

Perinatal stimulation and adaptation of the neonate

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The present report describes psychobiological studies of behavior around the time of birth. An adaptive, ecological perspective is presented in which stimulation of the fetus and newborn is purported to instigate adaptive postpartum behavior. Studies describing the perinatal sensory environment are reviewed, with a consideration of emergent sensory function of the fetus. It is asserted that afferent input associated with parturition perturbs the fetus and neonate, producing a general arousal state that facilitates breathing, suckling, and early learning. The view developed herein is that perinatal sensory input induces and canalizes the newborn's behavior, thereby regulating adaptive postpartum function. Deviations in afferent input may alter ontogenetic trajectories and compromise developmental outcome by reducing availability of conditions necessary for adequate postpartum adaptation. □ *Arousal, breathing, learning, postpartum adaptation, suckling*

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Upon leaving the womb, the neonate must initiate novel behaviors. The first breath of air, the first nipple attachment, and the expression of learning are all essential beginnings to the fetus's adaptation to postpartum life. Yet, how these behaviors emerge and are quickly set into motion remain mysteries. We believe that a psychobiological perspective on postpartum adaptation offers new understanding of these fundamental puzzles. In the present report, we integrate existing knowledge of perinatal sensory function with the onset of neonatal behaviors essential to the process of adaptation to the postpartum environment.

Our framework is derived from the concept of ontogenetic adaptation (1, 2), a perspective based in behavioral biology that emphasizes habitat and function during development. According to this view, mammalian ontogeny occurs within a series of distinct environments or habitats, and the young mammal is specifically adapted to its habitat at each developmental stage. The fetus's habitat is the uterus, within which physiological functions are supported largely by the mother. Yet, even *in utero*, the fetus is a behaving organism, and some fetal behaviors have functional consequences; some may be self-regulating. For example, fetuses routinely swallow amniotic fluid, a behavior which plays an important role in digestive organ development (3). In this way, the fetus is specifically adapted to the uterine context.

At birth, the fetus abruptly enters a natal habitat which differs markedly from the womb. Oxygen, nutrition, warmth are no longer supplied automatically and continuously by the mother. New behaviors emerge and old behaviors take on new forms as the fetus undergoes the process of postnatal adaptation, adjusting to the new habitat outside of its mother's body. Air-breathing

begins within seconds, and steadily develops its cyclicality and regulatory capacities. Soon thereafter, the newborn seeks, locates and attaches to a nipple, thus initiating the process of suckling. These behaviors are specific adaptations to the postpartum environment, and are the behaviors upon which this report will focus.

The transition from fetus to newborn is a universal event in mammalian development. As psychobiologists whose approach is derived from an adaptive, ecological perspective, we will rely largely, but not exclusively, on behavioral studies of the Norway rat. The rat mother and her offspring can be viewed as an adaptive, ecological system: during gestation and parturition, the mother provides the fetus's environment. Her movements and physiological functions generate afferent input to fetal sensory systems [e.g. tactile, vestibular, proprioceptive (4)].

The mother's postpartum care provides sensory input to the newborn. Once the newborn exits the birth canal, she removes the birth membranes and cleanses the pup's body, then provides warmth and access to mother's milk. The mother and infant can be viewed as a functional system throughout gestation and during postpartum life, and, as we will describe, the mother's actions are biologically meaningful to the neonate. Our interests in the rat are not to describe a small replica or demonstrate a model of the human; but rather, we seek general biological principles or universals of mammalian development applicable to the human condition. Even more important, perhaps, this adaptive, ecological view may provide methodological and conceptual insights into clinical inquiries of the human fetus and newborn. Through discussions of basic behavioral and physiological processes of the developing rodent, we hope to

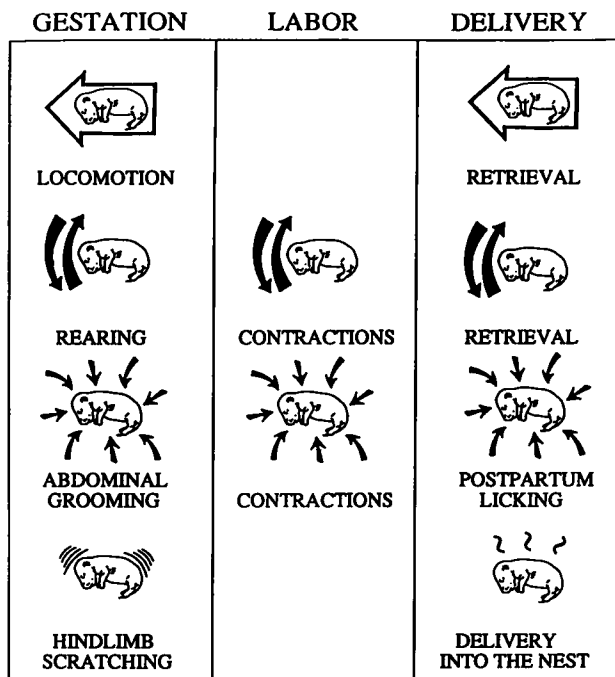


Fig. 1. An overview of stimuli available to the Norway rat (*Rattus norvegicus*) during gestation, labor and delivery.

further understanding of the behavioral biology of the perinate, and pathological conditions which may emerge when the developmental processes have gone awry.

This report is organized around three major themes. First, *mothers stimulate fetuses*. The mother's behavior and physiological functions provide many different forms of afferent input to fetuses *in utero* (5, 4). Second, *fetuses experience*. Despite the fact that fetal sensory systems are both morphologically and functionally immature, fetuses have the capacity to sense, perceive and even recall stimuli encountered *in utero* (5–9). Third, *perinatal sensory experience induces and canalizes the emergence of adaptive postpartum behavior*. Several examples are presented which elucidate some of the sensory controls of postpartum breathing and suckling, and illustrate the critical inductive and formative roles of perinatal stimulation in emergent postpartum functions.

Maternal stimulation of fetuses

There is now a large body of evidence showing that significant amounts of afferent input are available to the fetus *in utero*, with maternal behavior and physiology making a major contribution to the pool of available stimuli (4–7, 10–14). In our studies of the Norway rat, we have identified sources of sensory input to which the rat fetus is exposed during gestation, labor and delivery (4). These stimuli and their sources are illustrated in Fig. 1. During gestation (left panel), fetuses

in utero are exposed to tactile and vestibular stimuli associated with the mother's behavior. Specifically, fetuses are exposed to linear acceleration as the dam ambulates, angular acceleration as the dam rears, compression as the dam grooms her abdomen, and vibration as the dam scratches with her hindlimb. These maternal activities occur at high levels throughout pregnancy, exposing fetuses to hundreds of sensory inputs each day, many of which occur within 24 h of birth. During labor (middle panel), fetuses are pitched and rotated by uterine contractions, and repeatedly exposed to strong compressions, culminating as the newborn is squeezed through the birth canal. Upon delivery from the birth canal (right panel), the dam removes the birth membranes, enabling air to reach pups' nares for the first time. She licks and handles pups, removing amniotic fluid from the skin as she lifts and rotates them, providing extensive cutaneous stimulation and bouts of linear and angular acceleration. The postpartum thermal environment is much cooler than the intrauterine environment (21°C vs. 37.5°C), causing thermally fragile newborn pups to cool to room temperature within minutes of birth (15). The rat dam typically does not gather her pups into the nest and warm them until the entire litter has been delivered, a process which usually requires more than an hour (4).

The human perinate is similarly exposed to physical stimulation associated with maternal movement, labor contractions and postpartum handling. Sensory development is relatively more advanced in the human baby than in the infant Norway rat [see (16, 12)]. Unlike most rodents, the auditory and visual systems of the human neonate are functional at birth, providing additional channels for pre- and postnatal sensory input. Although we will focus our discussion on the physical stimuli that impinge upon the fetal and newborn Norway rat, it is important to note that our intention is to provide a general model of perinatal stimulation which does not preclude a role for stimuli arising from other sensory modalities.

Fetal sensory experience and function

Early sensory function (whether intrinsic or stimulated) is a critical element in the development of sensory systems and of neural systems [see Purves (17)], and therefore, in the regulation of behavior ontogenesis. It has long been known that embryonic behavior can be provoked by stimulation. In classic work with human embryos, Humphrey (18) reported that tactile stimuli elicit movement responses in late gestation fetuses. Prenatal rats respond to punctate stimulation of the snout with movement responses on Gestational Day (GD) 16 of the 22-day gestation period (19). Milk, lemon, and other chemical cues presented through an intraoral cannula elicit changes in movement in prenatal rats on GD 17. Fetuses also respond to chemosensory cues with heart rate (HR) deceleratory responses (20).

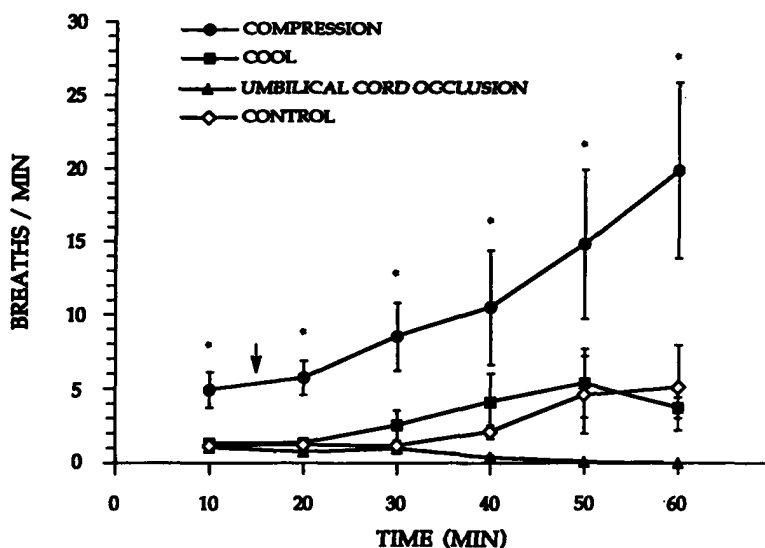


Fig. 2. Effects of compression, cooling and umbilical cord occlusion on respiratory behavior of perinatal rats. ($N = 8-12$ per group).

Studies of prenatal sensory competence are essential for ascertaining the extent to which available stimuli might be transduced by fetal sensory systems. However, the most accurate understanding of prenatal sensory experience is derived from studies which utilize ecologically-relevant stimuli. For a variety of mammalian species, much of the stimulation present *in utero* appears to fall within fetal sensory detection thresholds (10, 13, 14, 21-23). Ecologically-relevant cues have been presented to externalized rat fetuses (9). These cues included tilts that match maternal rearing and circling, vibration to match intrauterine events during maternal grooming, controlled bouts of mechanical compression to match contractions of the uterus during labor, stroking to mimic maternal licking at birth, and cooling to match the postpartum thermal environment. Each form of biologically-matched stimulation evoked robust cardiac and behavioral responses from perinatal rats. The fetus's HR and behavioral responses provided evidence for prenatal transduction of stimuli normally encountered during fetal and neonatal life, and showed that functional linkages to efferent systems are in place prior to birth.

Fetal experience can be viewed as an epigenetic mechanism intrinsic to the regulation of developmental processes. Early sensory experience is fundamental to the development of sensory, neural and behavioral systems. Premature sensory experience can influence perceptual development (24, 25). Reductions in embryonic limb movements, even for a relatively brief period, can permanently block joint flexibility. Limb movements are part of the formative process of the musculoskeletal apparatus (26, 27). Similarly, manipulations that disrupt fetal swallowing or early respiratory movements have been directly associated with impairments in gastrointestinal and pulmonary development (3). Fetal

sensations appear to instigate fetal movements, suggesting the possibility that onset and/or maintenance of developmentally adaptive behavior may be regulated by fetal sensory experiences.

Perinatal experience and postpartum adaptation of the newborn infant

Immediately after birth, the newborn must breathe on its own and, soon thereafter, locate and ingest nutrients. The findings that we have discussed thus far suggest that stimulation of the mammalian fetus during gestation and birth can affect function, and thus contribute directly and necessarily to the development of behavior. In this section, we look at behaviors which must be initiated by the newborn in its new habitat.

Perinatal experience and the induction of breathing in the newborn

The movement of air in and out of the lungs is accomplished by the contraction and extension of voluntary muscles (28). Breathing movements begin during prenatal life (29), at which time lung fluid, rather than air, is moved through the trachea (30). Although unrelated to gas-exchange functions, prenatal respiratory movements are thought to contribute to the remarkable postnatal ability of the respiratory musculature to maintain vigorous, continuous, coordinated function after birth (3, 31). Numerous factors have been hypothesized to trigger the onset of continuous breathing at birth, including hyperoxia (32), umbilical cord occlusion (32, 33), cutaneous cooling (34), and somatic stimulation (35-37). From a psychobiological perspective, it is important to recognize the actual forms and levels of biological stimuli that accompany the birth

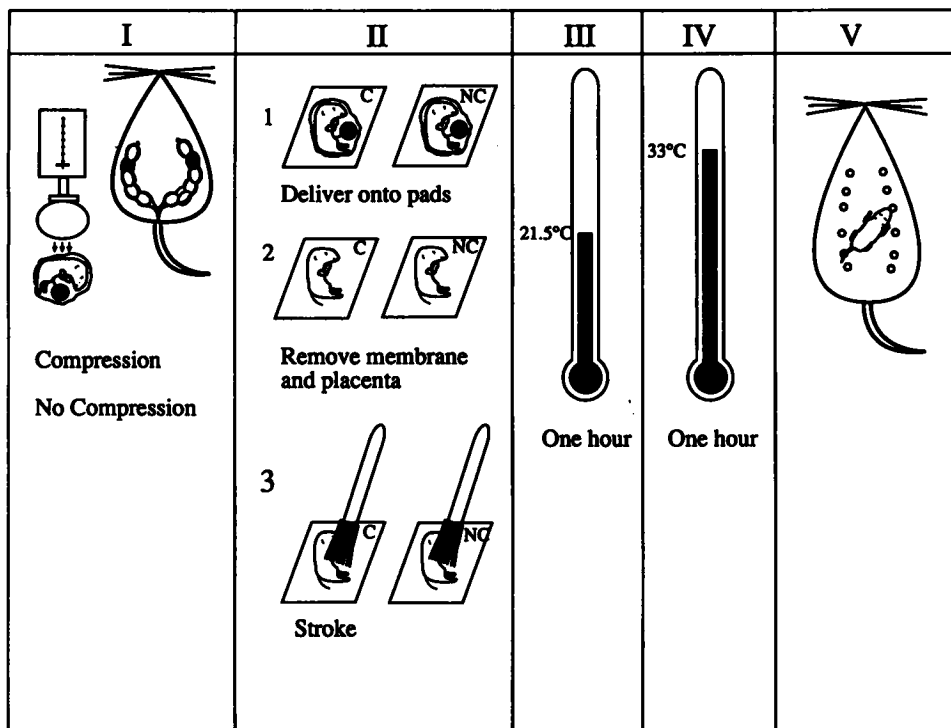


Fig. 3. Experimental protocol for studying factors controlling suckling onset in the Norway rat (*Rattus norvegicus*).

process, and the roles these stimuli may play in the expression of adaptive behavior by the neonate. In this section, we present some of our own studies that illustrate how perinatal stimulation can induce a vital postpartum function, namely, respiratory behavior.

Components of the birth process were isolated and presented singly or in combination to perinatal rats, and effects on postpartum breathing were assessed (35). Using procedures for directly observing fetal rats, GD 21 pregnant dams were given a chemical transection of the spinal cord to eliminate sensation and movement below the ribcage. Fetuses were externalized from the uterus, the amniotic sac was gently removed, while maintaining intact umbilical connections to the dam. The fetus was placed in a small cup, and exposed to one of three parturitional elements: (1) compressions simulating uterine contractions; (2) cooling (26°C) to match postpartum nest temperature; or (3) umbilical cord occlusion. Fetuses in a control condition were exposed to air heated to intrauterine temperature (37.5°C).

Figure 2 shows that fetuses in each group displayed some respiratory behavior, but compression significantly elevated respiratory rate compared to the other experimental conditions. All subjects in each group were respiring after 1 h, except for pups receiving umbilical cord occlusion without additional stimulation. The 100% attrition rate of the Cord Occlusion-alone group was reversed by combining cord occlusion with compression (with or without cooling), but not by combining cord occlusion with cooling. Pups exposed to all

three factors (compression, cooling and cord occlusion) breathed at rates which were identical to normal, vaginally-delivered pups. The absence of prenatal mechanical stimulation greatly compromised the viability of postnatal rat pups. Indeed, fetuses that were exposed to cord occlusion alone never displayed reliable breathing, and did not survive the first postpartum hour.

Newborn rat pups are typically exposed not only to compression, umbilical cord occlusion, and cooling, but also to cutaneous stimulation arising from the dam's vigorous licking during delivery and the immediate postpartum period. We reasoned that the effectiveness of compression might derive from either mechanical effects on the head, chest and organs or from cutaneous stimulation of skin, and on this basis, we compared the effects of compression and stroking (36). Pups that were either stroked or compressed and those that were both stroked and compressed, breathed at high rates relative to non-stimulated controls.

Cutaneous stimulation without direct body compression is sufficient for the establishment of postpartum breathing and survival in rats. Prenatal and postpartum breathing are influenced by a host of physiological, behavioral, and environmental factors. The physiological status of the perinate, the sensory concomitants of parturition, alterations in the fetus associated with the conversion to neonatal physiology, and the change from an aquatic to pneumatic environment are all relevant to the production of respiratory behavior. In contrast to most earlier investigations, a psychobiological approach

emphasizes the role of naturally-occurring sensory experience in the induction of perinatal breathing. Sensory factors can trigger the chain of adaptive physiological events required for the onset of postpartum breathing.

Perinatal stimulation captures and canalizes adaptive behavior

The newborn's second postpartum challenge is to obtain food via suckling. A nipple must first be apprehended. Newborn infants placed between their mother's breasts locate the nipple soon after birth without assistance (38), and prefer maternal nipples that emanate the natural odor to nipples from which the odor has been eliminated (39). In the case of the Norway rat, olfactory cues are essential for nipple location. During parturition, the dam licks her ventrum, spreading amniotic fluid and her own saliva along the nipple lines. Olfactory cues associated with amniotic fluid are essential for the suckling behavior (40). When presented with an anesthetized mother, pups attach readily to fresh (unmanipulated) maternal nipples. If the nipples are washed, suckling success drops precipitously, but suckling is reinstated when the wash extract is replaced, or when either maternal saliva or amniotic fluid are present.

Pedersen and Blass (41) subsequently demonstrated that a novel odor added to the amniotic fluid prior to birth could also come to control nipple attachment in rats. In that study, an odorant, citral, was injected into the amniotic sac of GD 20 rat fetuses. Two days later, pups were delivered by Cæsarean section and their nipple attachment behavior was evaluated. Three conditions were reported to be necessary for the expression of successful suckling: Prenatal exposure to citral, postnatal exposure to citral, and postnatal cutaneous stimulation, applied with brush strokes. Their studies indicated that these combined, pre- and postnatal experiences are, together, necessary and sufficient to produce an adaptive, conditioned behavioral response to the citral odor. This form of learning and behavioral control presumably involves some aspect of behavioral activation, which was evoked by stroking the postnatal pups in the presence of citral. Pederson and Blass (41) suggested that *postpartum* stimulation of newborn pups associated with the dam's removal of the birth membranes and vigorous licking arouses pups and provides a basis for neonatal learning. We hypothesized that *pre-natal* stimulation of pups associated with maternal behavior and uterine contractions, essentially uncontrolled sources of physical stimulation which coincided with citral exposure, may have contributed to the olfactant's control over pups' behavior. By bringing prenatal physical stimulation under control, we were able to investigate its role in the emergence of this early adaptive behavior. We first demonstrated that simulated uterine contractions promote attachment to normal nipples. Rat dams were prepared with a chemical transection of the spinal cord, as described earlier. The dam's

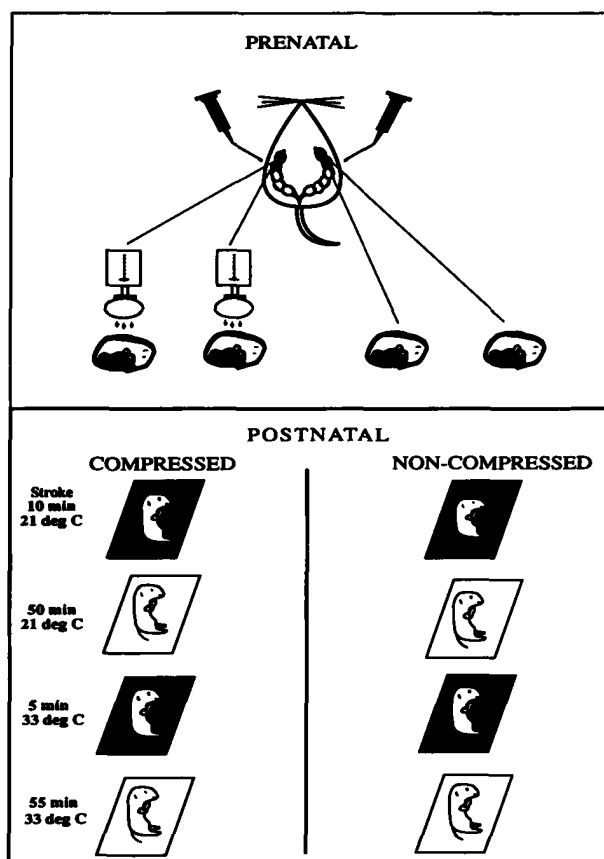


Fig. 4. Experimental protocol for studying suckling onset and the expression of early learning in the Norway rat (*Rattus norvegicus*).

uterine horns were externalized into a heated saline bath. Figure 3 shows the experimental protocol. A fetus in one uterine horn was exposed to compression for 10 min to simulate uterine contractions; a fetus in the opposite horn was not compressed (Panel I). Fetuses were delivered onto gauze pads, their amniotic sacs removed and their umbilical cords tied, and then stroked with a brush to establish breathing (Panel II). Pups were then exposed to room temperature (21°C) for 1 h (Panel III), followed by nest temperature (33°C) for 1 h (Panel IV) to mimic natural postpartum thermal dynamics. Nipple attachment was tested at 2 h postpartum (Panel V).

Simulated uterine contractions produced a high rate of nipple attachment (89%) relative to the non-compressed condition (39%). Compression greatly facilitated attachment rates to normal nipples. Prenatal physical stimulation activates fetuses and may increase the probability that the suckling response is emitted.

We next tested the hypothesis that stimuli canalize or direct suckling behavior by conditioning the suckling response to a novel odor. Warm citral solution was injected into the amniotic fluid of all subject fetuses

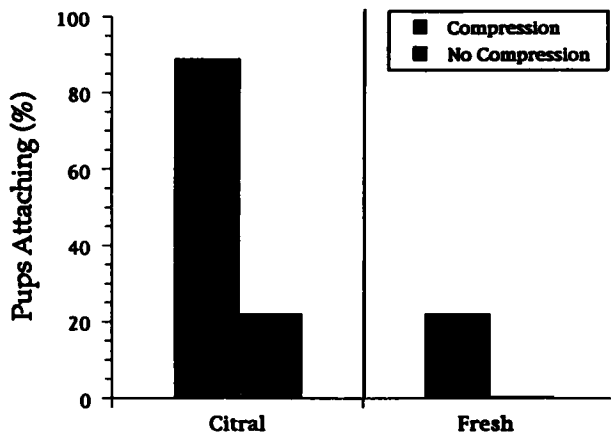


Fig. 5. Effects of citral exposure and compression on nipple attachment in rats. Attachment probabilities of compressed and non-compressed pups to Citral-scented nipples (left panel) or Fresh (nonmanipulated) nipples (right panel). ($N = 11-13$ per group).

immediately following externalization of the uterine horns as described earlier.

Figure 4 shows the protocol used in this experiment. Prenatal exposure conditions are shown on the top. The shaded areas indicate the presence of citral in the amniotic fluid. Fetuses in one horn were compressed, fetuses in the opposite horn were not. Postnatal exposure conditions are shown in the lower panel. The shaded rectangles represent postnatal citral exposure. Compressed and non-compressed pups were exposed to citral for 10 min, accompanied by a brief period of stroking to stimulate breathing. Citral was then removed and, to mimic birth conditions, pups remained at room temperature (21°C) for an additional 50 min. During the second hour, pups were exposed to nest temperature (33°C), with citral presented for the first 5 min of the hour.

Exposure to citral virtually eliminated attachment to fresh (normal, non-scented) nipples, regardless of exposure to compression (left). In contrast, the percentage of pups attaching to citral-scented nipples was dramatically increased by compression, relative to non-compressed subjects (right). Importantly, the attachment rate for these pups is equivalent to that of compressed pups without citral exposure, and to those of vaginally-delivered pups to normal nipples.

Prenatal stimulation is fundamental to the assembly of sensory and behavioral reactions that comprise nipple attachment, and operates by inducing and canalizing the suckling response. The key element appears to be activation, or arousal. In the past 15 years, there have emerged in the literature reports describing instances of generalized behavioral activation in infant rats. Various kinds of stimulation have been reported to induce behavioral activation: milk infusion into the mouth (42, 43), stroking the body with a soft brush (44-46), milk odor (47), electrical brain stimulation (48), and the odor of

maternal saliva (49). This phenomenon of stimulus-induced activation is particularly enticing because each form of activating stimulation was also found to function as a reward and supported learned appetitive associations. In the late 1980s, the attendant issues were cogently summarized (e.g. Sullivan and Hall, 46): behavioral activation may not be reinforcing, *per se*, but the infant's behavioral activation may reveal the occurrence of reward (50), or of an arousal state that accompanies "... a behavioral state that is conducive to learning" (46, p. 222; emphasis added).

Fetal and newborn rats are activated by simulated uterine contractions (9, 35). Behavioral activation produced by uterine contractions appears to be a manifestation of a generalized "arousal state" that facilitates learning about suckling-related odors. In an investigation of activation and odor conditioning in 3-day-old rats, it was found that stroking and amphetamine were equally effective in promoting odor-induced suckling (44). Additional work will be necessary to further characterize the role of birth stimuli in arousal processes and early learning.

Conclusions

Our findings show that sensory stimulation provides the necessary and sufficient conditions for initiating sustained, postpartum respiratory behavior, and directing suckling onset in rats. It is not known at this time whether our findings are specific to somatosensory afferent stimulation, or represent an adaptive behavioral response to sensory input in general. However, it is clear that perinatal stimulation, especially stimulation associated with birth, exerts important functional effects on the neonate.

Perinatal stimulation appears to play a predominant role in establishing behavioral and physiological organization in the newborn. The neonate possesses few totally independent regulations, and relies on stimulation from the mother for induction and maintenance of normal behavior and physiology (51). In this regard, physical stimulation appears to have particular biological relevance. Stroking alters basic biological processes of infant rats, including ornithine decarboxylase levels in brain, heart, liver (52-54), adrenocortical activity (55, 56), heart rate (57, 58), and blood pressure (59). Physical stimulation reduces pup body and brain temperatures by increasing ventilatory heat exchange, a maneuver which, in turn, increases convective and evaporative heat loss (46, 60). Pups require licking and other maternally-produced stimuli for recruitment of this physiological thermoregulatory system. Human babies show a surge of plasma catecholamines associated with the "stress of being born", a physiological response to labor and squeezing through the birth canal which has been strongly implicated in the neonate's adaptation to the postpartum world (61, 62).

In conclusion, the stimulation associated with gestation and birth plays a key role in assisting the fetus's transition to postnatal life, by inducing and canalizing specific postpartum behaviors, and thereby operating as a critical link in the chain of adaptive adjustments required for adaptation to the postnatal habitat. Fetal sensory experience appears to set into motion physiological processes that permit the onset of postpartum behavior and the expression of early learning.

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