General Article

THE PRENATAL ORIGINS OF BEHAVIORAL ORGANIZATION

By William P. Smotherman and Scott R. Robinson

Recognition that organisms have a developmental history, exhibit behavior that is uniquely suited to or constrained by features of their immediate environment, and adapt to new environments is central to current psychobiological thought. Unfortunately, these concepts have in the past been restricted largely to the study of postnatal behavioral development. However, recent extension of these concepts to the fetus as an active and interactive organism that resides within a specialized, intrauterine niche is proving to be a profitable approach toward understanding the origins of behavioral organization during development.

The existence of behavioral organization in the mammalian fetus implies that many of the motor, sensory, and learning abilities that typically are associated with the behavior of mature mammals have their origins in the prenatal period. However, the behavioral literature is replete with examples of experimental design, reasoning, and conclusions that convey the implicit assumption that the prenatal period is irrelevant to the postnatal expression, function, or development of behavior. Efforts to replace simplistic dichotomies in the study of behavior, such as the everlasting distinction between nature and nurture, with a more sophisticated perspective of behavioral epigenesis (Oyama, 1985) seem continually thwarted by the widespread lack of appreciation for the early development of behavior. For no portion of the life history of an animal is this lack of appreciation more evident than for the prenatal period.

A considerable body of evidence collected in the last decade is revising our view of the behavioral abilities of the fetus (Smotherman & Robinson, 1988a). Research on sensory development in human and nonhuman fetuses has demonstrated prenatal chemosensation (Pedersen, Greer, & Shepherd, 1988) and audition (Fifer & Moon, 1988) in utero. Research on the importance of experience during prenatal life (Smotherman & Robinson, 1987c) has documented the ability of fetuses to respond to changes in the intrauterine environment, to learn by association of stimuli, and to retain prenatal experiences into postnatal life. Research concerned with the patterning of prenatal behavior has discovered temporal rhythms in fetal activity, the emergence of motor coordination before birth, and the prenatal development of species-typical action patterns (Robertson, 1988; Smotherman & Robinson, 1987a). It has become apparent that the behavior of mammals has its roots in the prenatal period and that a complete understanding of behavioral development must include investigation of the behavioral capabilities of the fetus (Smotherman & Robinson, 1988c).

Any improvement in our understanding of prenatal behavioral development must be attributed to the new tools and concepts that recently have been applied to fetal investigation. Efforts to improve methods for directly observing healthy fetuses have provided experimental preparations that closely approximate an undisturbed fetal environment. Viewing prenatal behavior under such naturalistic conditions has revealed that the fetus is more than a passive passenger during gestation; it is an active organism responsive to changes within its intrauterine environment. Certain features of the fetal environment can facilitate the expression of organized behavior; other features constrain or inhibit behavioral production. Further, the behavior expressed by the fetus can have functional consequences. Some organized motor patterns emerge prenatally, in anticipation of postnatal function, whereas other patterns are expressed in utero as ontogenetic adaptations to the special demands of the intrauterine environment. These facts imply that the behavior of the fetus is inextricably connected to the environment in which it has developed, to the environment in which it currently exists, and to the succession of predictable environments that will follow in the course of its life history.

METHODOLOGICAL CONSIDERATIONS

Viviparity presents numerous obstacles to the study of prenatal behavior. Because the fetus is dependent for life support on placental connection to the mother's uterus, protocols for placing the fetus in a situation conducive to observation by necessity must include provisions for preparation of the mother. In humans, technological advances in external monitoring and real-time ultrasonography have made the maternal abdomen electronically transparent, permitting noninvasive description of fetal activity, postures, and simple movement patterns

Send correspondence and reprint requests to William P. Smotherman, Center for Developmental Psychobiology, Department of Psychology, SUNY-Binghamton, Binghamton, NY 13901.

Prenatal Origins of Behavioral Organization

(Prechtl, 1985). Methods for controlled manipulation of the sensory environment of human fetuses are less well developed, however, and opportunities for employing true experimental designs are limited by practical and ethical concerns.

These limitations can be circumvented by study of nonhuman fetuses, such as laboratory rats. Surgical blockade of the spinal cord insensitizes the lower abdomen of the pregnant rat and permits surgical exposure of the uterus while avoiding the activity-suppressing effects of general anesthesia (Smotherman & Robinson, in press). When immersed in a temperature-regulated physiological fluid, healthy fetuses may be directly observed (Figure 1). Studies that focus on the response of the fetus to naturally occurring changes within the uterus involve observation through the transparent wall of the uterus (in utero environment). Studies that require manipulation of the amniotic fluid surrounding the fetus are facilitated by delivery of the intact amniotic envelope into the saline bath while maintaining the integrity of the placental-uterine attachment (in amnion). Direct presentation of tactile or intraoral chemical stimuli to the fetus is possible after further removal of the chorionic and amnionic membranes that envelop the fetus, thereby suspending the fetus freely within the saline bath (ex utero). It is feasible to observe healthy fetuses in any of these environments from the time of the earliest embryonic movement (day 16 in laboratory rats) through the end of gestation (day 21). The advent of these improved methods is providing
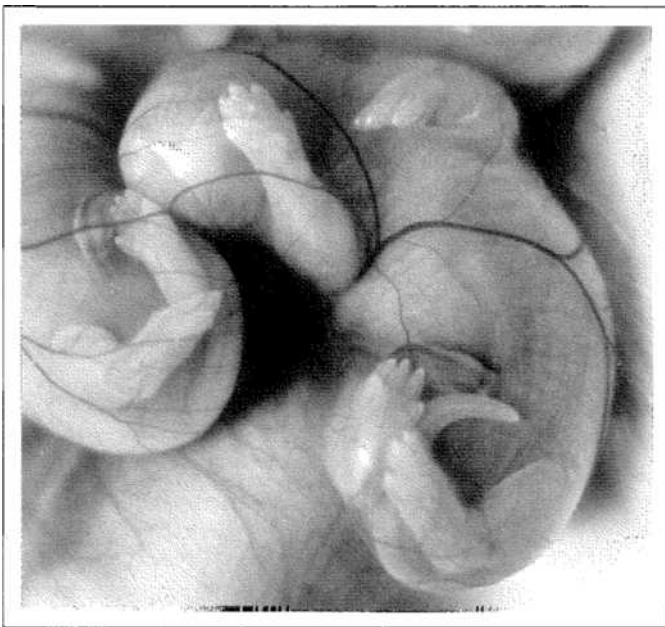

Fig. 1. Photograph of a 20-day-old rat fetus observed through the amniotic membrane. The fetus is engaged in synchronous head and forelimb movements. (From Smotherman, Richards, & Robinson, 1984)

a window on prenatal development through which the fetus may be studied in its natural environment.

MOTOR ACTIVITY BEFORE BIRTH

Fetuses move spontaneously within the uterus. This simple observation, which is self-evident to any pregnant woman, has been objectively documented in humans through the use of external fetal monitors and real-time ultrasonography (e.g., deVries, Visser, & Prechtl, 1985). However, the mere presence of motor activity, or motility as it is sometimes termed, in embryos does not imply behavioral organization. Many of the early behavioral embryologists, with noteworthy exceptions, were convinced that much of the motor activity of the fetus is reflexive, and that truly spontaneous movements lack pattern or orientation (Hamburger, 1963; Oppenheim, 1982). Such nonquantitative assessments of behavioral organization in the fetus have been perpetuated to the present day. For instance, a frequently quoted study of rat fetuses concluded that prenatal movements "give the impression of unintegrated, aimless movements in the sense that the movement of different parts, such as the head, anterior, posterior trunk and face and hindlimbs, tail and mouth are not related to each other as in clearly integrated action patterns such as walking" (Narayanan, Fox, & Hamburger, 1971). A consequence of such generalizations is that embryonic motor activity, while useful as an index of neural and muscular development, has been viewed widely as an epiphenomenon of the developing nervous system. This perspective has created a qualitative distinction between prenatal and postnatal behavior.

Among the early behavioral embryologists, undoubtedly the strongest proponent of the opposing view that prenatal behavior is critically important in the development of postnatal behavior was Zing-Yang Kuo. In a series of studies beginning in the 1930s with chick (*Gallus domesticus*) and duck (*Anas platyrhyncos*) embryos (Kuo, 1967) that pioneered the modern study of prenatal behavioral development, Kuo qualitatively described numerous instances of organized motor patterns that are present before hatching and are associated with presumptive sensory events in the embryo's environment within the egg. Among Kuo's conclusions are: (a) Organs begin to function while only in a rudimentary form; (b) the configuration of body structures influences the patterns of movement that are expressed during development; (c) non-organismic, external factors also influence action patterns of the embryo; and (d) the embryo is continually subjected to self-produced and external stimuli throughout development. For example, the avian embryo exhibits combined movements of the bill, head, wings, legs, and tail that emerge during the second week of incuba-

William P. Smotherman and Scott R. Robinson

tion. The occurrence of these movements is influenced by events within the egg environment, such as contractions of the amnion or movements of the yolk sac. As the period of incubation draws to a close, general embryonic activity gives way to stereotypic prehatching and hatching movements, including head-tucking and pipping (Oppenheim, 1973). These movements are configured by the relative position of the head and wings and are directed toward and limited by specific features of the external environment, namely the shell. Observations such as these led Gottlieb and Kuo (1965, p. 187) to conclude: "The above facts would seem to support the view that the ontogeny of behavior is gradual and continuous and that sequences of action occurring in embryo are significant precursors to the 'preadapted' quality of action patterns in postnatal life."

RESPONSE TO ENVIRONMENTAL CHANGE

Considerable evidence now exists to support Kuo's suggestion that fetuses can sense and alter their behavior in response to conditions within their immediate environment. In some respects, the prenatal environment of the developing mammal is buffered from perturbations arising in the environment outside the mother. On the other hand, the internal milieu is subject to considerable variation during gestation, and in most species the fetus must co-occupy a niche with littermates that share the same needs for space and life support (Smotherman & Robinson, 1988f). The amniotic fluid that surrounds each individual fetus, for example, is subjected to both physical modification (fluctuation in fluid volume and viscosity) and chemical alteration (short-term and long-term variation in composition resulting from changes in maternal diet and fetal physiology) throughout gestation. Experimentation has confirmed that rat fetuses are responsive to both physical and chemical modification of their amniotic fluid environment.

Rat fetuses begin to exhibit spontaneous movement on day 16 of gestation. During the first days of fetal activity amniotic fluid increases in volume, providing a relatively open space between the fetus and the surrounding membranes enveloping the fetus. Amniotic fluid achieves its peak in volume around day 19 and diminishes rapidly over the last two days of gestation, nearly disappearing by term (day 21). Overall fetal activity reaches a peak at the time of maximum fluid volume, but remains high through term. However, other aspects of fetal behavior in utero change qualitatively as amniotic fluid becomes scant and the free space surrounding the fetus disappears. Behavioral organization is evident in movement synchrony, which involves simultaneous movement of two or more body regions of the fetus. Movement syn-

chrony occurs infrequently on days 16–17, but on days 18–20 the incidence of synchrony far exceeds levels that can be ascribed to chance association of independent movements, indicating the emergence of an underlying coordination of motor activity. Interestingly, the rate of synchronous movement is substantially less than predicted by chance when fetuses are observed within the uterus on the last day of gestation (day 21). But the ability of fetuses to continue to exhibit behavioral organization is revealed by delivering the fetus outside the uterus into an unconfining fluid environment (ex utero). Under these conditions the rate of synchronous movements is well above chance levels. These environmental manipulations illustrate how behavioral organization, as evidenced by movement synchrony, exists but is not expressed by motorically immature fetuses under conditions of physical restraint within the uterus (Smotherman & Robinson, 1988b).

We have further explored fetal sensory responsiveness by presenting chemical stimuli to fetuses under controlled conditions. Presentation of chemical fluids to immature rats has been made possible through development of intraoral cannulation techniques (Hall & Rosenblatt, 1977). These procedures involve installing a fine polyethylene tube in the mouth of the fetus and connecting the free end to a syringe, permitting delivery of fluids in microliter volumes at specified times (Smotherman & Robinson, in press).

A variety of chemical fluids elicit behavioral responses in rat fetuses as early as day 17 of gestation (Smotherman & Robinson, 1988a). Early responses consist of an immediate increase in overall activity following infusion and a subsequent decrease in movement over the ensuing 30–60 s. Fetuses continue to respond to infusions through term, although the magnitude of the behavioral activation and the pattern of activity vary with age. In addition to a general effect on fetal activity, more specific patterns of behavior are elicited by infusions in older fetuses (days 20–21). Facial wiping, for example, is a stereotypic, species-typical pattern of behavior involving movement of the forepaws in contact with the face, which closely resembles behavioral patterns employed by adult rats during grooming or aversion sequences (Smotherman & Robinson, 1987a). In the rat fetus, facial wiping is consistently elicited by infusion of a variety of solutions, such as extracts of lemon (Figure 2), mint, citral, and cyclohexanone. The stretch response is a second fetal action pattern that is elicited only by infusions of milk (bovine light cream, which is similar in composition to rat milk). The stretch response is characterized by an extension of the body trunk and rear legs and is similar to the behavior exhibited by neonatal rat pups in response to milk letdown at the nipple (Lau & Henning, 1985). Both the facial wiping and stretch responses exhibit a sudden

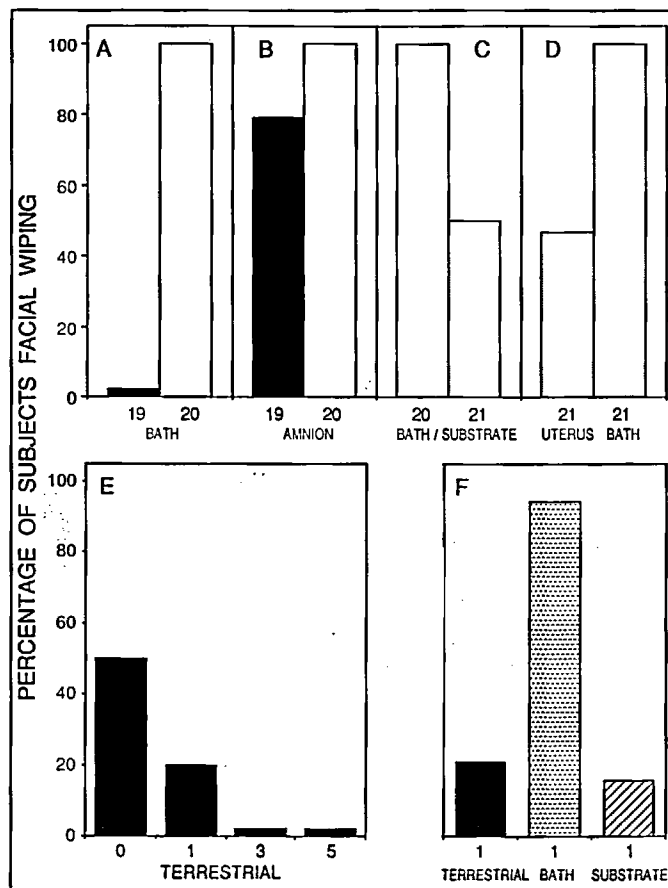Prenatal Origins of Behavioral Organization

Fig. 2. Expression of facial wiping by the rat fetus and neonate in response to intraoral lemon infusion in different environmental contexts. (A) Facial wiping emerges abruptly between gestational days 19 and 20 when infusions are administered to fetuses suspended in a physiological saline solution. (B) Infusion elicits facial wiping on gestational day 19 when fetuses are tested within the amniotic sac. (C) Fetuses are first responsive to the presence of a solid substrate on day 21 of gestation. (D) Increased physical restraint within the uterus suppresses the expression of facial wiping at term. (E) After birth, facial wiping gradually disappears when pups are infused in a terrestrial environment. (F) Immersion of pups in a buoyant fluid medium reinstates facial wiping on postnatal day 1, but testing pups on a submerged substrate within the fluid medium inhibits wiping.

ontogenetic onset, emerging over a period of 1–2 days late in gestation.

The existence of distinctive and reliable responses such as facial wiping, to stimulation has permitted the experimental assessment of prenatal sensory function. One feature shared by all of the solutions that elicit facial wiping is a strong olfactory component. Citral especially has been described as a tasteless odor cue. This commonality suggests that prenatal facial wiping may be governed by an olfactory sense. Other liquids, such as sucrose, saline, and quinine hydrochloride, which lack strong odors, fail to elicit facial wiping at concentrations tested

to date. Experimental transection of the main and accessory olfactory bulbs eliminates facial wiping while sparing the effect of infusion on overall activity. Presentation of cyclohexanone, a peppermint odor, in gas phase also elicits facial wiping. These behavioral findings augment physiological and anatomical evidence (Pedersen, Greer, & Shepherd, 1988) that fetuses possess a functional olfactory sense in utero.

The ability of the fetus to detect and respond to sensory stimuli potentiates the adaptive modification of behavior as a result of sensory experience. The question of whether fetuses are capable of learning, however, remained little more than a theoretical possibility until very recently, when techniques that permit manipulation of chemical cues within the fetus's amniotic milieu became available (see Smotherman & Robinson, 1987c, for a review). Amniotic fluid is an obvious source of chemical stimuli; because it surrounds and bathes the fetus, amniotic fluid gains access to the oral, pharyngeal and nasal cavities, and the vomeronasal organ. Immediately after birth, rat pups exhibit a preference in a two-choice situation for amniotic fluid collected from siblings over fluid from unrelated rats. Discrimination of amniotic fluid, therefore, may be involved in the development of kin recognition (Hepper, 1987). Amniotic fluid has also been demonstrated to play a role in directing the first attachment to the nipple by newborn rats. During parturition, the mother licks her perineum and ventrum, and thereby distributes amniotic fluid onto the teats (Dollinger, Holloway, & Denenberg, 1980). Under experimental conditions, pups attach to nipples that bear the odor of amniotic fluid but fail to attach to nipples that lack fluid (Blass & Teicher, 1980). These results suggest that fetal experience with amniotic fluid before birth may contribute to the development and expression of adaptive postnatal behavior.

Manipulation of the amniotic fluid environment has confirmed that prenatal experience with constituents of amniotic fluid can shape postnatal preferences. Substances present in the diet of pregnant rats, for instance, can be transported into the amniotic fluid. Hepper (1988) has shown that introduction of garlic into the food of pregnant rats results in offspring that exhibit an enhanced preference for garlic odor when tested 12 days after birth. More direct manipulation of the prenatal environment is possible through intra-amniotic injection. Injection of citral (a lemon odor) into the fluid, in conjunction with immediate postnatal exposure to citral, induces a preference in pups to attach to nipples painted with citral (Pedersen & Blass, 1982). Injection of other odor cues (orange, apple) into the amniotic fluid also can influence postnatal orientation and drinking preferences in juvenile and young adult rats (Hepper, in press; Smotherman & Robinson, 1987c). The studies cited previously all em-

William P. Smotherman and Scott R. Robinson

ployed prenatal training coupled with postnatal testing to assess evidence for fetal learning. Combining techniques for manipulating the amniotic environment with procedures for observing fetuses later in gestation has provided further evidence for the expression as well as acquisition of associations in utero. Pairing of a chemical stimulus with intraperitoneal injection of lithium chloride (LiCl) on day 17 alters the behavior of fetal rats that are re-exposed to the same stimulus two days later. Re-exposure to a mint stimulus paired earlier with LiCl results in a conditioned suppression of fetal activity. Similarly, pairing of sucrose with an infusion of lemon extract, which elicits a sudden increase in activity, produces conditioned behavioral activation upon re-exposure of the sucrose stimulus. In both instances, not only are changes in overall activity apparent, but specific behaviors expressed at the time of testing are similar in form to behaviors exhibited at the time of conditioning (Smotherman & Robinson, 1985). Studies such as these have conclusively demonstrated that fetuses are capable of associating stimuli and altering their behavior as a result of such experiences in utero.

Experimental demonstrations that rat fetuses possess olfactory and tactile senses that are functional as early as day 17 of gestation imply that events within the intrauterine environment contribute to the organization of behavior before birth (Smotherman & Robinson, 1987b). The fetal environment undergoes considerable change during gestation, with stimuli from the world external to the mother penetrating to the fetus indirectly, via maternal physiology (e.g., chemicals transported across the placenta) or transmitted directly through maternal tissues (e.g., acoustic and mechanical stimuli) (Smotherman & Robinson, 1988f). Interaction of external stimuli with events within the uterus, such as accidental transient compression of the umbilical cord, may be sufficient to support fetal learning under naturalistic conditions in utero. Because fetuses can retain and express associations in utero, it is evident that they are not only sensitive to immediate features of their environment, but produce behavior shaped by a history of interaction with that environment.

ENVIRONMENTAL CONSTRAINTS ON BEHAVIORAL PRODUCTION

Environmental context now is recognized as a factor that can either constrain or facilitate the expression of behavior during ontogeny. Experiments in which context is manipulated have indicated that the measurement of behavioral abilities is strongly influenced by the environment in which the subject is tested. It is a common finding that a particular behavior is expressed at an earlier age when the subject is tested in a supportive environ-

ment. For example, human infants normally progress from crawling locomotion to standing and then to walking. Thelen and colleagues (Thelen, 1988; Thelen & Fisher, 1982) have used this research approach to demonstrate that infants are capable of performing coordinated stepping movements shortly after birth. Immersion of the lower half of the infant's body in water provides buoyant support for the legs, permitting the infant to perform stepping movements at an age normally characterized by crawling. Similarly, Rochat and Stacy (1989) have traced the development of one-handed reaching directed toward external objects in human infants. Typically, bimanual reaching is expressed at an earlier point in development than one-handed reaching. But one-handed reaching occurs much more frequently in young infants (six months) when they are externally supported in a seated posture. A third example is taken from Stehouwer and Farel's work on the development of terrestrial locomotion in bullfrogs. Tadpoles swim with undulatory movements of the tail, whereas mature frogs utilize hindlimbs in either stepping or jumping locomotion. Even though the hindlimbs differentiate at a developmental stage well before the tadpole emerges from the water, hindlimb locomotor behavior is not ordinarily observed prior to emergence. Hindlimb stepping may be evoked in tadpoles up to five developmental stages earlier than normally expressed by placing them on a moist, hard surface (Stehouwer & Farel, 1984). These and many related findings indicate that the age-typical environment of immature organisms either constrain or lack appropriate stimuli to elicit behavioral abilities ordinarily associated with more mature individuals.

The opposite research strategy—searching for infantile or embryonic behavioral patterns in older individuals—has been adopted less often, but there are some remarkable examples nonetheless. Pfister, Cramer, and Blass (1986) have found that young rats will continue to suckle from a lactating female well after the normal weaning age (up to 70 days of age) if they remain associated with littermates of normal suckling age. Similarly, Lichtman and Cramer (1989) have shown that two daily exposures to an anesthetized milk-laden rat are sufficient to promote the expression of suckling behavior into the seventh postnatal week. These findings document that reproductively mature rats retain the motor patterns unique to suckling if tested in an appropriate context. Even more striking is the experiment of Bekoff and Kauer (1984) in which chickens, up to 63 days after hatching, are "folded" into an embryonic posture and replaced in an artificial glass egg. Even though they would ordinarily never encounter this environment, chickens exhibit head and neck movements that characterize the hatching movements of chick embryos in ovo. This experiment demonstrates that embryonic patterns of behavior may

not disappear from the repertoire, but simply fail to be expressed owing to lack of appropriate eliciting stimuli.

Context-dependent expression of facial wiping by the rat fetus and neonate may illustrate both of these research strategies (Smotherman & Robinson, 1989). Although virtually all rat fetuses exhibit the wiping response to lemon infusion on day 21 of gestation (Figure 2d, e), the incidence of facial wiping is reduced by 50% in newborn rat pups tested only a few hours after birth. Within 24 hours, the wiping response disappears almost completely and remains absent from the behavioral repertoire of pups until the end of the second week of life (Figure 2e). The neonatal disappearance of facial wiping coincides with the transition to a terrestrial environment and with the emergence of behavioral patterns, such as an active contact-righting response, that permit the pup to orient within such an environment.

The transient disappearance of facial wiping behavior in neonatal laboratory rats has recently been confirmed in other rodent species. Cotton rats (*Sigmodon hispidus*) and spiny mice (*Acomys cahirinus*), which bear offspring that are well-furred and ambulatory at birth, also exhibit the wiping response to lemon infusion well before birth. In these precocial species, the incidence of facial wiping in response to infusion diminishes as components of the contact-righting response and other stereotypic limb behavior, such as quadrupedal locomotor movements, emerge during late gestation. The result is a prenatal disappearance of the facial wiping response. These findings argue that interaction among elements of the behavioral repertoire and features of the environment influence the expression of behavior during the prenatal as well as the early postnatal period.

Although neonatal laboratory rats do not exhibit facial wiping when tested in an age-typical, terrestrial environment, placement in a buoyant fluid medium reinstates the expression of facial wiping in response to lemon infusion (Figure 2f). This effect may be interpreted either as the result of eliminating physical constraints on the expression of postnatal wiping or of recreating key features of the prenatal environment, facilitating the postnatal expression of a fetal pattern of response. Because testing immersed pups on a submerged substrate also inhibits the wiping response, the absence of facial wiping during the immediate postnatal period is related to the presence of a solid substrate. This inhibitory substrate effect evidently emerges prenatally. Rat fetuses exhibit a sharply reduced wiping response when tested on day 21 on a submerged surface (Figure 2c).

Recently, experiments employing contextual supports have similarly extended the earliest age at which fetuses will exhibit facial wiping. Testing fetuses that are freely suspended within a fluid medium originally indicated an abrupt emergence of the facial wiping response on day 20

of gestation. However, when lemon infusions are delivered to 19-day-old fetuses that remain within the intact amniotic envelope, facial wiping is elicited at least one day earlier in development (Figure 2a, b). Most likely, the enclosure of the amnion alters the posture of the fetus and thereby promotes the expression of the wiping response. The opposite effect is achieved when fetuses are tested on day 21 of gestation within the uterus. Under the conditions of intrauterine restraint existing at term (Figure 2d), the incidence of facial wiping in response to infusion is sharply reduced (Held & Smotherman, 1989).

The foregoing examples argue that descriptions of the behavioral phenotype of the fetus or neonate are not absolute, but are contingent on the environmental conditions present at the time of measurement. Manipulation of environmental context can enhance our understanding of behavioral organization when applied either to immature or mature members of a species. By either eliminating environmental constraints or providing contextual supports, precocial expression of behavioral organization may be facilitated in immature animals (Rochat & Stacy, 1989; Smotherman & Robinson, 1989; Stehouwer & Farel, 1984; Thelen & Fisher, 1982). Conversely, unique elements of the developing organism's repertoire are not necessarily eliminated as the individual matures and occupies new age-typical environments; fetal or neonatal behavioral patterns may simply fail to occur due to absence of appropriate environmental context. If context-dependent expression of behavior is a common feature of development, then the potential behavioral repertoire of an animal at any given age must be much larger than is normally expressed within an age-typical environment.

ANTICIPATION OR ONTOGENETIC ADAPTATION

Given an epigenetic approach to studying development and improved methods for discovering the behavioral repertoire of immature animals, behavioral sophistication in the neonate demands an ontogenetic explanation that is rooted in the prenatal period (Hall & Oppenheim, 1987; Smotherman & Robinson, 1988c). This is fundamentally a question of continuity: To what extent are the motor and sensory capabilities of the neonatal rat dependent upon prenatal behavioral development? Numerous studies have documented the behavioral ecology of the newborn rat (Alberts, 1986). Although born blind and deaf, the infant rat enters into an active symbiotic relationship with its mother to provide for its subsistence. Prenatal antecedents have been identified for many of the behavioral characteristics that contribute to this relationship. Young rats are capable of rudimentary locomotion and orientation toward the mother and siblings (Alberts & Brunjes, 1978; Altman & Sudarshan,

William P. Smotherman and Scott R. Robinson

1975); the rat fetus exhibits head and limb motor synergies characteristic of postnatal locomotion (Bekoff & Lau, 1980). Pups rely heavily on olfaction for orientation and recognition (Coopersmith & Leon, 1988); olfaction is a functional sense in utero and can serve as the basis for fetal discrimination between different odor stimuli (Smotherman & Robinson, 1987c). Location of the nipple is specifically facilitated by an odor component of pup saliva (Pedersen & Blass, 1981); odor components of amniotic fluid, to which the fetus is exposed during late gestation, function to direct the first nipple attachment after parturition (Pedersen & Blass, 1982). Attachment to the nipple is facilitated by rooting behavior of the pup (Hall & Williams, 1983); rooting may be elicited in the fetus by perioral tactile stimulation. Suckling behavior of the pup consists of rhythmic mouth movements followed by a stereotypic stretch response upon milk letdown (Lau & Henning, 1985); the sequence of rhythmic mouth activity and the stretch response are elicited by intraoral infusion of milk to the fetus (Smotherman & Robinson, 1987a). Elimination by the newborn rat requires maternal anogenital licking, which is promoted by the leg-extension response (LER) (Moore & Chadwick-Dias, 1986); the LER is elicited in utero by tactile stimulation of the anogenital region (Smotherman & Robinson, 1988d). Olfactory information present during bouts of suckling by the newborn can influence olfactory-based preferences in adult reproductive (Fillion & Blass, 1986) or ingestive behavior; fetuses demonstrate an ability to form associations based on olfactory stimuli present in utero and to retain these associations into adulthood (Smotherman & Robinson, 1985,1987c).

Close scrutiny of one example of fetal behavior illustrates the anticipation of postnatal behavior in prenatal activity. Neonatal rats do not readily exhibit forward locomotion, but do exhibit oriented movement in the form of pivoting or punting (Altman & Sudarshan, 1975). Punting locomotion is sufficient to enable neonatal rats to approach preferred objects such as the nipple and to regulate their position relative to littermates in the nest (Alberts & Cramer, 1988). The motor pattern of punting consists of the pup turning its head in one direction while simultaneously sweeping the contralateral foreleg in the opposite direction. Because the rear legs serve as a point of anchor, extension of one foreleg and flexion of the other result in a pivoting motion in the direction the head is turned (Figure 3). Punting is a characteristic stage in the development of quadrupedal locomotion in altricial mammals, but it is not simply an immature form of walking, as it involves a unique synergy of head and limb movement. Slow motion examination of videotape records of rat fetuses on day 20 of gestation indicates that the motor pattern of punting, as distinct from the walking step cycle, is also expressed before birth (see Figure 1).
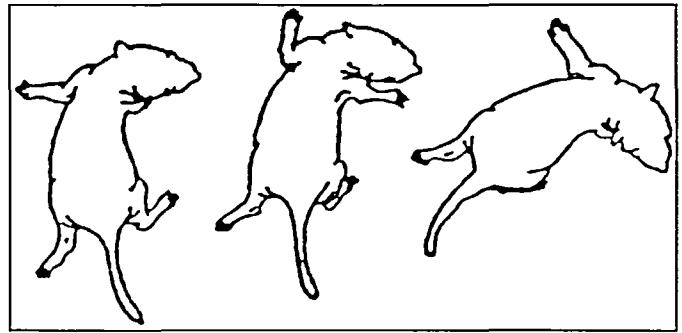

Fig. 3. Early locomotion by punting can be broken down into three units: (a) turning the head to the right; (b) pulling the right foreleg out from under the head and placing it to the right; (c) pushing the shoulder region to the right with the left forelimb. (From Altman & Sudershan, 1975).

Further, head and forelimb movements necessary for punting are synchronized earlier than any other combination of movements. Punting thus illustrates how a form of behavior that is first expressed in a functional context by the neonatal rat emerges during the prenatal period. Whether or not behavioral continuity exists between prenatal and postnatal life is no longer in question, but only the extent to which postnatal behavior has its origins before birth.

But the developing organism not only prepares for adult life; it also survives within and must adapt to a particular environment that may exist for a brief period of early development. The fetus, for example, inhabits an intrauterine niche that is not constant and occasionally poses hazard to fetal well-being (Mann, 1986; Smotherman & Robinson, 1988f). If the behavior of the fetus exhibits greater organization than once thought, then the existence of behavioral adaptations that promote survival within the specialized intrauterine environment may be expected. Behavioral or anatomical structures that promote survival of immature organisms during a limited period of development have long been recognized in species that undergo metamorphosis (Gould, 1977) and are termed ontogenetic adaptations (Alberts, 1987; Oppenheim, 1984). A putative ontogenetic adaptation that has been identified in ultrasound studies of human fetuses is turning to the vertex position (head down) immediately before parturition, an orientation that is achieved by organized limb and body movements of the fetus (Suzuki & Yamamuro, 1985). Sensitivity of the human fetus to acoustic stimuli such as human speech has been suggested to promote parental recognition and facilitate bonding, adaptive processes that begin immediately after birth (DeCasper & Fifer, 1980; Fifer & Moon, 1988).

The stereotypic fetal response to hypoxia induced by umbilical cord compression may function as an ontogenetic adaptation in rodent fetuses (Robinson & Smother-

man, 1989; Smotherman & Robinson, 1988e). Placement of a microvascular clamp on the umbilical cord produces a stereotypic response in the rat fetus that consists of three consistently identifiable phases of behavior. Immediately following occlusion of umbilical circulation, fetal activity is suppressed and a pronounced deceleration in heart rate is evident. This period of inactivity gives way to hyperactivity consisting predominantly of exaggerated flexions of the body trunk. The overall rate of fetal movement during this phase increases to nearly five times that of spontaneous activity. The hyperactive phase ultimately is followed by a secondary suppression of fetal activity as trunk movements decline in frequency and rostral extensions of the head ("head-tosses") become evident. The hypoxic response is apparently an organized pattern of behavior: the alteration in fetal behavior is virtually immediate following cord compression, and the occurrence of the principal components of the motor response, namely trunk flexions and head tosses, are patterned in time and in spatial relation to other body regions. Further, the pattern of behavioral activation and cardiac deceleration that characterizes the fetal hypoxic response is exactly contrary to the motor and physiological response of neonatal rats deprived of oxygen (Eden & Hanson, 1987). Therefore, the organization inherent in the fetal hypoxic response is unlikely to exhibit continuity with any postnatal pattern of behavior. These motor patterns may be adaptive in utero in alleviating accidental cord compression produced by fetal posture or pressure against siblings or maternal structures.

NICHE-CONTINGENT EXPRESSION OF BEHAVIORAL ORGANIZATION

The previous sections argue that an understanding of behavioral development is incomplete without knowledge of the history of the organism, points of interaction between the organism and its current environment, and new environments that the organism will inhabit in the future. Such information fosters a view of the developing organism as occupying a succession of ontogenetic niches (West & King, 1987). Periods of adaptation to a particular niche are interrupted by transitions to subsequent niches. Development within an ontogenetic niche is characterized by increasing behavioral diversity and organization, while periods of transition between niches may result in temporary slowing or regression of measures of developmental improvement. Viewing ontogeny as a process that incorporates adaptation to a succession of niches predicts not only that disruption in behavioral organization will occur during the period of adjustment that immediately follows a sudden transition to a novel adaptive mode, but also that a period of behavioral dis-

organization may occur in anticipation of an imminent transition between niches.

Undoubtedly the best example of this process is provided by the dramatic transition of birth. In the rat, this transition is presaged by changes in fetal behavior that would seem to indicate a reduction in overall behavioral organization. Although the rat fetus at term remains dependent on its prenatal life support system, it exhibits diminished behavioral components of the hypoxic response to umbilical cord occlusion (less activity, delayed peak of activity, fewer lateral trunk movements). Although central and peripheral neural structures subserving sensory and motor responsiveness continue to mature, rat fetuses on day 21 are less responsive to novel olfactory stimulation and exhibit fewer spontaneous movements and less synchronous activity within the uterus. It is also at this age that the presence of a hard substrate begins to inhibit the expression of fetal facial wiping. Thus, evidence for fetal behavioral organization assessed only at this age (a reasonable approach from a strictly maturational approach), would lead to inaccurate conclusions about fetal behavioral abilities.

Fetal study presents a unique opportunity for understanding behavioral development. At its inception, fetal movement is characterized by randomness (Robinson & Smotherman, 1988). Late in gestation, considerable organization is evident and species-typical action patterns are expressed. The task of developmental research is to chart the events that lead randomly ordered elements of movement to become organized into an integrated system of behavior. As more information becomes available, it is increasingly apparent that the expression of organized behavior by the fetus is not rigidly determined, but rather is contingent on both historical and immediate circumstances. The influence of prenatal sensory experience on subsequent behavior demands that the fetus be seen in historical perspective. For instance, much of the behavioral sophistication evident in the neonate is directly traceable to the prenatal period. At the same time, behavioral production by the fetus is sensitive to both the quality of impinging sensory stimuli and the physical context of the prenatal environment. Recognition of the roles of context, anticipatory development, and ontogenetic adaptation argues that a broader perspective of the life history and ecology of the fetus must be incorporated into an adequate theory of behavioral development.

REFERENCES

Alberts, J.R. (1986). New views on parent-offspring relationships. In W.T. Greenough & J.M. Juraska (Eds.), *Developmental neuropsychobiology* (pp. 449–478). New York: Academic Press.

Alberts, J.R. (1987). Early learning and ontogenetic adaptation. In N.A. Krasnegor, E.M. Blass, M.A. Hofer, & W.P. Smotherman (Eds.), *Perinatal development: A psychobiological perspective* (pp. 11–37). Orlando: Academic Press.

Alberts, J.R., & Brunjes, P.C. (1978). Ontogeny of thermal and olfactory determinants of huddling in the rat. *Journal of Comparative and Physiological Psychology, 92*, 897–906.

Alberts, J.R., & Cramer, C.P. (1988). Ecology and experience: sources of means and meaning of developmental change. In E.M. Blass (Ed.), *Handbook of behavioral neurobiology, Vol. 9, Developmental psychobiology and behavioral ecology* (pp. 1–39). Plenum Press.

Altman, J., & Sudarshan, K. (1975). Postnatal development of locomotion in the laboratory rat. *Animal Behaviour, 23*, 896–920.

Bekoff, A., & Kauer, J.A. (1984). Neural control of hatching: fate of the pattern generator for the leg movements of hatching in post-hatching chicks. *Journal of Neuroscience, 11*, 2659–2666.

Bekoff, A., & Lau, B. (1980). Interlimb coordination in 20-day-old rat fetuses. *Journal of Experimental Zoology, 214*, 173–175.

Blass, E.M., & Teicher, M.H. (1980). Suckling. *Science 210*, 15–22.

Coopersmith, R., & Leon, M. (1988). The neurobiology of early olfactory learning. In E.M. Blass (Ed.), *Handbook of behavioral neurobiology, Vol. 9, Developmental psychobiology and behavioral ecology* (pp. 283–308). New York: Plenum Press.

DeCasper, A.J., & Fifer, W.P. (1980). Of human bonding: newborns prefer their mothers' voices. *Science, 208*, 1174–1176.

deVries, J.I.P., Visser, G.H.A., & Prechtl, H.F.R. (1985). The emergence of fetal behaviour. II. Quantitative aspects. *Early Human Development, 12*, 99–120.

Dollinger, M.J., Holloway, W.R., Jr., & Denenberg, V.H. (1980). Parturition in the rat (Rattus norvegicus): Normative aspects and the temporal patterning of behaviours. *Behavioural Processes, 5*, 21–37.

Eden, G.J., & Hanson, M.A. (1987). Maturation of the respiratory response to acute hypoxia in the newborn rat. *Journal of Physiology, 392*, 1–9.

Fifer, W.P., & Moon, C. (1988). Auditory experience in the fetus. In W.P. Smotherman & S.R. Robinson (Eds.), *Behavior of the fetus* (pp. 175–190). Caldwell, NJ: Telford Press.

Fillion, T., & Blass, E.M. (1986). Infantile behavioural reactivity to oestrous chemostimuli in Norway rats. *Animal Behaviour, 34*, 123–133.

Gottlieb, G., & Kuo, Z.-Y. (1965). Development of behavior in the duck embryo. *Journal of Comparative and Physiological Psychology, 59*, 183–188.

Gould, S.J. (1977). *Ontogeny and phylogeny*. Cambridge, MA: Belknap Press.

Hall, W.G., & Oppenheim, R.W. (1987). Developmental psychobiology: Prenatal, perinatal, and early postnatal aspects of behavioral development. *Annual Review of Psychology, 38*, 91–128.

Hall, W.G., & Rosenblatt, J.S. (1977). Suckling behavior and intake control in the developing rat pup. *Journal of Comparative and Physiological Psychology, 91*, 1232–1247.

Hall, W.G., & Williams, C.L. (1983). Suckling isn't feeding, or is it? A search for developmental continuities. In J.S. Rosenblatt, R.A. Hinde, C. Beer, & M.C. Busnel (Eds.), *Advances in the study of behavior, Vol. 13* (pp. 218–254). New York: Academic Press.

Hamburger, V. (1963). Some aspects of the embryology of behavior. *Quarterly Review of Biology, 38*, 342–365.

Held, F.P., & Smotherman, W.P. (1989, October). *Context-dependent expression (or lack of expression) of a species-typical action pattern—facial wiping.* Paper presented at the meeting of the International Society for Developmental Psychobiology, San Francisco, CA.

Hepper, P.G. (1987). The amniotic fluid: An important priming role in kin recognition. *Animal Behaviour 35*, 1343–1346.

Hepper, P.G. (1988). Adaptive fetal learning: Prenatal exposure to garlic affects postnatal preferences. *Animal Behaviour, 36*, 935–936.

Hepper, P.G. (in press). Prenatal exposure learning in the rat. *Quarterly Review of Experimental Psychology B*.

Kuo, Z.-Y. (1967). *The dynamics of behavior development: An epigenetic view*. New York: Random House.

Lau, C., & Henning, S.J. (1985). Investigation of the nature of the "stretch response" in suckling rats. *Physiology and Behavior, 34*, 649–651.

Lichtman, A.H., & Cramer, C.P. (1989). Relative importance of experience, social facilitation, and availability of milk in weaning rats. *Developmental Psychobiology, 22*, 347–356.

Mann, L.I. (1986). Pregnancy events and brain damage. *American Journal of Obstetrics and Gynecology, 155*, 6–9.

Moore, C.L., & Chadwick-Dias, A.-M. (1986). Behavioral responses of infant rats to maternal licking: Variations with age and sex. *Developmental Psychobiology, 19*, 427–438.

Narayanan, C.H., Fox, M.W., & Hamburger, V. (1971). Prenatal development of spontaneous and evoked activity in the rat. *Behaviour, 40*, 100–134.

Oppenheim, R.W. (1973). Pre-hatching and hatching behavior—a comparative and physiological consideration. In G. Gottlieb (Ed.), *Studies on the development of behavior and the nervous system: Behavioral embryology* (pp. 163–244). New York: Academic Press.

Oppenheim, R.W. (1982). The neuroembryological study of behavior: Progress, problems, perspectives. In R.K. Hunt (Ed.), *Current topics in developmental biology, Vol. 17, Neural development*, part 3 (pp. 257–309). New York: Academic Press.

Oppenheim, R.W. (1984). Ontogenetic adaptations in neural development: Toward a more "ecological" developmental psychobiology. In H.F.R. Prechtl (Ed.), *Continuity of neural functions from prenatal to postnatal life* (pp. 16–30). Philadelphia: Lippincott.

Oyama, S. (1985). *The ontogeny of information*. Cambridge: Cambridge University Press.

Pedersen, P.E., & Blass, E.M. (1981). Olfactory control over suckling in albino rats. In R.N. Aslin, J.R. Alberts, & M.R. Peterson (Eds.), *The development of perception: Psychobiological processes* (pp. 359–381). Hillsdale, NJ: Erlbaum.

Pedersen, P.E., & Blass, E.M. (1982). Prenatal and postnatal determinants of the 1st suckling episode in albino rats. *Developmental Psychobiology, 15*, 349–355.

Pedersen, P.E., Greer, C.A., & Shepherd, G.M. (1988). Early development of olfactory function. In E.M. Blass (Ed.), *Handbook of behavioral neurobiology, Vol. 8, Developmental psychobiology and developmental neurobiology* (pp. 163–203). New York: Plenum Press.

Pfister, J.F., Cramer, C.P., & Blass, E.M. (1986). Suckling in rats extended by continuous living with dams and their preweanling litters. *Animal Behaviour, 34*, 415–420.

Prechtl, H.F.R. (1985). Ultrasound studies of human fetal behaviour. *Early Human Development, 12*, 91–98.

Robertson, S.S. (1988). Mechanism and function of cyclicity in spontaneous movement. In W.P. Smotherman & S.R. Robinson (Eds.), *Behavior of the fetus* (pp. 77–94). Caldwell, NJ: Telford Press.

Robinson, S.R., & Smotherman, W.P. (1988). Chance and chunks in the ontogeny of fetal behavior. In W.P. Smotherman & S.R. Robinson (Eds.), *Behavior of the fetus* (pp. 95–118). Caldwell, NJ: Telford Press.

Robinson, S.R., & Smotherman, W.P. (1989, October). *Prenatal behavioral heterochrony in altricial and precocial rodents: A novel approach for identifying ontogenetic adaptations of the fetus.* Paper presented at the meeting of the International Society for Developmental Psychobiology, San Francisco, CA.

Rochat, P., & Stacy, M. (1989, April). *Reaching in various postures by 6- and 8-month-old infants: The development of mono-manual grasp.* Paper presented at the meeting of the Society for Research on Child Development, Kansas City, KS.

Smotherman, W.P., Richards, L.S., & Robinson, S.R. (1984). Techniques for observing fetal behavior in utero: A comparison of chemomyelotomy and spinal transection. *Developmental Psychobiology, 17*, 661–674.

Smotherman, W.P., & Robinson, S.R. (1985). The rat fetus in its environment: Behavioral adjustments to novel, familiar, aversive and conditioned stimuli presented in utero. *Behavioral Neuroscience, 99*, 521–530.

Smotherman, W.P., & Robinson, S.R. (1987a). Prenatal expression of species-typical action patterns in the rat fetus (*Rattus norvegicus*). *Journal of Comparative Psychology, 101*, 190–196.

Smotherman, W.P., & Robinson, S.R. (1987b). Prenatal influences on development: Behavior is not a trivial aspect of fetal life. *Journal of Developmental and Behavioral Pediatrics, 8*, 171–176.

Smotherman, W.P., & Robinson, S.R. (1987c). Psychobiology of fetal experience in the rat. In N.A. Krasnegor, E.M. Blass, M.A. Hofer, & W.P. Smotherman (Eds.), *Perinatal development: A psychobiological perspective* (pp. 39–60). Orlando: Academic Press.

Smotherman, W.P., & Robinson, S.R. (Eds.). (1988a) *Behavior of the fetus*. Caldwell, NJ: Telford Press.

Smotherman, W.P., & Robinson, S.R. (1988b). Behavior of rat fetuses following chemical or tactile stimulation. *Behavioral Neuroscience, 102*, 24–34.

Smotherman, W.P., & Robinson, S.R. (1988c) Dimensions of fetal investigation. In W.P. Smotherman & S.R. Robinson (Eds.), *Behavior of the fetus* (pp. 19–34). Caldwell, NJ: Telford Press.

Smotherman, W.P., & Robinson, S.R. (1988d). Fetal expression of the leg extension response to anogenital stimulation. *Physiology and Behavior, 43*, 243–244.

Smotherman, W.P., & Robinson, S.R. (1988e). Response of the rat fetus to acute umbilical cord occlusion: An ontogenetic adaptation? *Physiology and Behavior, 44*, 131–135.

Smotherman, W.P., & Robinson, S.R. (1988f). 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.

Smotherman, W.P., & Robinson, S.R. (in press) Accessibility of the rat fetus for psychobiological investigation. In G.A. Barr, M.A. Hofer, & H. Shair (Eds.), *Developmental psychobiology: Current methodological and conceptual issues* New York: Oxford University Press.

Smotherman, W.P., & Robinson, S.R. (1989). Cryptopsychobiology: The appearance, disappearance and reappearance of a species-typical action pattern during early development. *Behavioral Neuroscience, 103,* 246–253.

Stehouwer, D.J., & Farel, P.B. (1984). Development of hindlimb locomotor behavior in the frog. *Developmental Psychobiology, 17,* 217–232.

Suzuki, S., & Yamamuro, T. (1985). Fetal movement and fetal presentation. *Early Human Development, 11,* 255–263.

Thelen, E. (1988). On the nature of developing motor systems and the transition from prenatal to postnatal life. In W.P. Smotherman & S.R. Robinson (Eds.), *Behavior of the fetus* (pp. 207–224). Caldwell, NJ: Telford Press.

Thelen, E., & Fisher, D.M. (1982). Newborn stepping: An explanation for a "disappearing reflex." *Developmental Psychology, 18,* 760–775.

West, M.J., & King, A.P. (1987). Settling nature and nurture into an ontogenetic niche. *Developmental Psychobiology, 20,* 549–562.