

# Maternal Contributions to Sensory Experience in the Fetal and Newborn Rat (*Rattus norvegicus*)

April E. Ronca, Christopher A. Lamkin, and Jeffrey R. Alberts

*Using videographic analyses, we identified and quantified maternal contributions to the sensory environment of the perinatal rat (*Rattus norvegicus*) by analyzing, from the offspring's perspective, the dam's activities during gestation, labor, and delivery. Our observations indicate that pregnant females remain highly active during the final week of gestation, as compared with nonpregnant control animals. Exploratory movements, feeding, drinking, self-grooming, and other activities of the rat dam pitch, turn, accelerate, and expose fetuses to mechanical pressures. During parturition uterine contractions and maternal licking and handling provide vigorous tactile and vestibular stimuli to pups. Newly born pups are exposed to intense thermal stimulation, cooling rapidly to the temperature of the postnatal environment. Our results suggest that fetal and newborn rats are exposed during development to a broad range of maternally produced stimuli.*

Traditionally, the intrauterine environment has been characterized as dark, warm, and silent (Bichat, 1827; Carmichael, 1970; Preyer, 1937; Windle, 1940). Within the liquor amnii (amniotic fluid), the fetus was thus thought to develop undisturbed, buffered and protected from extrinsic influences. Then, on its emergence from the womb, "the baby, assailed by eyes, ears, nose, skin, and entrails at once, feels it all as one great blooming, buzzing confusion" (W. James, 1890, p. 488), as though experience begins suddenly at the moment of birth.

In contrast to this conventional scenario, more recent empirical studies suggest a different view, that the intrauterine world is complex, changeable, and replete with stimulation. For instance, Bench (1968) and others (see Fifer & Moon, 1988, for a review) have made intrauterine acoustic recordings with small microphones in humans and animals and have reported sounds of varying pitch, at levels exceeding 80 dB. Amniotic fluid, which bathes fetal olfactory and gustatory receptors (Bradley & Mistretta, 1975), is a chemosensory melange of nutritional and immunological factors (Abbas & Tovey, 1960; Lev & Orlic, 1972), fetal waste products (Jeffcoate & Scott, 1959), and other substances (Mellor & Slater, 1971; Tam & Chan, 1977; Wirschafter & Williams, 1957; for a review, see Smotherman & Robinson, 1988b). The intrauterine thermal environ-

ment varies as well. In sheep the fetal thermal environment follows the maternal circadian cycle of body temperature variation (Dawes, 1973).

There is little doubt that the physical environment provides many forms of stimulation to developing offspring prior to birth. To what extent can the fetus experience events of prenatal stimulation? Fetal sensory systems are morphologically (and functionally) immature (Bradley & Mistretta, 1975) and thus may be insensitive to the available levels of stimulation or may simply be inoperative.

Pioneers of behavioral embryology have provided some clear examples of sensory-evoked reflex action prior to birth or hatching (Coghill, 1929; Kuo, 1932; Preyer, 1937; for an exhaustive review of earlier work, see Carmichael, 1970). Although the inaccessibility of the fetus within the womb has impeded knowledge of mammalian sensory competence prior to birth, it is now recognized that fetuses in a variety of species are able to transduce sensory information (rat, Narayanan, Fox, & Hamburger, 1971, and Smotherman & Robinson, 1988a; guinea pig, Carmichael & Smith, 1939, and Vince, 1979; lamb, Vince, Billing, Baldwin, Toner, & Weller, 1985; cat, Windle & Fish, 1932; human, Decasper & Fifer, 1980, and Hooker, 1952).

The clearest and strongest support for prenatal sensory competence comes from studies in which intact fetuses have been carefully stimulated and found to show reliable autonomic and behavioral responses. Narayanan et al. (1971) studied tactile sensitivity in externalized fetal rats by gently probing discrete body areas. Beginning on Embryonic Day 16 (E16) of a 22-day gestation period, rats displayed movement responses to punctate stimulation of the snout, but also responded to caudal stimulation sites later in gestation. Smotherman and Robinson (1988a) investigated chemosensitivity in prenatal rats by presenting milk, lemon, and other chemical cues to pups through an intraoral cannula. Beginning around E17, pups responded to stimulation with changes in movement. It has been found that intraoral infusion of a dilute lemon solution evokes robust heart rate deceleratory responses in fetal rats (Ronca & Alberts, 1990; Smotherman, Robinson, Ronca, Alberts, & Hepper, 1991). Decasper and Fifer (1980) and Pederson and Blass (1982)

---

April E. Ronca, Christopher A. Lamkin, and Jeffrey R. Alberts, Department of Psychology, Indiana University.

This research was supported by National Institute of Mental Health Grant MH 46485 to Jeffrey R. Alberts and April E. Ronca and Grant MH 28355 to Jeffrey R. Alberts. Portions of this work were presented at the 1991 annual meetings of the American Psychological Association and the International Society for Developmental Psychobiology.

We gratefully acknowledge the comments of William Timberlake during the inception of this work and Mark Blumberg for suggestions about data presentation. We thank Kelley Knapp, Anthony Michael, and Patrick Neer for assistance with data analysis. Illustrations were created by Deborah Hamilton.

Correspondence concerning this article should be addressed to April E. Ronca, Department of Psychology, Indiana University, Bloomington, Indiana 47405.

showed that fetuses can detect certain cues that normally impinge on it within in the uterine environment. Thus, prenatal organisms can detect and respond to sensory cues. However, the sensory aspects of the uterine environment are poorly understood.

The mother's behavior and physiology are almost certainly the major sources of fetal sensory experience. Maternal contributions to the intrauterine acoustic environment have been demonstrated in such species as humans and sheep, in which auditory function has prenatal onset. Decasper and Fifer (1980) demonstrated newborns' recognition of specific acoustic events, based on prenatal auditory experience. Other features of the intrauterine acoustic environment that may hold salience for the fetus include the maternal heartbeat, pulse, and borborygmi, that is, the audible by-products of digestion (Fifer & Moon, 1988; D. Walker, Grimwade, & Wood, 1971). Tactile, kinesthetic, and vestibular concomitants of maternal speech, movement, and physiology may provide especially potent sources of prenatal sensory stimulation. Prenatal transduction of these and other forms of sensory stimuli may intensify as birth approaches (Bradley & Mistretta, 1975).

Early in gestation, the fetus is surrounded by a fluid-filled amniotic sac that can buffer the impact of stimulation. Near term, there is a dramatic decline in amniotic fluid volume in relation to increases in fetal body size, and offspring are

increasingly susceptible to extrinsic stimuli as the amniotic cushion shrinks. Locomotion and other activities of the mother may pitch, turn, accelerate, and expose fetuses to mechanical pressures. During parturition, uterine contractions create intense mechanical pressures, squeezing, and moving the fetus along the birth canal. On delivery the newborn is exposed to a range of novel sensory experiences as the mother licks, handles, and carries offspring.

Tactile, vestibular, and thermal sensitivities may play special roles during perinatal life. These modalities are among the first to emerge in vertebrate development (Alberts, 1984; Gottlieb, 1971). Even in altricial species, such as the Norway rat, these early developing systems begin to operate prenatally and thus provide the earliest forms of sensory experience.

To identify specific tactile and vestibular stimuli to which the fetus and newborn are normally exposed, we have begun to examine in the rat maternal contributions to the perinatal sensory environment. In contrast to previous studies of rodent maternal behavior (Beach & Jaynes, 1956; Rosenblatt & Lehrman, 1963; Weisner & Sheard, 1933), our observations were made from the offspring's point of view. In particular, we quantified maternal stimulation of fetal and neonatal rats by analyzing the dam's activities during gestation, labor, and delivery of pups. Thus, the goal of these studies is to describe qualitatively and quantitatively mater-

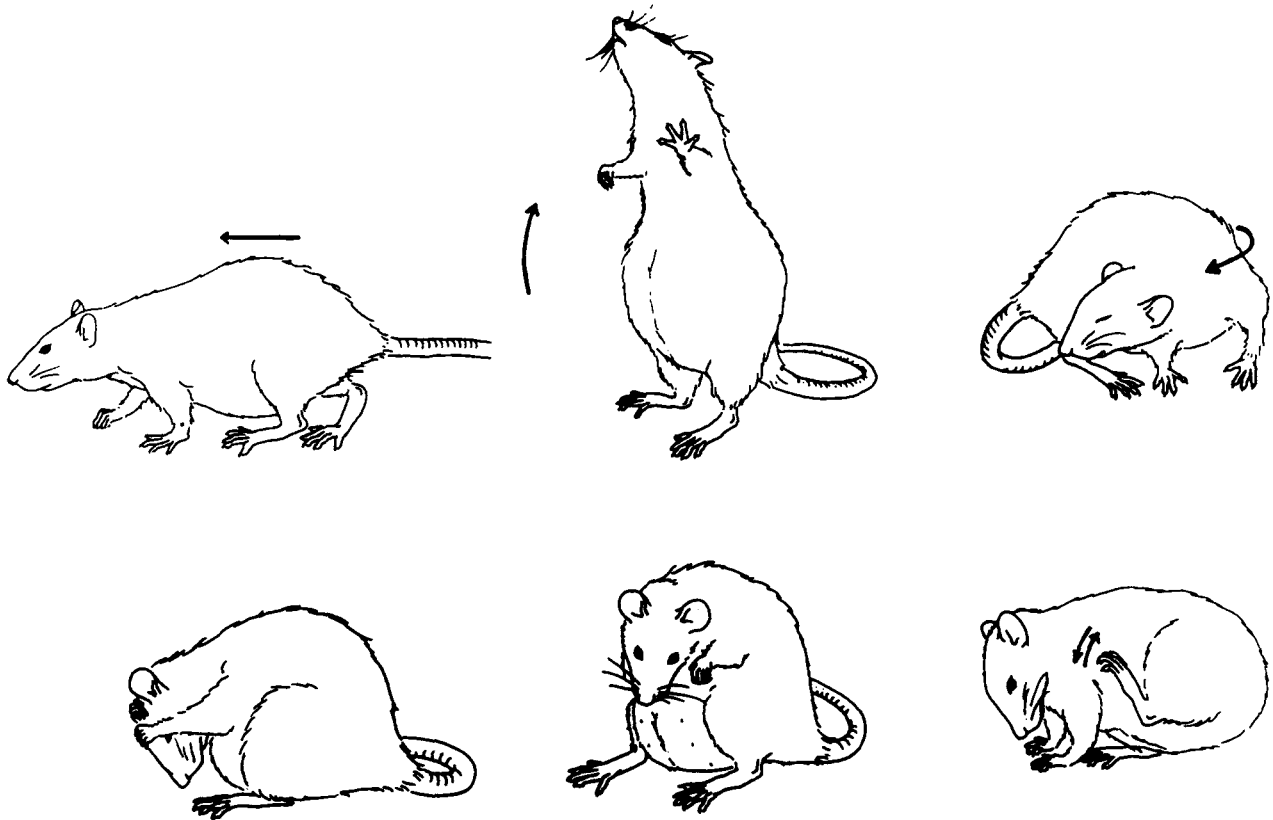


Figure 1. Behavioral activities of females that stimulate offspring in utero: Locomotion (top left), rearing (top center), stirring (top right), head and body grooming (bottom left), abdominal grooming (bottom center), and hindlimb scratching (bottom right).

Table 1  
Criteria Used to Quantify Behavior of Pregnant and Nonpregnant Rats

Category	Description
General activity	The subject explores, feeds, drinks, grooms, or nest builds. The amount of time that each subject was quiescent (sleeping or resting) was subtracted from the total observation time.
Locomotion	The subject crosses a line which bisects the habitat into two equal squares.
Rearing	The subject elevates both forequarters and forepaw from the floor, then returns to the prone position.
Stirring	The resting subject arises, rapidly circumrotates the nest area, and then resumes the resting posture.
Head and body grooming	The subject adopts an upright posture and grooms the forepaws, head, and dorsum.
Abdominal grooming	The subject grooms the ventrum within the area bounded by the ribcage and the anogenital area.
Hindlimb scratch	The subject rapidly scratches the lateral aspect of the abdomen with a single hindpaw.

nal activities that can contribute to the stimulating conditions of the fetal environment.

Experiment 1: Stimulation During Gestation

In the first experiment, we observed and quantified eight categories of maternal behavior that potentially provide to fetuses different forms of tactile and vestibular stimulation. To determine the relative frequencies of such provocative maternal activities, identical measurements were made with late-pregnant and nonpregnant female rats. As the dam engages in exploration, nest-building, grooming, and consummatory behaviors, it locomotes and rears on its hindlimbs (Figure 1, upper left). During its ambulatory activities, fetuses move through a variety of vectors. With the dam's forward locomotion, fetuses are exposed to vestibular cues in the form of linear acceleration. During rearing, as the dam raises its body, and as it returns to all fours (Figure 1, upper center), it produces angular accelerations of pups in utero. The dam's resting or behavioral quiescence is frequently interrupted by brief rotations, followed by resumption of the resting posture (Figure 1, upper right); these episodes of stirring may also provide vestibular stimulation to offspring.

Fetuses may receive stimulation during the dam's self-grooming. When grooming the head and body, a female balances on its hindlimbs (Barnett, 1963; Figure 1, lower left) and may remain vertically oriented for nearly a minute, which exposes fetuses to protracted episodes of vestibular stimulation. A pregnant female spends considerable amounts of time licking its ventrum, particularly along the nipple lines (Roth & Rosenblatt, 1967; Figure 1, lower center). During such self-licking, the dam exerts mechanical pressure on its abdomen and the underlying fetuses in utero. During hindlimb scratching, a rat focuses on the fur overlying the abdominal region (Barnett, 1963; Figure 1, lower right). The rapid vibrations of the dam's body associated

with hindlimb scratching may produce both tactile stimulation and vestibular oscillations of fetuses.

We observed pregnant dams during the final week of a 22-day gestation period. This interval coincides with two notable events likely to influence sensory experience in the developing rat: (a) the emergence of tactile, vestibular, and (possibly) thermal function (Alberts, 1984; Kirby, 1979; Lane, 1917; Narayanan et al., 1971) and (b) a period of decline in amniotic-fluid volume (60% from E15 to E22)

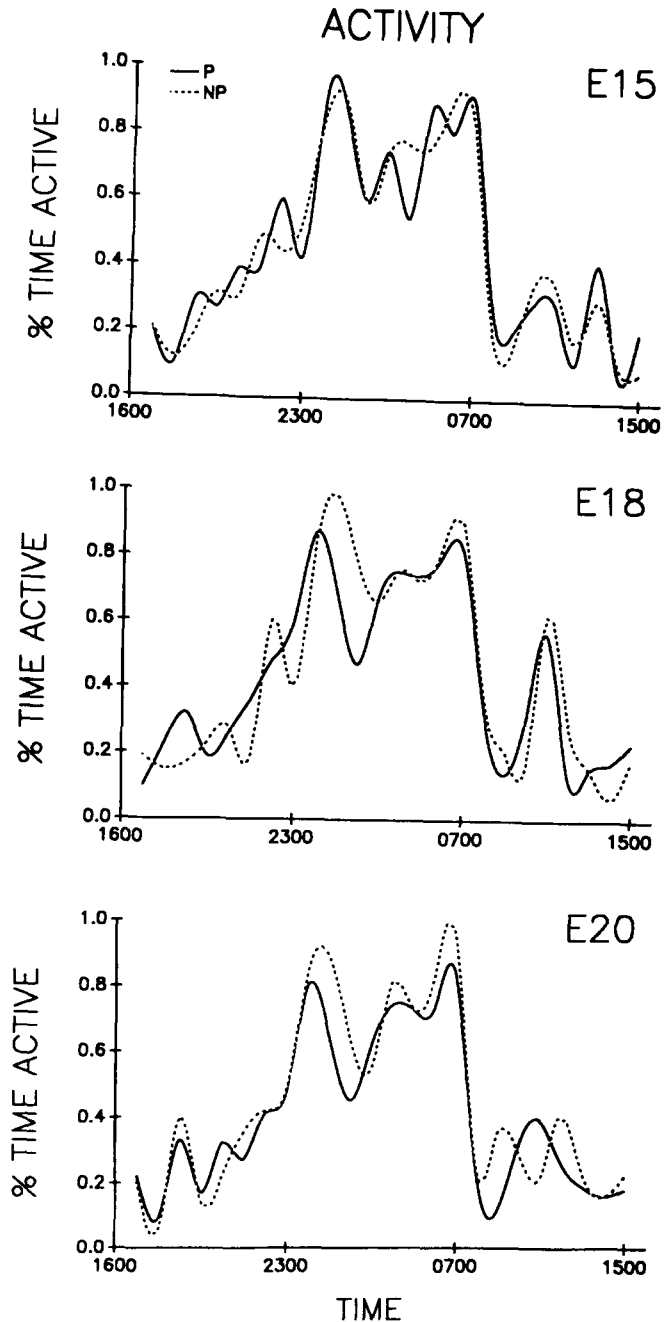
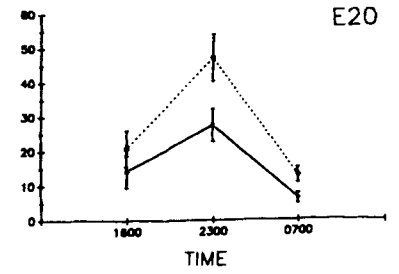
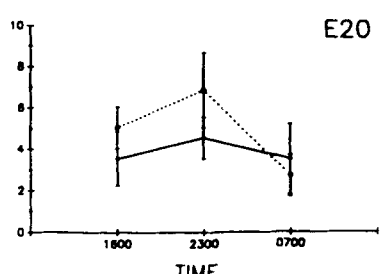
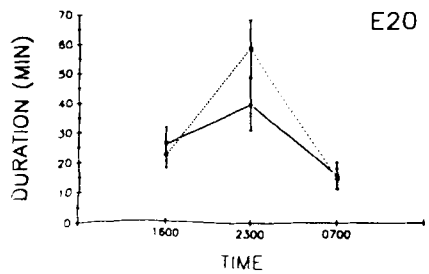
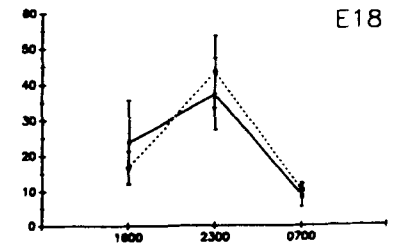
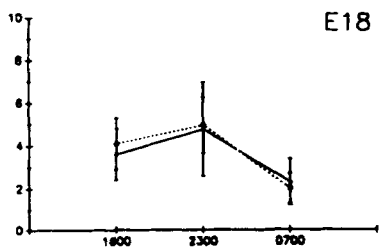
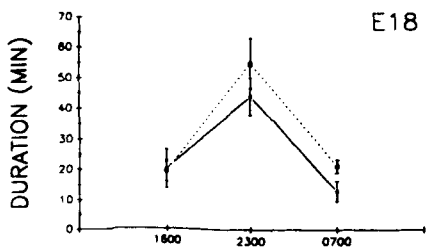
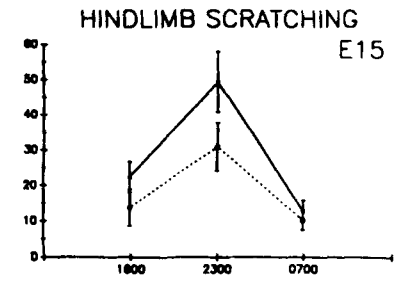
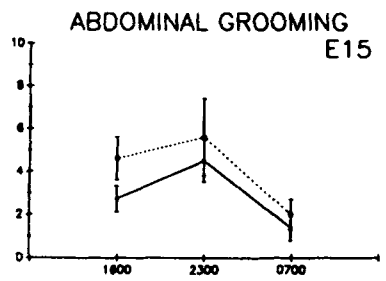
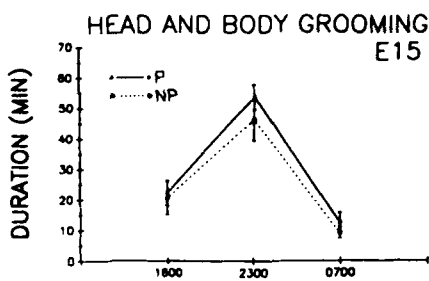
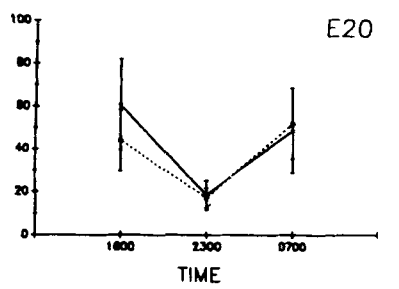
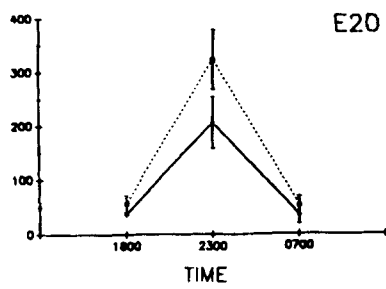
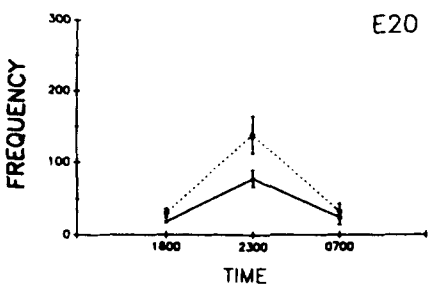
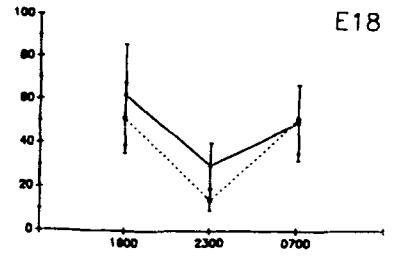
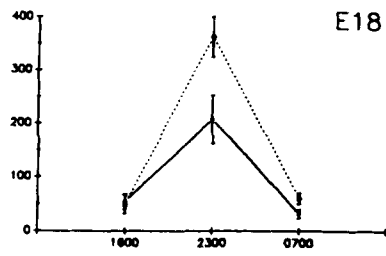
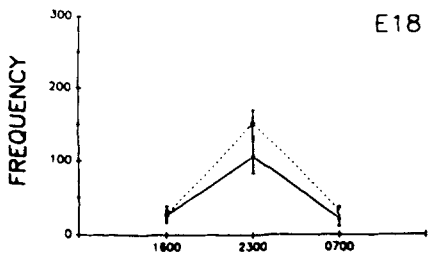
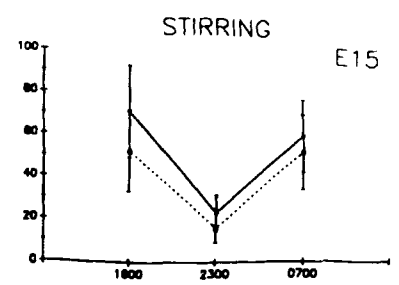
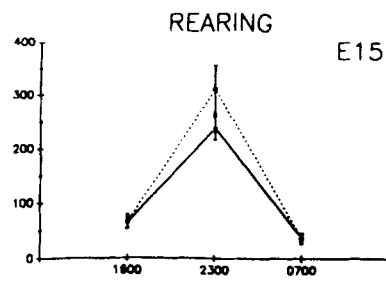
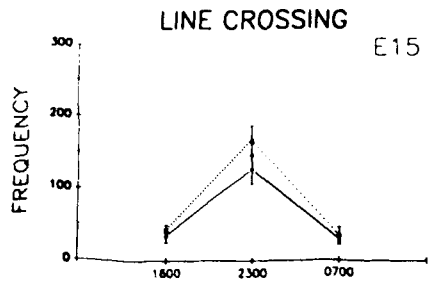


Figure 2. Activity levels during 24-hr observation periods for pregnant (P) and nonpregnant (NP) rats on Embryonic Days (E) 15, 18, and 20. (n = 8 per group.)



and rapid fetal growth (95% increase in body weight; Tam & Chan, 1977).

A key assumption underlying our hypothesis that maternal activities stimulate the fetus is that the gestating rat is behaviorally active. A matter of concern then were reports that pregnant rats become increasingly lethargic and inactive as birth approaches (Rosenblatt & Lehrman, 1963; Weisner & Sheard, 1933). Such suggestions, if accurate, may justify a reconsideration of our ideas about the importance of maternal stimulation prior to birth. Nonpregnant rats were observed in tandem with late-pregnant subjects. Activity profiles were derived from time-lapse videorecords.

### Method

**Subjects.** Sixteen virgin female Sprague-Dawley rats (*Rattus norvegicus*; 70–80 days), bred in the Indiana University colony, were used in this experiment. Females were time-mated to Sprague-Dawley males (day of conception = E0; day of birth = E22). Females were housed in standard polyurethane maternity tubs in a temperature- and humidity-controlled colony room (16:8-hr light–dark cycle). Purina Rat Chow and water were available ad lib.

**Apparatus.** Testing was conducted in an observation room maintained under similar conditions. Two 10-gal. (7.6-L) glass aquaria (50 × 25 × 30 cm) lined with wood chips served as test chambers. A mirror was angled at the rear of the habitat to maximize visibility of the subject. Visual contact between subjects was prevented by placing a shield between adjacent aquaria. A 25-W red lamp was continuously illuminated approximately 12 cm above each chamber to permit low-light video surveillance during the 8-hr dark phase of the daily cycle.

A video camera (Panasonic WV-1500; Cosmicar 25-mm 1:1.4 lens) was positioned approximately 1 m from each test chamber. The output of each camera was fed through a screen splitter (Pelco VSS100DT) to a time-lapse videocassette recorder (Gyr TL1400) set to a record:playback ratio of 12:1. This configuration permitted simultaneous recording of a pair of experimental and control subjects on a single video screen.

**Procedure.** We selected from our breeding population 8 females that conceived and 8 females that were mated but not impregnated. On E14, a pregnant female and nonpregnant control animal were yoked and adapted to adjacent test habitats. On E15, E18, and E20, the behavior of pregnant females and yoked control animals was recorded for 24 hr with time-lapse videography. Females resided in the test habitat for the duration of the experiment.

**Data analysis.** Each videorecord contained 24 hr of continuous recording and was viewed in 2 hr of playback time (12:1 record:playback). Trained observers used a microprocessor to encode the frequencies and durations of a variety of behaviors, which were computed for successive 1-hr segments.

One behavioral category was resting or sleeping. All other time comprised the parameter termed *general activity*, which was the total time that the animal was not categorized as quiescent. Nonquiescent categories included stirring, which often punctuated bouts of rest as the rat roused and turned in small circles before resettling. Locomotion was quantified with a measure of linear movement. Rearing to a vertical orientation was counted.

Head and body grooming was measured separately from abdominal grooming and from hindlimb scratching, during which the abdomen is stroked by rapid, unilateral movements of the hindpaw. Table 1 describes the operational definitions used to quantify each behavioral parameter. Interobserver reliability correlation among the persons who analyzed the videorecords was calculated at .97.

### Results and Discussion

Overall activity was equivalent between pregnant and nonpregnant rats. Both pregnant and nonpregnant females were generally active for an average of 9–12 hr during each 24-hr observation period (pregnant,  $11.3 \pm 1.1$  hr; nonpregnant,  $10.8 \pm 0.7$  hr). In addition to the behavioral categories that were recorded, females spent their time exploring, nest building, grooming, and feeding and drinking.

Figure 2 illustrates the overall activity of pregnant and nonpregnant females across the circadian cycle on the 3 observation days. A repeated measures analysis of variance (Group × Day × Hour) revealed no differences in overall activity either between groups or across days ( $F_s < 1$ ). A main effect of hour was obtained from this analysis,  $F(23, 1058) = 72.30, p < .0001$ , which reflects the high rate of activity during the dark phase of the cycle for both subject groups (Newman-Keuls test,  $p < .01$ ). Activity levels during the two light phases of the daily cycle did not differ from one another. Thus, our findings indicate that the general activity level of pregnant dams is more similar to that of nonpregnant rats than previously thought.

Figure 3 provides a visual summary of the activity profiles of pregnant and nonpregnant females on each observation day. For purposes of analysis, data for each category were parsed into three 8-hr intervals (beginning at 1600, 2300 and 0700 hr) corresponding to cycle phase. A repeated measures analysis of variance (Group × Day × Cycle Phase) was run for each behavior. In each case, the activities were observed in pregnant dams at similar or slightly reduced frequencies of occurrence, as compared with nonpregnant females.

Pregnant females ambulated somewhat less on each observation day than did nonpregnant females (Figure 3, upper left). Analysis of variance revealed a main effect of group,  $F(1, 14) = 5.18, p < .04$ , and a Group × Cycle Phase interaction,  $F(2, 28) = 10.03, p < .001$ . A Newman-Keuls post-hoc analysis revealed that line crossing by pregnant dams was reduced during the dark phase of the cycle ( $p < .01$ ). Compared with nonpregnant females, pregnant dams reared less frequently across days during the dark phase of the cycle (Figure 3, upper middle): group,  $F(1, 14) = 6.45, p < .05$ ; Group × Cycle Phase,  $F(2, 28) = 7.56, p < .01$  (Newman-Keuls test,  $p < .01$ ). Stirring was observed at similar frequencies in both subject groups (Figure 3, upper right; group,  $F < 1$ ), as was head and body grooming (Figure 3, lower left; group,  $F < 1$ ). Episodes of abdominal grooming by pregnant females also occurred at

Figure 3. Frequency or duration of behaviors displayed by pregnant (P) and nonpregnant (NP) rats during each 8-hr phase of the circadian cycle on Embryonic Days (E) 15, 18, and 20. (Line crossing is the measure of locomotion.)

frequencies comparable with those of nonpregnant females (Figure 3, lower middle; group,  $F < 1$ ). Hindlimb scratching was displayed at comparable rates by both subject groups on E15 and E18 but declined in the pregnant group on E20 (Figure 3, lower right): group,  $F < 1$ ; Group  $\times$  Day,  $F(2, 28) = 6.01$ ,  $p < .01$  (Newman-Keuls test,  $p < .01$ ).

The repeated measures analyses of variance (Group  $\times$  Day  $\times$  Cycle Phase) just described also revealed a significant effect of cycle phase. For both subject groups all activities (with the exception of stirring) were observed far more often during the dark phase of the daily cycle, as compared with each light phase: line crossing,  $F(2, 28) = 22.94$ ,  $p < .001$ ; rearing,  $F(2, 28) = 141.73$ ,  $p < .001$ ; head, forelimb, and back grooming,  $F(2, 28) = 80.00$ ,  $p < .001$ ; hindlimb scratching,  $F(2, 28) = 99.00$ ,  $p < .001$ ; abdominal grooming,  $F(2, 28) = 18.41$ ,  $p < .001$ . Stirring, associated with periods of rest, occurred almost exclusively during the light phase of the cycle,  $F(2, 28) = 16.10$ ,  $p < .001$ . (In each case Newman-Keuls tests were significant,  $p < .01$ ).

In Weisner and Sheard's (1933) classic monograph, they reported that parturition in the rat is preceded by a 1- to 3-day interval during which females "appear to be sluggish and show a reduction in spontaneous activity" (p. 21). Similarly, Rosenblatt and Lehrman (1963) described the rat dam's "growing lethargy" and "reduced responsiveness to the cage surroundings" (p. 15) that begins around E19. In contrast, by our criteria, dams were as active on E20 as they were on E15 and E18 (see Figure 2).

The discrepancy between previous characterizations of relative inactivity during late pregnancy and our findings of equivalent levels of general activity help to focus attention on the methodological differences that might contribute to different results. Earlier investigations relied on direct, time-sampled observations of dams' behavior during the light phase of the daily cycle. In contrast, time-lapse video technology and the use of computer-assisted behavioral encoding eliminated observer presence and enabled us to monitor the animals continuously.

Although previous researchers have provided general descriptions of the dams' behaviors, they did not specify the particular maternal activities that declined during late gestation. In our study pregnant dams ambulated and reared less frequently than nonpregnant controls. Hindlimb scratching was reduced on the final observation day. Observations of dams late on E21 and prior to delivery (described in Experiment 2) revealed a more general suppression of activity as parturition approached.

Because the overall measure of general activity was equivalent between the groups on each day, it was apparent that pregnant rats had made compensatory increases in activities that were not included in our eight behavioral categories. This, in addition to specifying the kinds of maternal activities that might stimulate fetuses, led to further examination of the data.

Additional analyses of the videorecords showed that pregnant females spent more time engaged in nest-building activities, such as digging within the nest area and manipulating woodchips. With the exception of hindlimb scratching, grooming durations were similar in pregnant

and nonpregnant rats (Figure 3, lower panel). Roth and Rosenblatt (1967) found that the overall amount of time that dams engage in grooming does not change during late gestation, however there are intriguing alterations in the pattern of self-licking displayed by pregnant females. Over the final week of pregnancy, licking of the pelvic region, nipple lines, and anogenital area increases, whereas licking of other body areas (head and forepaws and back and sides) declines. In this study we observed no such increase in dams' self-licking of the abdomen over gestational days. However, we measured grooming of the entire abdominal area, which may have obscured specific increases in nipple line grooming. Because the rat's nipple lines overlie the uteri, Roth and Rosenblatt's (1967) observations provide additional support for the view that the dam's self-grooming may stimulate the fetuses throughout late gestation. We are currently testing this hypothesis by directly measuring intrauterine pressure during nipple-line grooming of late gestation dams.

Rearing was displayed frequently by pregnant dams throughout the final third of gestation. To estimate the in utero angular acceleration delivered to fetuses during the dam's rearing behavior, we quantified the body rotation of pregnant females during rearing. We selected at least five videographic samples of rearing on each observation day. Samples were restricted to those instances of rearing in which the rat could be observed in a lateral view. A single locus on the midpoint of the dam's abdomen was used as an estimate of central fetal positions. The trajectory of this fetal locus was tracked with frame-by-frame analysis during episodes of maternal rearing. A rearing episode was considered initiated as the paws left the ground. Time was read from a counter on the videoscreen, and distance traveled was computed from the point at which all four paws were in contact with the floor to that of maximal elevation of the forebody. The rat's hindpaws were used as a reference. This analysis revealed that during rearing, fetuses in utero travel an average distance of  $63^\circ (\pm 3^\circ)$  or  $1.10 \text{ rad} (\pm 0.05 \text{ rad})$ , at an angular velocity equal to  $0.56 \text{ rad/s}$ . Dams retained an upright posture for durations of 1–18 s. These values provide a general estimate of fetal excursions during rearing episodes; the precise amount of stimulation may vary with uterine position. Fetuses residing at the ovarian end of each uterine horn would travel the greatest distance and at the greatest velocity, whereas fetuses at progressively more caudal sites would make smaller and slower excursions.

Extrauterine stimuli may impinge on fetuses differently at different points during gestation. Amniotic-fluid volume decreases during late gestation, whereas the fetus itself increases in size (Smotherman & Robinson, 1988b). The net result may be that the fetus is less buffered late in gestation. Thus, the behavior of parturient dams may provide the most direct and intense stimulation to fetuses during late gestation. We suggest that the kinds of maternal activities described in this study, namely, locomotion, rearing, stirring, face and head grooming, abdominal grooming, and hindlimb scratching, impose on fetuses specific forms of stimulation. On the final observation

day, when the supply of amniotic fluid is nearly exhausted, fetuses receive an average of 150 linear accelerations produced by the dam's locomotor activities, 600 angular accelerations associated with rearing and the upright posture adopted by dams during grooming of the head and body, approximately 10 min of mechanical pressure during abdominal grooming, and 125 episodes of vibration produced by hindlimb scratching. To the extent that maternal activities transmit to fetuses sensory experiences of acceleration, pressure, and vibration, our results indicate that the uterine environment is highly stimulating to offspring during late gestation.

### Experiment 2: Fetal Stimulation During the Hours of Labor

Fetuses are compressed and pitched during labor as the contracting uterus squeezes and shifts its contents. A few hours prior to birth in the rat, infrequent, low-amplitude uterine contractions become regular and increase in intensity, signaling the onset of labor (Fuchs, 1969). Direct measurements of intrauterine pressure suggest that near parturition the rat fetus is exposed to contractions at intensities that approach 20 mm/Hg (Fuchs, 1969). Accelerative forces on the fetus provide an additional sensory component to uterine contractions.

Dollinger, Holloway, and Denenberg (1980) described several behaviorally distinct types of uterine contractions. During a lordosis contraction the dam lies on its ventrum and elongates its body, often arching its back and lifting its outstretched hindlimbs off the ground (Figure 4, top). These contractions predominate prior to the birth of the first pup and are thought to transport the fetal rat into the lower birth canal (Dollinger et al., 1980; Rosenblatt & Lehrman, 1963). In addition to the contraction component, in utero fetuses are likely compressed under the weight of the dam's body during a lordosis contraction. Vertical contractions, observed in close proximity to pup births, are observed as a series of rapid, bilateral abdominal lifts (Figure 4, center). A third form of uterine activity observed during labor appears as a wave of peristalsis along the lateral aspect of the abdomen (Fuchs, 1969; Rosenblatt & Lehrman, 1963). Peristaltic waves are observed as quick rotary movements along the abdomen (Figure 4, bottom).

In Experiment 2, we measured in parturient females the frequency and duration of each contraction type in order to describe quantitative and temporal aspects of mechanical stimulation of the fetus during labor.

### Method

**Subjects.** Eight time-mated pregnant female rats, as described in Experiment 1, were used in this experiment.

**Apparatus.** Observations were made using time-lapse videography, as described in Experiment 1. Each subject was taped with a continuous time-date display on a single video screen at a 12:1 (record:playback) ratio.

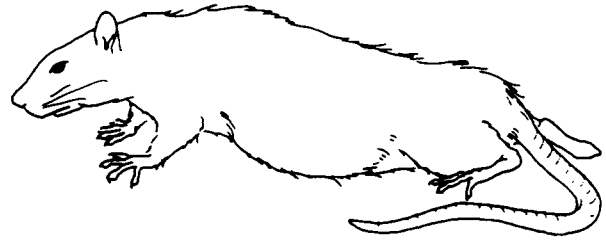


Figure 4. Behavioral expression of labor contractions in parturient rats: lordosis contraction (top), vertical contraction (center), and peristaltic waves (bottom).

**Procedure.** On E20, pregnant females were adapted to the test chamber. Beginning on E21, the behavior of females was recorded continuously until birth. During the course of the experiment (2–4 days), an experimenter quietly entered the taping room each day to check food and water availability. This evaluation was always made prior to the onset of labor.

**Data analysis.** Behavioral data were analyzed from videotape for the 6-hr period before delivery of the first pup. Data were encoded by trained observers into a microcomputer. This permitted us to create a complete chronological record of labor, in which the occurrence, onset, and offset of each contraction type was measured. Contraction types were defined as follows: (a) lordosis contraction, body extension along the floor, often with arching of the back and elevation of anterior and extremities (Figure 4, top; also see Dollinger et al., 1980); (b) vertical contraction, rapid bilateral lifts of the abdomen (Figure 4, center; also see Dollinger et al., 1980); and (c) peristaltic waves, quick rotary movements along the lateral aspect of the abdomen (indicated by the arrow in Figure 4, bottom; also see Rosenblatt & Lehrman, 1963).

### Results and Discussion

Parturition occurred in all 8 dams within 12 hours of E22 (E21, 12%; E22, 63%; E23, 25%). These results closely match the temporal distribution of parturition reported in rats by Dollinger et al. (1980).

*Uterine contractions prior to the delivery of pups.* During the 6 hr prior to the birth of the first pup, we observed an average of 84.0 ( $\pm 8.3$ ) lordosis contractions, 16.1 ( $\pm 7.8$ ) vertical contractions, and 44.8 ( $\pm 7.9$ ) episodes of peristalsis (Figure 5, top). Lordosis contractions occurred significantly more often than other contraction types, and peristalsis more often than vertical contractions,  $F(2, 21) = 20.80$ ,  $p < .001$  (Newman-Keuls test,  $p < .01$ ). Contraction types also differed in duration, averaging between 7 and 31 s in duration (Figure 5, bottom). Lordosis contractions and episodes of peristalsis were significantly longer in duration than vertical contractions,  $F(2, 21) = 44.50$ ,  $p < .001$  (Newman-Keuls test,  $p < .01$ ).

Each form of uterine activity followed a distinct time course during labor. Peristaltic activity was present during the first few minutes of the 6-hr observation interval, beginning an average of 5.8 ( $\pm 0.2$ ) hr before the delivery of the first pup. The finding that peristaltic waves were present so early in the observation interval suggests that they may have begun more than 6 hr prior to birth. Unfortunately, we are unable to specify from our records the precise onset of contractions. Lordosis contractions

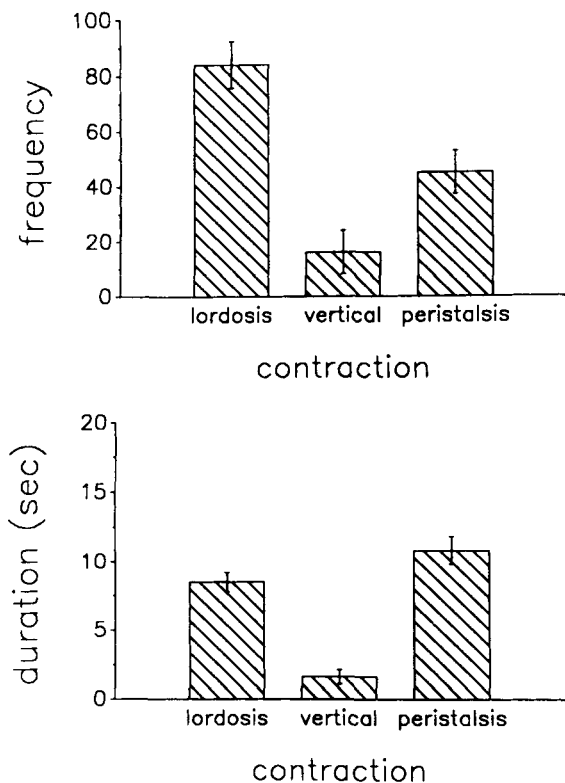


Figure 5. Frequency and duration of labor contractions in parturient dams during the 6-hr period prior to pup delivery.

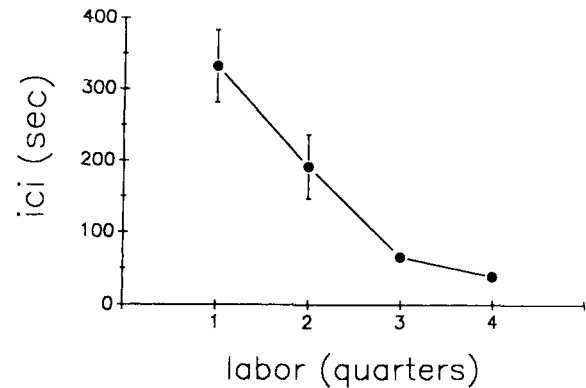


Figure 6. Intercontraction intervals (ICI) across quarters of pre-birth labor in parturient dams.

emerged next, approximately 3.9 ( $\pm 0.8$ ) hr prior to the onset of delivery. Finally, vertical contractions appeared last in the sequence, appearing about 52.5 ( $\pm 55.4$ ) min prior to the first birth.

Although each type of contraction persisted throughout prebirth labor, most of the active contractions were concentrated within the hour before actual parturition: 80% of lordosis contractions and 100% of vertical contractions occurred within the final hour before delivery, whereas peristaltic contractions showed a relatively stable rate of occurrence.

An analysis of intercontraction intervals was used to determine the exact time course of labor-related stimulation. Because the actual duration of labor differed for each subject, we partitioned into four segments (for each dam) the interval bounded by the first and the last uterine contractions prior to delivery. Figure 6 illustrates the rate of pooled uterine activity, as measured by intercontraction intervals, over the course of prebirth labor.

A repeated measures analysis of variance revealed a significant decline in intercontraction intervals across pre-birth labor,  $F(3, 21) = 15.90$ ,  $p < .001$ . A Newman-Keuls post hoc analysis indicated that each interval differed from every other ( $p < .01$ ). The overall increase in contraction rate can be attributed primarily to cumulative effects of different forms of uterine activity, rather than to specific patterns of activity associated with each contraction type. Among individual categories of activity, only lordosis contractions contributed to the overall decline in intercontraction intervals. In contrast, peristaltic waves were observed at a low, constant rate throughout the 6-hr observation period. Vertical contractions, which during prebirth labor occurred exclusively in the hour prior to delivery, did not show any systematic change over time.

Contraction duration also increased over the prebirth interval. Lordosis contractions increased from 8.3 s ( $\pm 1.4$  s) in the first quarter of labor to 13.4 s ( $\pm 4.8$  s) in the final quarter. This increase was significant,  $F(3, 21) = 4.24$ ,  $p < .02$ . Comparison of contraction duration across the quarters of labor for other types was not significant ( $F < 1$ ).

*Uterine contractions during pup delivery.* Contractions continued during pup delivery. We observed an average of 27 ( $\pm 22$ ) lordosis contractions, 13 ( $\pm 7$ ) vertical contractions, and 3 ( $\pm 4$ ) episodes of peristalsis (only one half of the dams continued to display peristaltic activity after the birth of the first pup). We otherwise observed no systematic trend in the frequency or duration of individual contraction types. Contractions occurred at a steady rate across pup births (approximately 3 contractions per birth), first vs. second half of pup births,  $F(1, 7) = 2.02$ , *ns*. Contraction duration was 7 s ( $\pm 1.4$  s) for lordosis contractions, 2.6 s ( $\pm 1.7$  s) for vertical contractions, 6 s ( $\pm 8.1$  s) for peristalsis.

Our results indicate that in the rat, as in other species, the process of labor is characterized by frequent uterine contractions. Lordosis contractions, which have been suggested to play a role in the transport of the rat fetus from the uterus to the birth canal (Rosenblatt & Lehrman, 1963) increased in frequency and duration during prebirth labor. In conjunction with other contraction types, uterine activity occurred at an increasingly rapid rate as the birth of the first pup drew near. Uterine activity reached maximal frequency of about 1 contraction per 40 s before the onset of delivery, when all pups of a litter were still in utero. The available data suggest that labor contractions impinge directly on the conceptus (Fuchs, 1969) and thereby expose the fetus to repeated episodes of mechanical stimulation.

We are not able to determine at this time whether differential sensations are associated with each contraction type. These observations do suggest, however, that during prebirth labor there is significant mechanical stimulation of pups. As compared with tactile and vestibular cues, which may be derived from other maternal activities during gestation (e.g., Experiment 1), the frequency and periodicity of uterine contractions associated with labor undoubtedly provide a unique pattern of sensory input to prenatal offspring. Mechanical pressures to which fetuses are exposed during labor are believed to produce a notable elevation of plasma catecholamines, which possibly assist the newborns' adaptation to the postnatal environment (Lagercrantz & Slotkin, 1986). Although an unexplored area of inquiry, we expect that delivery-associated stimulations may exert specific effects on sensory processes, as well.

### Experiment 3: Maternal Stimulation of the Newborn Rat During Delivery

The rat dam's behavior is an important part of the birth process (Rosenblatt & Lehrman, 1963; Weisner & Sheard, 1933). When a pup begins to emerge from the birth canal, the mother typically adopts a head-between-heels posture, which facilitates delivery by enabling the dam to grasp the newborn with its teeth and extract it from the vagina. The dam licks and handles the pup (Figure 7, top), removing and consuming the embryonic membranes that surround it, and thereby produces intense cutaneous stimulation and exposes pups to cooler temperatures associated with evaporation. During the interval between births, which ranges from 1 to

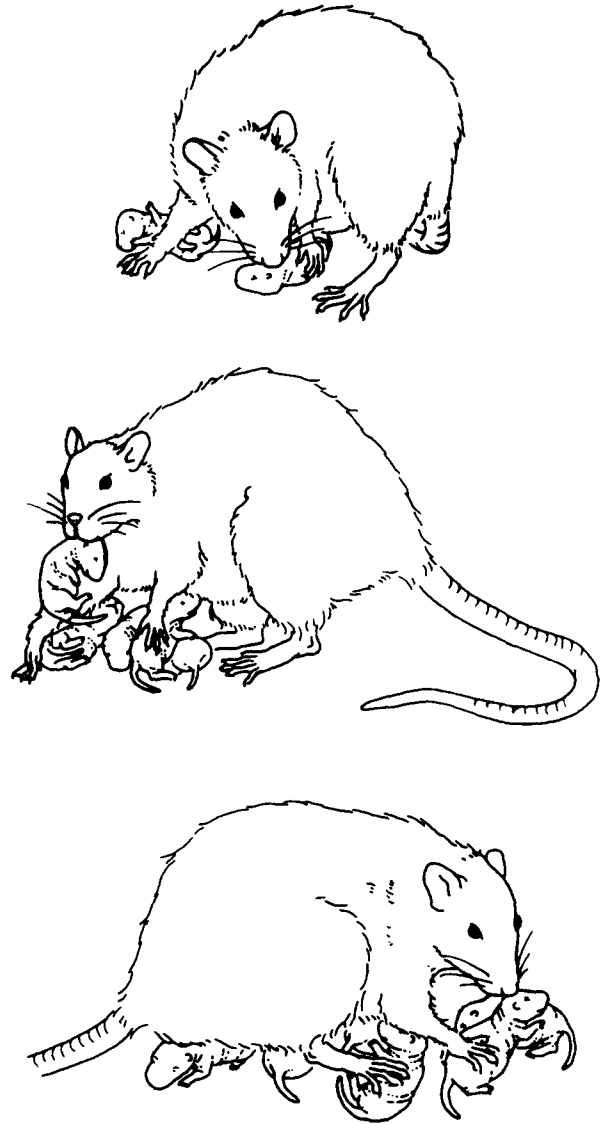


Figure 7. Behaviors of parturient dams that stimulate newborn pups: licking and handling of pups (top), pup retrieval (center), and vicarious stimulation (bottom).

29 min (Blandau & Soderwall, 1941; Dollinger et. al, 1980; Fuchs, 1969), previous newborns may become the focus of additional licking and handling, or they may be retrieved from a remote birthsite into the nest area (Figure 7, center). Alternatively, while the dam engages in placentophagia, it may ignore pups and leave them exposed to room temperature, which constitutes a drop from 37.5 °C (intrauterine temperature) to about 25 °C. Pups may also become the recipients of vicarious stimulation generated by the dam's behavior. Thus, a newborn may be suspended by the umbilical cord while the dam consumes its placenta or compressed under the dam's body weight as the dam undergoes labor contractions or attends to siblings (Ronca & Alberts, unpublished observations; Figure 7, bottom). As parturition draws to a close, the dam assembles the pups within the nest and huddles over them in the nursing posture. Thus,

throughout parturition the dam's behavior provides to offspring novel tactile, vestibular, and thermal stimulation. In Experiment 3, we sought to quantify stimuli associated with birth.

### Method

**Subjects.** The parturient (E21–23) dams observed in Experiment 2 also served as subjects in this experiment.

**Apparatus.** Deliveries were videorecorded with a color camera (Sony DXC-101) with a manual zoom lens (1:12/12.5–75 mm). The camera lens was positioned through an opening in a black cloth curtain that served to visually isolate the observer from the subjects. The curtain was used to minimize the possibility that observers' movements would interfere with on-going behavior of the dam.

**Procedure.** After the onset of labor, pregnant females were monitored every few minutes on a closed circuit television located at a site remote from the test habitat. When contractions began to occur in close succession (a sign of impending delivery), the experimenter quietly entered the test room and from behind the isolation curtain manually operated the camera lens to maintain a close-up view of each birth. Real-time recordings were made for the full duration of delivery.

**Data analysis.** The dams' behavior was observed during playback of the videotape for the period beginning 6 hr before the onset of delivery and until all pups were delivered.

Videorecorded observations were scored during playback for the interval bounded by the first birth and 10 min after the last birth. We measured the duration of selected maternal activities directed at newly born offspring (the most recently delivered pup) or previously born offspring (any pup with a younger sibling) and other characteristics of natal environment that might provide sensory cues to offspring. The following maternal activities were scored: (a) licking pups, the dam's tongue was in contact with a pup's body; (b) handling pups, the dam manipulated or retrieved pups with its forepaws or mouth; (c) vicarious stimulation of pups, the dam suspended a pup by its umbilical cord or stepped, sat, or lay on a pup.

### Results and Discussion

The total duration of the delivery phase of parturition (first to last birth) ranged from 40 to 136 min ( $M \pm SD$ , 90.6  $\pm$  29.6 min). Dams gave birth to an average of 10.1 ( $\pm$  1.1) pups. Delivery duration and litter size were positively related ( $r^2 = .73$ ,  $p < .01$ ). Pups births were separated by intervals from 0 to 22.5 min ( $M \pm SD$ , 9.9  $\pm$  2.3) and were evenly distributed over the delivery period (average interval between births during the first half of delivery, 9.8  $\pm$  2.6; during the second half, 9.5  $\pm$  3.4). This result is in contrast with the finding of Dollinger et al. (1980) that 36% of pup births occurred during the first half of the delivery period.

In accord with previous reports (Rosenblatt & Lehrman, 1963; Weisner & Sheard, 1933), dams adopted the head-between-heels posture during pup births and assisted the newborn's passage from the birth canal into the nest by licking and tugging at the pup. Dams also provided postpartum licking and handling. Figure 8 illustrates the amounts of pup stimulation produced by the dam's behavior during the entire delivery process. Dams provided about 2 min of continuous attention to each newborn while par-

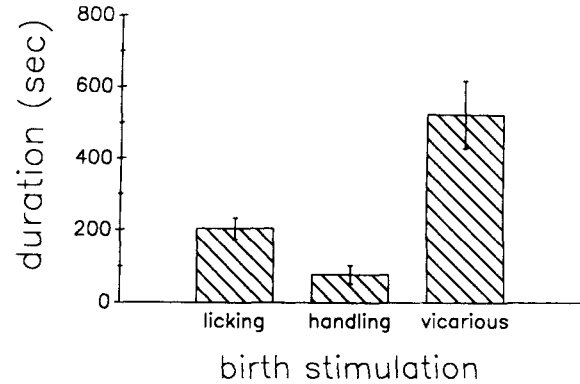


Figure 8. Duration of maternal licking, handling and retrieving, and vicarious stimulation of newborn pups.

ticipating in its delivery. Nearly all pups were born in the vertex position; thus initial stimulation derived from licking was typically directed at the offspring's head. Each pup received frequent vestibular stimulation as the dam rotated its body and systematically consumed the products of gestation.

During this period of intense tactile and vestibular stimulation, pups were, at first, unresponsive. On removal of birth membranes, particularly from the head and face, pups began to show the robust gasps, which characterize the onset of independent respiration (Mortola, 1986), and soon thereafter gross movement and audible vocalizations. After immediate postpartum licking and handling of the each newborn, the dam often focussed her attention on previous newborns, providing each with an additional 2½ min of licking and handling, which were delivered to pups in short bouts across the remainder of parturition. Overall, licking by dams was distributed equally across pups' bodies: head, 39% ( $\pm$  19%); body, 24% ( $\pm$  17%); anogenital area, 32% ( $\pm$  19%), ANOVA,  $F(2, 23) = 1.20$ , *ns*.

Vicarious stimulation became increasingly frequent as the size of the postnatal litter expanded within the nest. Each pup received about 9 min of vicarious stimulation associated with dams' activities during partus. Vicarious stimulation appeared in various forms: Pups were dragged through the nest after birth while still attached to their undelivered placenta or suspended in midair while the dam consumed the placenta of a still attached pup; other newborns were compressed against the floor under the weight of the dam's feet and body. In general, firstborns were exposed to more vicarious stimulation than were later born pups. It is noteworthy that pups actually spent only a small percentage of the 1- to 2-hr parturition process in direct physical contact with the dam. Episodes of contact were generally brief, as dams moved continuously about the nest, undergoing labor contractions and delivering new offspring. Thus, virtually for the entire duration of delivery, pups were exposed without insulative protection to an ambient temperature of 25 °C.

These findings help to specify sensory events to which the newborn rat is exposed during birth. Each pup receives a protracted bout of repetitive tactile and vestibular stimula-

tion associated with the dam's licking and handling immediately on delivery from the womb, followed by repeated brief episodes of postpartum licking and handling. During parturition, offspring are also exposed to seemingly hostile forms of stimulation associated with cooling and with compression under the weight of the dam's body.

General Discussion

Our results share many features with previous observations of parturient behavior in the rat (Dollinger et al., 1980; Rosenblatt & Lehrman, 1963; Weisner & Sheard, 1933), and other species (Lickliter, 1985; Schneirla, Rosenblatt, & Tobach, 1963; Tinklepaugh & Hartman, 1930). However, the experiments we report here differ from previous work in the rat in two important respects. First, we used videographic techniques, which permitted us to monitor the behavior of late-gestation and parturient rat dams across the circadian cycle and to compile extensive behavioral profiles. Secondly, our analysis of dams' behaviors emphasized the offsprings' perspective and highlighted maternal contributions to the perinatal sensory environment.

Maternal Stimulation

The findings of these studies suggest that the behavior of pregnant and parturient dams generate specific tactile, vestibular, and thermal stimuli that provide sensory experience to gestating and newborn rat pups.

Figure 9 is an iconographic chronology across the perinatal period of maternally produced stimuli that impinge on the offspring during gestation, parturition, and early postnatal life. As we have seen, dams are active throughout late gestation, engaging in activities similar to those of nonpregnant females. Locomotor behavior, rearing, head and body grooming, and stirring by pregnant dams during quiescent periods provide in utero accelerations. Abdominal grooming and hindlimb scratching may produce in fetuses sensations of pressure and vibration. We have not considered potentially related uterine events, such as provocative stimuli from adjacent fetuses.

During parturition, repetitive uterine contractions pitch and compress fetuses at an increasingly rapid rate as delivery approaches. As each pup is born, it is licked, handled, and carried by the dam and thereby exposed to additional cutaneous and vestibular stimuli. Offspring also receive vicarious stimulation of these modalities as the dam steps or sits on pups within the nest or as she suspends or drags delivered pups that remain attached to their umbilical cords. Finally, newly born pups are exposed to thermal stimulation, as they rapidly cool to the temperature of the postnatal environment.

Perinatal Perceptions in Utero and ex Utero

There is little question that the perinatal rat is able to detect tactile, vestibular, and thermal stimulation (Alberts, 1984; Kirby, 1979; Lane, 1917; Narayanan et al., 1971;

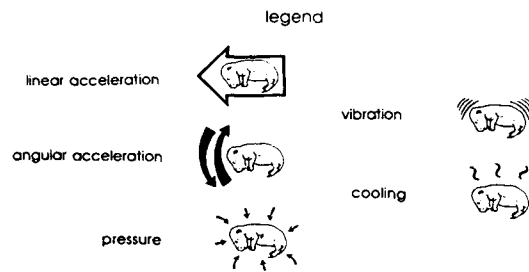
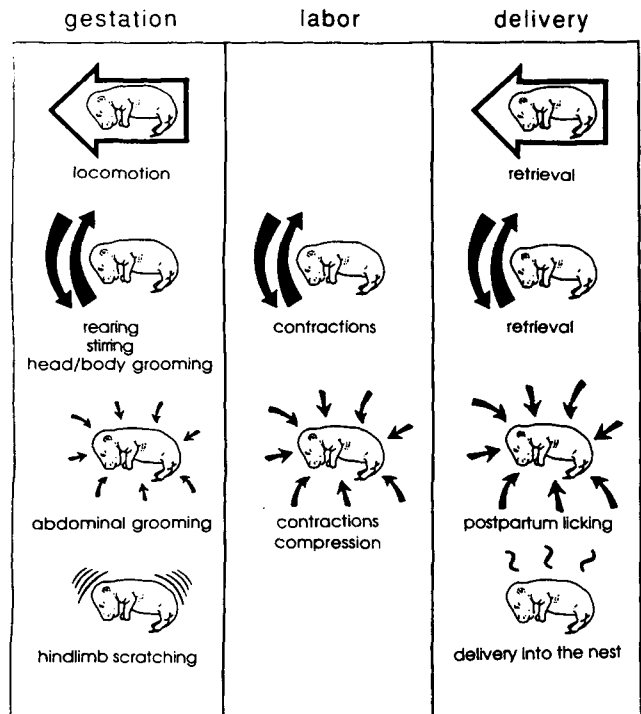


Figure 9. Chronological appearance of maternal sources of pup stimulation across the perinatal period.

Smotherman & Robinson, 1988a), but the degree to which these subjects are able to process stimulation is unknown. During the perinatal period the rat undergoes substantial physical growth and neural maturation. Corresponding improvements in sensory-perceptual function can be presumed from neurobiological analyses; however, there exist virtually no empirical data with which to assess the development of sensory-perceptual function in these subjects (see Alberts, 1984). Thus, it is presently impossible to determine the impact on perinatal offspring of stimuli present within the fetal and newborn habitats.

There is a similar lack of data with which to quantify specific tactile, vestibular, and thermal cues that impinge on perinatal organisms. We have recently begun to make direct measurements of such stimuli in the rat (Ronca & Alberts, 1991), and can offer some preliminary comments on the nature of available stimulation.

Maternal activities during gestation, labor, and delivery constitute a significant portion of the prenatal and natal environments. Over the course of gestation, episodes of tactile and vestibular stimulation are likely amplified by

alterations of the amniotic surround. Between prenatal Days 19–21, amniotic fluid volume declines from maximal levels to one fifth of this amount (Tam & Chan, 1977); this decline constitutes a lost physical buffer around the fetus. Rather than floating within a fluid-filled sac, the fetus is now tightly encased within the uterine sheath, where both cutaneous and vestibular receptors receive potentiated stimulation. Indeed, responsiveness of the human fetus to maternal activity and locomotion is well documented (Hofer, 1981).

The onset of partus occurs after the fetus' protective buffer diminishes and exposes it to the direct impact of labor contractions (Fuchs, 1969). On delivery the pup's cutaneous receptors are directly exposed to provocative environmental features, such as the rough surface of the dam's tongue. The fetus' delivery from the amniotic sac influences vestibular sensation in new ways, as well. Stimulation of the semi-circular canals and otolith organ produce more complex vestibular experiences *ex utero*, as novel gravitational forces operate in tandem on the newborn's musculoskeletal system.

Consideration of these additional factors suggests that stimuli normally present within the perinatal habitat become increasingly intense and complex as development proceeds and undergo massive potentiation during and after birth. Although low levels of stimulation may be sufficient to activate sensory systems around the time of their functional onset, it is possible that we must consider the hypothesis that buffering prenatal stimuli may protect fragile sensory apparatus. Support for this interpretation can be derived from studies of premature human babies who may suffer negative effects of extreme levels of environmental stimulation (Lott, 1989), although moderate levels of stimulation may produce beneficial consequences (Schanberg & Field, 1987). It is possible that under normal conditions, newly operative sensory receptors are exposed to controlled levels of stimulation in advance of birth.

### *On the Functional Significance of Perinatal Sensory Stimulation*

Moderate stimulation may promote useful levels of activity in fetal organisms, and there is increasing evidence that prenatal movement is an important determinant of normal development. Depressed fetal activity is associated with numerous morphological anomalies, including contractures of the joints, lung hypoplasia, facial anomalies, and growth retardation (Moessinger, 1988). Tongue movements associated with fetal swallowing are required for normal development of the palate (B. E. Walker & Quarles, 1962). Fetal respiratory movements move fluid through the lungs, stimulating pulmonary development and the neuromuscular action associated with breathing prior to the onset of independent respiration. Prenatal sensory factors may play a role in the regulation of these fetal behaviors.

The intense stimulation associated with labor and delivery may contribute to the newborn's transition from prenatal to postnatal life. At birth, the newborn must abruptly adapt to the loss of the maternal life support system. Circulatory, metabolic, and digestive functions conform to meet postna-

tal needs; however, the most essential and immediate neonatal requirement is the onset of independent respiration. In particular, contractions of the uterus prior to birth may play a key role in the newborn's adaptation to the postnatal environment. Mechanical pressure on the head during uterine contractions can stimulate sympathoadrenal activity in animals (see Lagercrantz & Slotkin, 1986). The resulting surge in catecholamines may protect offspring from the debilitating effects of birth asphyxia and promote the onset of postnatal breathing. In fetal sheep, increased catecholamine levels associated with labor have been shown to inhibit the natural production of fetal lung liquid and promote the absorption of existing liquid (Oliver, Strang, & Walters, cited in Lagercrantz & Slotkin, 1986). Indeed, human newborns that undergo labor contractions inspire greater volumes of air during the first 6 hr after birth (Boon, Milner, & Hopkin, 1981).

The role of sensory factors in promoting the newborn's successful adaptation to the conditions of postnatal life is recognized in the delivery room, where the newly born human is held in a head-down position and may be slapped on the rump or soles of the feet to initiate breathing and crying (L. S. James & Adamsons, 1989). The rat dam's postpartum licking and handling may supply similar important sensory input to offspring. Pederson and Blass (1982) reported that the absence of tactile stimulation at birth reduced the survivability of rat pups by 40%. Thus, perinatal sensory events may play critical roles in the regulation and maintenance of sensory development and the initiation of essential postnatal functions.

### *Directions for Future Research*

Taken together, these studies suggest that maternal behavior during perinatal life provides to offspring a rich source of stimuli. These results provide a detailed framework for empirical studies in which specific features of maternal stimulation important to the normal behavioral and physiological development can be identified. Of particular interest is the impact of stimulation on the development of fetal sensory systems and the role of sensory experience in promoting adaptive behavior in the fetus and neonate. In studies currently underway, we are measuring the transduction of maternally produced stimuli in utero and the effects on neonatal respiratory behavior.

### References

- Abbas, T. M., & Tovey, J. E. (1960). Proteins of the liquor amnii. *British Medical Journal*, 2, 476–479.
- Alberts, J. R. (1984). Sensory-perceptual development in the Norway rat: A view toward comparative studies. In R. Kail & N. S. Spear (Eds.), *Comparative perspectives on memory development* (pp. 65–102). Hillsdale, NJ: Erlbaum.
- Barnett, S. A. (1963). *The rat: A study in behavior*. Chicago: Aldine.
- Beach, F. A., & Jaynes, J. (1956). Studies of maternal retrieving in the rat: I. Recognition of young. *Journal of Mammalogy*, 37, 177–180.
- Bench, J. (1968). Sound transmission to the human foetus through

- the maternal abdominal wall. *Journal of Genetic Psychology*, 113, 85–87.
- Bichat, M. F. X. (1827). *Physiological researches upon life and death*. Boston: Richardson and Lord.
- Blandau, R. J., & Soderwall, A. J. (1941). Postparturitional heat and the time of ovulation in the albino rat: Data on parturition. *Anatomical Record*, 81, 419–431.
- Boon, A. W., Milner, A. D., & Hopkin, I. E. (1981). Lung volumes and lung mechanics in babies born vaginally and by elective and emergency caesarean section. *Journal of Pediatrics*, 98, 812–815.
- Bradley, R. M., & Mistretta, C. M. (1975). Fetal sensory receptors. *Physiological Reviews*, 55, 352–382.
- Carmichael, L. (1970). Onset and early development of behavior. In P. H. Mussen (Ed.), *Carmichael's manual of child psychology* (3rd ed., pp. 447–563). New York: Wiley.
- Carmichael, L., & Smith, M. F. (1939). Quantified pressure stimulation and the specificity and generality of response in fetal life. *Journal of Genetic Psychology*, 54, 425–434.
- Coghill, G. E. (1929). *Anatomy and the problem of behavior*. Cambridge, United Kingdom: Cambridge University Press.
- Dawes, G. S. (1973). Breathing and rapid eye movement sleep before birth. In R. S. Comline, K. W. Cross, G. S. Dawes, & P. W. Nathanielsz (Eds.), *Foetal and neonatal physiology: Proceedings of the Sir Joseph Barcroft centenary symposium* (pp. 49–62). Cambridge, United Kingdom: Cambridge University Press.
- Decasper, A. J., & Fifer, W. P. (1980). Of human bonding: Newborns prefer their mothers' voices. *Science*, 208, 1174–1176.
- Dollinger, M. J., Holloway, W. R., & Denenberg, V. H. (1980). Parturition in the rat (*Rattus norvegicus*): Normative aspects and the temporal patterning of behaviors. *Behavioural Processes*, 5, 21–37.
- Fifer, W. P., & Moon, C. (1988). Auditory experience in the fetus. In W. P. Smotherman & S. R. Robinson (Eds.), *Behavior of the fetus* (pp. 175–188). Caldwell, NJ: Telford Press.
- Fuchs, A. R. (1969). Uterine activity in late pregnancy and during parturition in the rat. *Biology of Reproduction*, 1, 344–353.
- Gottlieb, G. (1971). Ontogenesis of sensory function in birds and mammals. In E. Tobach, L. R. Aronson, & E. Shaw (Eds.), *The biopsychology of development* (pp. 67–128). New York: Academic Press.
- Hofer, M. A. (1981). *The roots of human behavior: An introduction to the psychobiology of early human development*. San Francisco: Freeman.
- Hooker, D. (1952). *The prenatal origin of behavior* (18th Porter Lecture Series). Lawrence: University of Kansas Press.
- James, L. S., & Adamsons, K. (1989). The neonate and resuscitation. In J. R. Scott, P. J. DiSaia, C. B. Hammond, & W. N. Spellacy (Eds.), *Danforth's obstetrics and gynecology* (pp. 675–690). Philadelphia: Lippencott.
- James, W. (1890). *Principles of psychology* (Vol. 1). New York: Holt.
- Jeffcoate, T. N. A., & Scott, J. S. (1959). Polyhydramnios and oligohydramnios. *The Canadian Medical Association Journal*, 80, 77–86.
- Kirby, M. L. A. (1979). A quantitative method for determining the effects of opiates on fetal rats in utero. *Problems of Drug Dependence, NIDA Research Monograph*, 27, 191–197.
- Kuo, Z. Y. (1932). Ontogeny of embryonic behavior in Aves: I. The chronology and general nature of the behavior of the chick embryo. *Journal of Experimental Zoology*, 61, 395–430.
- Lagercrantz, H., & Slotkin, T. A. (1986). The "stress" of being born. *Scientific American*, 254, 100–107.
- Lane, H. H. (1917). The correlation between structure and function in the development of the special senses of the white rat. *University of Oklahoma Bulletin, New Series 140, University Studies*, 8, 1–88.
- Lev, R., & Orlic, D. (1972). Protein absorption by the intestine of the fetal rat in utero. *Science*, 177, 522–524.
- Lickliter, R. E. (1985). Behavior associated with parturition in the domestic goat. *Applied Animal Behavior Science*, 13, 335–345.
- Lott, J. W. (1989). Developmental care of the preterm infant. *Neonatal Network*, 21–28.
- Mellor, D. J., & Slater, J. S. (1971). Daily changes in amniotic and allantoic fluid during the last three months of pregnancy in conscious, unstressed ewes with catheters in their foetal fluid sacs. *Journal of Physiology, London*, 217, 573–604.
- Moessinger, A. C. (1988). Morphological consequences of depressed or impaired fetal activity. In W. P. Smotherman & S. R. Robinson (Eds.), *Behavior of the fetus* (pp. 163–173). Caldwell, NJ: Telford Press.
- Mortola, J. P. (1986). Breathing patterns in newborns. *Journal of Applied Physiology: Respiratory and Environmental Exercise Physiology*, 56, 1533–1540.
- Narayanan, C. H., Fox, M. W., & Hamburger, V. (1971). Prenatal development of spontaneous and evoked activity in the rat. *Behavior*, 40, 100–134.
- Pederson, P. E., & Blass, E. M. (1982). Prenatal and postnatal determinants of the first suckling episode in albino rats. *Developmental Psychobiology*, 15, 349–355.
- Preyer, W. (1937). Embryonic motility and sensitivity (G. E. Coghill & W. K. Legner, Trans.). *Monographs of the Society for Research in Child Development*, 2, 1–115.
- Ronca, A. E., & Alberts, J. R. (1990). Heart rate development and sensory-evoked cardiac responses in perinatal rats. *Physiology and Behavior*, 47, 1075–1082.
- Ronca, A. E., & Alberts, J. R. (1991, November). *Sensory experience of the perinatal rat*. Paper presented at the meeting of the International Society of Developmental Psychobiology, New Orleans.
- Rosenblatt, J. S., & Lehrman, D. S. (1963). Maternal behavior in the laboratory rat. In H. L. Rheingold (Ed.), *Maternal behavior in mammals* (pp. 8–57). New York: Wiley.
- Roth, L., & Rosenblatt, J. S. (1965). Changes in self-licking during pregnancy in the rat. *Journal of Comparative and Physiological Psychology*, 63, 397–400.
- Schanberg, S. M., & Field, T. M. (1987). Sensory deprivation stress and supplemental stimulation in the rat pup and preterm human neonate. *Child Development*, 58, 1431–1447.
- Schneirla, T. C., Rosenblatt, J. S., & Tobach, E. (1963). Maternal behavior in the cat. In H. L. Rheingold (Ed.), *Maternal behavior in mammals* (pp. 122–168). New York: Wiley.
- Smotherman, W. P., & Robinson, S. R. (1988a). Behavior of rat fetuses following chemical or tactile stimulation. *Behavioral Neuroscience*, 102, 24–34.
- Smotherman, W. P., & Robinson, S. R. (1988b). The uterus as environment: The ecology of fetal behavior. In E. M. Blass (Ed.), *Handbook of behavioral neurobiology: Vol. 9. Developmental psychobiology and behavioral ecology* (pp. 149–196). New York: Plenum Press.
- Smotherman, W. P., Robinson, S. R., Ronca, A. E., Alberts, J. R., & Hepper, P. (1991). Heart rate responses of the rat fetus and neonate to a chemosensory stimulus. *Physiology and Behavior*, 50, 47–52.
- Tam, P. P. L., & Chan, S. T. H. (1977). Changes in the composition of maternal plasma, fetal plasma and fetal extraembryonic fluid during gestation in the rat. *Journal of Reproduction and Fertility*, 51, 41–51.

- Tinklepaugh, O. L., & Hartman, C. G. (1930). Behavioral aspects of parturition in the monkey (*Macacus rhesus*). *Journal of Comparative Psychology*, *11*, 63-98.
- Vince, M. A. (1979). Postnatal effects of prenatal sound stimulation in the guinea pig. *Animal Behavior*, *27*, 908-918.
- Vince, M. A., Billing, B. A., Baldwin, B. A., Toner, J. N., & Weller, C. (1985). Maternal vocalisations and other sound in the fetal lamb's sound environment. *Early Human Development*, *11*, 179-190.
- Walker, B. E., & Quarles, J. (1962). Palate development in mouse foetuses after tongue removal. *Archives of Oral Biology*, *21*, 405-412.
- Walker, D., Grimwade, J., & Wood, C. (1971). Intrauterine noise: A component of the fetal environment. *American Journal of Obstetrics and Gynecology*, *109*, 91-95.
- Weisner, B. P., & Sheard, N. M. (1933). *Maternal behavior in the rat*. London: Oliver and Boyd.
- Windle, W. F. (1940). *Physiology of the fetus: Origin and extent of function in fetal life*. Philadelphia: Saunders.
- Windle, W. F., & Fish, M. W. (1932). The development of the vestibular righting reflex in the cat. *Journal of Comparative Neurology*, *54*, 85-96.
- Wirtschafter, Z. T., & Williams, D. W. (1957). Dynamics of the amniotic fluid as measured by changes in protein patterns. *American Journal of Obstetrics and Gynecology*, *74*, 309-313.

Received January 24, 1992

Revision received March 17, 1992

Accepted March 20, 1992 ■



## AMERICAN PSYCHOLOGICAL ASSOCIATION SUBSCRIPTION CLAIMS INFORMATION

Today's Date: \_\_\_\_\_

We provide this form to assist members, institutions, and nonmember individuals with any subscription problems. With the appropriate information we can begin a resolution. If you use the services of an agent, please do NOT duplicate claims through them and directly to us. **PLEASE PRINT CLEARLY AND IN INK IF POSSIBLE.**

PRINT FULL NAME OR KEY NAME OF INSTITUTION \_\_\_\_\_

MEMBER OR CUSTOMER NUMBER (MAY BE FOUND ON ANY PAST ISSUE LABEL) \_\_\_\_\_

ADDRESS \_\_\_\_\_

DATE YOUR ORDER WAS MAILED (OR PHONED): \_\_\_\_\_

CITY \_\_\_\_\_

STATE/COUNTRY \_\_\_\_\_

ZIP \_\_\_\_\_

P.O. NUMBER: \_\_\_\_\_

PREPAID \_\_\_\_\_ CHECK \_\_\_\_\_ CHARGE \_\_\_\_\_

CHECK/CARD CLEARED DATE: \_\_\_\_\_

YOUR NAME AND PHONE NUMBER \_\_\_\_\_

(If possible, send a copy, front and back, of your cancelled check to help us in our research of your claim.)

ISSUES: \_\_\_\_\_ MISSING \_\_\_\_\_ DAMAGED

TITLE \_\_\_\_\_

VOLUME OR YEAR \_\_\_\_\_

NUMBER OR MONTH \_\_\_\_\_

*Thank you. Once a claim is received and resolved, delivery of replacement issues routinely takes 4-6 weeks.*

(TO BE FILLED OUT BY APA STAFF)

DATE RECEIVED: \_\_\_\_\_

DATE OF ACTION: \_\_\_\_\_

ACTION TAKEN: \_\_\_\_\_

INV. NO. &amp; DATE: \_\_\_\_\_

STAFF NAME: \_\_\_\_\_

LABEL NO. &amp; DATE: \_\_\_\_\_

SEND THIS FORM TO: APA Subscription Claims, 750 First Street, N.E., Washington, DC 20002

PLEASE DO NOT REMOVE. A PHOTOCOPY MAY BE USED.