

# Cryptopsychobiology: The Appearance, Disappearance, and Reappearance of a Species-Typical Action Pattern During Early Development

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Late in gestation, intraoral infusion of lemon elicits a facial wiping response from rat fetuses. This facial wiping response is isomorphic with that of older pups and adult rats exposed to aversive oral stimulation. Most studies of the postnatal development of aversive responses have demonstrated that facial wiping does not appear in the repertoire of rat pups until the second postnatal week. In certain test situations, however, wiping can be elicited from neonatal rats. This fact suggests that the expression of facial wiping by neonates is constrained or facilitated by the environmental conditions present at the time of testing. In this report, a series of seven experiments is described that document the wiping response of rat fetuses and pups in age-typical environments, and an environmental constraint hypothesis is examined. Examination of the ontogeny of facial wiping in this manner highlights issues that should be addressed in studies of behavioral continuity between the prenatal and the postnatal periods.

Recent investigations of the behavior of the rat fetus have traced the early ontogeny of certain species-typical action patterns, originally described from the behavior of pups or adult rats, to the prenatal period. These demonstrations have important implications for understanding the origin of the considerable behavioral sophistication now recognized in neonatal rats (see Hall & Oppenheim, 1987, for review). Among the action patterns that have been identified in the fetus are the stretch and leg-extension responses. Stretches occur after intraoral infusion of milk to fetuses on Day 20 or 21 of gestation (Smotherman & Robinson, 1987) and appear isomorphic with the stretch responses exhibited by pups after milk ejection at the nipple (Lau & Henning, 1985). The leg-extension response is performed by infant rats during episodes of anogenital licking by the mother (Moore & Chadwick-Dias, 1986) and can be elicited from 20-day-old fetuses by tactile stimulation of the anogenital region with a soft brush (Smotherman & Robinson, 1988a). Because these action patterns are expressed late in gestation and immediately after birth, there is little doubt that the behavior is continuous across the transition from prenatal to postnatal life. This conclusion agrees with other recent experiments that have demonstrated a role for prenatal experience in the ontogeny of postnatal behavior. Hepper (1987) for instance, found that cesarean-delivered rat pups prefer the odor of amniotic fluid collected from their own mother to the fluid collected from a strange female. Amniotic fluid is known to facilitate the

first nipple attachment by newborn rats (Blass & Teicher, 1980) and to influence adult sexual behavior (Fillion & Blass, 1986), and it may play a role in kin recognition.

A third action pattern that has been described in the rat fetus is facial wiping, which can reliably be elicited by intraoral infusion of novel solutions, such as lemon (Smotherman & Robinson, 1987). Although young rat pups perform a variety of foreleg motions in response to aversive oral stimulation (Johanson & Shapiro, 1986), facial wiping has previously been described only for older pups (during the second postnatal week) and adult rats. Because there is an apparent lack of facial wiping in very young pups, the continuity between the wiping behavior of fetuses and the aversive behavior of older rats is equivocal.

In the present study, the question of continuity between prenatal and postnatal facial wiping in the rat (*Rattus norvegicus*) was investigated in a series of experiments. Specifically, these experiments were designed to (a) replicate the original finding of an abrupt prenatal emergence of facial wiping on Day 20 of gestation, (b) examine whether the wiping response is specific to the lemon stimulus, (c) test for the expression of wiping in pups 0-11 days after birth, and (d) explore a specific mechanical hypothesis to explain the apparent discontinuity between prenatal and neonatal facial wiping.

## Method

### Subjects

Subjects were the progeny of female Sprague-Dawley rats bred to Long-Evans males (Charles-River Laboratories, Wilmington, Massachusetts). The day of conception was determined by examining vaginal smears taken daily during the period of breeding (the date of the first sperm-bearing smear was defined as Day 0 of gestation). Female rats were housed in groups of three in polycarbonate cages (33 × 38 × 10 cm) within a temperature- and humidity-controlled

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colony room under a 12:12 hr light/dark photoperiod regimen (lights on at 0700) with ad-lib food and water. Pregnant rats were rehousing individually 24 hr prior to birth (on Day 21.5 of gestation). The condition and care of breeding rats and experimental subjects at all times met or exceeded established guidelines for animal care established by the National Institutes of Health (1985) and the Animal Behavior Society (1986).

Fetuses were tested on Day 19, 20, or 21 of gestation. Pups were tested on Day 0 (the day of birth), 1, 3, 5, 7, 9, or 11. On Day 0, testing was conducted within 4 hr of either vaginal or cesarean delivery. Because all testing occurred between 1300 and 1700, fetuses on Day 21, cesarean-delivered pups, and vaginally delivered pups on Day 0 were all approximately the same postconceptional age.

### *Maternal Preparation*

The age at which subjects were to be tested dictated the type of maternal preparation. Fetuses were observed after the pregnant rat received a chemomyelotomy, which produces irreversible blockade in the L1-L2 region of the spinal cord, eliminating sensation from the lower body (see Smotherman & Robinson, in press, for detailed description of this procedure). Following chemomyelotomy, the rat was placed in a holding apparatus and immersed in a warm (37.5 °C) bath containing a buffered isotonic saline solution (Locke's solution). The uterus was externalized through a midline laparotomy to remain freely suspended within the saline bath (Smotherman, Richards, & Robinson, 1984).

Rat pups were tested after vaginal or cesarean delivery. Vaginal births were not interrupted to obtain subject pups. Completion of parturition was determined when mothers had ceased grooming activities and had assumed a nursing posture. Cesarean section was performed after humanely sacrificing pregnant rats at term by rapid cervical dislocation. Conceptuses were quickly removed from the uterus and cleared of surrounding membranes, after which time the umbilical cord was tied and separated from the placenta. Immediately after cesarean delivery pups were placed in a warm (32 °C), humid incubator.

### *Subject Preparation*

Individual fetuses were observed following removal from the uterus into the surrounding saline bath, with care taken to preserve umbilical circulation and placental attachment to the uterus. The extraembryonic membranes were carefully stripped away to permit implantation of the cannula and clearer observation of fetal behavior. A maximum of 2 subject fetuses were observed from each mother. Fetuses ( $n = 138$ ) were tested after a delay of at least 20 min after maternal preparation. On the day of testing, 4-6 pups were removed from the home cage to provide subjects for study. Pups were placed together in a square plastic dish (12 × 12 cm) within the incubator. Pups ( $n = 205$ ) were tested after a standard period of separation from the mother, which was arbitrarily set at 60-90 min.

### *Presentation of Stimuli*

Fetuses were experimentally exposed to the solutions of lemon (prepared as a 1:3 dilution from pure lemon extract, Schilling brand), mint (prepared in identical fashion from mint extract, Schilling brand), citral (1:200 dilution of pure extract, obtained from McCormick & Co., Hunt Valley, Maryland), sucrose (either 10% or 30% solutions, w/v), or isotonic saline (Smotherman & Robinson, 1988b) presented at ambient temperature (22 °C). Pups were exposed to the same solution of lemon. Presentation of solutions was accomplished by infusion through an intraoral cannula. Cannulas were implanted in

fetuses immediately after removal from the uterus and in pups shortly after initial placement in the incubator. The cannula consisted of a length of polyethylene (PE-10) tubing (diameter = 0.61 mm) inserted through the midline of the lower jaw with the flanged tip resting on the dorsal surface of the tongue in an anterior position (Kehoe & Blass, 1985). A length of PE-50 tubing connected the free end of the cannula to a micrometer syringe. With this infusion apparatus a precise volume of the test solution could be delivered directly into the mouth of the subject fetus or pup. Infusions consisted of a 1-2-s pulse of 20  $\mu$ l (Days 19-Postnatal Day 1), 30  $\mu$ l (Day 3), 50  $\mu$ l (Days 5-7), or 60  $\mu$ l (Days 9-11) of the test solution. All experiments involved delivery of a single infusion during a 2-min period of observation at the beginning of the second minute.

### *Testing Environments*

Fetuses were tested in one of two environments, designated ex utero and substrate. Fetuses ex utero were observed while suspended within the warm saline bath and connected by way of the umbilical cord to the placenta and uterus (Smotherman & Robinson, 1986, 1988b). In the ex utero condition, subject fetuses lacked systematic orientation to the external surface of the uterus, the ventrum of the mother, or the holding apparatus, although they occasionally came into contact with these surfaces. In the substrate condition, fetuses were positioned with the feet and ventrum in contact with a hardware cloth substrate, which was held at a 45° angle above the floor of the bath and remained completely submerged. Fetuses always were positioned beneath the water surface. Fetal position on the substrate was maintained by manipulating the cannula with forceps without placing strain on the umbilical cord.

Pups were tested in one of three environments, designated terrestrial, water, and substrate. In the terrestrial condition, individual pups were placed on a horizontal floor in a 12 × 12 cm dry plastic dish within the incubator. When tested in water, pups were immersed to the neck in the same saline bath used for observation of fetuses. The head was held above the water's surface by gripping the intraoral cannula with forceps. Pups suspended in this way typically adopted a supine floating posture (Figure 1, left). For testing on a substrate, pups were placed in the saline bath and immersed to the neck, with the feet and ventrum positioned in contact with the hardware cloth substrate (Figure 1, right). For pups, the substrate remained fixed at a 45° angle, with the top edge of the substrate 5-10 mm above the surface of the water. Pups were positioned on the substrate so that the head was maintained above and the body below the water surface.

### *Behavioral Method*

Fetuses and pups were observed directly, and instances of behavior, including facial wiping, were categorized and entered into a microcomputer serving as a real-time event recorder. This procedure is highly reliable in recording the incidence of fetal movements and accurately shows the activity of young rat pups (Smotherman et al., 1984). Facial wiping is a distinctive action pattern that is readily distinguished from other patterns of limb movement during observation sessions. Typically, wiping consists of a noncontact stroke in which both forelegs are positioned lateral to the head, followed by a contact stroke in which the forepaws are simultaneously drawn forward while remaining in contact with the face (see description and photograph, Smotherman & Robinson, 1987). Instances of facial wiping were operationally defined as any movement in which one or both forepaws contacted the face during motion in a rostral direction. Although the total number of movements as well as the frequency of wiping were recorded, for the purpose of this report

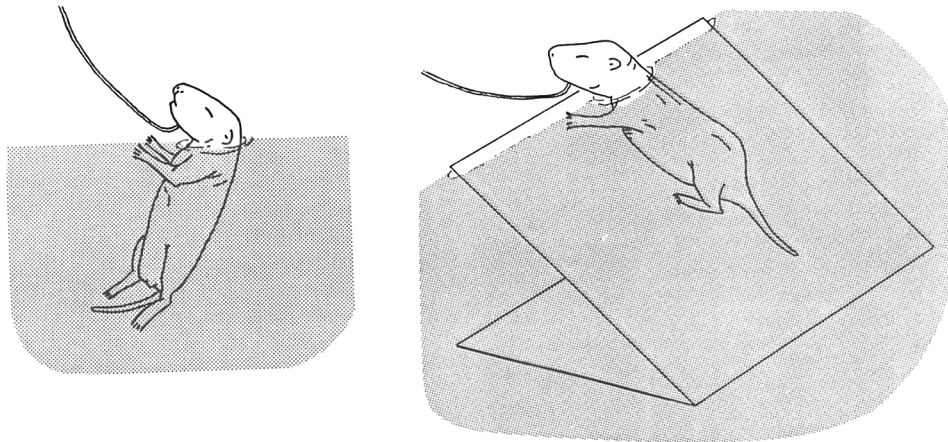


Figure 1. Line drawings depicting the testing environments of rat pups suspended in the saline bath (left) or positioned on a submerged substrate within the bath (right).

data were reduced to reflect simply the presence or absence of facial wiping by an individual fetus or pup.

### Experimental Design and Analysis

No more than one fetus from a pregnant rat was assigned to the same experimental condition. Similarly, no more than one pup from a litter was assigned to the same condition. These restrictions were employed to eliminate the confounding of treatment with litter effects. In different experiments, conditions comprised 10–24 subjects. In some instances, data were collected in independent replications involving different fetuses and pregnancies. When replicates were employed, they were found not to differ. Therefore, data from replicate groups were collapsed for analysis of treatment effects. In all experiments, contingency tables were constructed to compare the number of subjects exhibiting with the number failing to exhibit facial wiping under different experimental conditions. Chi-square tests of independence (Siegel, 1956) were employed to judge significance.

### Experiment 1: Emergence of Fetal Response to Lemon

This experiment was designed to replicate our earlier finding that fetuses exhibit a species-typical action pattern in response to intraoral infusion of lemon (Smotherman & Robinson, 1987). That study identified the abrupt emergence of facial wiping between Day 19 and Day 20 of gestation. Fetuses in Experiment 1 were infused with lemon or isotonic saline on Day 19 or Day 20 and observed ex utero.

No wiping was observed in response to saline infusions at either gestational age. Although wiping after lemon infusion was also absent on Day 19 of gestation, lemon infusions reliably elicited facial wiping on Day 20,  $\chi^2(1, n = 44) = 30.6, p < .001$  (Figure 2). Lemon typically resulted in a flurry of facial wiping that occurred within a few seconds of the moment of infusion. These data successfully replicate the

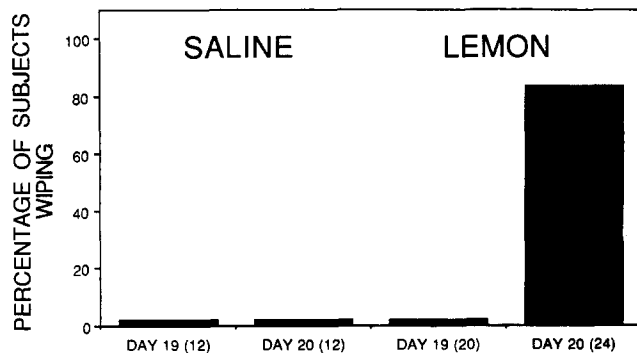


Figure 2. Facial wiping response of rat fetuses tested ex utero to lemon infusion. (Values in parentheses [in this and all subsequent figures] refer to the number of subjects in each experimental condition.)

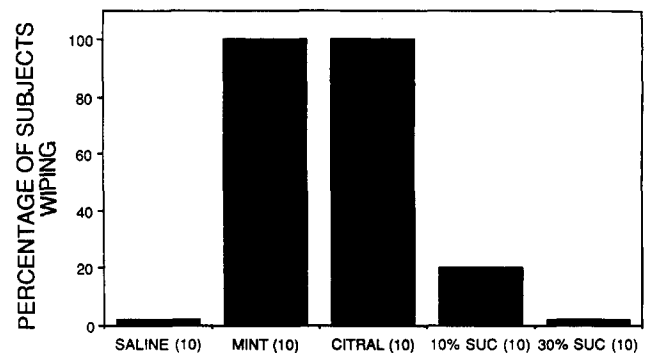


Figure 3. Facial wiping response of Day 21 rat fetuses tested ex utero to various solutions. (SUC = sucrose.)

previous finding of an abrupt ontogenetic onset of facial wiping.

### Experiment 2: Stimulus Specificity of Fetal Wiping Response

Lemon is effective in eliciting facial wiping on Day 20. Previous data suggest that wiping is just as effectively elicited by infusion of lemon on Day 21 (Smotherman & Robinson, 1987). The purpose of this experiment was to extend this finding and assess the generality of stimulus-induced facial wiping. In Experiment 2, Day 21 fetuses were observed *ex utero* after infusion of one of five solutions: saline, mint, citral, 10% sucrose (w/v), or 30% sucrose.

As on Day 20, saline infusion failed to elicit any facial wiping on Day 21. Precisely the opposite pattern of results was evident following infusion of mint or citral, which elicited wiping from all fetuses tested. Only low rates of wiping were evoked by a 10% solution of sucrose and no wiping by a more concentrated sucrose solution (Figure 3). The expression of facial wiping following infusion of these solutions was indeed different,  $\chi^2(4, n = 50) = 43.5, p < .001$ . It is evident that the fetal wiping response is elicited by stimuli other than lemon, but not by all sapid solutions.

### Experiment 3: Postnatal Disappearance of the Wiping Response

Fetuses exhibit facial wiping before birth when exposed to appropriate forms of stimulation. If fetal facial wiping were ontogenetically continuous with adult aversion behavior (Grill & Berridge, 1985), one might expect to be able to elicit facial wiping in rat pups at early postnatal ages. This expectation is consistent with recent reports that rat pups on Days 1 and 3 exhibit "forelimb-flailing," a rapid movement of both forepaws past the mouth and nose, but fail to exhibit "paw-treading" or "chin-scraping" in response to infusions of citric acid and quinine hydrochloride (Johanson & Shapiro, 1986). Although there are difficulties in reconciling different descriptions of pup aversive responses, it is clear that aversion sequences, as described for adult rats, are incompletely expressed during the first few days after birth. The purpose of this experiment was to measure the expression of facial wiping by using the same procedures and nomenclature developed for fetuses. In Experiment 3, pups were infused with lemon while in a warm, humid incubator. Testing in this terrestrial environment took place on Day 0 (following cesarean or vaginal delivery), Day 1, or Day 3.

Experiment 2 showed that on Day 21 virtually all fetuses exhibit facial wiping following infusion. Results of this experiment indicated that within a few hours after birth there was a discernible reduction in the tendency for newborn pups to wipe in response to lemon. No difference was apparent in the wiping response of cesarean-delivered and vaginally delivered pups; data for these groups were pooled for analysis. On Day 1, expression of wiping was much reduced, and by Day 3 wiping was completely absent,  $\chi^2(2, n = 57) = 10.4, p < .01$  (Figure 4). Pups appear to lose the tendency to respond to infusion with facial wiping, which occurs in con-

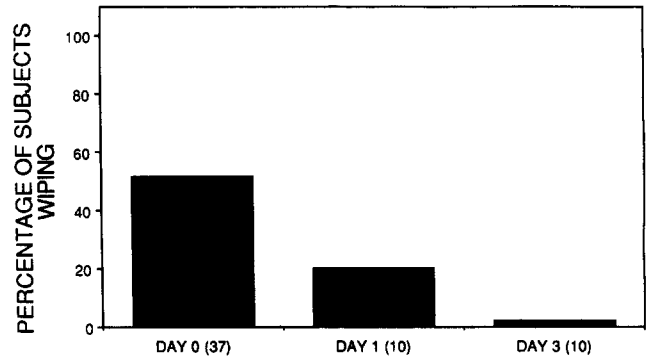


Figure 4. Facial wiping response of rat pups tested in a terrestrial environment to lemon infusion.

cert with a gradual adaptation to the terrestrial environment that takes place after birth. The incomplete expression of an adultlike aversion response, as exemplified in this experiment by infrequent facial wiping, has been interpreted as evidence for "immaturity in pups younger than 12 days of the neural substrates subserving these aversive responses" (Johanson & Shapiro, 1986, p. 593). Regardless of the underlying mechanism, it is clear that facial wiping disappears in a terrestrial environment as neonates perform facial wiping less frequently than fetuses.

### Experiment 4: Facial Wiping by Pups in Water

Although the expression of facial wiping is less common immediately after birth, as demonstrated in Experiment 3, there are indications that the incidence of wiping by neonates may be increased under specific experimental conditions. Newborn mice, for instance, exhibit adultlike facial grooming if externally supported in an upright posture that frees the forepaws (Golani & Fentress, 1985). This observation suggests that the environmental context of testing may be an important factor in the expression of species-typical action patterns. The topography of the wiping response within a terrestrial environment requires that the forelegs be freed from supporting the pup to permit wiping. The postural adjustments required for the pup to balance on its hindquarters, freeing the forelegs, are beyond the motor competence of newborn pups. In order to test the influence of postural constraint on the reduced expression of facial wiping by neonates, pups in Experiment 4 were suspended in a buoyant water medium, in which the forelimbs were not involved in postural support. As in the previous experiment, pups were tested in water on Day 0, following either cesarean or vaginal delivery, Day 1, or Day 3.

Suspension in water resulted in more pups at all ages performing facial wiping in response to lemon infusion. When pups of all ages were considered as a group, wiping was observed in 69% of pups tested in water but only 37% of pups in the terrestrial environment. However, the effect of testing pups in water was influenced by the age of pups,  $\chi^2(2, n = 68) = 11.3, p < .01$  (Figure 5). On Day 0, only a slight increase in the incidence of wiping was evident in both cesarean and vaginally delivered pups. Testing in water had its

most pronounced effect on Day 1, when 90% of pups exhibited wiping compared with only 20% in a terrestrial environment. However, testing in water had less influence on wiping on Day 3. The results of this experiment indicate that testing pups in water, thereby freeing the limbs from a support function, is effective in increasing the incidence of facial wiping.

#### Experiment 5: Facial Wiping by Pups in Contact With a Submerged Substrate

One feature that is present in a terrestrial environment but absent in the water bath is the existence of a hard substrate on which the pup must support itself. If the presence of a solid substrate is sufficient to inhibit the expression of wiping, then simultaneous immersion of pups and placement on a substrate should eliminate the effect of testing in water on facial wiping. This hypothesis was explicitly tested in Experiment 5, in which lemon infusions were delivered to pups on a submerged substrate on Day 0, Day 1, or Day 3.

When tested in water on an angled substrate, only 10% of all pups exhibited facial wiping. This reduction in wiping was evident at all three ages (Figure 6) but was most pronounced on Day 1. A chi-square analysis (involving recombination of a portion of the data from Experiments 3, 4, and 5) comparing the incidence of facial wiping on Day 1 in the terrestrial, water, and substrate environments was significant,  $\chi^2(2, n = 50) = 26.0, p < .001$ . These experiments support the hypothesis that contact with a substrate, whether terrestrial or submerged, is responsible for inhibiting the expression of facial wiping by Day 1 rat pups.

#### Experiment 6: Postnatal Reappearance of the Wiping Response

By Postnatal Day 3, facial wiping is not exhibited by pups tested in a terrestrial environment. If prenatal and neonatal facial wiping is indeed continuous with the aversion behavior of adult rats, then lemon infusion should elicit facial wiping at a subsequent point in development. The purpose of this experiment was to document the earliest postnatal reappearance of facial wiping. Pups were tested at 2-day intervals beginning at Day 5 (Figure 7).

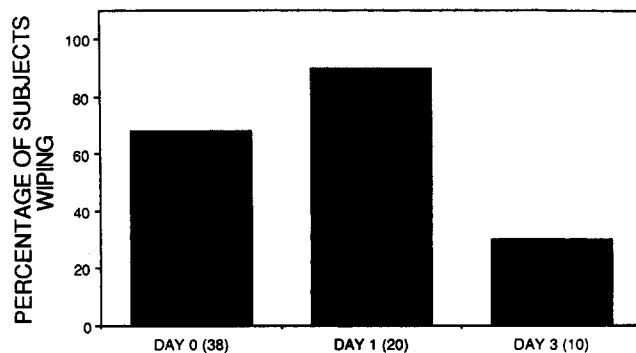


Figure 5. Facial wiping response of rat pups tested in the saline bath to lemon infusion.

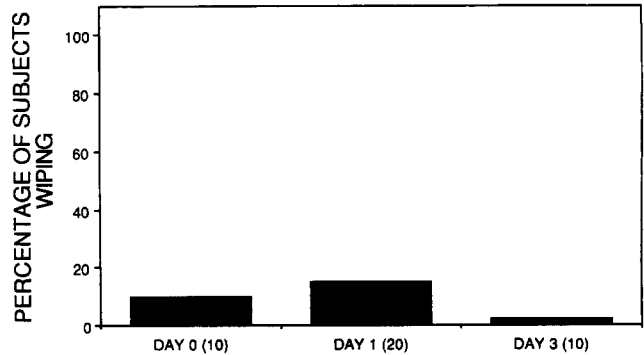


Figure 6. Facial wiping response of rat pups tested in water on a submerged substrate to lemon infusion.

Little or no facial wiping was evident in pups tested on Days 5, 7, and 9, but on Day 11 50% of the pups tested exhibited facial wiping,  $\chi^2(3, n = 40) = 13.3, p < .01$ . The reappearance of facial wiping on Day 11 is consistent with published descriptions of the ontogeny of aversive responses in rats (Johanson & Shapiro, 1986).

#### Experiment 7: Facial Wiping by Fetuses in Contact With a Substrate

Fetuses ex utero exhibit frequent facial wiping in response to lemon infusion. After birth, the incidence of wiping is reduced, apparently promoted by contact with a solid substrate. These two observations raise the question of whether fetuses would respond in the same way to the presence of a substrate by exhibiting lower rates of facial wiping. In Experiment 7, Day 20 or Day 21 fetuses were positioned on a substrate, while preserving the umbilical connection to the placenta, and received infusions of lemon.

The presence of a substrate affected facial wiping in an age-dependent fashion. Contact with a substrate had no discernible effect on Day 20; all of the fetuses presented with lemon at this age exhibited wiping. On Day 21, however, testing on a substrate resulted in a diminished wiping response to lemon,  $\chi^2(1, n = 20) = 7.1, p < .01$  (Figure 8). Under these conditions of testing, the wiping response of fetuses on Day 21 is virtually indistinguishable from that of pups on Day 0. Apparently, the rat fetus's response to a substrate emerges between Day 20 and Day 21 of gestation.

#### Discussion

These experiments provide new information about the early ontogeny of facial wiping behavior. Wiping in response to lemon exhibits an abrupt ontogenetic emergence on Day 20 of gestation. The absence of a wiping response to saline indicates that fetuses are responding not to the mechanical or thermal stimulation produced by the infusion but to the chemical characteristics of the solution that is infused. The absence of a wiping response on Day 19 cannot be attributed to an inability of the fetus to detect the lemon infusion, because fetuses at this age do respond to lemon with an increase in overall activity (Smotherman & Robinson, 1988b).

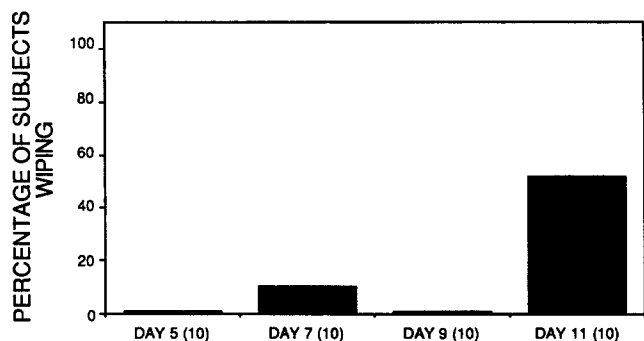


Figure 7. Facial wiping response of rat pups tested in a terrestrial environment to lemon infusion.

Similarly, the lack of a wiping response to sucrose solutions on Day 21 cannot be due to an inability of the fetus to sense this stimulus, because fetuses can be conditioned to respond to sucrose (Smotherman, 1987a). In contrast, facial wiping is consistently elicited on Day 21 by solutions of mint or citral. Facial wiping by the fetus therefore is not a specific response to lemon or a response that is elicited by all sapid solutions. Although evidence indicates the involvement of olfaction in the general behavioral response of fetuses to such solutions, the results of olfactory bulb transection experiments suggest that other sensory modalities (e.g., trigeminal pathways) are also involved in the fetal wiping response (Smotherman, 1987b).

Although Day 21 fetuses consistently exhibit facial wiping ex utero, Day 0 pups, which are the same postconceptional age, perform facial wiping far less often. The tendency to perform wiping in response to lemon is further reduced on Day 1. The factor that appears to be most influential in suppressing facial wiping on Day 1 is contact between the pup and a solid substrate. Even when tested in water, pups in contact with a submerged substrate exhibit wiping infrequently. The responsiveness of young rats to a substrate extends into the prenatal period, as evidenced by the reduced incidence of facial wiping by Day 21 fetuses tested ex utero on a substrate. The fact that wiping was observed in all fetuses tested on a substrate on Day 20, and in some older subjects, argues that the procedure involved in positioning a subject on the hardware cloth does not physically preclude the performance of the wiping response.

The developmental chronology of facial wiping suggests that several independent behavioral variables undergo transition during the late prenatal and early postnatal periods. The response to intraoral infusion changes suddenly on Day 20 of gestation with the first appearance of facial wiping. The tendency to exhibit wiping in age-typical environments, however, attains a peak during the prenatal period and is sharply reduced after birth. A different pattern of development is evident in the response to a substrate that suppresses facial wiping; a substrate response first appears on Day 21 of gestation and becomes more pronounced after birth. The proclivity of pups to alter their behavior on a substrate may be related to the early ontogeny of a righting reflex and negative geotaxis. A reasonable hypothesis, therefore, is that the de-

velopment of substrate-oriented and vestibular reflexes during the perinatal period results in a constraint of posture that interferes with the expression of facial wiping.

A postural constraint hypothesis argues that early during the postnatal period the pup's forelegs are preempted for a support function to maintain a stable, prone posture (Altman & Sudarshan, 1975) and are therefore unavailable for facial wiping. The results of this study are consistent with this hypothesis. On Day 0, pups exhibit some facial wiping in a terrestrial environment. This occurs at a time when their ability to maintain a prone posture is poorly developed and pups roll to their backs more readily, especially during the bouts of intense activity that occur after lemon infusion. When in a supine posture, the forelegs are freed from supporting the pup and become available for facial wiping. On Days 1 and 3, pups tested in a terrestrial environment do not wipe, a finding that agrees with a gradual improvement in the pup's ability to maintain a stable posture. It is interesting that facial wiping on Day 3 is not greatly facilitated by immersing pups in water. The reduced expression of wiping on Day 3 may indicate that postural constraint exerts an effect only on Day 1. Alternatively, postural constraint may exist on Day 3 but be overshadowed by a qualitatively different response of the Day 3 pup to immersion in water. Indeed, Day 3 pups were much more active when tested in water, a result suggesting that the supine posture of floating pups provokes a more pronounced righting reflex or that immersion elicits other competing behavioral responses that interfere with the expression of facial wiping.

Contact between the forepaws and a substrate, a nearly ever-present feature of the pup's relation to its terrestrial environment, may also have prenatal roots. The intrauterine environment undergoes dramatic changes immediately before parturition, including reduction in amniotic fluid and fetal growth. On Day 20, amniotic fluid completely bathes the fetus and provides a physical buffer between the fetus, its enveloping membranes, and the uterine wall. By Day 21, growth of fetuses and an almost complete disappearance of amniotic fluid result in the fetus's coming into more intimate contact with its siblings and the wall of the uterus (Smotherman & Robinson, 1988c). Reduction in free space within the uterus on Day 21 thus promotes an elastic bond between the fetus and the uterine wall. This bond between fetus and

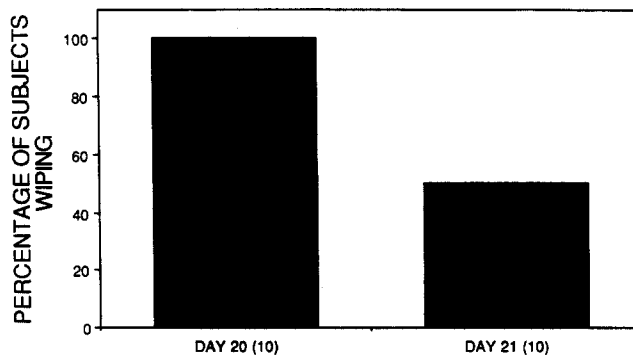


Figure 8. Facial wiping response of rat fetuses tested ex utero on a substrate to lemon infusion.

uterine substrate may be analogous to that of a pup gravitationally bound to a terrestrial surface. The appearance of a substratelike environment in utero coincident with the emergence of a fetal substrate response is intriguing. To our knowledge, however, the possible role of fetus-uterus interaction in the development of substrate-oriented responses has not previously been considered.

With the reappearance of facial wiping on Day 11, the development of the wiping response assumes a pattern of presence-absence-presence. Manipulation of the testing environment can effectively reinstate facial wiping during the period of its apparent absence. This strategy for uncovering organized motor patterns that have disappeared during development also has been adopted by other investigators. Thelen and Fisher (1982) argued that the familiar "stepping-reflex" of human neonates, which disappears by the second postnatal month, is in fact isomorphic with later walking behavior. Coordinated stepping movements can be elicited from 3-month-old infants, who normally show little evidence of stepping, when the effective mass of the legs is reduced by immersion in water (Thelen, Fisher, & Ridley-Johnson, 1984; Thelen & Fogel, in press). Bekoff and Kauer (1984) elicited stereotypic prehatching movements in chickens up to 61 days after hatching by folding the chicken into an embryonic posture within a glass egg, thereby recreating features of the chick's environment within the egg. These examples argue that the temporary disappearance of a movement pattern is not unique to this study of facial wiping but may be a common process in the ontogeny of motor behavior.

Erroneous conclusions may be drawn about the ontogeny of a behavioral pattern that is constrained by the testing environment and therefore appears to be absent from the animal's repertoire. It is common in developmental research for investigators to adopt a strategy that involves testing animals at progressively earlier ages. Typically, experiments are halted when an age is encountered at which the focal behavior is no longer evident. The conclusion frequently drawn from studies of this sort is that the ontogenetic origin of the behavior has been identified. As others have pointed out, however, early ontogeny can entail reversible changes in behavior (Golani, Bronchti, Moualem, & Teitelbaum, 1981; Golani & Fentress, 1985). The present study illustrates how the interaction between different behavioral variables during early development can result in a developmental pattern of presence-absence-presence that masks underlying behavioral continuity and obscures the true origins of a particular behavioral pattern.

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