

REACTIVITY OF THE SYRIAN GOLDEN HAMSTER TO
ULTRASONIC PURE TONES AND CONSPECIFIC
PAIN VOCALIZATIONS

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1975

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Submitted to the faculty of the Graduate College
of the Oklahoma State University
in partial fulfillment of the requirements
for the degree of
DOCTOR OF PHILOSOPHY
May, 1978



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ACKNOWLEDGMENTS

I wish to express my thanks to Dr. Arthur E. Harriman, committee chairman, for his encouragement, guidance, constructive criticism and investment of time. I am also indebted to Dr. Larry Hochhaus, Dr. Robert Weber and Dr. Richard Lowery for their assistance.

Special appreciation is extended to the zoology department who provided me with the necessary equipment for completion of this project.

Finally, I would like to thank my wife, Dena, for her morale support and typing skills during the completion of this project.

J. R. N.

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CHAPTER I

INTRODUCTION

Behavior patterns in the animal kingdom often have a communicative function. Their effectiveness is often enhanced by conspicuous morphological structures such as feathers or manes. R. Schenkel (1947) stated that the richness and variability of the facial expressions in the wolf argue against the validity of the concept of fixed action patterns in mammals. In a reply, K. Lorenz (1953) showed that in the dog's facial expression, the combination of the intentional movements to flee with those to fight, leads to a great variety of expressions. The intention to flee is characterized by pulling back the corners of the mouth, retracting the upper lip, and wrinkling the muzzle and forehead. Elements of both expressions can be superimposed in varying degrees. Fighting and fleeing are often activated simultaneously, so one usually sees a combination of the two expressions, rather than a pure expression of either.

Animals within a group frequently maintain vocal contact (Eibl-Eibesfeldt, 1970) as do males and females of many species that are mated, as well as the maternal family. These calls which serve to maintain group cohesion, are called contact calls. Many animals learn to recognize the voice of their partner individually. Sea lions and sheep recognize the call of their young individually, and only this individual familiarity keeps them together (Eibl-Eibesfeldt, 1955).

It may be possible after close observation and analysis of such vocal interactions, at various phylogenetic levels, to find characteristics common with that of human communication systems in regard to structural, motivational, and adaptive mechanisms. Only when a type of *lingue franca* can be established at more than one phylogenetic level can behavioral scientists ever hope for cognitive data to verify their behavioral measures (Griffin, 1976). This may well prove to be the most difficult step to take in the comparative behavioral sciences not only due to the initial dearth of information and past research, but also due to out present philosophies on the subject of consciousness and intelligent thought.

The fact that man communicates with men is not a unique zoological phenomenon. Most vertebrates have inter and intraspecies communication systems and among mammals there is often vocal communication. However, animal communication cannot be ordered like a genetic tree and the phylogenetic relations among vertebrates, derived from comparative morphology, is not reflected in any taxonomy of their communication. Many species have evolved highly specialized communication systems, such as the honey bee, many bird species, and dolphins. Neither of these systems nor a dog's or a horse's response to human commands represent even primitive stages of human communication. The empirically determined primitivity of language in man is behaviorally very different from the signals that animals emit for each other. Animal communication systems are special offshoots, as is man's, and cross-species comparisons must be carried out with great caution. The ethological mechanism of animal noises have only been studied in a few animals. We are still ignorant about the biological significance, the releasing

mechanism, and the vital functions of even the most common animal noises.

Historical Review

It has been noted by Anderson (1954) over twenty years ago that rodents, other than bats, emit ultrasonic cries. Initially then, the primary section of this review will concern itself with a description of this phenomena in various rodent species. Following the description the review will address itself with possible motivational factors which may underlie ultrasonic vocalization in rodents and also how the calls themselves vary with this factor which is situationally determined. Ultimately this review relates several current theories, each of which attempts to explain the vocalization phenomenon across motivational states. The phenomenon has been observed in a number of species such as Mus musculus (Ralls, 1967), Peromyscus (Dice, 1955), and albino mice (Noirot, 1968), Mesocricetus auratus and Rattus mervegicus (Sewell, 1970). Pure ultrasonic calling has thus far been noted in only one suborder Myomorpha, or Rodentia, which includes mice, rats, gerbils, hamsters and their allies (Sales and Pye, 1974). Within this suborder, ultrasounds have been noted in only the following two families: Muridae (rats, mice and allied species) and Cricetidae (hamsters, voles, gerbils, and lemmings, among others).

Sewell (1969) reported that ultrasounds vocalized by adults in various species of the family Muridae differed somewhat in their length and frequency patterns although much interspecies overlap was noted. The same finding was noted for cricetid rodents. A much greater difference existed between the patterns of calling in infant rodents of the

family Muridae and Cricetidae. All of the cricetid rodents thus far studied produced some purely ultrasonic calls with a single frequency component. These formed the majority of the calls emitted by Merione shawi from birth until day 18 when pulses of more than one harmonic component appeared. Sewell (1970) observed that gerbils Meriones unguiculatus produced cries which consisted of some longer pulses, up to 200 msec., that initially were composed of two to five harmonics. A noisy wide-band structure also occurred for a short duration, and in many of these pulses, the lowest frequency components fell within the normal range of human hearing.

In hamsters, (Mesocricetus auratus), purely ultrasonic calls with a single component were rarely produced by young pups, but they became more common as the pups grew older. Sales (1970) reported that golden hamsters produced wide-band, 80 to 120 msec. long calls during aggressive behavior, with a band width up to 50 kHz and a maximum frequency range of 60 kHz. These cries consisted of both "audible" and ultrasonic components which were usually harmonically unrelated.

The motivational factors underlying ultrasonic vocalization in rodents include cold stress and hunger in infant rodents (Zippelius and Schliedt, 1956; Hart and King, 1966; Noirot and Pye, 1969), and aggression (Sewell, 1967, 1969) and sexual encounters (Sewell, 1972; Barfield and Geyer, 1972) in adults. A detailed study of the effects of cold stress upon infant rodent vocalizations has been made by Okon (1970, 1971, 1972). Okon's initial investigation was concerned with the relationship between body temperature during the development of homothermy and ultrasonic emission in infant albino mice.

The quantitative analysis of behavior changes with age in young

mammals has been delimited by their poorly defined response patterns, their rapidly changing sensory capacities and motor abilities, and the interaction of experimental factors with innate behavior patterns. Whereas the impact of various experiences during neonatal development upon subsequent physiological and behavioral development has been well documented (e.g., Bell, Geisner, and Linn, 1961; Denenberg and Karas, 1959; Levine and Lewis, 1959), attempts to define the mediating mechanisms underlying the phenomena have been handicapped by an inability to systematically examine neonatal responses to stimulation.

One class of neonatal responses which shows promise as a quantifiable age-dependent behavior is the ultrasonic vocalizations exhibited by infant rodents, since their maturational changes involve consistent parameters of the signals, e.g., frequency, duration, intensity, and rate. These signals have been observed in several subspecies of mice and in albino rats and have been reported to vary as a function of handling (Bell, Nitschke, Gerry and Zachman, 1971), isolation (Zippelius and Schleidt, 1956; Noirot, 1968), cold stress (Allin and Banks, 1971), and active retrieval by the mother (Noirot, 1966). They appear to function as distress calls serving as guides to lost pups (Zippelius and Schleidt, 1956) and stimulating nest building and retrieval by the mother (Noirot, 1964).

Bell, Mitschke, Gerry and Zachman (1971) suggested that ultrasounds by pups could act as a mediator of early handling phenomena. They removed Peromyscus pups from the litter, placed them in small individual compartments for 3 min., and then replaced them in the nest. From this moment they obtained simultaneous video and audio 30-sec recordings. Handled pups emitted great quantities of relatively long

ultrasounds whereas nonhandled controls gave only some shorter audible calls. The ultrasounds by the previously handled pups were apparently emitted in response to contact and handling by the mother since they occurred when the female was retrieving or grooming the pups. Bell et. al. thus considered the possibility that these calls might mediate early handling effects in a manner as originally described by Richards (1966), namely by alteration of the mother's behavior for a more or less prolonged period. In this case, they suggested that the mothers might, in response to ultrasonic distress calls, behave differently with handled (i.e., calling) and with non-handled pups. There exist three basic stages of development of homothermy in baby mice (Lagerspetz, 1962; Okon, 1971). For 5-6 days after birth the pups are poikilothermic. Specifically, they have no control over their own body temperature and adopt a temperature similar to that of their surroundings. During this period, they are very resistant to hypothermy. From day 6-7 until day 14, the pups begin to regulate body temperatures endogenously. They are then much less resistant to hypothermy, therefore, it becomes more important that they are not exposed to sharp reductions in ambient temperature for prolonged lengths of time. The final stage of development of homothermy lasts from day 14 until day 19-20, when full homothermy is acquired.

Okon's results (1970) show that isolated baby mice produce very few ultrasonic calls when they are most resistant to cold stress. He suggests that it may not be so important for the pups to elicit maternal retrieval at this time. Ultrasound production increases markedly at this time when pups are most vulnerable to cold and only decreases again when the pups become able to regulate their own body temperature.

This research supports earlier notions (Noirot and Pye, 1969; Hart and King, 1966), that the production of ultrasounds by isolated pups is closely related to the development of homothermy.

Okon (1971) noted analogous patterns in the development of homothermy and changes in ultrasound emission in rat and hamster pups. Both species showed very slight ultrasonic responsiveness to cold stress for the first few days after birth. Rats, like mice, increased ultrasound production from days 6-8. Hamsters did not show the increase until day 9-12. It may be significant that Nissa and Lagerspetz (1962) and Okon (1971) showed that homothermy in hamsters does not begin to develop until this age. The rat pups developed self-regulation by day 20 and ceased ultrasounds, even at 2-3°C., at this age. Hamsters, however, did not achieve full homothermy until day 23. This relatively late development of homothermy may be regulated to the short gestation period of hamsters (16 days) which means that they are born at an earlier stage than are either rats or mice which have a mean gestation period of 19 and 21 days, respectively.

Okon (1970, 1971) also studied the ultrasonic responses of baby rodents to the following different kinds of tactile stimuli: Holding and lifting them loosely between two fingers, tapping or pressing the tail lightly against the surface of the dish containing the pups, and lightly pinching the scruff of the neck. Okon confirmed the earlier observations of Sewell (1968, 1969), that ultrasonic "handling" calls are louder than the "isolation" calls of young pups and also that they are produced for some time after the eyes open.

Infant rats produced very few calls in response to tactile stimuli during the first few days after birth. Most of these calls were wide-

band signals, and were audible. From day 4 to days 14-16, all methods of handling elicited ultrasonic calls. After this age, the response declined rapidly, and few calls were elicited after day 20. Hamsters also produced mainly audible sounds in response to tactile stimulation during day 1-3. As with their acoustic response to temperature changes, the audible calls decreased, and the ultrasonic calls increased as the pups grew older. Normal handling failed to facilitate vocalizations after day 6-7, but pinching and tapping elicited calls until 20 or later. Acoustic responses in hamster pups to maternal retrieving decreased from birth onwards and ceased by day 8.

Noirot (1972) noted rodent pups in distress emit 2 different types of ultrasonic calls. One is given in response to cold; the other in response to unusual tactile stimulation. The effects of these calls on adult behavior can also be classified into 2 categories. Some exert positive effects attracting the adult to the pup in distress and stimulating searching, retrieving, and nest-building. Other cause withdrawal of the adult from the pup thereby causing cessation of rough handling or aggression. The ultrasounds elicited by cold could exert the positive effects whereas those elicited by tactile stimulation produce the withdrawal effects.

King (1963) noted that as the infant mouse loses body temperature the incidence of signaling increases until lowered metabolism gradually reduces the signaling. Thus, signaling is a curvilinear function of body temperature loss, and may account for Schaefer's (1963) findings of curvilinear effects of infantile cold stress upon subsequent responsiveness to stress.

Allin and Banks (1972) reported effects of infant ultrasounds on

adult albino rats investigated through playback of recorded pup calls. Adults were exposed to a 90 sec. recording of either ultrasonic calls and background noise (experimentals) or of noise alone (controls). Males and virgin females merely oriented to the sound source. However, 50 per cent of lactating females left the nest at least once in response to recorded pup calls. Unlike controls, experimental lactating females localized the sound source accurately in terms of direction. The results suggest that ultrasounds are capable of inducing lactating females to leave the nest and to engage in searching behavior, as well as of guiding them to a vocalizing pup.

Sewell (1967, 1969) noted that rats emit ultrasonic vocalizations during aggressive encounters. The twelve animals used in the study produced two distinctly unique types of pulses. The so-called 'long' pulses were described as ranging up to 700 ms in duration and occurring at a frequency of about 25 kHz. "Short" pulses of about 3-60 ms duration and 45-70 kHz were produced by 38 rats (including two of those that had produced long pulses). "Short" pulses were emitted when the animals were rolled onto their backs and restrained. This posture resembled the full submissive posture of a defeated rat (Seward, 1945; Grant and Mackintosh, 1963). These ultrasounds produced by these adults may have been in association with aggressive ("long") responses to the experimenter.

According to Sales (1972) who has studied murid rodents, aggressive behavior was observed in Apodemus sylvaticus when young males were introduced into an established group of adults. Ultrasonic calls were detected when two adults of this species, a male and a female, postured aggressively towards one of the strangers, and when they chased and

fought with him in turn. Both narrow-band and wide-band calls were detected from cricetid rodents during aggressive behavior. Gerbils, Meriones shawi, produced both types of calls during boxing, chasing, and aggressive posturing. Wide-band "creaking" sounds, containing audible and ultrasonic components, were emitted while attackers were fended off. Often one of the ultrasonic components was more intense than the others, and the pulse ended on this single frequency. Some pulses consisted of several components, 5-12 kHz apart, with possible harmonic relationships. Hamsters produced only wide-band calls during aggressive behavior. These calls consisted of many harmonically unrelated components. Some audible, which usually ended on a purely ultrasonic note, between 25-35 kHz.

Ultrasonic calling during periods of aggression in rodents appears to be related to the social structure of the different species rather than to their taxonomic or, probably, their evolutionary standing (Sales and Pye, 1974). Species which are said (Walker, 1964) to live in colonies or to show some degree of mutual tolerance, such as rats, Meriones and Gerbillus, produced pure ultrasounds in aggressive situations. Rats, which have fairly stable dominance-subordination relationships, however, produced ultrasonic cries in submissive situations.

No pure ultrasounds were detected during aggressive behavior in hamsters, laboratory mice, Mus minutoidus, Microtus, Praemys or Lagurus. Mice and hamsters appear to live solitarily within established territories if space permits. In mice, the apparent absence of ultrasounds during aggressive behavior may be correlated with the fact that there appears to be no clear submissive posture in this species (in experimental situations, dominant males often are intolerant of submissive

males, and often attack them). The possible value of ultrasounds may lie in establishment of social order within a group (Mackintosh, 1970).

During a comparative survey carried out by Sales, (1972) on aggressive behavior, it was reported that several species of myomorph rodents emitted ultrasonic cries during investigation of the genital area or attempted mounting of one animal by another. This finding led Sewell (1972) to investigate the emission of ultrasounds during mating behavior in rodents. The ultrasonic calls produced during mounting appeared to be emitted by the male. Observations with the "bat-detector" showed that the pulses seemed to be related to the pelvic thrusts of the males and to audible cries emitted by the females. The ultrasonic cries that were detected during these heterosexual encounters appeared to be emitted only by the males with a very high level of sexual motivation.

Mounting and intromission occurred in five species of Myomorph rodents and was accompanied by ultrasound emission in four of these. In *Acomys*, ultrasonic calls were detected when a male chased a female prior to mounting and during the early part of mounting and intromission. These pulses were emitted for up to 300 msec at a time. In *Apo-demus*, chasing and intromission were accompanied by the emission of sequences of pulses which contained both long drifts in frequency and some brief frequency fluctuations. These calls were of very low intensity. *Peromyscus* emitted short pulses with a single frequency component during nosing and genital sniffing of the female by the male as well as during mounts with intromission. The pulses often contained marked frequency drifts downward which were occasionally followed by an upward drift. A few very low intensity pulses were produced during

intromission in Clethrionomys (which was observed on two different occasions when females were introduced singly into a cage containing several males).

Golden hamsters emitted purely ultrasonic calls on encounters that involved females in behavior oestrous. During two different encounters between an oestrous female and an anoestrous female, low intensity ultrasounds were detected as each oestrous female nosed the other in the intervals between adopting the rigid mating posture (several times in succession). On each occasion, the anoestrous female was then replaced by a male, and ultrasonic calls were detected as the female nosed the male. The calls were noted most commonly after the female had maintained the rigid mating posture without being mounted. No ultrasounds were detected at the time of actual mounting by the male. Most of the pulses produced during the heterosexual encounters consisted of a single component in the range between 25-50 kHz.

In the golden hamster, visual as well as auditory signals serve as possible communication links within and between species (Johnston, 1976). In golden hamsters, the dark transverse patches of fur on their chests, which contrasts with the otherwise white ventral pelage, are purported to be threat stimuli (Grant, Mackintosh and Lerwill, 1970). This function was first inferred from two studies. The first involved a descriptive study of the agonistic behavior of hamsters (Grant and Mackintosh, 1963). The other was an experimental study on the effects of enlarging and darkening chest patches (Grant, Mackintosh and Lerwill, 1970). Johnston (1976) pointed out the shortcomings of both two studies and forwarded the opinion that the darkening of the chest patches served to inhibit the attack of the aggressor.

Illustratively, golden hamsters in the Grant, Mackintosh and Lerwill (1970) study were not matched for weight; yet, body weight is an important determinant of fight outcome among hamsters (Payne and Swanson, 1970; Drickamer and Vandenberg, 1973) as well as a major factor in the activity level of many rodents (Nevitt and Harriman, 1977).

When the phenomenon of ultrasonic vocalization in rodents is explored across motivational states one notices two outstanding theories which seek to summarize the literature. The first of these is exemplified by the writings of Sales (1972) and has advanced the opinion that ultrasonic sounds probably serve an important role in the establishment of social hierarchies in many species of myomorphic rodents. From hereon out the theory of Sales (1972) will be referred to as the "social sound" theory. Bell (1974) reported a more parsimonious theory by indicating that the acoustic parameters previously described were simply arousal-producing and arousal produced. From time to time the theory of Bell (1974) will be referred to as the "sympathetic sound" theory because of its speculated association with arousal and the sympathetic nervous system. Griffin (1976) has stated that the communication behavior of certain animals has been discovered to be surprisingly complex, versatile, and, to a limited degree, symbolic. He further states that it may be appropriate at this time to extend previous attempts to communicate with certain species, using methods analogous to those of anthropologists seeking to establish communication with conspecifics who are assumed to speak a language, but one in which no words are yet shared. Symbolic communication might, if suitably developed, provide us with a "window" through which to examine the properties of an animal's templates, Gestalten, or mental images. Griffin states that

the data gathered in this way should be validated by comparison with conventional stimulus-response experiments.

The Role of the Golden Hamster in Research

The golden hamster, Mesocricetus auratus, was described as a new species and named originally Cricetus auratus by Waterhouse in 1839. It is the most generally used of several related species, such as the Chinese hamster (Cricetulus griseus) and, the grey hamster (Cricetulus migratorius), which have been newly bred in captivity and have been subsequently introduced into the biological and medical research laboratory (Hoffman, 1968).

The discovery of the golden hamster as a laboratory research animal dates back to Professor I. Aharoni of the department of Zoology, Hebrew University, Jerusalem, who collected a litter of eight golden hamsters near Aleppo, Syria, in 1930. Three litter mates (one male and two females) survived and were bred easily in the laboratory. Accordingly to the best known sources, all the golden hamsters now in use as laboratory animals in Europe and America originate from the previously mentioned three litter mates of 1930 (Adler, 1948).

The unique characteristics of the golden hamster include immunogenetic tolerance to homologous, heterologous and human tumors, parasites, viruses, and bacteria. Its possession of aspirated eversible cheek pouches serves as natural windows for detailed microscopic investigation of blood flow and growth of transplanted tumors and embryonic organs. Also, the phenomenon of hibernation in the species has been exploited increasingly in the biological laboratories of universities, research foundations, and institutes throughout the world.

Statement of the Problem

The review of the literature demonstrates that a possible system of communication exists in many forms of myomorph rodents. The literature is quite divergent on the question of motivational components underlying the phenomenon of ultrasonic emission (Okon, 1971; Sales, 1970) and the adaptive value of such vocalizations (Sales, 1972; Bell, 1974).

Ultrasounds appear to be important signals for altricial infant rodents. They seem, for example, to initiate infant retrieval by the dam in rats (Allin and Banks, 1972) and to coordinate maternal behaviors in mice (Noirot, 1972).

Bell (1974) has emphasized that ultrasounds reflect high arousal in infants and induce arousal in the dam. At a time when the infant is unable to thermoregulate, to see, or to ambulate well, the infant ultrasound seems to serve as a distress signal to the dam. In the rat, ultrasounds diminish at the age at which the pup gains the ability to thermoregulate, open its eyes, and begins to leave the nest, at which time a chemical signaling system involving a maternal pheromone is said to predominate.

It was the purpose of the present study to investigate the effects of ultrasonic pure tones and audible pain vocalizations on Mesocricetus auratus, a species of cricetid rodent that does not appear to organize as rigidly into colonies as do Rattus nervegucus, Mus musculus and other members of the family Muridae. Logically, the adaptive value of ultrasonic calling in the establishment of social hierarchies would be rather low in such a "solitary dwelling" rodent. An operant task, bar pressing, was used to test the arousal properties of ultrasonic alone

and conspecific vocalization motivated by high arousal with the ultrasonic components removed.

Past research investigations have reported that fear conditioned by Pavlovian procedures can affect instrumental behavior (Hammond, 1966, 1967). The procedure in question involves the establishment of a conditioned fear signal (CS+) by explicitly pairing a signal with electric shock and then looking for a facilitation by CS+ of a previously learned avoidance response.

A somewhat related procedure involves the presentation of a signal (CS-) which explicitly "predicts" the non-occurrence of shock and then looking for a suppression of avoidance responding in the aversive conditioning test trials whenever CS- is presented. This particular procedure has been confirmed utilizing canines (Rescorla, 1967) as well as laboratory rats (Grossen and Bolles, 1968).

In the present study, an escape paradigm was employed to facilitate the formation of a light CS- to be later utilized during the testing phase of the experiment. The successful decrement of the dependent variables in all groups during the trials in which CS- alone was presented to the subjects would indicate the possibility of either fear inhibition or some sort of positive reinforcement effect. Rescorla and LoLordo (1965) suggest that the occurrence of a CS- may be a reinforcing event similar in some way to when happens when a subject makes an avoidance response that takes it out of the danger situation and into a safe place. It was speculated that if arousal of behavior components were detected in either the ultrasonic pure tone or the conspecific pain vocalizations that they would interact with a CS- to produce an alteration in frequency, force or duration in bar pressing.

CHAPTER II

METHOD

Subjects

The subjects were twelve male and twelve female adult golden hamsters (Mesocricetus auratus) with a mean weight of 81.06g., S. D. 30.2g. The animals were housed separately in elevated cages, separated by 3/8 in. wire mesh, in a Percival environmental chamber. Ambient temperature inside the chamber was 24.5°C, air humidity was kept at 50.0 percent and the room was lighted from 8:00 A.M. to 8:00 P.M. daily. All animals were fed Purina Laboratory Show ad libitum and were watered via 140 ml. Wahmann drinkers attached to the front of each cage.

Apparatus

All animals were trained to bar-press in a modified operant chamber to escape 24v D. C., 1 mA., continuous footshock delivered to each of 16 grid bars spaced 1/2 inch apart by a shocker-scrambler Model A 102 (Scientific Prototype Mfg. Corp). A cue light (25 watt) inside the chamber was controlled via the same apparatus.

Time spent on the bar in the chamber was measured by a microswitch connected to a 14-15 digital .01 second timer (Marietta Apparatus Co.). Peak force of bar press was determined by a Grass Force Displacement Transducer, Model FT03C, connected to a low level D. C. amplifier

(Model 7-PID), which, in turn, was connected to a polygraph D.C. driver amplifier (Grass Instruments, Model 7DAEF).

Ultrasonic tones were produced by means of a 3 inch ultrasonic speaker which connected to a Lafayette 11-watt Model P.A. 420 amplifier. The amplifier in turn was wired to a R. C. A. Model Wa-44C sine-wave/square wave generator. Ultrasonic waveforms were monitored by a R. C. A. oscilloscope system and a Heathkit frequency counter. Pulse duration and interpulse intervals were controlled with a Lafayette interval and repeat second timer. Pain vocalizations were recorded during training on a Akia tape recorder and were subsequently played back during testing periods through two three inch Pioneer speakers mounted on top of the operant chamber. The chamber was placed inside a plexiglass box insulated with foam rubber, and on top of a sheet of foam rubber to reduce incidental noise and vibrations in the testing room.

Procedure

All subjects were trained to depress a lever in a modified operant chamber to escape 24v D.C., 1 mA continuous footshock. Animals were trained in a series of 500 second periods, 24 hours apart, to depress the bar with at least 25g of force (minimum force required to activate the micro-switch). The criterion which was established in each animal before termination of training was defined as follows: The subject had to depress the lever for no fewer than 300 seconds in two consecutive 500 second training periods. During training a small, frosted 25 watt lightbulb was illuminated upon each barpress and, thus, was paired with termination of shock. The sequence of events is depicted in Appendix I.

Upon reaching the training criterion, the subjects were equilibrated for sex of animal, in each group and were then randomly divided into three groups of eight animals each. Every subject in each group was tested in the operant chamber for four 60 second periods spaced 24 hours apart. Footshock was not administered during the test periods. Each animal was tested under a group specific, auditory stimulus (ultrasonics, vocalizations or control) on and stimulus off conditions both in the presence and the absence of the illuminated cue light used during training. The order of trials was presented to each group of eight subjects after the fashion of a latin-square design so that every treatment would occupy the same position, in presentation order, the same number of times.

The subjects in Group 1 were exposed to a 30 kHz tone at 60 dB during the stimulus on-light on and stimulus on-light off test periods and served as their own within subject controls during the stimulus off-light on and stimulus off-light off test periods. The ultrasonic tone was pulses in 200 msec. pips. Intertone interval was kept at 200 msec. similarly.

The subjects in Group 2 were exposed to tape recordings of pain vocalizations that had been recorded during the training periods. These vocalizations contained only audible components with a mean frequency of 5.2 kHz, S.D. 1.5 kHz. The pain vocalizations were played back to subjects during the stimulus on testing periods at an average intensity of 60 dB.

Subjects in Group 3 were exposed to no type of auditory stress, and the group was maintained for between subject control purposes. The control group was used to establish baseline data concerning

frequency of bar-pressing, time spent on bar, and peak force of bar-press. Results from the experiment were analyzed by the technique of analysis of variance for a multifactor mixed design having repeated measures on two elements (Winer, 1971).

CHAPTER III

RESULTS

Training Trials

All groups were equated during training for amount of time spent on the lever according to a series of one way analyses of variances utilizing data obtained for all three groups on each separate trial. The respective F tests, from first to last trial were as follows: ($F=.053$, $df=2,21$, $p \gt .05$), ($F=1.23$, $df=2,21$, $p \gt .05$), ($F=1.53$, $df=2,21$, $p \gt .05$) and ($F=1.51$, $df=2,21$, $p \gt .05$). The mean amount of time spent on the bar by all subjects during the last trial was 330.46 seconds with a standard deviation of 50.57 seconds. All groups were also equated for frequency of bar press. A series of one way analyses of variance from the first to the last trial yielded the following values: ($F=.321$, $df=2,21$, $p \gt .05$), ($F=.648$, $df=2,21$, $p \gt .05$), ($F=3.30$, $df=2,21$, $p \gt .05$) and ($F=.115$, $df=2,21$, $p \gt .05$). The mean frequency of bar press for last trial data was 80.49 with a standard deviation of 46.14 (Table I summarizes the performance data for each separate training trial in regard to both duration and frequency of bar press).

Testing Trials

A split-plot analysis of variance for time data yielded a significant between-groups effect ($F=3.81$, $df=2,21$, $p \lt .05$). Table II

depicts the group means and standard deviations for duration of bar presses. The effect over all three groups due to the presence or absence of an auditory stimulus proved to increase the amount of time spent on the bar significantly in the experimental groups ($F=7.59$, $df=1,21$, $p < .05$). The effect over all three groups due to the presence or absence of an auditory stimulus proved to be significant ($F=7.59$, $df=1,21$, $p < .025$). Likewise, the effect due to the presence or absence of the light safety signal proved significant ($F=7.12$, $df=1,21$, $p < .025$) as did the light x auditory stimulus interaction ($F=3.70$, $df=2,21$, $p < .05$).

Separate sub-plot analyses of time data for each group showed a significant light x auditory stimulus interaction ($F=13.51$, $df=1,7$, $p < .01$) and a significant subjects x light interaction ($F=49.23$, $df=7,7$, $p < .001$) for the ultrasonic group. A second split-plot factorial analysis of variance revealed significance in the frequency data for the presence or absence of auditory stimuli ($F=9.60$, $df=1,21$, $p < .01$). All other effects for frequency data based on a collapse of data for all three groups failed to reach significance.

Table III presents the means and standard deviations for the frequency data for all three groups. Separate subplot analyses of the frequency data revealed a strong light x auditory stimulus effect ($F=12.60$, $df=1,7$, $p < .01$) as well as a subject x light effect ($F=14.00$, $df=7,7$, $p < .01$) and a subject by auditory stimulus effect ($F=7.60$, $df=7,7$, $p < .01$). A significant effect due to the presence or absence of the cue light was noted in the control group ($F=29.84$, $df=1,7$, $p < .001$).

An analysis of variance for force of bar press data indicated a

significant difference related to the presence or absence of the cue light safety signal ($F=148.75$, $df=1,21$, $p < .001$). The effect over all three groups due to the presence or absence of auditory stimuli was likewise significant ($F=12.50$, $df=1,21$, $p < .005$). The auditory stimulus x group interaction revealed a significant difference ($F=5.16$, $df=2,21$, $p < .025$). Similarly, the light safety signal x auditory stimulus x group interaction was significant ($F=8.83$, $df=2,21$, $p < .005$).

Table IV reports the mean and standard deviation data for peak force of bar press in all three groups during testing. Separate subplot analyses of variance for each individual group yielded a significant bar press effect due to auditory stimulus ($F=16.82$, $df=1,7$, $p < .005$) and a significant bar press effect due to light alone ($F=7.81$, $df=1,7$, $p < .05$), auditory stimulus alone ($F=37.91$, $df=1,7$, $p < .001$) and light x auditory stimulus interaction ($F=6.46$, $df=1,7$, $p < .05$) was noted for the conspecific pain vocalization group. A significant difference in bar press due to cue light on vs. cue light off ($F=8.00$, $df=1,7$, $p < .05$) was noted for the control group.

TABLE I
 GROUP MEANS AND STANDARD DEVIATION FOR BOTH TIME
 AND FREQUENCY DATA DURING TRAINING TRIALS

Training Trial	1		2		3		4	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Bar Presses Control	32.7	35.9	66.7	38.0	90.7	34.5	97.5	68.5
Bar Presses Pain Vocal.	42.0	35.0	71.5	15.1	90.7	46.1	79.0	59.1
Bar Presses Ultrasonic	32.7	24.3	71.0	62.4	73.7	36.0	66.6	28.7
Seconds Control	134	148	240	125	352	40.6	375	36.9
Seconds Pain Vocal.	76.2	97.7	243	157	304	110	347	61.5
Seconds Ultrasonic	64.0	61.8	211	132	322	70.0	357	28.1

TABLE II
 GROUP MEANS AND STANDARD DEVIATIONS FOR TIME
 DATA DURING TEST TRIALS

Test Condition	Cue Light Audit. Stim.		Cue Light		Audit. Stim.		Control	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Control	17.9	17.2	7.8	11.1	10.1	16.1	15.5	23.3
Ultrasonic	15.4	23.7	3.79	3.92	21.9	24.9	1.76	2.03
Pain Vocal.	4.32	5.80	2.87	3.63	20.8	23.6	3.46	4.58

TABLE III
 GROUP MEANS AND STANDARD DEVIATIONS FOR FREQUENCY
 DATA DURING TEST TRIALS

Test Condition	Cue Light Audit. Stim.		Cue Light		Audit. Stim.		Control	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Control	3.25	1.80	4.00	6.16	3.25	4.08	15.5	23.9
Ultrasonic	15.4	2.50	3.79	1.41	21.9	1.89	1.76	1.50
Pain Vocal.	4.32	4.50	2.87	.95	20.8	1.25	3.46	2.70

TABLE IV
 GROUP MEANS AND STANDARD DEVIATIONS FOR FORCE OF BAR
 PRESS DATA DURING TEST TRIALS

Test Condition	Cue Light Audit. Stim.		Cue Light		Audit. Stim.		Control	
	Mean Kg.	SD Kg.	Mean Kg.	SD Kg.	Mean Kg.	SD Kg.	Mean Kg.	SD Kg.
Control	.46	.31	.28	.34	.62	.51	.88	.45
Ultrasonic	.53	.34	.44	.17	1.16	.34	.25	.24
Pain Vocal.	.33	.38	.21	.14	.85	.37	.42	.33

CHAPTER IV

DISCUSSION

As previously stated in chapter I the "social sound" theory of ultrasonic vocalizations in rodents have been presented by Noirot (1972) and Sales (1972). The former considered the available data on neonatal ultrasounds and their effects on maternal behavior. The latter presented information regarding adult ultrasounds for a variety of rodents species and the presumer role in controlling aggressive behavior. In a similar article, Bell (1974) stated that such reviews of the available literature were overstated in terms of the available behavioral data.

Noirot (1972) presented an analysis of ultrasounds emitted by rodent pups and postulated 2 distinct types of signals which elicit 2 distinct maternal responses. This classification of vocalizations was based upon the following categorization: (1) the stimuli which are effective in eliciting the signals (e.g. cold stress vs. novel tactile stimulation), (2) different functions for cold-elicited vs. tactually elicited signals; and (3) the observation that neonatal signals which may elicit maternal retrieval if the pup and mother are not in physical contact may cause the mother to break off contact if these signals occur while they are in physical contact.

Sales' (1972) review of ultrasonic signaling by adult rodents has led her, like Noirot (1972), to hypothesize 2 distinct types of signals

with 2 distinct meanings. Sales also based her interpretation upon: (1) the stimulus circumstances which elicit the signals, fighting (suggesting an "aggressive" signal) vs. following a fight (suggesting a "submissive" signal); and (2) acoustical properties of the signals. This latter criterion is probably more appropriate for the adult signals than for the neonatal signals because in the former the acoustical properties of the signals are quite different.

The "sympathetic sound" theory, as previously mentioned, proposed by Bell (1974) is a theory which has the advantage of simplicity, demanding less in terms of the animals' capabilities of decoding and encoding of vocal information, and which deals with both neonatal and adult vocalizations in a single conceptual scheme. Bell's theory states that the acoustical properties of high frequency signals such as those emitted by rodents and other small mammals suggest certain potential communicative properties. These signals are quite intense (often measured in the 80-110 dB range), are hyperdirectional, and have a limited carrying range. If their occurrence and acoustical properties are related to degree of arousal, they may well convey such information to members of their own species in the near vicinity (e.g., degree of arousal and location). Their intensity suggests that the occurrence of these signals triggers a similar degree of arousal in those animals which hear them. The specific behavioral consequences of hearing these signals almost certainly depends upon the degree of arousal triggered in the recipient animal, the persistence of the signaling, other organismic characteristics of the recipient animal (e.g. lactation, oestrous, androgen level, corticosterone activity), other stimulus features of the situation (e.g., contact, odors), and

previous experiences associated with the stimulus complex rather than specific information-coded signal characteristics.

In a recent article, Amsel (1977) reported that rats rewarded for crawling by being allowed to suckle on the dry nipple of a paralyzed dam showed a decreasing rate of ultrasound production during acquisition. An increasing rate of ultrasound production was noted during extinction. Many studies of adult animals show that extinction following appetitive learning increases arousal, presumably because of the frustrating effects of non-reward following a history of reward (Amsel, Spence and Spence, 1967). If ultrasounds were a measure of a state of internal arousal, as suggested by Bell (1974), one would expect ultrasounds to increase during extinction of a learned appetitive response. Amsel's article was the first measure ultrasound production during infant learning. The work provided evidence which supports an active conception of appetitive extinction in neonatal rats.

During acquisition, ultrasounds in the goal box were recorded as the pups crawled towards the anesthetized dam. Ultrasounds recorded during extinction and trials were recorded until the pup failed to reach the goal box in 100 seconds. If one accepts the hypothesis that ultrasounds reflect arousal, the increase in ultrasound in extinction argues against an arousal decrement interpretation of extinction in infant rats. Informal observations by Amsel provided additional evidence that extinction entailed increasing rather than decreasing arousal in 11-day-old pups as it does in adults. During extinction, the pups moved down the alley, hesitated, retraced, and attempted to climb out of the apparatus. Even when they were not ambulating, they made curious chewing movements, sneezed vigorously, and groomed. Often they

oriented towards the goalbox and moved the front limbs forward and backward while their hind limbs remained planted. Such activities, which never occurred during late acquisition trials, seemed to demonstrate conflict and suggest that the pups actually learned not to approach the goalbox.

In light of the research of Bell (1974), and Amsel (1977), the experimental results of this study offered at least partial support to the notion of ultrasonic arousal production. Upon examination of Table II, one notes a definite rise in time spent bar pressing, in the presence of auditory stimulation, for both the ultrasonic group and the conspecific pain vocalization group. Upon sub-plot analysis, however, it was noted that only performance by the ultrasonic group achieved statistical significance. It was previously indicated that during training both of these groups were statistically equivalent on each trial for the dependent variable (duration of bar press). The overall main effect of the conditioned safety signal (CS-) was also reported to have reached a high level of significance during testing. The sub-plot analysis attributes this to the light by auditory stimulus interaction in the ultrasonic group (which contributed a majority of the variation in the overall analysis of all three groups).

An interpretation of the experimental results might be best handled by espousing the hypothesis of Rescorla and LoLordo (1965) which states that the occurrence of a CS- could perhaps be positively reinforcing in the same manner as an avoidance response might be. It was noted that during training time spent on the bar dropped off sharply in all groups. In the presence of auditory stimulation, however, a significant performance rise was seen, which could be accounted for

mainly by the ultrasonic group.

It would appear that once avoidance conditioning is established, a behavioral measure of arousal, i.e., time spent on bar, drops below baseline, in the presence of the CS-. Conversely, one notices facilitation of the behavioral measure of arousal during exposure to auditory stimulation in the two experimental groups.

Table III displays group data for a second measure of behavioral arousal, frequency of bar pressing during a sixty-second test trial. An overall pattern similar to the duration data in Table II may be noted. In the presence of the light CS-, the frequency for barpressing in the ultrasonic and conspecific pain vocalization group dropped drastically. In the presence of an auditory stimulus, the frequency of bar pressing rose once again for both experimental groups. If behavioral arousal is facilitated by the presence of ultrasonic pure tone or tape recorded pain vocalizations, it should be manifested on several discrete measures of the same complex behavior pattern, such as time spent on bar and the total frequency of bar presses. Again the ultrasonic group contributed almost totally to the significance of the variance of the light by auditory stimulus interaction for the dependent variable frequency of bar press.

The "sympathetic sound" theory of Bell (1974) and Amsel (1977) which deals with arousal production via the ultrasonic mode seem consistent with the results thus far. Specifically, ultrasonic pure tone and, to a lesser degree, conspecific pain vocalizations seem to facilitate two of the behavioral measures of arousal used in the study. The theories of Bell (1974) and Amsel (1977) assume that a state of internal arousal is created upon the perception of certain frequencies of

ultrasonic pulses. This arousal is externalized in the natural state by means of similar ultrasonic pulses, which, presumably serve some adaptive function such as alerting a social group to the presence of possible predators. In the laboratory setting of the present study, the internalized arousal was externalized, not only by ultrasonics, but also by means of a learned avoidance response (the barpress) which was acquired under circumstances of a similar state of arousal. The subjects acquired a response which became stereotyped and reinforced during training by the removal of electroshock. According to the theory of Rescorla and LoLordo (1965), and consistent with notions of classical conditioning, when a stimulus such as a cue light is repeatedly paired with this period of reinforcement, it acquires the properties of a secondary reinforcer. Reinforcement in the present study may be thought to be related to a reduction of a high state of internal arousal in the subject. Thus, it has been previously noted that on two separate measures of behavioral arousal (time and frequency of bar press), that the presence of a CS- in the testing situation reduced learned behavioral measures of arousal.

The inference which might be made at this point concerning the reduction in magnitude of the behavioral indices is that a certain ambient arousal state associated with the task setting was reduced by the cue light in testing due to its acquired secondary reinforcer properties. The apparent increase in the behavioral indices of arousal in the ultrasonic group and to a lesser degree in the conspecific pain vocalization group, in the presence of their respective auditory stimuli, is consistent with the prediction of arousal production in the organism by Bell (1974) and Amsel (1977). The strength of the arousal

production phenomenon was tested by placing the auditory stimulus condition at odds with the CS- condition during testing. In both Table III, the frequency of bar press for CS- and auditory stimulation are shown to have approached the same magnitude as the frequency data for the auditory stimulus condition alone. Thus, the phenomenon appears to have an all-or-none characteristic under this particular behavioral indice. In Table II, the duration of bar press in the CS- condition and the auditory stimulation condition seem to combine in the CS- plus auditory stimulation condition to produce a degree of duration which is intermediate to either condition viewed separately.

In Table IV, the characteristic pattern noted in Table II and Table III is readily seen again. In the presence of a CS-, the force of bar press falls below baseline level; however, in the auditory stimulus condition an abrupt rise in the force of bar press (peak deflection per 60 second test trial) is noted for both experimental groups. Sub-plot analysis of variance indicated significant difference in force of bar press between conspecific pain vocalization and ultrasonic groups over the four test trials. Thus, once again, behavior indicators seem to verify the notion of arousal production by ultrasonic stimulation. When the CS- and the auditory stimulus are included in the same trial, a pattern similar to that noted in Table II is evident. The force of bar press assumed an intermediate value in both the conspecific pain vocalization group and the ultrasonic group. This intermediate value resembled the baseline measurements more than any other single condition during testing. Upon examination of the behavioral measures of arousal in the experimental groups, one notes a similar pattern which is consistent with arousal production theory.

In the dependent variables of duration, frequency, and force of bar press, a similar trend in response to CS- conditions and auditory stimulus conditions was noted. A dissimilarity was noted in the CS- plus auditory stimulus condition upon comparison of the three dependent variables, however. In both force of bar press and duration of bar press indices of arousal, an intermediate value of the dependent variable was assumed approximately mid-way between the elevated values obtained during the auditory stimulus alone trials and the CS- alone trials. This pattern was evident for both experimental groups. Upon examination of the frequency of bar press data for these groups, an all-or-none responsiveness above the baseline level was noted whenever the auditory stimulus was presented and whether or not the CS- was present. Initially, this seems inconsistent with the previously formulated notion of arousal facilitation and reduction. It would seem logical, if the behavior indices are indeed a measure of a generalized state of arousal, and if a divergence in measures is noted in correlation with a divergence in conditions designed to facilitate such a divergence, that when these conditions are combined the behavioral indices should reach an intermediate mean value. A post hoc explanation for the absence of this type of pattern in the case of frequency might be supported on the basis of the nature of any type of frequency measurement when compared to continuous variables such as those of duration and force. The measure frequency is a discrete variable. Because of the nature of such a measure and the brief period involved in a test trial, the behavioral measure was in the form of an all-or-none response. Specifically there was either a bar press (+) or there was none (-) during every 60 second trial in testing. No intermediate

value was allowed expression in a majority of the cases during testing trials. As a result, the group mean for each trial reflected this general characteristic.

In a study by Nevitt and Harriman (1977), a significantly greater amount of bar pressing was seen in a group of hamsters exposed to a 30 kHz tone than in a control group treated identically to the experimental group during training trials. A similar analysis for force of bar-press data indicated a significant group by trial interaction which could be interpreted as the result of differential states of arousal and habituation in the two groups.

During testing trials the mean and body temperature for the experimental group was significantly greater than the mean temperature of the control group. An analysis of the data for the initial testing trial revealed significantly fewer fluctuations from baseline temperature and a significantly lower magnitude of fluctuation from the baseline. A deduction from a general theory of arousal production, such as that of Bell (1974), would predict an increase in the general metabolism of the rodent upon exposure to an ultrasonic stimulus similar to that of the pulses emitted by conspecifics. Presumably, this general state of heightened physiological functions would lead to the adaptive production of the species typical ultrasonic cries.

The generalized increase in anal body temperature noted by Nevitt, Truby and Harriman (1977) upon exposure of hamsters to a 30 kHz tone is in close agreement with the findings of Rosenmann and Morrison (1974) who stimulated Peromyscus maniculatus with a 20 kHz tone. It was noted that in such animals a 20% increase in oxygen consumption was evident. These indices of increased metabolism during exposure to ultrasonic and

near ultrasonic tone support the hypothesis of Bell (1974) and Amsel (1977) that sounds in this range are arousal-producing, as well as arousal-produced, in a variety of rodent species.

The adaptive function of ultrasonic vocalization may perhaps be several-fold in rodents and other small mammals. First, such vocalizations might serve to communicate arousal levels (Bell, 1974; Barfield, 1972). Such a notion would certainly seem parsimonious in explaining the behavior of species such as Mesocricetus auratus but does not discount the importance of the role of ultrasonics in establishing social hierarchies (Sales, 1972; Nevitt, Truby and Harriman, 1977). Secondly, it has been demonstrated by Riley and Rosenweig (1956) that rats are capable of maze navigation by means of ultrasonic echolocation. In the study, by R. and R. at a choice point rats could go to either of two paths, one or the other of which was blocked by a barrier 20 cm. from the choice point. The subjects learned to avoid the blocked path and detected the barrier from the choice point evidently by using echoes of sounds they made. Performance in the maze rose and fell when efforts were made to facilitate or inhibit using echoes as directional cues. The authors suggest that the ability of rats to echolocate may have been the basis of some performance which has been attributed to visual discrimination. This fact along with the newly initiated line of ultrasonic research (Sales and Pye, 1974) would seem to call for a reevaluation of orientation research.

In conclusion, it seems feasible to the writer that ultrasonic vocalizations reflect a heightened state of arousal and have been selected for by the environment due to several adaptive merits. Ultrasonics cause a general increase in metabolism of various rodents

(Nevitt et. al., 1977; Rosenmann and Morrison, 1974). This increase in metabolism, if accompanied by rapid shallow breathing, may lead indirectly to ultrasonic pulse production as a mere result of the physiological state of the organism alone. Such an involuntary mechanism would have adaptive value over any sort of stimulus interpretative or decision making system when an entire colony of rodents are to be alerted on the basis of the initial arousal of a single member.

Such a general system of arousal communication when voluntarily modified by the organism could form the basis of a system of dominance-submissive signals. Sales (1972) first noted the golden hamster Mesocricetus auratus produced only wide-band calls during aggressive behavior. They were described as consisting of many apparently harmonically unrelated components, both audible and ultrasonic, and were noted often to end on a purely ultrasonic note at 25 to 35 kHz. The audible component was described as having a "huff" like sound and might well correspond to the "ffff-ff" calls described by Rowell (1960). Sales noted that ultrasonics could not be used as social signals unless they had some effect on other animals of the same species. Noting that Barnett (1967) reported that posture and bodily contact of wild rats in a colony, Sales (1972) speculated that long ultrasonic pulses are important in inhibiting the aggression of other animals for long periods of time and that this allows the submissive animal to perform 'essential' activities such as feeding and cleaning even when in the close proximity of the aggressive rat.

To summarize, the present study has offered support to the "sympathetic sound theory" of Bell (1974) and Amsel (1977). It was noted that ultrasonic pure tones and conspecific pain vocalizations could (1)

facilitate an increase in several behavioral indices of arousal, (2) these increases in arousal appropriately interacted with a CS- in a consistent manner, and (3) these interactions were in agreement with a general theory of arousal production.

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APPENDIXES

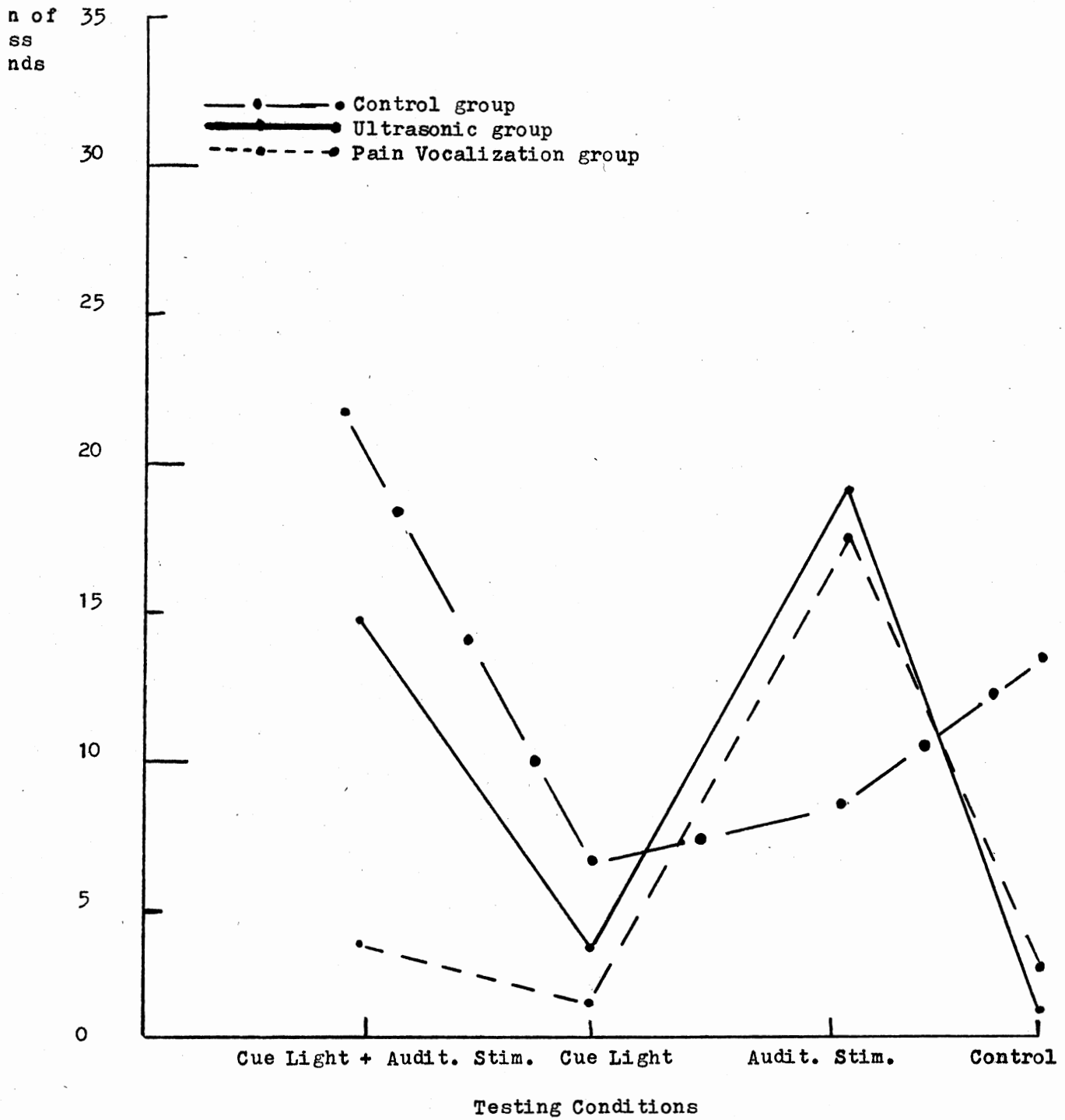


Figure 1. Group Means and Standard Deviations For Time Data During Test Trials

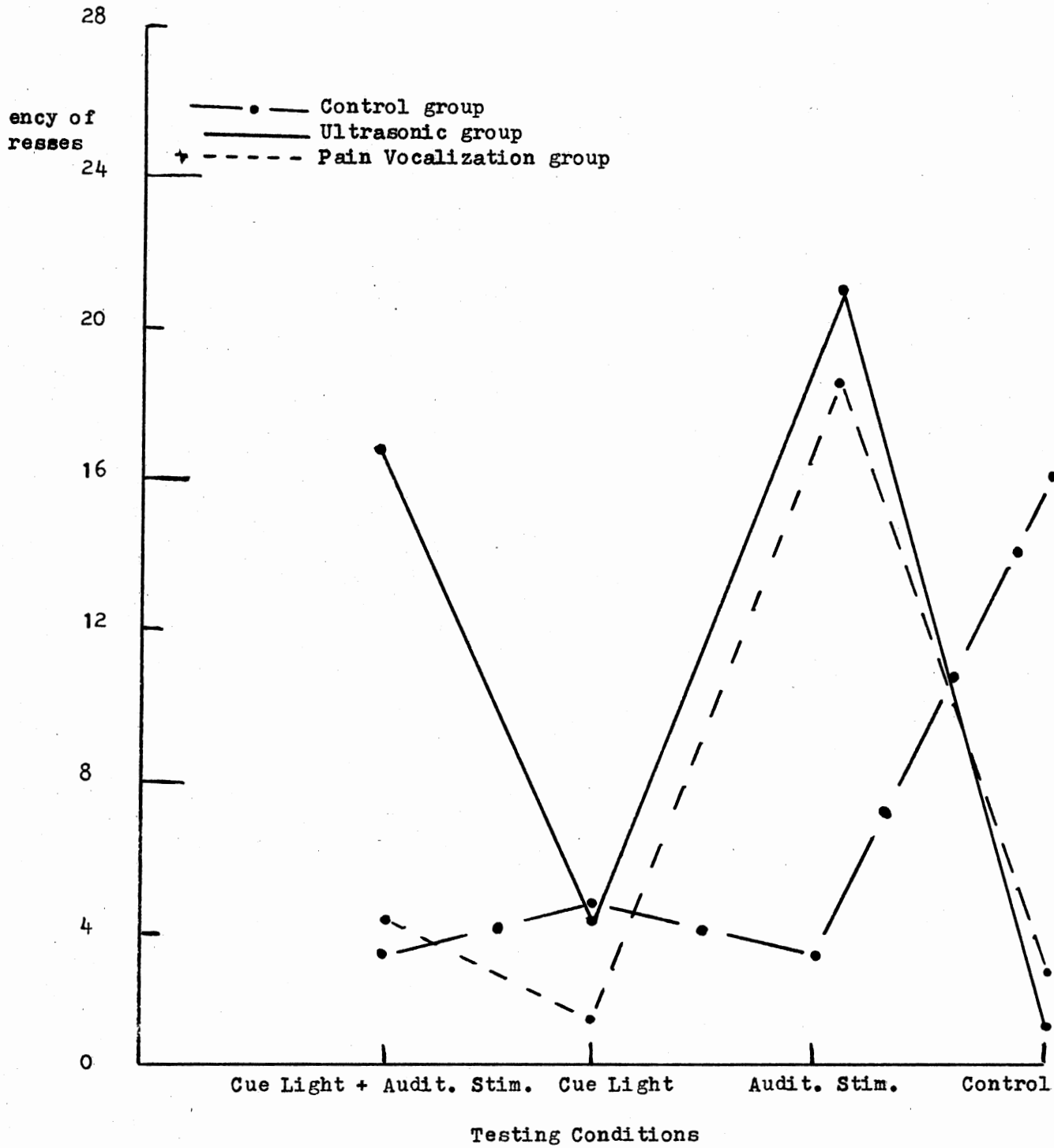


Figure 2. Group Means and Standard Deviations for Frequency Data During Test Trials

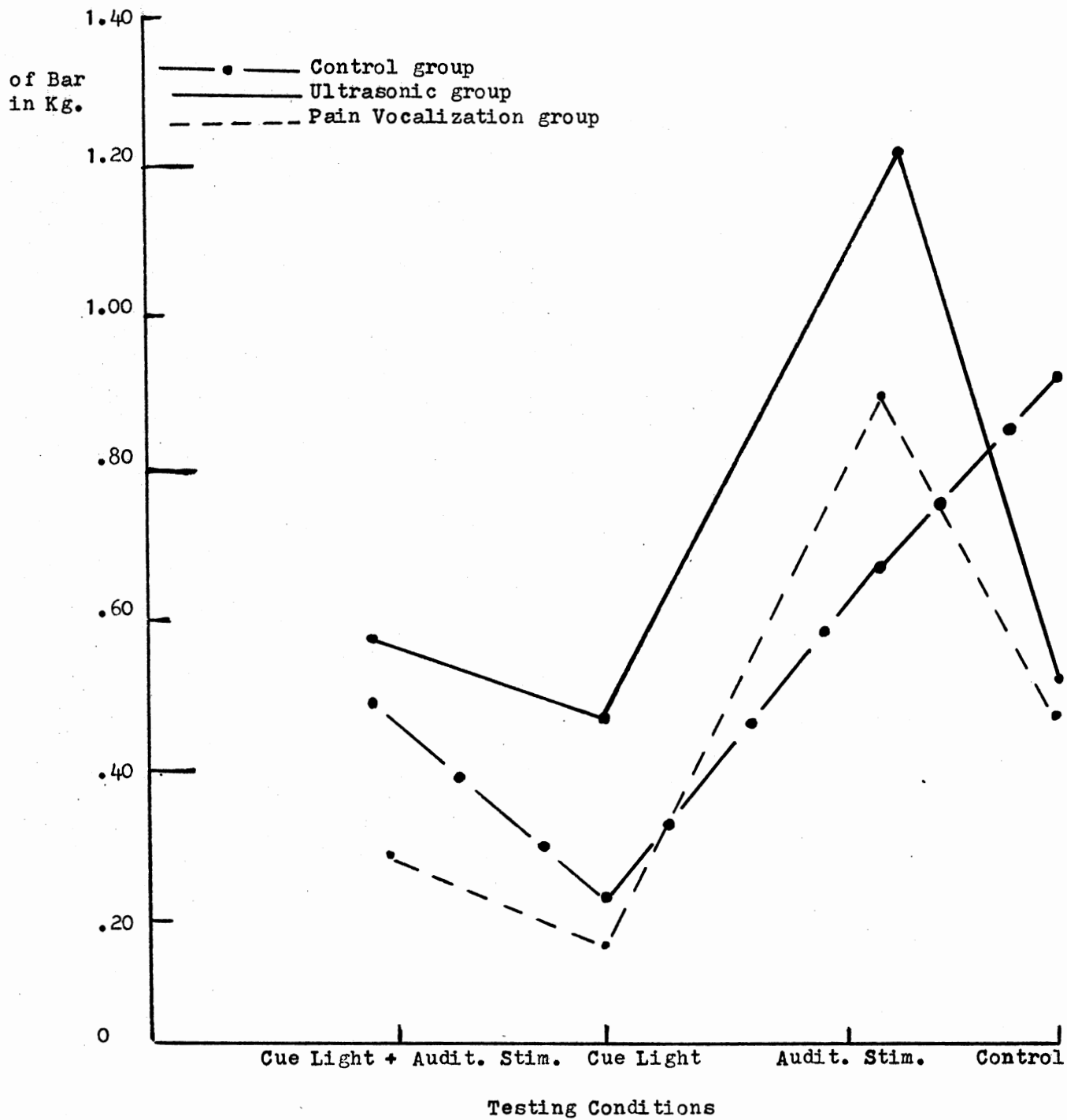


Figure 3. Group Means and Standard Deviations for Force Data During Test Trials

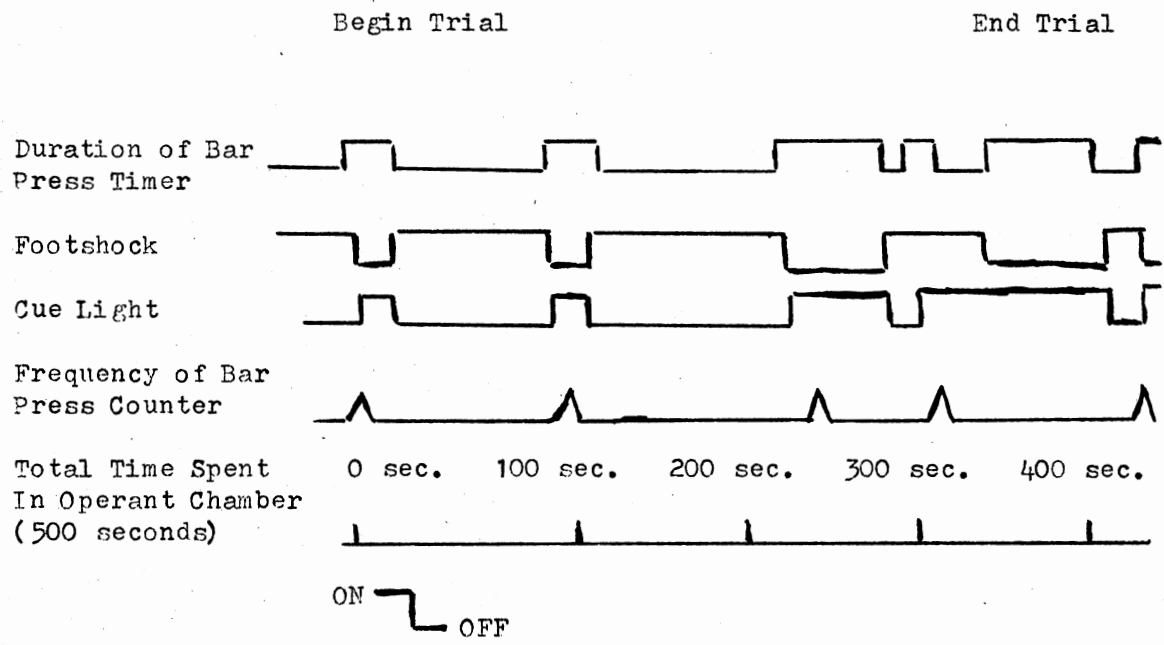


Figure 4. A Typical Training Trial

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Candidate for the Degree of

Doctor of Philosophy

Thesis: REACTIVITY OF THE SYRIAN GOLDEN HAMSTER TO ULTRASONIC PURE TONES AND CONSPECIFIC PAIN VOCALIZATIONS

Major Field: Psychology

Biographical:

Personal Data: Born in Fort Scott, Kansas, July 24, 1953, the son of Dr. Kem R. and Twyla M. Nevitt.

Education: Graduated from Fredonia Sr. High School, Fredonia, Kansas, in 1971; attended Independence Jr. College, Independence, Kansas, 1971-73; received the Bachelor of Science degree from Pittsburg State University, Pittsburg, Kansas, with a major in Psychology, May, 1975; received the Master of Science degree from Oklahoma State University, with a major in Psychology, December, 1976; completed requirements for the Doctor of Philosophy degree in May, 1978 at Oklahoma State University.

Professional experiences: Served as departmental assistant at Oklahoma State University, 1976-1978; member of the Southwestern Psychological Association, 1977.