

- ($Y < 15$ seconds $< X$), and presence (Y) or absence (X) or a response to rapidly moving stimuli of appropriate contrast (dark for OFF-surround, light for ON-surround cells). As in normal tree shrews, most cells (53 percent) consistently responded on these tests with either X- or Y-cell properties without an exception. An exception on one test occurred in 37 percent of the classified X- and Y-cells, and in a few instances (10 percent) two exceptions in the five tests were tolerated when the other responses were well within either the X or Y range. Thus, for instance, a cell might fail to respond to rapid movement but still be classified as a Y-cell because it had a large receptive-field center and short latencies and gave a very transient response to standing contrast. We did not use a test for receptive-field linearity in the tree shrews. However, recent experiments in one of our laboratories have shown that when a test for receptive-field linearity [see p. 538 in C. Enroth-Cugell and J. G. Robson, *J. Physiol. (London)* **187**, 517 (1966)] is used in the cat lateral geniculate nucleus, the X- and Y-cells classified by methods used in this study have, respectively, linear and nonlinear receptive-field properties (K. E. Kratz, S. V. Webb, S. M. Sherman, in preparation).
8. When focusing the animals on the tangent screen with contact lenses, we consistently found that the deprived eye was strongly myopic (about 20 diopters) relative to the normal eye [S. M. Sherman, T. T. Norton, V. A. Casagrande, *Brain Res.* **124**, 154 (1977)]. As a result we took great care in focusing both the deprived and normal eye on the tangent screen with retinoscopic tests. In addition, we tested the responses and receptive-field size of several cells with a range of spectacle lenses to find the optimal correction, which always agreed with our retinoscopic determination. Many X-cells driven by the deprived eye had small receptive fields and responded to fine gratings. We are thus confident that our results do not reflect incorrect focus during the recording sessions.
 9. By a χ^2 test the proportion of binocular-segment Y-cells was lower than the proportion in the nondeprived laminae ($P < .01$) and lower than the proportion in laminae innervated by the contralateral eye in normal animals ($P < .001$).
 10. We used t -tests for receptive-field diameter, chiasm latencies, and cortex latencies, and χ^2 tests for responses to standing contrast and moving stimuli.
 11. Although only three X-cells were recorded in the deprived monocular segment, we have no evidence for a loss of X-cells there since this was not significantly lower than the proportion in the monocular segment of normal tree shrews by an χ^2 test (4).
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 15. We used two additional monocularly deprived tree shrews from another experiment and tested their visual behavior 1 or 2 days after opening the deprived eye and suturing the normal eye closed to force the animals to use the deprived eye.
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 17. Sixty-six cells were sampled, but two abnormal cells could only be generally located in the binocular field and are not plotted. When plotting cells on this graph, we used the estimate (A. L. Humphrey, J. E. Albano, T. T. Norton, *Brain Res.*, in press) that the vertical meridian is 37.5° medial to the optic disk and 5° above the optic disk. We originally plotted all cells relative to the optic disk, so relative cell locations are unchanged by any errors in estimation of the area centralis location. We found the edge of the boundary between the binocular and monocular visual fields to be approximately 10° medial to the optic disk, or 27.5° from the area centralis.
 18. Supported by NIH grant EY 01085 and an Alfred P. Sloan Foundation research fellowship (T.T.N.), NIH grants EY 01565 and RCDA EY 00020 (S.M.S.), and NIH grant EY 01778 (V.A.C.). We thank T. Ferguson, B. Jeffers, and C. Pelham for histological assistance.

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Ultrasound Emission in Infant Rats as an Indicant of Arousal During Appetitive Learning and Extinction

Abstract. *Infant rats rewarded for crawling by being allowed to suckle on the dry nipple of an anesthetized dam showed a decreasing rate of ultrasound production during acquisition and an increasing rate during extinction. These results suggest that infant rats can be stressed and are aroused as a result of successive nonrewards just as adult rats are. In addition, these results do not support the hypothesis that infant rats lack inhibitory mechanisms related to poorly developed neural centers.*

Infants of most rodent species emit sounds at frequencies above the range of human hearing. These ultrasonic vocalizations, investigated in a number of species, typically occur when the infants are exposed to conditions of environmental stress (1, 2). Thermal and tactual stressors, unusual odors, pain, and hunger evoke the ultrasonic calls of infant rats (1, 3, 4). Developmentally, the rate of ultrasound production decreases as homiothermy is attained (4).

Ultrasonics appear to be important signals for altricial infant rodents. They seem, for example, to initiate infant retrieval by the dam in rats (5) and to coordinate maternal behaviors in mice (1). Bell (6) has emphasized that ultrasonics 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, ultrasonics diminish at the age at which the pup gains the ability to thermoregulate, opens its eyes, and begins to leave the nest, at which time a chemical signaling system involving a maternal pheromone (7) is said to predominate.

Some of our previous work (8, 9) has demonstrated (i) that 10- and 11-day-old rat pups can learn to approach an anesthetized dam in a heated alley with dry suckling as a reward and (ii) that the approach behavior is extinguished with successive nonrewarded trials. Extinction in these experiments indicates that at least one kind of response-suppressive mechanism is operating at an age at which centers responsible for "inhibition" are said to be not well developed in rat pups (10). It could be argued that the extinction in our experiments reflected decreased arousal resulting from any increasing period of no contact with the dam. Many studies of adult animals show that extinction following appetitive learning *increases* arousal, presumably because of the frustrating effects of nonreward following a history of reward (11). If the mechanisms of appetitive extinction in infant rats are similar to those in older rats—being characterized by active (frustrative) processes and con-

flict—and if ultrasonics indicate arousal in the pup (6), one would expect ultrasonics to increase during extinction of a learned appetitive response. This experiment is the first to our knowledge that measures ultrasound production during infant learning, and it provides evidence for an active conception of appetitive extinction in rats, even at 11 days of age.

The training apparatus is described in detail elsewhere (9). It consisted of a Plexiglas alley (38 cm long, 7.5 cm wide, and 10 cm high) and a goalbox (17 by 25 by 10 cm). A Plexiglas gate bisected the goalbox and could prevent the pup from reaching the rear half of the goalbox. Another gate at the end of the alley prevented retracing after the pup had reached the goalbox. Both alley and goalbox were maintained at 37°C by commercial heating pads located beneath the Plexiglas floor. Two photobeams positioned along the sides of the alley at 13 and 38 cm from the start position activated two clocks which recorded start and total times. Ultrasonics were detected by a condenser microphone (Bruel and Kjaer 4135) with a cathode follower (Bruel and Kjaer 2615), a microphone amplifier (Bruel and Kjaer 2604), and a bandpass filter (Krohn-Hite 310-C). The filtered amplifier output was monitored visually on an oscilloscope (Tektronix 465), and any ultrasound pulses in the range of 20 to 50 kHz (louder than 30 db) were counted by a specially constructed digital counter. The microphone was positioned over the intersection of the alley with the goalbox in such a way that ultrasonics anywhere in the apparatus were detected.

The subjects, eight albino rat pups bred in our laboratory but originally of Holtzman stock, were 11 days of age and weighed between 25 and 30 g. Each pup was separated from its dam 10 hours before runway training began and was kept in a covered plastic breeding cage maintained at 37°C . Approximately 20 minutes before runway training began, the dam was anesthetized with EquiThesin (2 ml per kilogram of body weight, injected intraperitoneally). Additional amounts of anesthetic were used as

needed to maintain a surgical level of anesthesia. Before the first trial, the pup was placed next to the dam in the rear portion of the goalbox and allowed to attach to a nipple for 30 seconds. With the dam so anesthetized and with a single pup suckling for only 30 seconds at a time, it is unlikely that a pup ever received any milk during the experimental session (12). In addition, each pup was weighed immediately before and after testing, and no pup was ever observed to gain weight during the period.

For each pup, 25 successive rewarded trials were followed immediately by 15 unsignaled nonrewarded trials. At the beginning of each trial the pup was placed at the end of the alley farthest from and facing away from the dam. The gate in the middle of the goalbox remained down and was opened only on rewarded trials after the second photobeam had been interrupted. Reward consisted of 30 seconds of dry suckling on one of the dam's nipples. Nonreward consisted of a 30-second detainment in the outer portion of the goalbox with the dam present in the other portion but inaccessible. At the end of a trial the pup was gently detached from the nipple or removed from the empty portion of the goalbox and placed in a 12 cm by 12 cm by 10 cm Plexiglas holding box for approximately 5 seconds while the experimenter positioned the gates for the next trial.

The time (to the nearest 0.01 second) from the placement of the pup in the alley until the first and second photobeams were interrupted (start and total approach times) and the number of ultrasounds emitted during those times were recorded for each trial. In addition, ultrasounds emitted in the goalbox during extinction were recorded. During acquisition, ultrasounds in the goalbox were not recorded because the pups sometimes emitted ultrasounds when the experimenter, on occasion, guided the pup in nipple attachment. During extinction pups were tested until they failed to reach the goalbox in 100 seconds.

Figure 1 shows the mean approach times and number of ultrasounds emitted by the pups during acquisition and extinction. All pups showed rapid acquisition of the approach response ($P < .001$). Paralleling the decrease in response time was a decrease in the number of ultrasounds emitted ($P < .001$). Since the pups reached the criterion for extinction of the approach response at different rates (between 9 and 15 trials), extinction times and ultrasounds in extinction were Vincentized into eight intervals. Analysis of variance

of the Vincentized extinction scores revealed a significant rise in approach times ($P < .001$) and a significant increase in number of ultrasounds ($P < .01$).

The close correspondence between the changes in approach time and ultrasounds might suggest that the number of ultrasounds is a simple reflection of time spent in the alley. A closer look at the extinction data shows that this is not the case. Figure 2 presents the mean start, run, and constant goal times and the corresponding mean number of ultrasounds emitted during those times. Although the time and ultrasound means

for the start and run measures are strikingly parallel, the production of ultrasounds also increased significantly in the goalbox, for which the detention interval was constant (30 seconds) for all trials ($P < .002$). An additional fact argues against attributing increased ultrasounds in extinction simply to time spent in the runway. The correlation between ultrasounds in the alley and time spent there on the last Vincent interval (when both were highest) was $-.25$ (13).

The approach-time data for acquisition and extinction are similar to those reported for other studies that used the same reinforcer and animals of the same

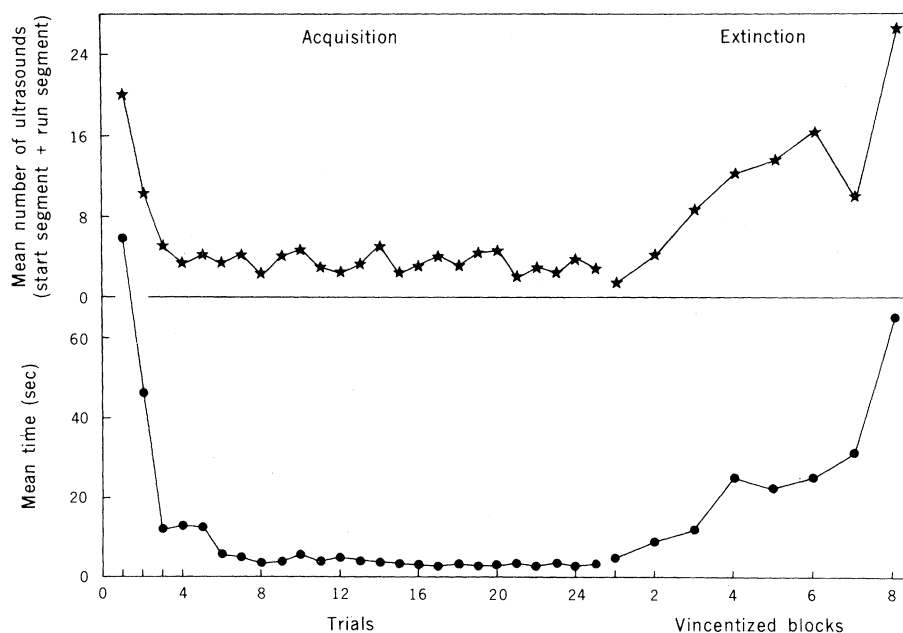


Fig. 1. Mean approach time (●) and corresponding mean number of ultrasound emissions (★) in acquisition and extinction.

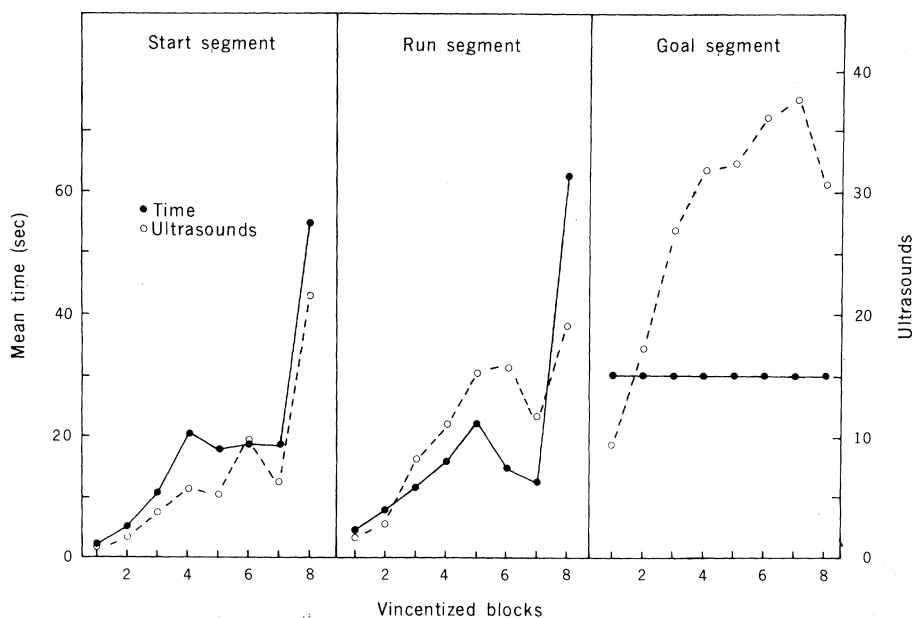


Fig. 2. Ultrasounds produced during extinction in the start, run, and goal segments of the apparatus, with corresponding time spent in each segment.

age (8, 9). The additional data on ultrasound production by infant rats during appetitive learning and extinction make this experiment especially interesting.

If one accepts the hypothesis that ultrasounds reflect arousal (6), the increase in ultrasounds in extinction, particularly over the fixed 30-second interval of goal-box detention, argues against an arousal-decrement interpretation of extinction in infant rats. Informal observation of the pups provides additional evidence that extinction entails not decreasing but increasing 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 toward the goalbox and moved the front limbs forward and backward while their hind limbs remained planted. Such activities, which never occurred on late acquisition trials, seemed to demonstrate conflict and suggest that the pups actually learned not to approach the goalbox.

Our findings of increased ultrasounds and other indicants of arousal in the appetitive extinction of infant rats do not support the hypothesis that the infant rat lacks inhibitory mechanisms nor that it is similar to the adult with a nonfunctioning hippocampus (10). Active suppression of

behavior is intrinsic to extinction in these pups as it is in adults; if extinction can be said to reflect inhibition in adult rats, it would be difficult not to attribute extinction to inhibitory mechanisms in infants as well.

ABRAM AMSEL, CATHRYN C. RADEK
MIKE GRAHAM, RICHARD LETZ
*Department of Psychology,
University of Texas, Austin 78712*

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13. Our ultrasound rate measure (ultrasound per second) provided data consistent with those of Fig. 2. These data, however, seemed to us less meaningful than mean ultrasounds because (i) correlations of the number of ultrasounds and response times were not consistent from one trial to the next and (ii) ultrasounds were not distributed evenly over the corresponding interval (time) scores but tended to occur in bursts, making rate measures somewhat misleading.
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Sociobiology of Rape in Mallards (*Anas platyrhynchos*):

Responses of the Mated Male

Abstract. *Male mallards respond to rapes of their mate by intervening aggressively against the rapist or rapists, by attempting to force a copulation with the rape victim, or both. Aggressive intervention is more likely against a solitary male than against a group, and forced copulations are more likely immediately after a rape and especially when the rape appears to have been successful. This behavior pattern reflects strategies consistent with maximizing individual male fitness.*

Rape may be defined as forced copulation. Among animals, this designation seems reasonable when the victim shows obvious resistance, copulation being preceded by vigorous struggle and escape behavior, and without the precopulatory courtship displays characteristic of "normal" mating between members of an established pair. Rape has been well described for the surface-feeding ducks, Anatini (1). Recently, McKinney (2) has pioneered the use of natural selection at the level of individuals to interpret duck reproductive behavior, an approach that will be pursued in this report. In particular, I shall present data on male re-

sponses to the rape of their mates, and show how such responses are consistent with the sociobiologic theorem that animals should behave in ways consistent with maximizing their inclusive fitness (3).

These data were gathered between 1 January and 1 June in the years 1974 through 1976, at the University of Washington Arboretum, a seminatural, suburban environment with approximately 15 breeding pairs annually; 558 observation hours were conducted from 0800 to 1600 hours. I obtained an index of females present by censusing them at 15-minute intervals and found a mean of 5.6 and a

standard deviation of 3.1. During this time, I observed 89 rapes, for a mean of .03 rape per female per observation hour. (Unless otherwise specified, "rapes" will be used to designate any rape attempt in which mounting occurred, without regard to presumed success in transferring sperm.) The monthly occurrence of rapes, per female per observation hour, was: January, 0.007; February, 0.01; March, 0.05; April, 0.05; and May 0.02. Males whose mates are being raped have two basic options, not mutually exclusive. (i) They can intervene aggressively, defending their mates and attempting to prevent or terminate the rape by dislodging the attacker or attackers. (ii) After the rape, they can introduce their sperm into their female as quickly as possible, so as to compete with those of the rapists.

Of the 89 observed rapes, 31 precipitated vigorous intervention by the mated male, whose response was usually grabbing the assailant by the neck and beating with the wings. In 30 of these 31 cases, this behavior was apparently successful in preventing sperm transfer by the rapist (that is, neither "bridling" nor "nod-swimming" occurred). Mated males failed to respond in the remaining 58 cases; this may be attributed to ignorance of the rape attempt, perceived female ability to defend herself, or unwillingness to incur the costs of such defense. In this regard, mated males never engaged aggressively against rapists when the female flew away to avoid rape (20 times), and did so in only 5 of 15 occasions when females responded to rape attempts by "repulsion" behavior, a characteristic, hunched posture, combined with loud and distinctive calls (1) which females give when approached by strange males during incubation. Such behavior apparently indicates that she is unlikely to be carrying fertilizable eggs (2). Finally, defense against multiple rapists is likely to be more costly in terms of physical injury to the defending male than is defense against a single rapist. Of the 89 observed rapes, 64 involved multiple males (range, 2 to 9; mean, 3.8; standard deviation, 2.1); mated males intervened aggressively during 14 of the 25 singleton rapes (.56) and 17 of the 64 multiple rapes (.27) [$\chi^2 = 5.63$, $\alpha = .05$, $P < .025$ (one-tailed test)].

Rapid sperm introduction is an additional possible strategy for the mate of a just-raped female. Among mallards, copulations between individuals of a mated pair are preceded by a variety of well-documented, mutual displays, notably "head-pumping" immediately before