

Maternal Responsiveness to Infant Norway Rat (*Rattus norvegicus*) Ultrasonic Vocalizations During the Maternal Behavior Cycle and After Steroid and Experiential Induction Regimens

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When removed from the nest and placed in a cool environment, Norway rat (*Rattus norvegicus*) pups emit ultrasonic vocalizations that can elicit maternal search behavior. The authors examined the behavior of pregnant dams, mothers, and virgin females during exposure to a pup that was either warm and silent or cool and vocalizing. Results indicate potentiated maternal reactions to a vocalizing pup: Mothers approached and maintained proximal orientation to a vocalizing pup far more than did virgin females. Elevated levels of proximal orientation appeared within hours of birth, increased during the 1st week postpartum, and declined by the time of weaning. Estrogen plus progesterone administration facilitated virgin females' proximal orientation toward vocalizing pups, whereas prolonged exposure to pups in the absence of hormones was without effect, suggesting that the ontogeny of the maternal response is regulated, at least in part, by maternal hormones.

Parent–offspring relations are a defining dimension in mammalian development. The expression and coordination of parental behavior is particularly important in altricial species such as the Norway rat in which infants rely on the mother for nourishment, warmth, shelter, and protection. In the present set of experiments, we examined one aspect of mother–infant interactions, specifically, the mother's behavioral response to ultrasonic vocalizations (USVs) emitted by infant Norway rat pups. We shall review briefly the empirical and conceptual precursors to the present experiments to provide background and to make explicit the interpretive framework.

There are numerous descriptive and empirical accounts of rat maternal behavior; most of these are focused on a subset of the mother's activities, such as nest building, nursing, pup licking, and the retrieval of young. Each of these activities can be defined operationally and can be studied quantitatively. Under standard, controlled laboratory conditions, nest-building behavior increases during the final days before parturition (Kinder, 1927; Rosenblatt & Siegel, 1975). Immediately after birth, pup-directed maternal behaviors (licking, retrieval, and nursing) are seen. Dams continue to display these maternal activities until the 3rd week postpartum, after which levels of maternal behavior wane gradually and systematically as weaning approaches (see Rosenblatt & Lehrman, 1963).

It is useful and important to distinguish between the overt display of maternal behavior, including its dynamic organization, that is, the *maternal behavior cycle*, and the corresponding internal states of an animal that render it differentially and specially likely to respond with species-typical behaviors to stimuli emanating from immature conspecifics. The term *maternal responsiveness* denotes an internal state or condition that is manifest by the expression of maternal behavior in the presence of cues from young (Rosenblatt, 1965). It should be understood that maternal responsiveness is a hypothetical construct; it cannot be directly observed. Nevertheless, it is a key motivational measure that has been rigorously explored and defined. We have invoked the construct here and use it to elucidate the development and the organization of the mother rat's responses to vocalizing infants.

Changes in mother–infant interactions during the postpartum period may result from changes in the mother's internal state or from the changing characteristics of her developing offspring (e.g., Jakubowski & Terkel, 1986). To isolate and examine the emergence and decline of maternal responsiveness as a process within the dam, testing must be conducted using foster pups of a particular age. Changes in a dam's responses toward standard, constant-age stimulus pups during tests conducted throughout the pre- and postpartum periods reflect changes in the dam's internal state because the characteristics of the stimulus pups remain the same, whereas the dam's maternal status varies. Most studies examining the development of maternal responsiveness use stimulus pups 10 days of age or less, because pups of this age usually receive vigorous care and because such young pups tend not to initiate contact with the dam. At these early stages, rat mothers approach their pups and initiate contact (Rosenblatt & Lehrman, 1963).

Although the emergence of maternal behavior normally coincides with the arrival of young, laboratory experiments have demonstrated that, in fact, heightened maternal responsiveness can be seen even earlier, as pregnant dams often lick, retrieve, and group stimulus pups placed in their nest shortly before giving birth (Mayer & Rosenblatt, 1984; Rosenblatt & Siegel, 1975; Slotnick,

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This research was supported by National Institutes of Health Grant MH28355 and the Indiana University Center for the Integrative Study of Animal Behavior. We thank Scott Bilstad for his artwork in Figure 1.

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Carpenter, & Fusco, 1973). The rapid initiation of maternal responsiveness around the time of birth (sometimes termed the *pregnancy effect*) appears related to endocrine changes associated with pregnancy, parturition, and lactation (see Rosenblatt, 1995). Another important tenet in this area of behavioral analysis is that hormones are not required for maternal responsiveness. Exposure to pups over the course of several days, a procedure referred to as *concaveation*, induces maternal responsiveness in virgin females, and this effect can be seen in virgins that have been both ovariectomized and hypophysectomized (Rosenblatt, 1967).

Most studies of maternal behavior and maternal responsiveness focus on a subset of all of the behaviors that might be considered maternal. One form of maternal behavior that has received relatively little developmental attention is the mother rat's response to the high-frequency acoustic emissions, that is, the USVs, emitted by her infants.

During the first 2 weeks postpartum, rat pups possess limited thermoregulatory capabilities and rely on their mother and littermates for maintenance of thermal homeostasis (Alberts, 1978). When young pups are removed from the nest environment, they cool rapidly and emit vocalizations (Blumberg & Alberts, 1990). These vocalizations are referred to as *ultrasounds* because they are typically 30 to 50 kHz in frequency and hence fall outside the human hearing range. Whereas the pups' vocalizations are inaudible to humans, they are easily detected by adult rats, which have peaks in cochlear and collicular sensitivity corresponding to the frequency range of pups' USVs (Brown, 1973; Crowley, Hepp-Reymond, Tabowitz, & Palin, 1965). It is generally agreed that USVs are a stimulus for the mother's retrieval of pups that have strayed from the nest. This stance is supported by the finding that mothers orient toward and approach sources of recorded USVs (Allin & Banks, 1972), particularly in the presence of pup odors (Smotherman, Bell, Starzec, Elias, & Zachman, 1974). As pups mature, they develop fur, insulation, and more advanced motor capabilities. During the 3rd week postpartum, USV production wanes (Blumberg, Efimova, & Alberts, 1992; Insel & Winslow, 1991), and early patterns of maternal care are progressively replaced by pup-initiated, mother-infant interactions (Rosenblatt & Lehrman, 1963).

Although there is evidence that mothers are more responsive to USVs than are virgin females (Allin & Banks, 1972; Smotherman, Bell, Hershberger, & Coover, 1978), most mothers used in previous USV experiments had extensive experience with pups before testing. Little is known about the development of the maternal response to USVs or the roles played in regulating this response by physiological variables and by experience with offspring.

In the present study, we established a behavioral assay to quantify maternal responsiveness to vocalizing pups. In Experiment 1, this assay is used to characterize a developmental trajectory for maternal responsiveness to vocalizing pups. Specifically, we examined the responses of pregnant dams, mothers, and nonmaternal virgin female controls at different points during the maternal behavior cycle. In Experiment 2, we used the same methodology to determine whether hormonal and experiential manipulations (long-term exposure to foster pups) that have previously been demonstrated to induce other forms of maternal responsiveness (retrieval, grouping, and crouching over pups) in virgin females would also induce responsiveness to vocalizing pups. We hypothesized that the ontogeny of maternal responsiveness to a vocalizing pup would

follow a time course similar to those seen for other forms of maternal responsiveness and that both steroid administration (estrogen and progesterone) and long-term exposure to foster pups would induce motherlike responses from virgin females.

Experiment 1: The Pre- and Postparturitional Development of Maternal Responsiveness to Vocalizing Pups

Though pup-directed maternal behaviors are normally first seen immediately after birth, studies examining maternal responsiveness to standard-age stimulus pups have revealed that in fact, pregnant dams retrieve, lick, and crouch over pups before giving birth, provided that testing is conducted within hours of birth (Mayer & Rosenblatt, 1984; Rosenblatt & Siegel, 1975; Slotnick et al., 1973). Furthermore, most studies examining maternal responsiveness during the 3rd and 4th weeks postpartum have demonstrated that mothers continue to retrieve, group, and crouch over young stimulus pups beyond the point in time when maternal behavior directed toward the mother's own litter normally declines (Bridges, 1975; Reisbick, Rosenblatt, & Mayer, 1975; Wiesner & Sheard, 1933).

The emergence of maternal responsiveness immediately before birth as well as numerous reports demonstrating that virgin females rapidly display maternal responsiveness after either transfusions of blood from newly parturient mothers (Terkel & Rosenblatt, 1972) or the administration of exogenous progesterone and/or estrogen (e.g., Bridges, 1984; Stern & McDonald, 1989) has led to the general belief that the initial expression of maternal behavior at the time of birth is due, at least in part, to endocrine changes that accompany pregnancy and parturition. The decline of maternal behavior around the 3rd week postpartum appears to result from the changing stimulus characteristics of the developing pups. Developmental changes that occur as pups mature alter the mother's experience and may also alter the release of prolactin (Amenomori, Chen, & Meites, 1970) and oxytocin (see Wakerley, Clarke, & Summerlee, 1988), hormones associated with lactation and milk release.

As a first step in examining maternal responsiveness to a vocalizing pup, we wanted to establish a developmental trajectory for this form of responsiveness by examining the behavioral responses of pregnant dams, mothers, and virgin female controls beginning shortly before birth and extending past the usual time of weaning (≈ 21 days postpartum). To do this, we developed an apparatus and methods that allowed us to observe simultaneously the behavior of a virgin control animal and either a pregnant dam or mother during exposure to a 6- to 8-day-old pup that was either warm and silent or cool and vocalizing. We chose 6- to 8-day-old rat pups as stimulus animals because pups of this age vocalize vigorously during cold exposure and readily elicit maternal behavior from mother rats. Furthermore, the results of at least one study (Smotherman et al., 1974) suggested that pup odors are required for mothers to approach USVs. Vocalizing pups provide the most natural complex of acoustic and olfactory stimuli. We used a single pup as the stimulus source because previous research has established that sensory cues associated with littermates attenuate USV production (Hofer & Shair, 1980, 1987, 1991).

To establish a developmental trajectory for maternal responsiveness to a vocalizing pup, we chose to examine the behavior of

pregnant dams both on the 20th day of gestation, typically 1 to 2 days before parturition in our laboratory, and on the day of birth, before birth (Gestational Day 21 or 22). We also tested mothers on the day of birth and on Postpartum Days 6–8, 21, and 41. We chose to examine the behavior of pregnant dams because to differing extents, these animals had undergone the endocrine and other physiological and experiential changes associated with pregnancy. The examination of the behavior of mothers within hours of birth extends this research to include animals that have experienced parturition but have minimal experience with offspring. Testing mothers on Postpartum Days 6–8 and 21 allows us to assess the effects of experience with pups and provides the opportunity to examine the behavior of animals both during the typical period of peak maternal behavior and around the time of weaning when maternal behavior is declining (Postpartum Day 21). Finally, we chose to test mothers at 41 days postpartum as these animals have been separated from their litter for 20 days in our laboratory. We hypothesized that, as with other forms of maternal responsiveness, responsiveness to vocalizing pups would emerge around the time of birth and would continue through lactation and weaning.

Method

Subjects. A total of 96 female Sprague-Dawley rats (*Rattus norvegicus*) were tested for behavioral responsiveness to a vocalizing pup. Forty-eight nulliparous, virgin females (> 80 days of age) were used to form control groups. The remaining 48 rats were pregnant females (primiparous) that were tested either on the 20th day of gestation ($n = 9$) or on the day of birth (before giving birth, $n = 7$) or mothers that were tested on the day of birth, Postpartum Days 6–8, 21, or 41 ($n = 8$ per group). Litters were culled to a total of 8 pups (4 males and 4 females when possible) at 3 days of age (day of birth = Day 0), and mothers were separated from their remaining offspring on the 21st day after parturition. For pregnant dams, the 1st day of pregnancy was determined by the presence of sperm in daily vaginal smears.

In addition to the adult rats, 48 pups (6 to 8 days old) were used for the production of stimulus USVs. At the beginning of experimental sessions, pups had visible milk bands signifying the recent ingestion of milk. Stimulus pups were always obtained from litters other than those of the mothers being tested.

All rats were bred in the Indiana University Bloomington Animal Behavior Laboratory from stock originally supplied by Taconic Laborato-

ries (Germantown, NY). Rats were housed in standard polycarbonate cages ($45 \times 25 \times 20$ cm) containing shredded aspen bedding and were maintained on a 12-hr light–dark cycle (lights on at 8:00 a.m.). Mothers were housed with their litters through the 21st day postpartum, after which time they were housed individually. Pregnant dams were housed individually, whereas virgin females were housed in groups of 4. The ambient temperature in the colony was maintained at 22 ± 2 °C, and food and water were available ad libitum.

Apparatus. Maternal responsiveness to a vocalizing pup was assessed using an apparatus that allowed the simultaneous observation of a virgin control rat and a pregnant or postparturient female during exposure to a pup that was either warm and therefore silent or cool and vocalizing. The apparatus, depicted in Figure 1, consisted of two Plexiglas observation cages ($32 \times 22 \times 23$ cm) and a double-walled glass cylinder (5 cm inner diameter; 8 cm long). The glass cylinder was used to house the stimulus pup during testing and functioned as an open-ended environmental chamber. Pups were confined to a plastic mesh enclosure inside the environmental chamber; however, this tube did not prevent pups from moving or turning around inside the apparatus. Ambient temperature inside the chamber could be controlled precisely by passing water from a thermostatically regulated water circulator between the inner and the outer walls of the glass cylinder. Air temperature inside the cylinder was monitored using a Type T thermocouple and thermocouple reader (Omega, Stamford, CT).

Observation cages were positioned 10 cm from both of the open ends of the environmental chamber containing the stimulus pup. The walls of the observation cages facing the stimulus pup were outfitted with a 10.2-cm-diameter mesh-covered hole that allowed the efficient passage of sounds generated by the pup. Ventilation inside the observation cages was further aided by perforations in the steel lid of the cage and a second mesh-covered ventilation hole (7.6 cm in diameter) cut in the wall opposite to the stimulus pup (1 cm from the front wall and 4 cm from the floor). An open-faced enclosure ($13 \times 13 \times 10$ cm) was positioned in the rear corner of each observation cage to provide a semi-enclosed nesting area that would not block the passage of sound from the stimulus pup. The two walls of this enclosure were constructed of clear Plexiglas (0.6 cm thick), and the roof consisted of a 13-cm² sheet of black Plexiglas (0.3 cm thick). Two perpendicular black lines (1 cm wide) were drawn on the front of each observation cage to aid in the quantification of motor activity. Each observation cage was illuminated with a reflective lamp, and a 40-W light bulb was positioned 9 cm above the center of the cage. Additional light was provided by a 52-W bulb located 1.93 m above the observation cages. A piece of cardboard was positioned on the roof of each observation cage to shade the half of the cage located farthest from the stimulus pup.

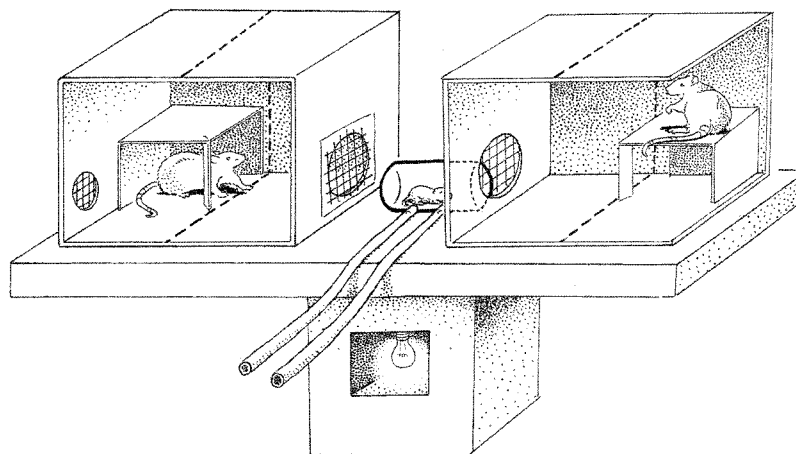


Figure 1. Apparatus used to test behavioral responsiveness to rat pup ultrasonic vocalizations.

Experimental sessions were recorded using a video camera (Sony DXC 151A or Panasonic BL200) connected to a time-lapse videocassette recorder (VCR; Gyrr, TLC 1400). USVs emitted by the stimulus pup were monitored using a microphone with a mylar diaphragm positioned at a 45° angle adjacent to one of the open ends of the environmental chamber. Output from the ultrasound microphone was passed through an ultrasound detector (Ultrasound Advice U30, London, England) set to detect sounds in a frequency range centered on 43 kHz. The signal from the tape output socket of the ultrasound detector was passed to an analog-to-digital (A/D) card housed in a Macintosh 7600 computer. A customized Labview software program (Labview, 2000) was used to detect the presence or absence of USVs that surpassed a predetermined threshold during a series of 2-s bins. When a vocalization was detected, a small red light (4 W) located beneath the observation cages was illuminated during the subsequent 2-s time bin. Activation of this light provided a video record of USV production that could be viewed in recordings of test sessions, even when played back at six times normal speed.

Procedure. At the beginning of each experimental session, the open-ended environmental chamber was warmed to between 35 and 37 °C, and the observation cages were cleaned with Roccal-D detergent (Pharmacia & Upjohn, Peapack, NJ) and water. After the ambient temperature inside the chamber had stabilized, a single 6- to 8-day-old stimulus pup was enclosed in a plastic mesh tube and placed inside the chamber. The pup habituated to the chamber for 20 min, during which time vocalizations ceased. Subsequently, a virgin female rat was placed inside one of the two observation cages, and a pregnant or postparturient female was placed in the other observation cage. The two adult rats were allowed to habituate to the apparatus for 40 min. During this habituation period, they typically became quiescent, settling on the side of the observation cage farthest from the stimulus pup. At the completion of the habituation period, the time-lapse VCR was started, and a 20-min baseline recording was made. During this baseline period, the pup remained warm and silent.

At the completion of the 20-min baseline period, the water supply going to the environmental chamber housing the pup was changed, causing the temperature inside the chamber to fall rapidly to ≈15 °C. The stimulus pup typically began to produce USVs within 1 to 5 min after the reduction in environmental chamber temperature. USV production was monitored, and a 20-min test session was videotaped, beginning with the production of the first USV. At the completion of testing, 20-min video recordings of adult behavior had been made during exposure to two different stimuli: a warm silent pup and a cool vocalizing pup.

The procedure outlined above was used to conduct a series of cross-sectional comparisons between virgin control rats and pregnant or postparturient females. Each pregnant and postparturient female was tested simultaneously with a virgin control rat. Rats were tested only once. A matched-pairs (yoked) experimental design ensured that both control and experimental rats received equivalent USV exposure from the shared stimulus pup. This design was crucial to interpreting differences in behavioral responsiveness to vocalizing pups because individual pups varied in their production of USVs.

After completion of the test session, video recordings of the 20-min baseline and test periods were replayed at six times normal speed. The major dependent variable coded during playback was the duration that each adult rat spent actively oriented toward the stimulus pup while in close proximity (<5 cm) to the mesh-covered hole adjacent to the pup (digging at the base of the mesh-covered hole was also included). This behavior is referred to as *proximal orientation*. Proximal orientation was only registered during active orientation; merely sleeping in proximity to the mesh-covered hole did not qualify. Additionally, general activity levels during the baseline period were estimated by quantifying the number of line crossings displayed by both the experimental rats and their matched virgin controls. Line crossings were registered when the entire head (nose to ears) of the rat being tested crossed either the vertical or horizontal line on the face of the observation cage. Behavioral coding was performed using

DOS-based software that automatically converted the duration of proximal orientation coded from time-lapse tapes to real-time values. Finally, a computerized record of the stimulus pup's USV production (the timing and number of light activations) was retained to estimate the percentage of time that stimulus pups spent vocalizing during the test period (number of 2-s bins containing vocalizations divided by the total number of bins, multiplied by 100).

Data from 10 rats (5 matched pairs) were excluded from analysis because the virgin control rat or the corresponding matched experimental rat had exceeded a predetermined level of proximal orientation (>600 s of baseline proximal orientation) to the silent pup during the baseline period. Data from three pairs of rats were excluded because of excessive baseline proximal orientation from control rats, and data from two pairs were excluded based on the behavior of pregnant dams or mothers. These rats are not represented in the group sizes listed above. Data on USV production from one stimulus pup were also excluded from analysis because of a failure of the ultrasound detection hardware.

Data analysis. Data are presented as means plus or minus standard error of the mean. The duration of proximal orientation during each baseline period was subtracted from the duration seen during the subsequent test period to yield a value reflecting the change in proximal orientation occurring as a result of exposure to USVs. Differences between mean values obtained from experimental rats and matched virgin controls were assessed for statistical significance using a series of paired *t* tests and were considered to be statistically significant if $p < .05$, two-tailed. Paired *t* tests were also used to make select comparisons between the baseline durations of proximal orientation displayed by experimental rats and matched virgin controls. Finally, a Pearson product-moment correlation coefficient was calculated using the line-crossing values obtained from experimental rats and matched virgin controls during the baseline period to assess the possibility that the activity levels of paired animals were systematically related as a consequence of being observed simultaneously.

Results and Discussion

During the baseline period (pup silent), virgin females, pregnant dams, and mothers spent an average of less than 3 1/2 min engaged in proximal orientation. Mean durations of proximal orientation displayed by groups of virgin females (six groups) during the baseline period ranged from 43.5 ± 39.3 to 184.5 ± 36.6 s, whereas baseline values for pregnant dams and mothers (six groups) ranged from 12.7 ± 8.5 to 133.5 ± 46.5 s. Although we attempted to maintain consistent conditions for these tests, it is possible that variability in baseline proximal orientation might be related to differences in the ambient temperature of the testing room or from related, seasonal differences in the noise emanating from the cooling and heating systems. Paired *t* tests revealed only one instance in which differences in baseline levels of proximal orientation for matched groups of experimental and control rats approached statistical significance: Pregnant dams tested on the 20th day of gestation displayed considerably less proximal orientation than did matched virgin controls, $t(8) = 2.21$, $p < .06$, two-tailed.

Lowering the temperature within the environmental chamber served as a potent stimulus for USV production. Whereas the pattern of vocalization for individual pups was quite variable, on average, pups vocalized vigorously throughout the 20-min test period. The percentage of time that stimulus pups spent vocalizing throughout the course of the test period is depicted in Figure 2.

During the test period, while the pup was vocalizing, mothers of newborns and mothers of 6- to 8-day-old pups typically responded with frequent bouts of proximal orientation. Whereas individual

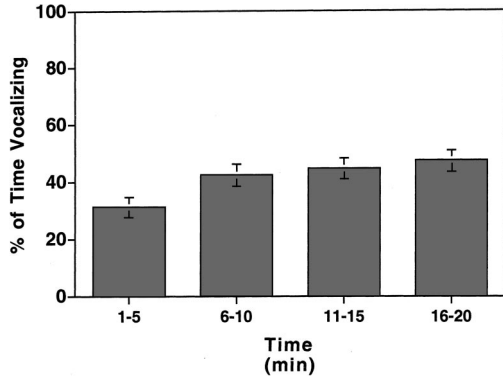


Figure 2. Percentage of time spent vocalizing by stimulus pups throughout the course of the 20-min test period. Data are presented as $M \pm SEM$.

response profiles varied considerably, these mothers often remained responsive to the pup throughout the duration of the 20-min test. Pregnant dams, mothers tested on Postpartum Days 21 and 41, and matched virgin controls generally displayed less intense responses to the vocalizing pup. The time course of proximal orientation by pregnant dams, mothers, and matched virgin controls during the test period is enumerated in Table 1.

The mean changes in proximal orientation displayed by pregnant dams, mothers, and matched virgin controls during the test period (pup vocalizing) indicate that potentiated responsiveness to a vocalizing pup emerges around the time of birth, increases during the 1st week postpartum, and declines by the 21st day after parturition. Figure 3, which shows mean increases in proximal orientation over baseline for each group, illustrates the initial emergence, rise, and subsequent decline of maternal responsiveness in reproducing rats, compared with the flat response profile

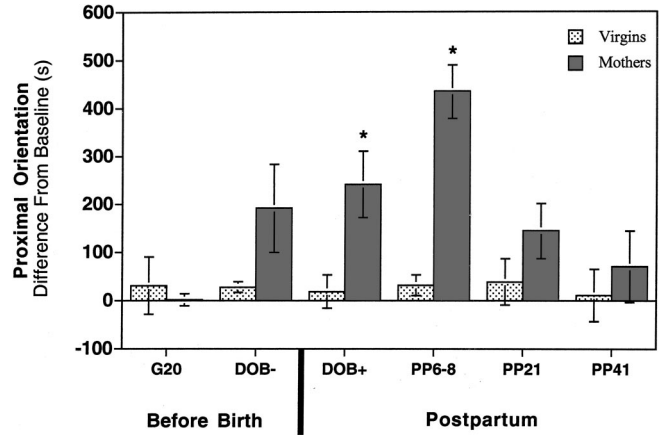


Figure 3. Duration of proximal orientation by pregnant dams tested on Gestational Day 20 (G20) or on the day of birth before birth (DOB-); and mothers tested on the day of birth after birth (DOB+) or on Postpartum Days 6-8 (PP6-8), 21 (PP21), or 41 (PP41). Histograms represent the mean difference between the 20-min test period (pup vocalizing) and the 20-min baseline period (pup silent). Error bars represent the SEM. All comparisons were made against matched virgin controls (* $p < .05$).

across the virgins. Virgin females consistently showed small (<40 s) average increases in proximal orientation during the test period (pup vocalizing). The extent to which proximal orientation increased in pregnant dams and mothers was highly dependent on gestational or postpartum status. Mean increases in proximal orientation ranged from 2 ± 12.9 s on the 20th day of gestation to a high of 435.8 ± 54.4 s when testing was conducted between Days 6 and 8 postpartum.

Paired t tests comparing the mean increases in proximal orientation displayed by pregnant dams to those exhibited by their

Table 1
Time Course During Ultrasonic Vocalization Exposure (Test Period) of Proximal Orientation by Pregnant Dams, Mothers, and Matched Virgin Controls

Time (in minutes)	Duration of proximal orientation (in seconds)											
	G20 ($n = 9$)		DOB- ($n = 7$)		DOB+ ($n = 8$)		PP6-8 ($n = 8$)		PP21 ($n = 8$)		PP41 ($n = 8$)	
	M	SEM	M	SEM	M	SEM	M	SEM	M	SEM	M	SEM
1-5												
Pregnant dams or mothers	8.7	5.9	88.3	39.3	73.5	26.5	141.8	27.5	79.5	19.9	63.8	34.9
Matched virgin controls	68.0	20.9	45.4	30.7	12.8	7.0	25.5	11.6	85.5	24.9	27.8	13.1
6-10												
Pregnant dams or mothers	5.3	3.7	60.0	32.6	69.0	23.8	140.3	11.1	84.0	21.2	54.0	13.6
Matched virgin controls	60.0	24.2	14.6	12.7	12.8	7.6	42.8	22.0	66.8	16.2	17.3	7.5
11-15												
Pregnant dams or mothers	0.7	0.7	42.0	22.0	77.3	20.9	110.3	19.9	52.5	14.2	36.0	15.0
Matched virgin controls	35.3	23.0	10.3	6.8	20.3	10.1	31.5	20.1	33.8	16.9	12.8	5.1
16-20												
Pregnant dams or mothers	0.0	0.0	22.3	15.9	68.3	26.7	96.8	24.3	62.3	11.5	42.8	24.4
Matched virgin controls	4.7	4.7	20.6	11.4	16.5	10.9	16.5	14.8	37.5	16.9	31.5	18.0
Total												
Pregnant dams or mothers	14.7	6.8	212.6	97.1	288.0	76.2	489.0	42.7	278.3	34.4	196.5	75.7
Matched virgin controls	168.0	61.7	90.9	59.4	62.3	25.6	116.3	49.5	223.5	59.4	89.3	38.1

Note. Pregnant dams were tested on Gestational Day 20 (G20) and on the day of birth before birth (DOB-). Mothers were tested on the day of birth after the birth (DOB+) and on Postpartum Days 6-8 (PP6-8), 21 (PP21), and 41 (PP41).

matched virgin controls failed to yield statistically significant differences. Proximal orientation on the day of birth (before birth) seemed to be enhanced, $t(6) = 1.65$, $p < .15$, however, and may warrant further investigation, particularly in light of our small sample size. Statistically significant levels of maternal responsiveness to vocalizing pups emerged shortly after birth, and responsiveness continued to increase during the 1st week after parturition. Paired t tests comparing the mean increases in proximal orientation displayed by mothers and virgins revealed statistically significant differences both on the day of birth, $t(7) = 2.53$, $p < .05$, and 6 to 8 days after parturition, $t(7) = 9.28$, $p < .01$. Maternal responsiveness to vocalizing pups declined by the end of the 3rd week postpartum, and comparisons between mean increases in proximal orientation failed to yield statistically significant differences between mothers and virgins at both 21, $t(7) = 1.48$, $p < .19$, and 41, $t(7) = 0.66$, $p < .54$, days after parturition.

The frequency with which pregnant dams, mothers, and matched virgin controls exhibited different magnitudes of change in proximal orientation is enumerated in Table 2. The majority of mothers tested on the day of birth and all of the mothers tested on Postpartum Days 6–8 displayed increases in proximal orientation in excess of 200 s. This stands in contrast to the changes displayed by the remaining mothers, pregnant dams (particularly on the 20th day of gestation), and matched virgin controls, which generally displayed smaller increases or decreases in proximal orientation while the stimulus pup was vocalizing.

The matched-pairs procedure used here had the advantage of exposing both experimental and control animals to the same stim-

ulus (pup vocalizations). The procedure, however, had the possible disadvantage of testing animals from the different groups in close physical proximity. To assess whether paired rats might have affected each other's behavior, a Pearson product-moment correlation coefficient was calculated between the number of line crossings displayed during the baseline period by the virgin rats and the pre- and postpartum mothers to which they were matched. This correlation (48 pairs) yielded an r value of .04, suggesting that interactions between mothers and virgins were of little consequence in these tests. Overt interactions between experimental animals and matched virgin controls were also not apparent during coding of the baseline and test periods; however, the possibility remains that rats were interacting in a way that was not captured by observation or the measure of general activity outlined above.

Experiment 2: Virgin Females' Responsiveness to Vocalizing Pups After Steroid Administration or Experience With Pups

The results of Experiment 1 indicate that maternal responsiveness to a vocalizing pup emerges rapidly around the time of birth, continues to increase during the 1st week of lactation, and declines around the time of weaning. The rapid onset of maternal responsiveness on the day of birth suggests that endocrine changes associated with the end of pregnancy and parturition may play a role in rendering mothers responsive to vocalizing pups. The further increase in responsiveness seen between the day of birth and the end of the 1st week postpartum may also be related to

Table 2
Frequency of Changes in Proximal Orientation Displayed by Pregnant Dams, Mothers, and Matched Virgin Controls During Ultrasonic Vocalization Exposure

Duration (in seconds) ^a	Gestational or postpartum period					
	G20 (<i>n</i> = 9)	DOB– (<i>n</i> = 7)	DOB+ (<i>n</i> = 8)	PP6–8 (<i>n</i> = 8)	PP21 (<i>n</i> = 8)	PP41 (<i>n</i> = 8)
Pregnant dams and mothers						
–300 to –201	—	—	—	—	—	—
–200 to –101	—	—	—	—	—	1
–100 to –1	2	—	1	—	2	2
0 to 99	7	4	1	—	1	3
100 to 199	—	1	1	—	—	1
200 to 299	—	—	1	2	4	—
300 to 399	—	—	2	1	1	—
400 to 499	—	1	1	2	—	—
500 to 599	—	1	1	2	—	1
600 to 699	—	—	—	1	—	—
Matched virgin controls						
–300 to –201	—	—	—	—	1	—
–200 to –101	2	—	1	—	—	2
–100 to –1	2	—	1	3	2	1
0 to 99	2	7	4	4	2	3
100 to 199	2	—	2	1	2	1
200 to 299	—	—	—	—	1	1
300 to 399	—	—	—	—	—	—
400 to 499	1	—	—	—	—	—
500 to 599	—	—	—	—	—	—
600 to 699	—	—	—	—	—	—

Note. Pregnant dams were tested on Gestational Day 20 (G20) and on the day of birth before birth (DOB–). Mothers were tested on the day of birth after birth (DOB+) and on Postpartum Days 6–8 (PP6–8), 21 (PP21), and 41 (PP41). — = no entry.

^a From test to baseline.

endocrine changes, but a second (and not mutually exclusive) possibility is that this increase in responsiveness is brought about by the mother's experience with her own litter.

Numerous studies conducted over the last 4 decades have demonstrated both an endocrine and an experiential basis for maternal responsiveness. Blood titers of estrogen and progesterone rise during pregnancy (see Bridges, 1990). Just before parturition, progesterone levels decline, while estrogen levels remain high. Treatment with estrogen alone reduces induction latencies in virgin females, but regimens of exposure to estrogen and progesterone that simulate hormonal changes during pregnancy and parturition yield greater reductions in maternal responsiveness latencies than do treatments using equivalent doses of estrogen alone (Bridges, 1984; Stern & McDonald, 1989). As was mentioned in the introduction, long-term exposure to foster pups (concoaveation) can induce in virgin females a state of maternal responsiveness that is not dependent on ovarian or pituitary hormones (Rosenblatt, 1967).

The present experiment was designed to determine whether hormonal and experiential manipulations that have been shown to induce other forms of maternal responsiveness would also increase levels of responsiveness to vocalizing pups. To address this question, we examined the behavioral responses of virgin females either after a regimen of estrogen and progesterone administration or after the experiential, concoaveation manipulation. We hypothesized that both of these induction regimens would enhance responsiveness to vocalizing pups in our paradigm.

Method

Subjects. In the present experiment, we used 46 virgin female Sprague-Dawley rats (*Rattus norvegicus*) and 23 stimulus pups (6 to 8 days of age). Rats used in the concoaveation experiment were at least 70 days of age at the time of testing. Rats in the steroid induction experiment were between 200 and 225 g on the day of ovariectomy. All experimental and control rats were housed singly in standard maternity cages for the duration of the experiment.

Procedure. Behavioral responsiveness to vocalizing pups was quantified using the procedures and apparatus described in Study 1. Eleven virgins were tested after ovariectomy and a regimen of steroid (estrogen and progesterone) administration designed to simulate hormonal changes associated with pregnancy and parturition (Bridges, 1984). Twelve additional virgins were tested for responsiveness to a vocalizing pup after concoaveation. Eleven ovariectomized virgins and 12 pup-naive virgins served as matched controls for steroid-treated and concoaveated virgins, respectively.

Steroid regimen. Virgin females were ovariectomized 1 week before hormone administration. The ovariectomy procedure involved making two dorsal incisions (1 cm) lateral to the midline, over the caudal poles of the kidneys. Tissue was resected, and a blunt dissection was performed to expose the ovaries. The fallopian tubes were then ligated with 4-0 silk, and the ovaries were removed. The muscle wall overlying the ovaries was closed with 4-0 silk, and cutaneous incisions were closed with surgical staples.

Steroid implants were prepared using the procedure of Smith, Damassa, and Davidson (1977). Implants were constructed from Silastic tubing (Dow-Corning, Model 602-305, Midland, MI) and were filled with either 17β -estradiol or progesterone (Steraloids, Wilton, NH). Implants were sealed with 5-mm wood dowels fashioned from the machined ends of applicator sticks (Baxter, A5000-1, Deerfield, IL) and silicone adhesive (Dow-Corning, Type A). Estrogen and progesterone capsules had pharmacologically active zones (excluding length of wood plugs) measuring 2 mm

and 30 mm, respectively. Implants were incubated in phosphate-buffered saline (pH 7.0) for 48 hr and washed in ethanol before implantation.

We chose to use a regimen of steroid administration similar to that used by Bridges (1984) because this procedure had been shown to produce physiologically realistic titers of circulating estrogen and progesterone and to reduce maternal responsiveness induction latencies in virgin females. One week after ovariectomy, virgin females were implanted with a single estrogen capsule and three progesterone capsules. Capsules were implanted under the skin of the back via two small (<1 cm) incisions. Wounds were closed with a single surgical staple. Fourteen days after implantation, progesterone capsules were removed, whereas estrogen capsules remained in place. Rats were tested for behavioral responsiveness to a vocalizing pup 1 day after removal of the progesterone implants. Ovariectomized control females underwent the same surgical procedures as steroid-treated virgins, except that they were implanted with blank capsules. All surgical procedures were performed under isoflurane anesthesia (4% in oxygen), delivered through a nonbreathing anesthesia unit, and took less than 10 min.

Concoaveation. On the 1st day of the concoaveation procedure, 3 healthy foster pups were placed in the cage of each virgin female. Twenty-four hours later, the cages containing the virgin females and their foster pups were removed from the colony and brought to a separate room, where they were tested for maternal responsiveness. At the beginning of this 1-hr test, the 3 foster pups were distributed in the three corners of the cage located farthest from the home nest (if present). Brief observations were conducted every 15 min for the next hour to determine whether the mother had retrieved, grouped, and crouched over the foster litter. After completion of the 1-hr test, original foster pups were returned to their mothers, and virgins were given 3 freshly fed pups. This procedure was repeated daily until virgins retrieved, grouped, and crouched over pups during two consecutive daily test sessions, at which point they were tested for responsiveness to a vocalizing pup. Four rats (not included in above group sizes) were not tested for maternal responsiveness to a vocalizing pup because they failed to display maternal responsiveness after 10 days of pup exposure. The remaining 12 females became maternally responsive to foster young after an average of 6.5 ± 1.0 days of pup exposure.

Results and Discussion

Hormonal changes associated with pregnancy and parturition appear to be sufficient for the development of maternal responsiveness to a vocalizing pup. As is depicted in Figure 4A, steroid administration caused enhanced responsiveness to the pup-generated USVs. Both steroid-treated females and ovariectomized controls displayed modest levels of proximal orientation during the baseline period, engaging in an average of 69.8 ± 34.0 and 98.7 ± 23.0 s of proximal orientation, respectively. During the test period, when the pup was vocalizing, steroid-treated virgins displayed an average increase in proximal orientation of 261.8 ± 77.9 s. In contrast, ovariectomized control rats engaged in only 106.4 ± 60.6 s of additional proximal orientation during USV exposure. A paired *t* test comparing the mean increases in proximal orientation displayed by steroid-treated virgins and control rats during the test period revealed a significant difference between the two groups, $t(10) = 2.43$, $p < .05$.

Although the rats used in the present experiment were never exposed to pups and consequently were not tested for other forms of maternal responsiveness, results from a parallel study indicated that the steroid regimen we used was very effective for inducing maternal responsiveness: The steroid-treated virgins used in the parallel study reliably retrieved, grouped, and crouched over foster pups after an average of 2.5 ± 0.8 days of pup exposure. In contrast, the majority of ovariectomized control rats remained

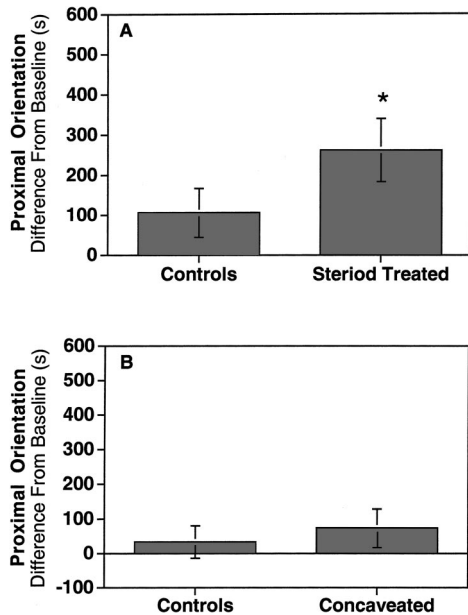


Figure 4. Duration of proximal orientation by steroid-treated (A) and concaveated (B) virgin females. Histograms represent the mean difference between the 20-min test period (pup vocalizing) and the 20-min baseline period (pup silent). Error bars represent the SEM. Statistical comparisons were made against matched controls ($*p < .05$).

unresponsive to young despite having been housed with 3 foster pups (3 to 8 days of age) for 10 days.

Unlike steroid administration, concaveation failed to induce enhanced responsiveness to vocalizing pups (see Figure 4B). During the baseline period, concaveated virgins and pup-naive control rats engaged in 46.5 ± 23.6 and 86.5 ± 37.6 s of proximal orientation, respectively. During the 20-min test period, concaveated virgins displayed an average increase in proximal orientation of 73.5 ± 55.1 s, whereas the proximal orientation of pup-naive virgins increased by 33.0 ± 47.2 s. The average increases in proximal orientation displayed by concaveated virgins and control animals were statistically equivalent, $t(11) = 0.7$, $p < .51$.

Hormonal changes associated with pregnancy and parturition appear to be sufficient for the development of maternal responsiveness to a vocalizing pup. Long-term exposure to foster young, although effective in inducing other forms of maternal behavior, failed to induce enhanced responsiveness to a vocalizing pup. In contrast, virgin females did exhibit an enhanced, motherlike response to USVs after steroid administration, despite the fact that these virgins had no prior experience with pups.

General Discussion

The results of Experiment 1 indicate that maternal responsiveness to a vocalizing pup, as measured by increased proximal orientation during the test period, emerges around the time of birth, continues to develop during the 1st week of lactation, and declines by the end of the 3rd week postpartum, around the time of weaning. The rapid emergence of responsiveness to vocalizing pups around the time of birth is consistent with reports regarding other forms of maternal responsiveness, including retrieval and

grouping of foster pups (e.g., Mayer & Rosenblatt, 1984; Rosenblatt & Siegel, 1975; Slotnick et al., 1973). Furthermore, the rapid emergence of responsiveness to vocalizing pups on the day of birth also suggests that endocrine changes accompanying pregnancy and parturition might play a role in mediating this behavior. Mothers began to respond to vocalizing stimulus pups before gaining extensive experience with their own litter.

The results of subsequent induction experiments suggest that endocrine changes associated with pregnancy are sufficient to increase maternal responsiveness to vocalizing pups and provide further support for an endocrine basis for the initial emergence of this form of responsiveness at the time of birth. Virgin females treated with a regimen of estrogen and progesterone designed to simulate changes in steroid titers characteristic of the latter stages of pregnancy respond to vocalizing pups with increases in proximal orientation approximating those displayed by mothers of newborns. Newly parturient mothers represent an appropriate group for comparison because they have experienced the endocrine changes associated with pregnancy but have minimal experience with their litters.

Unlike steroid-treated virgins, the virgin females that received long-term exposure to foster pups failed to display enhanced responsiveness to vocalizing pups, even though these virgins reliably retrieved and grouped stimulus pups on 2 consecutive days before testing. Previous research indicates that concaveation is not hormone dependent (Rosenblatt, 1967). Our results regarding proximal orientation to a vocalizing stimulus pup are consistent with previous reports indicating that concaveated virgins are less likely than lactating mothers to retrieve pups from the arms of a T maze attached to their home cage (Bridges, Zarrow, Gandelman, & Denenberg, 1972; Stern & Mackinnon, 1976). It is possible, however, that the maternal behavior displayed by our concaveated virgins was dependent on cues associated with the home cage environment. Indeed, most previous studies involving maternally responsive virgins were conducted in the home cage, so it might be revealing in future studies to test concaveated virgins for other forms of maternal responsiveness (e.g., licking, crouching over pups, and retrieving) in a novel testing environment.

The results of our developmental analysis also indicate that maternal responsiveness to vocalizing pups increases during the 1st week after parturition. The fact that our concaveation procedure failed to induce enhanced responsiveness to vocalizing pups despite having induced other forms of maternal responsiveness suggests that experience with pups in the absence of endocrine change is unlikely to explain the postpartum increase in maternal responsiveness to vocalizing pups. However, postpartum experience gained by mothers with their own offspring may have contributed substantially to their increase in responsiveness (Experiment 1, Figure 2). Unlike concaveated virgins, newly parturient mothers have experienced the hormonal changes associated with pregnancy and parturition and are lactating. Experiences with pups may yield different outcomes when obtained in the presence and absence of these hormonal changes. It must also be remembered that the kinds and amounts of experience derived from full mother-litter interactions involving milk transfer, nearly continuous contact, licking, and more may have consequences not seen after the exposure regimen used in the current procedures.

Another possibility is that pup stimulation during the 1st week postpartum may increase maternal responsiveness to vocalizing

pups as an indirect or secondary effect of its primary effects on the hormones of lactation and milk release. Stimulation associated with suckling and nursing is known to be a potent releaser for both prolactin (Amenomori et al., 1970) and oxytocin (see Wakerley et al., 1988). Therefore, while rearing a litter, mothers would be expected to sustain changes in prolactin and oxytocin levels that differ from those seen in pregnant dams, mothers of newborns, concaveated virgins, and steroid-treated virgins. Suckling-related stimulation might potentiate maternal responsiveness to vocalizing pups during the 1st week after birth by elevating prolactin and oxytocin titers. Conversely, reductions in prolactin and/or oxytocin release around the time of weaning may explain the decline of this behavior by the end of the 3rd week postpartum. Smotherman et al. (1978) reported that maternal approach toward recorded USVs in a Y maze declines after litter removal on Postpartum Days 1, 5, and 10, suggesting that pup stimulation is required for the maintenance of responsiveness to USVs.

The possible involvement of prolactin in the regulation of responsiveness to vocalizing pups is of particular interest because changes in prolactin titers around parturition might also explain the emergence of this behavior. Pregnant dams exhibit elevated prolactin titers shortly before giving birth (Amenomori et al., 1970; Bridges & Goldman, 1975; Linkie & Niswender, 1972). In addition, pregnant dams are also exposed to placental lactogen, a closely related compound (Robertson & Friesen, 1981). Recent studies suggest that prolactin (Bridges, DiBiase, Loundes, & Doherty, 1985; Bridges & Ronsheim, 1990) and placental lactogen (Bridges & Freemark, 1995) are involved in the rapid onset of maternal responsiveness around the time of birth. In fact, the rapid induction of maternal responsiveness in virgin female rats treated with estrogen and progesterone appears to be prolactin dependent (Bridges et al., 1985). Hypophysectomized virgins fail to display reduced induction latencies after estrogen and progesterone administration in the absence of exogenous prolactin administration or the implantation of ectopic pituitary grafts that release prolactin (Bridges et al., 1985).

The estrogen administered to virgin females, as part of our steroid regimen, should have increased prolactin release in addition to elevating estrogen titers (Bridges & Ronsheim, 1990). This increased prolactin may have, however, been insufficient to enhance further the hormone-treated virgins' responsiveness to vocalizing pups. Orpen, Furman, Wong, and Fleming (1987) reported that virgins treated with an estrogen, progesterone, and prolactin regimen displayed reduced induction latencies for nest building and retrieval of stimulus pups 7 days after the termination of hormone administration. Virgins that received only estrogen and progesterone failed to show similar reductions in induction latencies. Given that responsiveness to USVs and retrieval of pups may be related, it may be useful to determine whether the addition of exogenous prolactin to the hormone regimen would further augment responsiveness to vocalizing pups. Similar studies examining the effects of exogenous oxytocin administration may also prove fruitful in this regard.

These studies provide specific findings and overall patterns of results that bear on some general issues in the comparative psychology of parent-offspring relations. There has long been an overriding emphasis on the *producers* of USVs, that is, infant rodents, compared with the *receivers* of USVs (adult conspecifics). Consequently, there has emerged an overall perspective suggesting

that by emitting USVs, infant rodents can control the behavior of the mother. Within such a perspective, conventional terminology refers to the pups' vocal emissions as *distress vocalizations* and *calls* (e.g., Gardner, 1985; Hofer & Shair, 1987) and combines with the functional consequences of the vocalizations, such as solicitation of maternal attention, to reinforce the view that it is the stimulus that controls the dam's behavior. The results of the present experiments, in contrast, emphasize how the internal state of the mother rat renders her especially responsive to vocalizing pups. These kinds of findings emphasize the importance of the *receiver* in the functional organization of this parent-offspring relationship.

There is little question that there are functional and adaptive consequences to the infant rodent's emission of USVs in the presence of a maternal adult. It has recently been argued, however, that the production of the USVs may be an incidental by-product of homeostatic mechanisms internal to the infant and that the mother's responses are fortuitous consequences (e.g., Blumberg & Alberts, 1997; Blumberg & Sokoloff, 2001; Farrell & Alberts, 2000). The developing infant need not be equipped with intentional, directive behaviors that are shaped or intended to control the adult's behavior. The adult receiver may be equipped with internal mechanisms that extract information-laden cues from the sender. The present results suggest that such mechanisms and capabilities exist in the rat dam and that these may be sufficient to create adaptive parent-offspring interactions based on the complex of stimuli emitted by the infant. This general perspective is applicable to other species and other modalities.

When evaluating the results of the current study, it is important to recall that rats were exposed to a complex stimulus: a vocalizing pup. Although USV exposure was carefully controlled by manipulating the temperature of the environmental chamber housing the stimulus pup, pregnant dams, mothers, and virgin females were exposed to more than just USVs. Rats were also exposed to secondary pup cues including odors. Fleming (1986) has proposed that endocrine changes associated with the transition from pregnancy to motherhood make pup odors attractive to mothers. Consistent with this stance, Bauer (1983) reported that mothers display a preference for material gathered from the nests of other lactating dams relative to clean shavings, and similar findings have been reported for virgin females treated with estrogen and progesterone (Fleming, Cheung, Myhal, & Kessler, 1989). Furthermore, at least two previous reports indicate that pup odors enhance maternal approach toward USVs (Smotherman et al., 1974, 1978). In our companion article (Farrell & Alberts, 2002), we use the behavioral assay introduced in this study to examine the extent to which nonacoustic cues from pups contribute to the mother rat's responsiveness to vocalizing offspring, and we find that pup odors interact with USVs to elicit the enhanced maternal response. Therefore, changes in the dam's olfactory perception may also contribute to maternal responsiveness to vocalizing pups.

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Received May 9, 2001

Revision received January 25, 2002

Accepted January 30, 2002 ■

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