Characteristics of ultrasonic vocalizations emitted by rats during shock-elicited aggression

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Albino rats tested for shock-elicited aggression on occasion emitted periodic ultrasonic calls. The fundamental frequency of these calls was about 24 kHz, with harmonics appearing at 72 and 120 kHz, and the calls lasted as long as 3-4 sec. These calls were emitted by rats which had adopted an upright submissive posture following attack(s). These long 22-26-kHz calls may serve to inhibit or prevent unlearned behaviors in rats.

Attempts to control or modify aggression demand an understanding of the basic mechanisms by which agonistic behavior is generated. The first of two major explanations of agonistic behavior arises from a psychological tradition, arguing that organisms learn to be aggressive either through social modeling or by finding aggressive behavior instrumental to achieving some end (Bandura, 1973). A second ethological approach argues that vertebrates, including man, have evolved an inborn aggressive potential which is generated by unlearned, i.e., genetic, factors analogous to those important in other behaviors critical to species survival, e.g., sex (Tinbergen, 1968). The former position argues that learning variables should be most relevant in promoting or eliminating aggression, while the latter argues that aggression cannot be eliminated but, at best, be channeled into nondestructive areas. Indeed, Tinbergen (1968) has stated that "Lorenz is, in my opinion, right in claiming that elimination, through education, of the internal urge to fight will turn out to be very difficult, if not impossible" (p. 1418).

Ethological theory argues that specific sensory stimuli release or inhibit genetically based species-specific behaviors. It is proposed that levels of such unlearned behaviors, including aggression, may be lowered by eliminating those sensory events which "release" them or by producing those stimuli which "inhibit" them (Moyer, 1976). In attempting to elucidate the above theories using animal models of aggression, some evidence on the effects of reinforcement has been generated (e.g., Baisinger &

Roberts, 1972; Van Hemel, 1972), but little with respect to sensory control.

It is known that among myomorph rodents ultrasonic signals are correlated with behaviors that may be classified as unlearned. The importance of ultrasonic vocalizations emitted by rat pups in eliciting maternal behavior has been apparent for some time (Sales & Pye, 1974). Barfield and Geyer (1972) have shown that male rats emit an ultrasonic signal during the postejaculatory period following successful copulation. They suggest that this signal may inhibit the hopping and darting behaviors of the female that produce sexual arousal in the male and so serve as a signal to cease social contact. Sales (1972; Sales & Pye, 1974) has shown that two classes of ultrasonic signals are emitted when a foreign rat is introduced into the home cage of another. One class consisted of short-duration (3-60 msec), high-frequency (45-70 kHz) signals which occurred in the context of ongoing attack behavior. The second class consisted of long-duration (800-1,600 msec), low-frequency (22-30 kHz) signals which occurred in the context of non-attack behavior. Others have reported vocalizations having a 20-26-kHz component accompanying agonistic behavior and have also suggested that such signals may play an aggression-inhibiting role (Berg & Baenninger, 1973; Lore, Flannelly, & Farina, 1976).

It has been argued that shock-elicited aggression may fit ethological (or unlearned) explanations of agonistic behavior in that it is dependent upon critical sensory information for its elicitation. In untrained rats, tactual sensory information from the snout is critical for the occurrence of shock-elicited aggression; without such information, no aggression occurs (Thor, Ghiselli, & Lambelet, 1974). Olfaction plays a lesser eliciting role than tactual information, while visual cues appear irrelevant (Ghiselli & Thor, 1975). Thus, the occurrence of shock-elicited ag-

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gression is under highly specific sensory control (i.e., tactual) and so fits well into the theoretical explanation of agonistic behavior proposed by Moyer (1976). Audible vocalizations occur in the context of such fighting and are related directly to the level of fighting (Thor, Ghiselli, & Wilson, 1973) and, at least in individual animals, shock can be effective in eliciting ultrasonic calls (Barfield & Geyer, 1972; Lore et al., 1976). Thus, it seems likely that ultrasonic vocalizations, important sensory information in other behaviors, might be present in shock-elicited aggression. The present study sought to determine if ultrasonic vocalizations occurred in the shock-elicited aggression paradigm and, if so, to describe their characteristics and behavioral correlates.

METHOD

Subjects

Six male albino Sprague-Dawley rats, 150 days old and purchased from Holtzman Co., were subjects. All subjects had participated in a prior learning experiment for food. For the duration of the present study, all subjects were individually housed with ad-lib food and water.

Apparatus

Shock-elicited aggression was conducted in a Lafayette operant chamber ($28 \times 20 \times 20$ cm) with a grid floor of 1-cm stainless steel rods. The chamber was enclosed in a sound-attenuating chamber illuminated by a 100-W incandescent bulb. Constant-current shock was delivered to the grid floor from a Lehigh Valley Model 113-04 shocker and scrambler. A "Kuhl" type ultrasonic microphone was constructed after that described by Pye & Flinn (1964). In order to facilitate detection and analysis of ultrasonic signals, the microphone was attached to a frequency transformation circuit which allowed signals' frequency to be stepped down by as much as a factor of 15 to put them into a range audible to humans. Processed (i.e., stepped-down) output from the microphone was recorded on magnetic tape and subsequently analyzed in a Model 7029-A Sonagraph Spectrum (5-16,000 Hz) analyzer

(Kay Electric Co.) to determine frequency and temporal and amplitude characteristics of the signals.

Procedure

The subjects were formed into three pairs and were given 5-10 daily fighting sessions in the operant chamber. Each session consisted of 50 2.0-mA 0.5-sec shocks delivered 6.5 sec apart. Attack was defined as directed movement by at least one rat toward the other which resulted in physical contact and was subsequently followed by at least one of four acts: mutual upright facing postures, boxing, striking or biting at the opponent's snout with the teeth, or supine posturing by one animal. Fighting was expressed as the percentage of shocks effective in eliciting an attack.

RESULTS

Fighting occurred at relatively low levels, ranging from none to 50% over pairs and test sessions. All pairs emitted shock-correlated audible vocalizations and occasional audible vocalizations during the inter-shock interval when attacks occurred.

Monitoring of sessions indicated that two of the three pairs had ultrasonic signals occurring during the sessions. The stepped-down signals sounded as a complex periodic tone and lasted as long as 3-4 sec, averaging 1-2 sec. These signals were not audible to human beings, but correlated with flank movement of the rat emitting the signal. Figure 1 presents one of six examples of ultrasonic signals that were analyzed. It shows a time span of 2,400 msec, which contains two successive signals emitted by one member of a pair of rats. Each signal is of approximately 1,000 msec duration, and they are separated by a silent interval of 200 msec. Two formants (regions of prominent energy) are apparent: one centering about 23 kHz (F1) and a second centering about 72 kHz (F2). This confirms the human im-

Figure 1. Sound spectrograph of two ultrasonic vocalizations showing frequency characteristics over time.

pression that the ultrasonic signal is a periodic complex wave with at least one dominant frequency and one harmonic. It resembles a human fricative speech sound (e.g., f, s, or sh), in which there are dominant frequencies (formants) accompanied by wide-spectrum noise. The absence of this noise in the 200-msec silent period indicates it to be animal generated. Analyses of all signals showed F1 to range between 22.5 and 24.5 kHz, averaging 23.33 kHz, while F2 ranged between 67.5 and 72.0 kHz, averaging 71.0 kHz. The striking aspect of these signals is their constant nature. As may be seen in Figure 1, they show no onset or offset transients or frequency transitions and the dominant frequencies were very consistent both within and between signals. All signals analyzed in this manner showed a similar lack of transients or frequency change. The only noticeable change in signals were occasional irregularities in harmonics (e.g., Figure 1, F2 between 1,800 and 2,000 msec). To clarify these dominant frequencies, a spectrographic analysis of frequencies was made with respect to their energy level (amplitude). Such an analysis of second sample signal is presented in Figure 2. In this instance, F1 = 22 kHz, F2 = 67 kHz, and a third formant (F3), at 108 kHz, is also present. Analyses of signals indicated that this third formant was centered about 121.2 kHz as an average. In Figure 2, the peak of F2 is 2.5-3 dB below that of F1, and F3 is approximately 25 dB below F1. This, along with their average frequencies, suggests that F2 and F3 are harmonics of fundamental frequency F1. Figure 2 also shows that the signals sounded as complex periodic tones because the major formants essentially provide high signal-to-noise ratios. F1 is about 30 dB above ambient noise and F2 approximately 25 dB above ambient noise. Behaviorally, the ultrasonic signals never occurred while the rats were engaged in attack (i.e., when boxing, biting, or showing upright or supine posturing). These signals were not present when no rats were present or only one member of a pair was present during a session. The pair that emitted no ultrasonic signals also failed to show shock-elicited aggression. When ultrasonic signals occurred, they most commonly came from a rat that had adopted an "upright submissive" posture (e.g., Sales & Pye, 1974, Figure 7.9e) and usually followed one or more instances of attack. This posture differs from upright attack posture in that the rats are not mutually facing and the head of the rat emitting the signal is level or pointing down, while in attack postures it points up. In most cases, the second animal adopted a low crouch, the offensive or defensive nature of which was indeterminate. On a few occasions, both rats were upright but not facing when ultrasonic signals occurred.

Figure 2. Sound spectrograph of an ultrasonic vocalization showing amplitude characteristics as a function of frequency.

DISCUSSION

The present study demonstrated that rats exhibiting shock-elicited aggression emit ultrasonic signals. These signals are of long duration (up to 4 sec) and have a base frequency of about 24 kHz with a major harmonic (F2) at about 72 kHz and a minor harmonic (F3) about 120 kHz. The presence of these 24-kHz signals (F1) compares with Sales' (1972) report of long (3,400-msec) ultrasonic signals of about 25 kHz associated with submissive agonistic behavior and Barfield and Geyer's (1972) demonstration of long (1-3-sec) signals centering about 22 kHz associated with the absence of sexual behavior. The present results indicate the presence of other frequencies (F2, F3) that may be of important relevance.

Bordon, Walker and Latané (Note 1) have shown that social contact time by rats in an open field is the same for normal and deaf animals. The authors argue, therefore, that ultrasonic signals neither serve to attract rats to each other nor to regulate duration of social contact. The present study, along with the results of others investigating ultrasonic signals occurring in the context of sex (Barfield & Geyer, 1972) and aggression (Sales, 1972; Sales & Pye, 1974), suggest that ultrasonic signals have social significance. In the present study, the signals occurred only in the social context and not with single or no rats. For the most part, the signals occurred only after at least one attack had occurred. The lack of shock-elicited aggression, the absence of aggression against an intruder (Lore et al., 1976; Sales, 1972), and the lack of sexual behavior (Barfield & Geyer, 1972) suggest that long ultrasonic signals may serve to inhibit or prevent types of behavior which have been classified as unlearned and which are under the control of specific sensory events. Just as particular sensory information is required to "release" certain acts, e.g., agonistic or sexual behavior, the inhibition or prevention of such acts, necessary to main-

tain social order, e.g., dominance or pair bonding, should also be under specific sensory control (Chance, 1962; Moyer, 1976).

The present study demonstrated that ultrasonic signals are correlated with the absence of aggression following attack. Further, it appeared to be submissive animals which emitted such signals. The almost invariant nature of the signal's frequency (see Figure 1) requires that its physical production must also be similar within and across signals, suggesting the possibility of production through the nares. If the present hypothesis concerning the inhibitory nature of these ultrasonic signals is correct, their removal should increase behavior (agonistic or sexual) through disinhibition. Removal might be accomplished by deafening to prevent reception of the signal or a nasal block to possibly prevent signal production. Conversely, signal production via ultrasonic speakers (cf. McCue, 1961) should decrease these behaviors. Given the constant signal characteristics of the present study, production might be accomplished artificially with three sine-wave generators set at the dominant frequencies (24, 72, and 120 kHz) and mixed to generate the complex periodic signal. The high reliability of the shock-elicited aggression paradigm in eliciting attack across a wide variety of species would seem of value in potential investigations of this sort (Hutchinson, 1972). An initial attempt to elicit behavior or ultrasounds from a single rat in response to single-frequency ultrasonic signals was not successful (Sales, 1972).

Finally, Sales (1972; Sales & Pye, 1974) has reported that shorter duration (5-60-msec) higher frequency (45-70-kHz) ultrasonic signals correlate with attack behavior. No such signals were seen in the present study, nor were they seen when a strange rat was placed in a resident's home cage and fighting took place. The reason for their absence is unclear and may relate to ultrasonic apparatus, species, environment, or the actual absence of such signals in the shock-elicited aggression paradigm. Apparatus, environment, and strain differences may explain why F1 differs somewhat in its frequency from that reported elsewhere.

REFERENCE NOTE

1. Bordon, R. J., Walker, M. R., & Latané, B. *Ultrasounds and social attraction in rats: Concomitants, not determinants*. Manuscript submitted for publication, 1975.

REFERENCES

- BAISINGER, J., & ROBERTS, C. L. Reduction of intraspecies aggression in rats by positive reinforcement of incompatible behaviors. *Journal of the Experimental Analysis of Behavior*, 1972, 18, 535-540.
- BANDURA, A. *Aggression: A social learning analysis*. Englewood Cliffs, N.J.: Prentice-Hall, 1973.
- BARFIELD, R. J., & GEYER, L. A. Sexual behavior: Ultrasonic post-ejaculatory song of the male rat. *Science*, 1972, 176, 1349-1350.
- BERG, D. S., & BAENNINGER, R. Hissing by laboratory rats during fighting encounters. *Behavioral Biology*, 1973, 8, 733-741.
- CHANCE, M. R. A. An interpretation of some agonistic postures: The role of "cut-off" acts and postures. *Zoological Society of London*, 1962, Symposium No. 8, 71-89.
- GHISELLI, W. B., & THOR, D. H. Visual, tactual, and olfactory deprivation effects on irritable fighting behavior of male hooded rats. *Physiological Psychology*, 1975, 3, 47-50.
- HUTCHINSON, R. R. The environmental causes of aggression. *Nebraska Symposium on Motivation*, 1970, 20, 155-181.
- LORE, R., FLANNELLY, K., & FARINA, P. Ultrasounds produced by rats accompany decreases in intraspecific fighting. *Aggressive Behavior*, 1976, 2, 175-181.
- MCCUE, J. J. G. Ultrasonic instrumentation for research on bats. *Institute of Radio Engineers International Convention Record*, 1961, 9, 310-315.
- MOYER, K. E. *The psychobiology of aggression*. New York: Harper & Row, 1976.
- PYE, J. D., & FLINN, M. Equipment for detecting animal ultrasound. *Ultrasonics*, 1964, 2, 23-28.
- SALES, G. D. Ultrasound and aggressive behavior in rats and other small mammals. *Animal Behaviour*, 1972, 20, 88-100.
- SALES, G. D., & PYE, J. D. *Ultrasonic communication by animals*. New York: Halsted, 1974.
- THOR, D. H., GHISELLI, W. B., & LAMBELET, D. C. Sensory control of shock-elicited fighting in rats. *Physiology and Behavior*, 1974, 13, 683-686.
- THOR, D. H., GHISELLI, W. B., & WILSON, L. D. Vocalization as an objective measure of shock-elicited social aggression in rats. *Animal Learning & Behavior*, 1973, 1, 263-267.
- TINBERGEN, N. On war and peace in animals and man. *Science*, 1968, 160, 1411-1418.
- VAN HEMEL, P. E. Aggression as a reinforcer: Operant behavior in the mouse-killing rat. *Journal of the Experimental Analysis of Behavior*, 1972, 17, 237-245.

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