abruptly as the predator approaches to within a meter or so from the rat [13]. It is less prominent in laboratory rats but can be elicited by pain [12].

2. Rat vocalizations during predator–prey interactions

This lab has studied rat vocalizations largely in the context of defensive behavior, usually to predators. In particular this has involved USVs in rats in seminatural visible burrow systems (VBS), and sonic vocalizations in the context of responsivity to approach and contact by a potential predator, a human experimenter (for review of methods see [8,9,11,13,57]). The VBS enclosures contained an open area plus tunnels and chambers, and typically housed three male, two female groups of adult rats, sometimes including pups born in the habitats. After a week of group residence, a cat was placed in the open area for 15 min and USVs were recorded for 175 min following cat presentation. A control/sham exposure using a toy cat followed 2–3 days later, and this session was followed by a last 2–3 day (real) cat exposure.

Upon introduction of the cat into the open area of a VBS (cat day 1), rats quickly scattered and fled into the burrows, subsequently emitting 22 kHz USVs (actually 18–24 kHz USVs) [11]. These vocalizations continued until about 30 min after the cat was removed, declining thereafter. During this time and for several more hours, the rats showed reductions in non-defensive activities such as eating, copulation, or fighting and refrained from reentering the surface of the VBS. When a control (toy cat) stimulus was presented, a brief flight to the burrow system did occur, but rats showed only short-lived 22 kHz USVs and rapidly reentered the open area, resuming their regular activities. The second cat exposure induced responses virtually identical to the first, indicating that no habituation had occurred in the defenses elicited by predator presentation. Rats exposed individually to a cat both in an open field that provided no escape, and in a VBS, where escape to the burrows was possible (and quickly utilized), did not vocalize [11].

That these USVs occurred only when the rat was in a conspecific social setting is consonant with findings of alarm cries (also referred to as alarm calls) in other rodent species [16]. The ability of playback of 22 kHz USVs to induce a marked reduction in activity of the recipient rats is also consonant with a view of these as alarm cries directed at conspecifics [22]. Finally, playback of 22 kHz USVs also induces recruitment of cries from other conspecifics in a social group, including preweanling pups (Blanchard, unpublished observations) further contributing to a view that the 22 kHz vocalizations not only have a major impact on listening conspecifics, inducing attention and defensiveness, but also are directed at such conspecifics, occurring only when they are present. Preweanling rat pups responded to the playback by emitting USVs of approximately 27 kHz. This is in contrast to the typical 40 kHz pup call. Moreover, Takahashi [63], found

that 14-day-old pups inhibit typical circa 40 kHz vocalizations in response to a threatening stimulus (an adult male conspecific). These findings suggest distinct functional differences between 40 kHz pup vocalizations, which are inhibited by a threatening stimulus, and the observed 27 kHz vocalizations, which may be related to the classic 22 kHz vocalizations of adult rats.

It is useful to view these USV in the context of other defensive behaviors in the VBS. Aside from USVs, rats consistently exhibited four major subpatterns of defense in response to cat presentation in the VBS; namely withdrawal, movement arrest, risk assessment and suppression of ongoing non-defensive behaviors [9]. Risk assessment is a behavior pattern facilitating assessment of the threat potential of ambiguous threat sources or novel situations [10]. Risk assessment is typically measured as the time spent scanning a territory for possible threats, and is enhanced if a predator has been previously associated with a context [9]. In the VBS, a widely accepted measure of risk assessment is the number of head-outs, in which the subject would extend its head out of the tunnel and scan the surface.

Dominant males were always first to exit the burrow system following cat presentation (and removal). In addition, only dominant males exhibited corner runs, a sprint across the internal corners of the open area of the VBS, entering and exiting this area in a single, uninterrupted run. We interpreted corner running as a relatively safe way to assess whether the (unseen, having been removed) cat was still present by soliciting an attack. This behavior was nonetheless relatively safe because (1) the dominant invariably scanned the area prior to the corner run and never embarked upon the run when another animal blocked its exit through the adjacent opening and (2) the run itself was only a matter of a second or so, as the entry and exit to the open area were only a few centimeters away from each other. This tactic enables some clarification of whether the threat is present, although concealed, and is thus a form of risk assessment.

3. Sonic vocalizations to a predator

Sonic vocalizations to a predator occur on an equally predictable basis, but under very different circumstances. Rats adjust their defensive response in accordance with the proximity of the approaching threat (a human experimenter). Whereas distal threats produce flight or freezing responses, depending on the availability of an escape route, proximal threats – at about 1 m distant for wild *R. norvegicus* – progressively induce sonic defensive threat vocalizations (also referred to as defensive threat cries). If the threat stimulus moves even closer, defensive attacks and bites are elicited [13]. Similar cries (“screams”) have been recorded in aggressive agonistic encounters in captured wild Black rats (*Rattus rattus*), close relatives of *R. norvegicus* [34].

The function of this behavior appears to be straightforward: to discourage further approach from a dangerous opponent by threat of defensive attack. These sonic vocalizations are a virtual certainty when wild rats are approached by a human, regardless of whether they were wild-trapped or reared in a laboratory set-

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