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22–28 Khz ultrasonic vocalizations associated with defensive reactions in male rats do not result from fear or aversion

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Abstract. This study was carried out to determine whether 22–28 kHz vocalizations emitted during intermale interactions in adult rats were related with a state of fear, aversion or resulted from painful stimulation. Vocalizations in the 22–28 kHz range were measured in male rats during non-aggressive and aggressive social interactions; when given foot shock with a partner; during non-aggressive social interactions after an injection of (i) acetic acid (1%, IP); (ii) pentylenetetrazol (20–30 mg/kg, IP) and (iii) lithium chloride (63.8 mg/kg, IP). Ultrasonic vocalizations were consistantly detected in all rats while the animals displayed defensive or submissive postures when tested as intruders confronted with offensive residents or when administered foot shocks. Only occasional vocalizations were emitted, even in the presence of a partner, when the animals had received other painful or aversive treatments. These data support the hypothesis that 22–28 kHz vocalizations during intermale interactions are associated with defensive postures and are not the consequence of a state of fear or aversion.

Key words: Ultrasonic vocalizations – Defense – Pain – Fear – Aversion – Social interactions – Rat

Several studies have reported that rats, as other rodents, emit ultrasonic vocalizations during different natural and experimental situations and principally during social interactions (Sales 1972; Brown 1976; Nyby and Whitney 1978; Kaltwasser 1990). In particular, vocalizations in the range of 20–30 kHz, often referred as the "22 kHz call", have been described and have been shown to be associated with (i) maternal behaviour (Bell et al. 1971), (ii) male copulatory behaviour (Barfield and Geyer 1972; Nyby and Whitney 1978; White et al. 1990), (iii) intraspecific defensive and/or submissive behaviour (Lore et al. 1976; Nyby and Whitney 1978; Corrigan and Flannelly 1979; Thomas et al. 1983; Takeuchi and Kawashima 1986 and Kaltwasser 1990; Van der Poel and Miczek 1991) and (iv) antipredator defensive behaviour (Blanchard et al. 1990, 1991). Such vocalizations have also been associated with stressful and painful situations (Barfield and Geyer 1972; Francis 1977; Tonoue et al. 1986; Cuomo et al. 1988; Van der Poel et al. 1989; Van der Poel and Miczek 1991) and they have been proposed as a measure of fear and aversion (Tonoue et al. 1986; Cuomo et al. 1988).

Although some authors have proposed that the 22 kHz ultrasonic calls in rats reflect a state of arousal (Bell 1974) or are the by-product of a respiratory manoeuvre, the function of which is to cool brain stem structures (Blumberg and Alberts 1991), several reports have suggested that they play an important role in intraspecific communication in behavioral contexts of survival value (Sales 1972; Nyby and Whitney 1978; Barfield and Thomas 1986; Blanchard et al. 1990). The exact meaning and function of these vocalizations remain, however, to be elucidated.

Nevertheless, when measuring defensive reactions in laboratory conditions, ultrasonic vocalizations in the rat can be an objective and easily quantifiable variable accompanying emotive behavioural reactions. Using high-capacitance microphones, measurement of this variable has recently been used in the study of different types of pharmacological manipulations (Vivian and Miczek 1991; Depaulis et al. 1992). However, whether the 22 kHz vocalizations in the rat result from the aversive, stressful or painful aspects of aggressive encounter or are a physiological component of some defensive reactions has not been determined.

The purpose of the present study was to examine whether 22 kHz vocalizations in the adult rat are the expression of a state of fear or aversiveness or result from painful stimulation that may occur during agonistic encounters. To this aim, the effects of treatments known to be either aversive, fear promoting or painful on the emission of 22 kHz calls in male rats during social isolation or social interactions were examined. They were compared to a "resident-intruder" situation in which the intruder displayed different defensive postures.

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Materials and methods

Animals. Male Wistar rats (300–350 g) from our laboratory were used in this study. During the experiments, they were kept in single cage (25 × 30 × 35 cm) with food and water ad libitum and maintained under a 12/12 h light-dark cycle with light at 8:00 a.m. Male rats of a different group (350–450 g) were used as partners for the required tests.

Video and ultrasound recording. The behaviour of the animals during the different test situations was video recorded with the camera placed 1.5 m above the test cage in a room adjacent to the animal room. Ultrasounds in the 20–30 kHz range were made audible using a bat detector receiver (QMC Instruments, London) placed at the same distance as the camera from the test cage. This detector was set on a frequency of 25 kHz so that all ultrasonic signals in a 5 kHz range could be detected. The signal was fed into an electronic timer which allowed measurement of the total duration of ultrasound emission. It was also fed into the audio channel of the video recorder. When animals were tested with a partner, the rat emitting ultrasounds could be clearly identified by the high amplitude inspiration which occurs at the end of each ultrasonic vocalization (Roberts 1972; Sales 1972; Kaltwasser 1990). In our conditions, no ultrasounds were detected in the absence of this respiratory effort.

Isolation test. The animals were placed in a test cage similar to their own (25 × 30 × 35 cm) and their behaviour and vocalizations were recorded for 10 min.

Social interactions. The rats were confronted with a 20% heavier partner and their social interactions and vocalizations were recorded for 10 min. The test took place either in a test cage similar to their own cage (neutral cage) or, for one experiment, in the cage of another animal in the presence (intruder with resident) or absence (intruder without resident) of the partner.

Foot shocks. The animals were placed in a plexiglass cage (20 × 20 × 30 cm), the floor of which was formed by stainless steel bars of 3 mm diameter connected to a shock generator (Campden Instruments Ltd.). This generator was controlled by relayed programming equipment and supplied scrambled electric shock of specified intensity, duration and frequency to the grid floor of the test cage.

Drugs. Pentylenetetrazol (Sigma, USA) and lithium chloride (Merk, Germany) were both dissolved in 0.9% NaCl before the test and injected IP with a volume of 1 ml/kg. Acetic acid solution 1% was mixed with arabic gum (9 ml/1 g), and was injected IP with a volume of 5 ml/kg.

Protocols. In experiment 1, eight rats were placed for 10 min in the following four conditions: A: isolation test; B: in a neutral cage with a non-offensive partner; C: in the empty cage of a conspecific and D: as intruder with an offensive resident. The sequence of tests was allocated to each rat in a counterbalanced order. A delay of at least 3 days was allowed between two tests.

In experiment 2, six rats were placed either alone or paired with a partner in a foot-shock chamber in a counterbalanced order, a delay of 5 days being allowed between two tests. In each case, the animals received 20 shocks of 1 mA intensity and 1 s duration every 10 s. In these two test situations, the cumulated duration of ultrasonic vocalizations was measured from the video recordings using a stop watch. Only the vocalizations of the tested animals were thus taken into account.

In experiment 3, six rats were placed in four different situations. The rats were injected with a solution of acetic acid (5 ml/kg; Calvino and Le Bars 1986) in isolation or in social interaction in a neutral cage (conditions B and D, respectively). In conditions A and C (isolation or social interactions in a neutral cage, respectively), the rats were injected with arabic gum solution with a volume equal to injections of acetic acid. In all cases, the behaviour of the animals was recorded for 10 min, 30 min after the injection. The sequence of tests was allocated to each rat in a counterbalanced order. A delay of at least 5 days was allowed between two tests.

In experiment 4, eight rats were placed for 10 min, starting 5 min after the injection, in the following four conditions: A: isolation test with IP injection of NaCl 0.9%; B: isolation test with injection of pentylenetetrazol (20 mg/kg, IP); C: social interactions in a neutral cage after NaCl injection; D: social interactions in a neutral cage after injection of pentylenetetrazol (20 mg/kg, IP). The sequence of tests was allocated to each rat in a counterbalanced order. A delay of at least 5 days was allowed between two tests. A different group of ten rats was tested in the presence of a partner after they have received an injection of saline (A) or 30 mg/kg IP of pentylenetetrazol (B). For five of these rats, the ultrasound detector was set as usual (i.e. 25 kHz) whereas, for the other five rats, it was set on 20 kHz.

In experiment 5, ten rats were placed in the following four test situations: in conditions B and D, they received an injection of lithium chloride (63.8 mg/kg, IP) and were tested in isolation or with a partner in a neutral cage, respectively. In conditions A and C, they received an injection of saline with an equal volume and were tested in isolation or with a partner in a neutral cage, respectively. All animals were tested for 10 min, 20 min postinjection. The sequence of tests was allocated to each rat in a counterbalanced order. A delay of at least 5 days was allowed between two tests.

Statistics. The data were expressed in mean ± SEM or median and quartiles of total duration of 22 kHz ultrasounds. Comparisons between groups were performed using non parametric analysis for paired samples (Friedman and Wilcoxon tests; Siegel 1956).

Results

Experiment 1: effects of intraspecific attacks

The total duration of 22 kHz ultrasounds (Fig. 1) was significantly higher (Friedman test, $X = 15.34$, $P < 0.01$) when the animals were confronted as intruders into a resident's cage in the presence of a partner (condition D). During this condition, all intruders were attacked at least once and several offensive attacks from the residents were often observed (Mean ± SEM = 4.4 ± 0.9). All intruders emitted 22 kHz vocalizations but only after they have been attacked by the resident. These 22 kHz vocalizations mainly consisted of long pulse calls (800–3000 ms) and were detected concomitantly with three types of behavioural elements: (i) defensive upright postures, (ii) "on the back" or (iii) immobility when the rats displayed a crouching position. The first two behavioural elements were never observed in the other three test conditions (data not shown).

Experiment 2: effects of electric foot-shock

The total duration of 22 kHz vocalizations was significantly higher when the animals were tested with a partner (118.0 ± 9.8 s) as compared to when tested alone (40.5 ± 15.3 s: Wilcoxon test, $P < 0.05$). Flinch/jumps reactions and occasional backward movements were observed concomitantly with the shocks when the rats were individually tested. Between shocks, the animals were immobile and occasionally emitted ultrasonic vocalizations. When tested with a partner, after the first four or five shocks, all the animals displayed upright postures, often pushing the partner with the forelimbs. These pos-

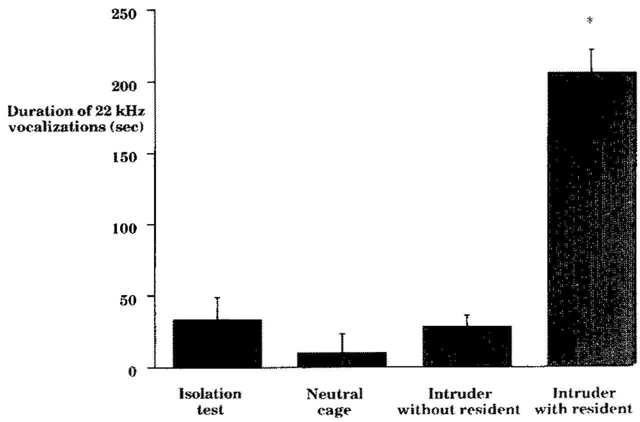

Fig. 1. Mean ± SEM of total duration of 22 kHz vocalizations emitted during 10 min in male adult rats ($N = 8$) in different test situations. $^{*}P < 0.01$ vs neutral cage with a non-offensive partner

tures were generally observed just at the end of a shock and generally lasted 3–4 s. They were similar to those displayed by intruders in the resident-intruder situation. Long pulse ultrasonic vocalizations were generally detected concomitantly with these postures in all the animals.

Experiment 3: effects of acetic acid

Intraperitoneal injection of acetic acid did not result in the production of 22 kHz ultrasounds whether the rats were alone or with a non-offensive partner (Friedman test, $X = 1.75$, $P > 0.5$; Table 1). Following acetic acid injection, the animals generally remained immobile and showed little interest for their environment or their partners (data not shown) and writhes and abdominal constrictions were regularly observed for about an hour after the injection, with a maximum between 30 and 60 min.

Experiment 4: effects of pentylenetetrazol

Injection of pentylenetetrazol did not result in the production of 22 kHz vocalizations whether the animals were tested in the isolation or in the social interactions conditions (Table 1; Friedman test, $X = 1.35$, $P > 0.7$). When treated with 20 mg/kg pentylenetetrazol, the animals showed no significant modifications of their behaviour in the isolation test and an increased duration of immobility in the social interaction test (data not shown). When treated with 30 mg/kg, no ultrasounds were emitted whether the detector was set on 25 or 20 kHz. At this dose, facial and forelimbs myoclonies were occasionally observed.

Experiment 5: effects of lithium chloride

Injection of lithium chloride, did not result in the production of 22 kHz vocalizations whether the animals were tested alone or with a partner (Friedman test, $X = 3.63$, $P > 0.3$). When the animals were re-exposed to the same test conditions, for 10 min, 2 days after the test and without any injection, no ultrasounds were detected.

Table 1. Median (quartiles) duration (s) of 22–28 kHz vocalizations emitted during 10 min rats in the following drug conditions: A: isolation after vehicle; B: isolation after drug treatment (1% acetic acid ($N = 6$); 20 mg/kg pentylenetetrazol ($N = 8$); 63.6 mg/kg lithium chloride ($N = 10$); C: social interactions in a neutral cage after vehicle; D: social interactions in neutral cage after drug treatment

Test conditions	A	B	C	D
Acetic acid	0 (0–1)	0 (0–0)	0 (0–0)	0 (0–14)
Pentylenetetrazol	0 (0–71)	0 (0–3)	0 (0–0)	0 (0–4)
Lithium chloride	0 (0–1)	0 (0–0)	0 (0–6)	0 (0–0)

Discussion

The results of the present study indicate that 22 kHz vocalizations are recorded in the male rats in situations where intraspecific defensive/submissive behaviours occur, whether they result from the attacks of a conspecific or from a somatic painful situation. In contrast, no such vocalizations were significantly produced, even in a social situation, following treatments that result in visceral pain or promote fear or aversiveness.

When the animals were tested as intruders in the presence of the resident (experiment 1), 22 kHz vocalizations were almost always recorded soon after the rats were attacked by the resident. These vocalizations were concomitant with defensive upright and on the back postures or while the animals remained immobile in a crouching position, especially after having been attacked. When animals received electric foot-shocks they also emitted 22 kHz vocalizations concomitantly with upright postures (experiment 2).

These data are consistent with previous reports, where long 22 kHz vocalizations were emitted by the intruders once being attacked by a resident (Sales et al. 1972; Thomas et al. 1983; Takeuchi and Kawashima 1986; Van der Poel and Miczek 1991). More especially, they are in agreement with the observation that intruder rats emit 22 kHz vocalizations along with submissive postures and boxing (Takeuchi and Kawashima 1986). Although from a different species, long pulse 22–28 kHz vocalizations have been shown to appear along with upright postures in *Rattus rattus* (Kaltwasser 1990). Data from experiment 2, using electric foot shocks, also confirm data from the literature obtained in similar test conditions (Barfield and Geyer 1972; Tonoue et al. 1986; Cuomo et al. 1988).

In contrast with the above mentioned situations, experimental situations where the animals were submitted to other painful, stressful or aversive treatments did not result in the production of ultrasonic vocalizations.

Intraperitoneal injection of acetic acid has been shown to induce nociceptive stimulation which can be associated to visceral pain (e.g., Calvino and Le Bars 1986). At the dose used in the present study, such treatment results in a long-lasting effect culminating at 40 min. The effectiveness of the treatment was confirmed by the signs of discomfort displayed by the animals (writhes, abdominal constrictions). However, this treatment did not result in 22 kHz vocalizations whether the rats were alone or with a partner. Although the rats never displayed any upright or on the back postures, they very often remained immobile as in a crouching position, a posture which could have been quite compatible with the emission of ultrasounds.

The fact that electric foot-shocks evoke 22 kHz vocalizations in rats tested alone whereas acetic acid injection had no effects, suggests that somatic rather than visceral painful stimulations participate in the triggering of these vocalizations. These two treatments also differ in their temporal aspects: foot shocks being short and recurrent stimulations whereas acetic acid is longer lasting and almost continuous. Electric foot shocks are certainly closer in nature to the types of painful stimulations (i.e., somatic, short and recurrent) that a rat may receive during agonistic encounters. Our data thus suggest that the modality of the painful stimulations is critical in the triggering of 22 kHz vocalizations in the rat.

That the aversive or fear states which may accompany agonistic encounters in rats do not appear to be sufficient to evoke 22 kHz vocalizations is suggested by the following data. In experiment 1, introduction into an empty resident's cage did not result in the production of 22 kHz calls. This result is in agreement with previous study (Corrigan and Flanelly 1979) which reported no ultrasonic calls when the rats were placed into the empty cage of an aggressive partner. In experiment 4, systemic injection of pentylenetetrazol does not result in 22 kHz vocalization. Administration of pentylenetetrazol is known to induce anxiogenic effects in humans (Rodin and Calhoun 1970) and has been shown to possess fear-promoting effects in animals (see Pellow and File 1984). At doses similar to those used in the present study, this compound has discriminative stimulus properties which have been used as an animal analogue of human anxiety (see Lal and Emmett-Oglesby 1983). In particular, cross-generalization has been recently reported between pentylenetetrazol discriminative stimulus and exposure to a predator (Gauvin et al. 1991). In our laboratory, similar doses enhanced freezing and submissive reactions of intruder rats towards offensive residents (Piret et al. 1992). Finally, systemic administration of lithium chloride, which is often used to evoke aversion in animals (Lett 1985), did not induce 22 kHz vocalizations. In the present study, the dose of lithium and postinjection delay were the same as for taste aversion procedure (Nachman and Ashe 1973).

The results of the present study thus strongly suggest that 22 kHz long pulse vocalizations occurring during intermale agonistic encounters in the rat are specifically associated with defensive reactions. These calls cannot be interpreted as a reliable correlate of fear or emotional/aversive state of the animals: in our test conditions they were detected only when the animals were engaged or had just been engaged in defending themselves. This conclusion is in contrast with previous studies which have proposed that such vocalizations could be used as a measure of the emotional state of the rat (Tonoue et al. 1986; Cuomo et al. 1988, 1992). For example, it was shown in a recent study that rats emit 22 kHz calls both during the presentation of the conditioned stimulus and the intertrial interval of a two-way avoidance task (Cuomo et al. 1992). However, when submitted to unavoidable or avoidable foot shocks, 25% of the rats never emitted ultrasonic vocalizations (Cuomo et al. 1988, 1992), whereas *all* animals vocalized in the ultrasonic range when they were engaged in defensive reactions, in the present study. Also, electric footshocks were used as the unconditioned stimulus in these studies. This kind of stimulus is known to trigger defensive reactions when the animals are paired and it is very likely that such a stimulus activates neural circuitries involved in defensive reactions (see Keay and Bandler 1992). Direct activation of these circuitries in the midbrain have been shown to evoke 22 kHz ultrasonic vocalizations (Depaulis et al. 1992).

It has been suggested (Blumberg and Alberts 1991) that 22 kHz long pulse vocalizations in the male rat are a by-product of a respiratory maneuver. By increasing gas exchange in the lungs, this mechanism is certainly beneficial for energy-consuming behaviours such as defense. In this respect, the data of the present study are in agreement with this hypothesis since ultrasonic vocalizations were detected only when the animals displayed or had displayed defensive reactions involving intense effort. However, it is not certain that respiratory patterns accompanying qualitatively different types of defense (e.g., upright postures, freezing, on the back) are identical. Furthermore, data from the literature (Blanchard et al. 1991) have shown that 22 kHz vocalizations can be detected in the rat in the absence of any defensive confrontation.

The data of the present study, along with reports from the literature, suggest that 22 kHz vocalizations in the male rat constitute a component of an integrated defensive reaction to exteroceptive stimuli (e.g., dangerous objects, presence of an offensive partner or a predator) but *not* to interoceptive noxious and/or aversive stimulation (e.g., acetic acid, pentylenetetrazol, lithium chloride). Although the communicative function of 22 kHz ultrasonic vocalizations remains to be elucidated, it has recently been suggested that they may act as an alarm cry (Blanchard et al. 1991) since they occur with a much greater incidence when rats are in a social context. In this respect, noxious exteroceptive stimuli are certainly more relevant for the conspecifics than interoceptive ones.

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