VLF radiation which is confined to the earth-ionosphere cavity and which has the effect of magnifying the effective power, provided absorption losses are not high. If the cavity effect and local conditions together act to concentrate the effective power in the vicinity of some observers, it should not be impossible to reconcile this power level with the amount of power available in the fireball wake. Also, if the generation of surface acoustic waves in the upper audible range by the varying electric field acting on objects close to the observer is as effective as laboratory trials suggest, it should be possible to reduce the power levels by a further factor of at least 10^2.

To confirm the existence of VLF emission from meteor fireballs, it will be desirable to compile and disseminate annual lists of fireballs (*45*). Each occurrence should be timed as accurately as possible to ensure positive identification of fireball events on the chart records of VLF receiving stations engaged on other work, such as whistler detection. VLF energy from a meteor fireball should propagate globally in the earth-ionosphere duct and have a distinctive time/frequency spectrum compared to lightning discharges or nuclear bomb detonations in the atmosphere. It seems more than likely that VLF receiving networks established for nuclear test monitoring must have already recorded many meteor fireballs, but they may not have been identified for want of fireball sighting data.

In 1 year only about 50 fireballs as large as the New South Wales fireball enter the earth's atmospehre, and of these fewer than three are observed and reported, the remainder being over the sea or unpopulated areas or behind clouds. From any given inhabited region such a fireball event will be seen on average at intervals of 30 to 100 years, depending on the cloud cover statistics of the region.

To sum up, it now appears to be certain that meteor fireballs are perceived aurally by a significant number of observers. The energy transfer appears to occur at very low frequencies in the upper audio range emitted by the fireball as electromagnetic radiation. Further work is now indicated to determine more precisely the mechanisms of electrostatic-to-acoustic transduction involved and the conversion of energy into VLF radiation from the energy of turbulence in the fireball wake.

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Suckling

Elliott M. Blass and Martin H. Teicher

Among mammals, suckling is the only behavior that is universal and characteristic. Because of its vital importance for survival and its putative contribution to normal psychosexual development, suckling behavior has provided researchers with a rich source of theories and debates concerning the role of nature versus nurture in human behavior and the needs of the developing child. As the debates spent themselves, attention focused on the mechanisms that control suckling behavior, on its incidence and form of occurrence, on the events that precipitate and terminate it, on the way stress affects it, and on the way that suckling changes during the individual's development (*1*). Scientists and pediatricians alike became more sensitive to the pronounced individual variability among normal infants in the efficiency of suckling, and a number of investigators studied suckling in nonhuman primates (*2*) and other mammals (*3*) in search of general principles.

This effort revealed the multiple facets and functions of the suckling act. While the most obvious function of suckling is for the infant to obtain nutrients and fluids from the mother's milk, it has other vital functions as well. As a source of maternal contact, suckling seems to comfort the infant. For certain nonhuman mammals, it contributes to escape from predators. Some marsupial and rodent mothers (wood rats, for example) exploit their pups' tenacious grip

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on the nipple to transport the litter from nest to nest at danger's onset (4). Similar predator-avoidance strategies are practiced by some smaller primates (5). Suckling also protects the infant from certain diseases since maternal milk, especially the colostrum formed during the earliest stages of lactation, contains antibodies that help defend the vulnerable newborn against infection (6).

Summary. Suckling is the only behavior that is common among mammals. In newborn albino rats it is originally elicited by amniotic fluid deposited by the mother during parturition. Subsequent suckling is stimulated by saliva deposited on the nipples by the infant rats. Internal controls over the volume of milk suckled do not appear until infant rats are about 2 weeks of age at which time gastric distension, milk, systemic dehydration, and the intestinal hormone cholecystokinin suppress milk intake derived through suckling. The development of controls over suckling appetite appears to parallel that of consummatory control. Until about 2 weeks of age infant rats choose to suckle a nonlactating nipple with the same frequency as a lactating nipple. Thereafter, the lactating nipple is unanimously chosen. These studies suggest differences and commonalities in the suckling behavior of laboratory rats and other mammals.

In order to understand the determinants of suckling behavior and use the term with precision, we describe the components of the suckling sequence that are common to infant mammals, changes in suckling behavior during development, and differences among species in suckling behavior. We also discuss experiments analyzing the controls of suckling in a representative mammal, the albino rat, and indicate commonalities apparent in other species, including the human infant, in order to provide a framework through which the stimuli controlling this fundamental behavior can be identified and understood.

The Suckling Sequence

The components and sequence of each suckling act (Fig. 1) may be described as follows: (i) establishing maternal contact, (ii) locating and attaching to the nipple, (iii) suckling, (iv) milk withdrawal and swallowing, and (v) cessation of suckling. This sequence and changes in the controls are discussed below.

Establishing maternal contact. Investigators (7, 8) have described three stages of contact development. At first the mother is the exclusive initiator of contact. Newborn cats and dogs, for example, are placed in the nest where the mother stays for long periods. In the case of laboratory rats, the mother may spend 80 to 90 percent of her time hovering over her nested young during the days immediately after parturition (9). Vocalizations of a cold or isolated kitten or pup may bring the mother back at this stage (10). By 15 days of age, when rat pups are well insulated with fur and fat and their eyes have opened, they are rarely retrieved by the dam.

The second stage, according to Rosenblatt and Lehrman (7), is characterized by mutual contact initiation. Rats and cats often leave the nest to approach the mother. Attraction to rat mothers appears to be predominantly under olfactory control. Leon (11) has demonstrated that rats 14 to 26 days of age are attracted to a volatile substance, caecotrophe, which rat mothers secrete in large quantities in the caecal portion of the large intestine at about the third week after birth and excrete with fecal material (12). Albino rats use their eyes, which open at about 14 days of age, to locate the mother when she is outside of the nest (13). Cats apparently do not need olfactory cues to locate the nest but can rely on thermal gradients (14).

In the third stage of the nursing-suckling relation, contact is initiated almost exclusively by the infant. In the laboratory, rat and cat mothers actively avoid the persistent young. Under natural circumstances the mother can better control her availability to the infants. Carnivore mothers, for example, leave their cubs or pups for long periods to hunt. They begin to feed the young partially digested prey by regurgitating their own meal in the lair. Next they return several times with fresh kill for the young who are then finally taken to hunt (15). Thus, although the source of contact initiation has shifted to the pup, the mother, in the wild, controls her availability as well as that of the nutrients offered to the developing animals.

Locating and attaching to a nipple. Once contact with the mother is estab-

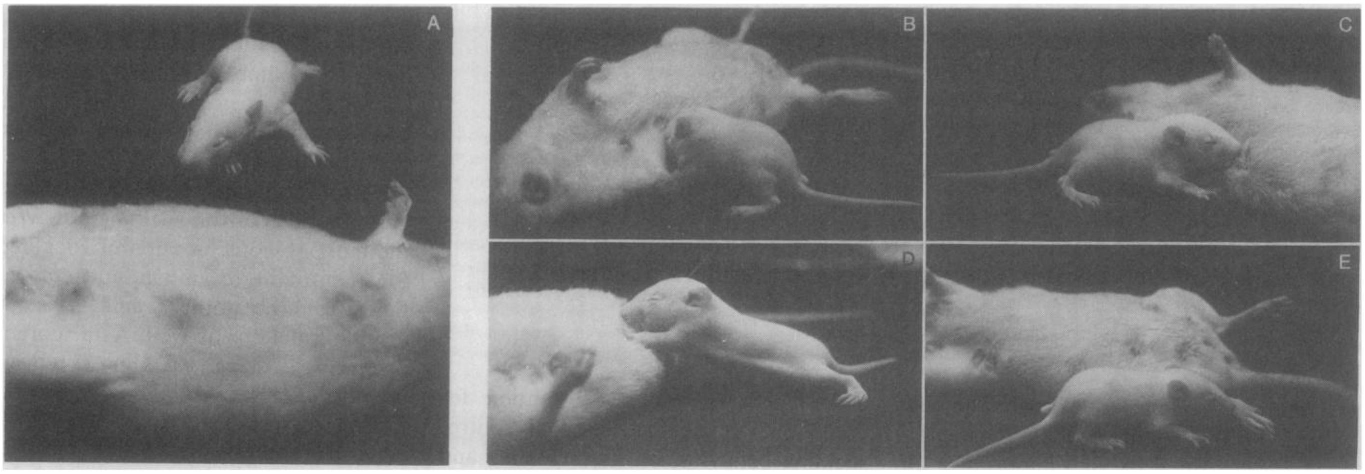

Fig. 1. The suckling sequence of a 10-day-old albino rat approaching and suckling its anesthetized mother. (A) The pup approaches its mother slowly at first and moves its head from side to side (scanning) until it is 3 to 4 cm from her; it then approaches more quickly. (B) The infant, using all four limbs, propels itself along the mother's body, scanning the surface with its snout until a nipple is contacted. While the infant continues to push with its hind limbs, it also flexes its neck and probes the nipple by tongue extention and vigorous licking. As the nipple becomes erect, the pup takes it deep into the oropharynx. (C) Suckling in the absence of milk let-down. The pup is at rest and except for occasional muscular twitches or repositioning, will suckle the nonlactating nipple continuously for up to 8 hours. (D) The "stretch" or milk withdrawal response. This response occurs when the engorged teat releases milk into the back of the mouth and allows the pup to drain the nipple of its contents. (E) Suckling termination. The sated infant has left the nipple and moves away from the dam.

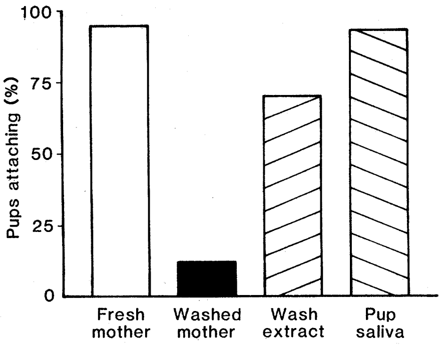

Fig. 2. The percentage of 4- and 5-day-old pups attaching to the nipple of their anesthetized mother under four conditions: on the fresh mother, that is, an anesthetized mother whose nipple area had not been altered; on the washed mother whose nipples were washed as described in (*19*); after wash extract was applied to the nipples; and after pup saliva, obtained from suckling-deprived pups or from an extract of the submaxillary and sublingual glands of siblings, was applied to the washed nipples ($N = 34$; $P < .001$). [Modified from Teicher and Blass (*18*)]

lished, infants must locate a nipple, attach to it, and suckle. In the case of young rats, contact elicits a characteristic "rooting" response through which the infant, using swimming-like motions, moves quickly across the mother's body, scanning the surface by moving its head from side to side until the pup contacts a nipple. At this time the scanning stops, and the pup probes the nipple area, extending its tongue and vigorously licking the nipple until it becomes erect, whereupon the pup suckles and becomes immediately quiescent.

Nipple attachment is not necessarily a simple feat for altricial mammals such as rats, which are blind at birth. Moreover, there are often more members of a litter than available teats, and rat mothers, unlike carnivore or primate mothers, do not assist their young to the nipple. Newborn rats, which are not only blind but also deaf at birth, must rely on chemical and tactile stimuli to provide information about nipple properties and location. We (*16*) investigated the possibility that rats identify the nipple through its contrast with the mother's fur. We eliminated the contrast by shaving the ventral surface of anesthetized rat dams and placed the infants in contact with the mother. The same number of rats attached to the nipples of the shaved mother as to the normal one, although there was a slightly longer latency (about 30 seconds) in the case of the shaved dam. The results were similar when we examined the role of maternal temperature and thermal gradients (*16*). The nipple and skin temperature of anesthetized dams was lowered from 34°C to 31° or 28°C (and quickly restored at the end of a test). Attachment to nipples was essentially unaffected. In fact, attachment on shaved dams whose temperature was cooled to 31°C was also normal throughout the entire nursing-suckling period of 30 days. Thus, attachment withstood marked alterations of the mother's thermo-tactile qualities. We then turned to the chemical senses.

The role of olfaction. We thought that olfaction might contribute to the process of nipple location and attachment because of reports (*17*) that suckling rats deprived of their olfactory sense, either by surgical removal of the olfactory bulbs or through destruction of the olfactory mucosa by intranasal injections of zinc sulfate, no longer suckled. We conducted the converse experiment. Instead of presenting a normal mother to pups that could not smell, we presented an altered mother to pups with normal olfaction (*18*).

If olfaction is important in locating and attaching to the mother's teat, then removing a scent coating the nipples should disrupt suckling. Returning the scent should reinstate suckling. To test this hypothesis, we studied how infant rats attached to the nipples of their anesthetized mother under three conditions: (i) immediately after anesthetization, when she bears the full complement of cues that elicit suckling in the nest; (ii) after her nipples were washed; and (iii) after an extract of the washing solution or some other substance was applied to the nipples. Complete washing of all 12 nipples took about 2 hours (*19*).

We found that 5-day-old rats, placed in contact with their anesthetized mother, located and attached to her nipples (Fig. 2). Washing the nipples, however, essentially eliminated attachment, indicating that some substance must coat the rat's nipples in order for attachment to occur. To ascertain that failure to suckle was not due to an aversive taste in the chemicals used to wash the nipples, a few drops of the washing solution were placed on each teat. Subsequent drying by evaporation resulted in normal attachment (*20*). Failure to attach reflects more than the inability of the infant rat to locate the nipple since attachment still did not occur when the rats were held in contact with the washed nipple. When an extract of the wash was applied to the nipples, however, suckling was reinstated. In fact, it was generally difficult to distinguish between the rat's behavior on the mother before she was washed and after an extract of the washing solution was applied in that activity, exploration, and the latency with which attachment took place were unaltered.

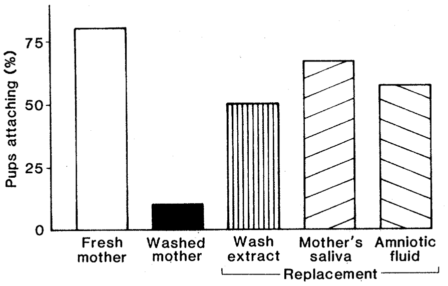

Fig. 3. Percentage of newborn rat pups attaching for their first suckling experience under different conditions: fresh mother, washed mother, and wash extract conditions as in Fig. 2; after mother's saliva was applied to washed nipples; and after amniotic fluid, obtained from a pup taken from the mother before she could strip the amniotic sac, was applied to the nipples. Each subject was tested once only ($N = 14$; $P < .001$). [Modified from Teicher and Blass (*23*)]

Thus, we had isolated a factor needed to elicit suckling. Some substance had either to be deposited on the nipple by the mother during the course of grooming, secreted by her, or placed on the nipple by the pups themselves. We found that painting an extract of rat pup saliva on the washed nipples fully restored suckling, but coating the washed nipples with a variety of wet, salty, or oily substances, including commercial milk, did not, an indication that the effects of the reinstatement are specific (*18*). It is unlikely that the saliva is effective because it contains mother's milk. According to Singh and Hofer (*21*), rat milk is not an effective stimulus for nipple attachment. In addition, we found that an extract from the salivary glands, uncontaminated with milk, was effective in restoring suckling. We repeated these experiments in rats 2 to 30 days of age and found that washing the nipples continued to disrupt suckling even in rats whose eyes had opened (*16*). Thus, pup saliva is a stimulus needed throughout the suckling period to elicit nipple attachment (*22*).

These findings raise questions about the rat's original suckling experience after parturition. Since pup saliva has not yet been deposited on the nipple, a number of possibilities could account for the first attachment. (i) No specific olfactory cue is necessary to elicit the first nipple attachment; (ii) a substance that contains the cue may be secreted by the nipples during parturition; (iii) the cue may be carried in the parturient mother's saliva; or (iv) the birth fluids may contain the cue (*8*). Another possibility is that any odor is sufficient to elicit suckling. To test these possibilities, we observed parturition and gently removed the pups from their mothers before any suckling took place (*23*). Then the dams were anesthetized and the newborn pups were hand held to the nipples (Fig. 3). Attachment on the freshly parturient dam was impressive; even holding the newborns to an anesthetized mother did not disrupt suckling. Washing the nipples, however, essentially eliminated the newborn's first attachment. It seems reasonable to conclude, therefore, that a substance on the nipples of the parturient mother is needed to initiate the first suckling episode. Thus, we may reject the first possibility.

Suckling could be elicited by applying an extract of the solution from the nipple washings. Furthermore, we found that maternal saliva and amniotic fluid were as effective in bringing about suckling as was the extract from the washings. That both maternal saliva and amniotic fluid were effective is to be expected. The parturient rat mother, between the birth of the pups, cleans and licks each newborn and her own anogenital area, both of which are coated with birth fluids. She also licks the nipple region and thereby deposits her saliva, now rich with amniotic fluids (*24*).

Because the three substances applied brought about the newborn's first nipple attachment, we investigated the possibility that the birth fluids hold the cue for specificity (Fig. 4). That neither urine from the parturient female nor saliva from a virgin rat was effective suggests that the stimulus that elicits the rat's first nipple attachment is quite specific. We have yet to evaluate the possibility that the mother is secreting a substance that is eliciting this first attachment. This is a reasonable possiblity, in that Singh and Hofer (*21*) found that older rats attach to the washed nipples of anesthetized dams that have been given large oxytocin injections.

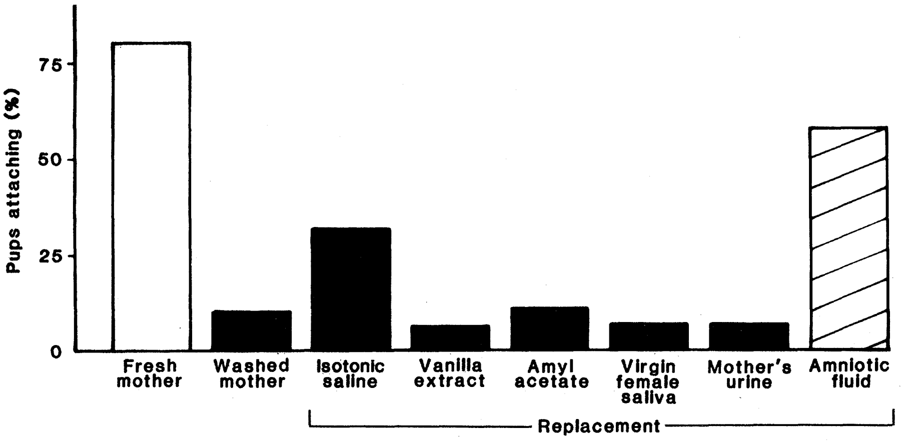

Fig. 4. Percentage of newborn pups tested for their first suckling experience on their anesthetized mother under various conditions: fresh mother, washed mother, and amniotic fluid data taken from Fig. 3; remaining data reflect attachment to the washed nipple after treatment with the indicated substance (N = 14 per column). Comparisons of the differences between fresh mother or amniotic fluid conditions and any of the treatments represented by the solid histograms were statistically significant, $P < .001$ or greater (*23*).

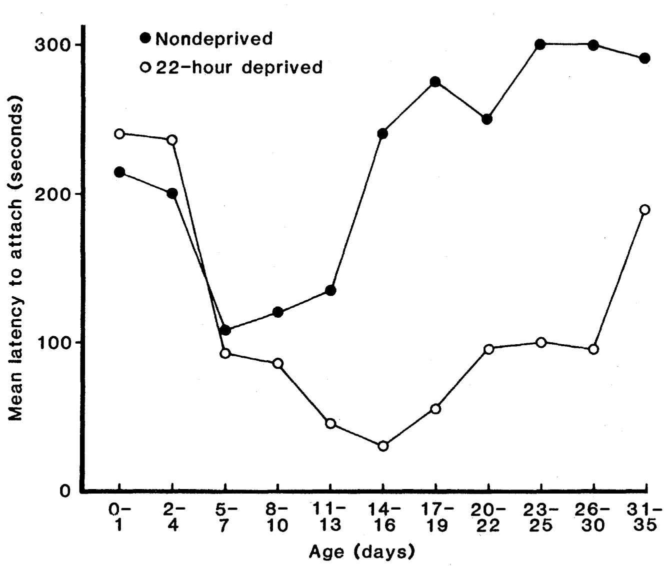

Fig. 5. Mean nipple-attachment latencies of rats of various ages to their anesthetized dams. Nondeprived rats were tested immediately after maternal anesthetization and had not been separated from the mother until the time of testing. Deprived rats were separated from the dam and from food and water for 22 hours before testing (N = 18 per data point; P's for age, deprivation, and their interactions < .01). [From (*34*), copyright 1977 by the American Psychological Association; reprinted by permission]

Our studies have started to show how newborn rats locate and attach to their mothers' teats. We believe olfaction is used throughout the suckling period even after the rat's eyes are open (*25*). The mechanism through which scent elicits suckling is under study. Saliva has at least two functions. It leads the rat to the nipple and then permits the tactile qualities of the nipple to gain control over the rat's behavior (*26*) presumably via the trigeminal sensory field (*27*). In the absence of the volatile substance that coats it, the nipple does not elicit the mouth-opening, tongue-extension response that culminates in attachment. In its presence, the nipple does.

The use of olfaction by other mammals. A comparison of commonalities and differences in the suckling behavior of other mammals is instructive. A number of mammals, farm animals in particular, which are born with their eyes open and are capable of independent locomotion, are not as dependent on olfactory cues as rats. Rather, they appear to use kinesthetic and tactile cues even when suckling synthetic protuberances (*28*). Newborn cats and dogs, however, appear dependent at birth on olfactory cues to guide them to the nipples. Mothers in both species, after delivering the entire litter, lie on their sides and encircle it. They coax the newborns to the nipple line by coating their muzzles with saliva and, thereby, arousing them. Then the mother licks her own nipples and the newborns, with head-scanning movements, follow her scent until they contact a nipple (*29*).

Saliva is apparently important in human nursing as well. Human infants, under the most natural conditions of home delivery, spend 3 to 5 minutes licking the mother's breast before beginning to suckle (*30*). Even though newborn humans will accept substitutes for the mother's breast, the first apparently spontaneous behavior is to lick. Olfaction may also contribute to human mother-infant interaction. MacFarlane (*31*), for example, demonstrated that 6-day-old infants show a preference for a soiled breast pad over a clean one, and 8-day-old infants prefer their own mother's pad to that of a woman of identical lactational status. The early reports of Peto (*32*) indicated that infants rejected breasts contaminated with substances such as eau de cologne or asafetida. Gustatory cues might prompt this rejection, but we find this unlikely. For, according to Jensen (*33*), suckling from a rubber nipple was not disturbed by the addition of adulterants such as quinine to the milk.

It is clear that olfactory information contributes in various ways to the suckling-nursing bond in humans as well as some nonhuman mammals. In the case of rats, the presence of pup saliva on the nipple appears necessary for attachment after the first suckling experience. In contrast, olfaction does not appear to contribute to suckling behavior in farm animals born with their eyes open and capable of standing. Humans are intermediate in that they will accept a surrogate nipple but discriminate on the basis of olfaction, and changing the familiar scent can be disruptive.

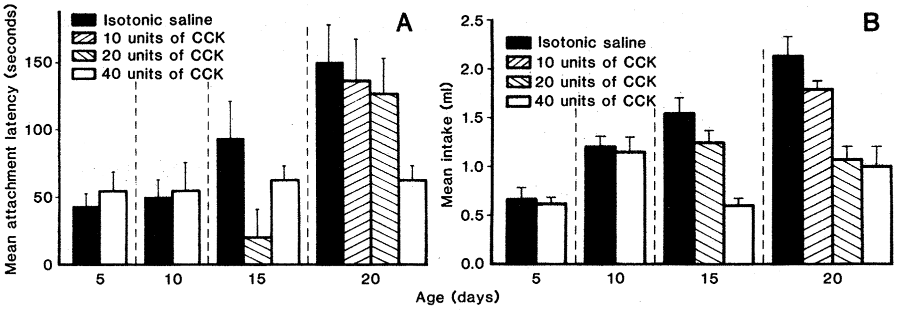

Fig. 6. (A) Mean nipple-attachment latencies of deprived rats 5, 10, 15, and 20 days of age after intraperitoneal injections of 10, 20, or 40 units of cholecystokinin (CCK) per kilogram of body weight. There appears to be no dose-response relation. If anything, CCK reduced the latency with which attachment occurred. (B) The attenuating effect of various doses of CCK on milk intake in the older rats ($N = 10$ per column; for intake, P for 40 units at days 15 and 20 was $< .01$, and for 20 units at day 20, $< .01$). [From (*42*), courtesy *American Journal of Physiology*]

Suckling, milk withdrawal, and sucking termination. We have discussed the characteristics of the mother that permit suckling to occur but not the circumstances under which it occurs and whether there is, in fact, more than one form of suckling. The questions we must answer include: What antecedent conditions are necessary and sufficient to elicit and sustain suckling? What conditions are necessary and sufficient to terminate suckling? Do these conditions change with age? Before we can answer these questions, however, we must identify the internal mechanisms that control suckling behavior. We must also determine whether they are the same as the controls of feeding or drinking behaviors and whether they change with development.

The role of internal mechanisms in controlling suckling behavior was revealed by Hall, who, together with Cramer and Blass (*34*), investigated changes in nipple-attachment behavior during development and its relation to deprivation. Nipple attachment was studied in rats from the day of birth until the time of weaning at 35 days of age. The rat pups were deprived of the opportunity to suckle for 0, 4, 8, or 24 hours before the suckling test on anesthetized, nonlactating dams (Fig. 5). Suckling privation not only prevents rats from engaging in a highly preferred activity but also deprives them of the nutrients, minerals, and water in the mother's milk. During the first 12 days, the mean attachment latency for nondeprived rats was virtually identical to that of their deprived siblings. Latencies decreased with age regardless of privational status, indicating that nipple attachment is independent of the rat's immediate suckling history and hydrational and nutritional status. (More direct proof is presented below.) Then, at about 12 to 14 days, deprived rats continued to attach rapidly, but nondeprived rats did not. Between 15 and 25 days of age the nondeprived rats still suckled, but attachment to the nipple, in addition to occurring with longer latencies, appeared to differ qualitatively. It seemed almost casual in that the rats sniffed about the nipple, might lick it, and then walk away. Their behavior lacked the excitement characteristic of younger pups or deprived siblings. After the pups were 25 days of age, liberation from maternal sensory cues seemed complete (*34*).

Deprived pups showed another age-related difference in suckling behavior. Pups, 12 days of age and younger, did not leave a nonlactating nipple even after 8 hours of nonnutritive suckling. Starting at about day 15, they shifted from nipple to nipple in the absence of milk let-down. The incidence of shifting increased with deprivation and age, reaching its maximum in 21- to 24-day-old rats, in which shifting occurred about 50 times during the course of a 2-hour test (*35*).

Hall *et al.* (*34*) suggested that during the infant's first 2 weeks, attachment to the nipple may be an end in itself since the behavior of rats that have been suckling almost continuously is virtually indistinguishable from that of rats deprived for up to 24 hours. Moreover, continued attachment to the nipple is apparently not dependent on milk let-down or the amount in the stomach. For example, nondeprived rats that were intubated with milk to the point of observable stomach distension continued to attach rapidly to the mother's nipples (*36*).

These findings led Hall and Rosenblatt (*37*) to investigate whether the act that causes withdrawal of milk from the nipple was under the control of internal stimuli that determine adult food and water intake. They implanted a thin, polyethylene tube in the back of the rat pup's mouth through which they could inject a bolus of milk after the pup attached to a nipple. The injection of milk through this tongue cannula triggered the "stretch" response (Fig. 1D), which occurs naturally when the mother's milk is ejected from the nipple into the back of the pup's mouth (*38*). Hall and Rosenblatt (*37, 39*) recorded the amount of milk that rat pups at various ages accepted while attached to the nipple and the point at which the stretch response waned during repeated milk injections. They discovered that various internal stimuli (for example, stomach distension) that inhibit feeding in adult mammals do not affect milk withdrawal until rats are about 15 days old, the age that also marks the transitional point in nipple-attachment latency. In the case of stomach distension, Hall and Rosenblatt (*37*) found that the stretch response was often eliminated in 5- and 10-day-old rat pups only when their stomachs became so distended by repeated injections of milk that it refluxed up the esophagus. Many literally turned blue with asphyxia and struggled off the nipple. Moreover, they found that nutrient in the stomach, which differentially suppresses intake in adults, does not exert such an effect in younger rats (*39, 40*).

These findings are also related to the way in which the intestinal hormone cholecystokinin (CCK), which profoundly inhibits feeding in adults (*41*), affects attachment to the nipple and milk withdrawal (*42*) (Fig. 6, A and B). The largest dose of CCK (40 units per kilogram of body weight) did not increase the latency with which attachment to the nipple occurred in deprived rats at any of the ages tested. This supports the finding that attachment to the nipple and suckling occur in rats for reasons in addition to milk deprivation (*43*). The stretch response and, by inference, milk intake were not affected by CCK until rats were about 2 weeks old, when a 40-unit dose was effective in reducing milk intake. At this time the nascent controls discussed above, which inhibit feeding, start to emerge. By 20 days of age, a 20-unit dose of CCK was as effective in reducing milk intake in these young rats as it is in free-feeding adults. In addition, both suckling and the stretch response terminated "voluntarily" in the older pups. They behaved in a manner similar to adult rats at the end of a meal. They groomed, explored the cage, and eventually rested and slept.

The relation of suckling to feeding and drinking. The stomach distension data do not clarify this relation because distension reduces both food and water intake in adult rats (44). The CCK data suggest that by day 15, milk withdrawal is partially under the control of mechanisms that determine food intake. To assess this issue directly, Bruno (45) studied the effects of sudden dehydration on attachment to the nipple and the volume of milk taken through the implanted tongue cannula. On the basis of what is known about adult ingestion (46), several predictions could be made. If suckling is like feeding, then latency to attach to a nipple should increase and milk intake at the nipple should decrease in dehydrated rats. If it is like drinking, the opposite should hold. If suckling is related to neither, then dehydration treatments should not affect suckling. Bruno found that until rats were about 2 weeks of age, attachment latency was not affected by loss of either intracellular or intravascular fluid. By 20 days both sources of fluid loss increased attachment latency and decreased milk intake. Thus, suckling does not appear to be under the control of hydrational status until rats are about 2 weeks old. We have no evidence that suckling is ever an ingestive response to dehydration, and at least two lines of evidence (46) suggest that suckling at about 2 weeks is under the control of mechanisms that determine food intake in adult rats.

The Controls of Suckling Behavior

The components of the suckling act, namely, nipple attachment, nonnutritive suckling, and nutritive suckling (47), are differentially affected during ontogeny. Evidence derived from studies of attachment to the nipple and especially the willingness of young rats to remain attached to the nipple in the face of repeated milk injections (40) support the following conclusions regarding suckling in rats from birth until day 30.

From birth to day 10. The necessary and sufficient condition for nipple attachment during this period is that the nipple be coated with saliva. Deprivation does not facilitate attachment. Moreover, loading the stomach to the point of precipitating distress responses does not retard attachment to the nipple. The volume of milk taken through the indwelling tongue cannula is not responsive to the internal conditions that moderate either adult ingestive behavior or milk intake at the nipple in slightly older rats.

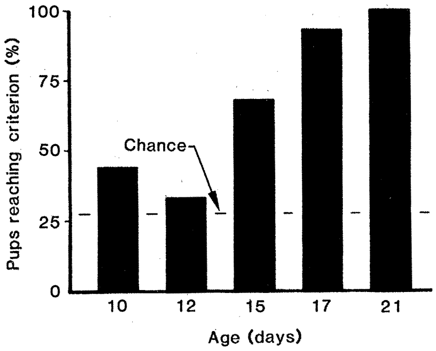

Fig. 7. Percentage of subjects preferring nutritive over nonnutritive suckling at 10, 12, 17, and 21 days of age ($N = 10$ per column; P, days 17 and 21, $< .001$). [From (49), copyright 1979 by the American Psychological Association; reprinted by permission]

Day 11 to day 20. This is an important period of transition. (i) Attachment to the nipple becomes responsive to deprivation (34). Findings by Williams, Rosenblatt, and Hall (48) suggest that deprivation affects attachment by virtue of separation from the mother and not because the rat is in need of either food or water. According to Williams *et al.* (48), nipple-attachment latencies in 15- to 20-day-old rats, separated from their dams and allowed free access to food and water, were indistinguishable from siblings that did not have food and water available during the separation period. As is the case with younger rats, the nipple must be coated with saliva in order for attachment to occur (even when the rats are deprived). (ii) Factors that modulate adult food intake (for example, dehydration, administration of CCK, or filling the stomach with food) start to reduce the amount of milk taken through the tongue cannula. (iii) Either cellular or extracellular dehydration reduces the percentage of pups that attach to nipples and increases the latency with which attachment occurs. The controls are not fully mature in that the magnitude of the reduction is not equal to that in adults receiving comparable treatment.

Day 21 to day 30. At 21 to 30 days suckling is similar to feeding. Although deprivation induces attachment to nipples, 25-day-old rats deprived of suckling no longer attach to nipples if they have eaten during the deprivation period (48). The events that inhibit feeding in adults very effectively control suckling in rats at the age of weaning.

Development of Suckling Appetite

The conclusions concerning internal controls over milk consumption lead to certain predictions about pups approaching the mother from a distance. Specifically, if appetite develops in parallel with consummatory controls, then the following should hold true. (i) The nonlactating nipple should provide a powerful incentive until at least day 20 for rats to solve a problem that allows them to suckle, and (ii) the same time course seen in the development of consummatory controls on milk intake should appear for the appetitive component of suckling. In other words, until about 2 weeks of age, rat pups should not discriminate between a nipple that does not yield milk and one that does. Thereafter they should choose the lactating nipple. Kenny *et al.* (49) investigated the possibilities by using a Y maze (50). In one experiment, rats 7 to 23 days of age were placed in the start box, the stem of the Y, and allowed to go to either goal box in the arms of the Y. The "correct" response was rewarded with a 30-second opportunity to suckle a nonlactating nipple. When rats chose the "wrong" arm, they found the anesthetized mother covered with gauze to prevent suckling. The rats did root into the gauze. Yet rats at all ages studied learned and remembered the path that offered them the reward of suckling the nonnutritive nipple (50). Thus, the opportunity to suckle a nonlactating nipple is sufficient to support appetitive behavior.

This finding led us to investigate whether the delivery of milk would influence the animal's behavior. The tongue-cannula technique was used to deliver a bolus of milk to the back of the rat's mouth when the correct arm of the maze was chosen and the rat attached to the nipple. When the other arm was chosen, the rats were allowed to suckle, but no injections of milk were made. The findings (Fig. 7) revealed that rats at days 10 and 12 did not discriminate in their choice of nipple. Their preference for the lactating nipple did not exceed chance performance. Starting at 15 days of age, and especially by day 21, the lactating nipple was preferred. Thus, as rat pups near the age of weaning, the mother becomes defined differently. At first, whether or not she provides milk, she is approached from a distance and suckled. After 2 weeks, appetitive behavior is also determined by the pups' nutritional status and by an apparent appreciation of the benefits of milk let-down so that the lactating nipple is preferred. In this connection, the studies of Martin and Alberts (*51*) should be considered. They found that rats younger than 20 days of age could not form an association between suckling and being made sick by injections of lithium. Yet, when these rats were made ill by lithium in association with other acts, such as swallowing milk injected into the mouth, they did not eat the substance that produced illness. Taken together, these findings suggest that during the first 2 weeks of life the infant rat's suckling behavior is exclusively under external control and that rats cannot associate suckling with potentially negative consequences.

Recent advances in our understanding of the mechanisms of learning and constraints on learning (*52, 53*) force us to alter our view of suckling. No longer can it be considered a reflexive act unmodified by experience and insensitive to certain affective consequences of its practice. As has been demonstrated above and by others (*54*), rats as young as 7 days of age actively and selectively approach the dam to suckle. Before 3 weeks of age, internal stimuli gain control over approach to the mother in that rats suckle milk-yielding nipples in preference to nonlactating ones. But, as is the case with other appetitive behaviors, there are bounds. (i) A rigid boundary is erected by the narrow range of stimuli that elicit the suckling act. Thus, although the motor components of suckling change with age, the sensory cues that elicit suckling do not. Even rats whose eyes have opened suckle only when the nipple is coated with saliva. (ii) Another bound relates to the failure to associate suckling with negative consequences of either severe gastrointestinal distension or lithium injections to toxicosis.

Parallels with Human Suckling

The many differences between human and rodent suckling (for example, acceptance of surrogate nipples by human infants) usually preclude comparisons between the species. We wish, nevertheless, to call attention to some similarities with the hope that understanding the behavior of one species will at least provide a framework for understanding the factors that might control the behavior of the other. Parallels will be restricted to two unanticipated findings from the rodent research (*34, 37, 50, 51*): (i) the apparent inability of young rats to appreciate negative consequences of suckling at a time that suckling's positive aspects can gain control over their behavior; and (ii) the seeming independence of suckling from internal control in younger animals, that is, the idea that suckling is the end in itself.

Human infants, younger than 3 weeks of age, also seem to have difficulty responding to negative effects of suckling. For example, they are unresponsive to salty or bitter adulterations of their formulas (*33*). Indeed, this inability to associate suckling with postingestive consequences resulted in the death of a number of infants in whose nursery formulas salt was accidently substituted for sugar. Six infants lapsed into a coma and died. While they presented a syndrome of encephalopathy, including convulsions and respiratory stress, the deaths were caused by continuing ingestion of the extremely concentrated salt diet (*55*). In the suckling context, the infants were not sensitive either to the taste of the diet or to the fact that it sickened them. Yet human infants can make positive associations and discriminations through suckling. Eight-day-old infants, for instance, recognized their mother's breast pad. Moreover, the rate of newborn suckling is very sensitive to gradations of glucose and sucrose concentrations (*56*).

In regard to suckling serving as an end in itself (*57*), suckling in younger animals appears to terminate with sleep and be reinstated on awakening, a pattern that is often seen in humans younger than 12 weeks of age. Rousing such children invariably leads to suckling (*32*). In children older than 12 weeks, suckling is not terminated by sleep. When rats enter the weaning period their behavior becomes more responsive to internal demands. By 20 days of age, rats that have not been deprived or are only mildly deprived do not suckle but pull at or lick the nipple and explore the mother and their surroundings. This is true of humans 12 to 24 weeks old. The infant may play with the nipples or bottle and hold them in different positions, but they no longer dominate the child's attention or elicit the motor patterns that culminate in nipple attachment. Moreover, nonnutritive suckling is considerably reduced in these children, and suckling starts to resemble adult ingestion in that it is more flexible. Suckling can still occur in the deprived subject, but as the stomach fills attention is directed elsewhere, and there are pauses for play with the parents or siblings.

In conclusion, our findings about suckling behavior in rats must be confirmed and our understanding extended to other species. Major issues concerning the neural mediation of suckling, the receptors that detect changes in hormonal levels or in the status of the gastrointestinal tract in relation to suckling, and the process of weaning have yet to be investigated experimentally. The important similarities and differences among mammalian newborns must be taken into account as we plan experiments to further our knowledge of this fundamental mammalian behavior.

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Computed Medical Imaging

Godfrey N. Hounsfield

In preparing this paper I realized that I would be speaking to a general audience and have therefore included a description of computed tomography (CT) and some of my early experiments that led up to the development of the new technique. I have concluded with an overall picture of the CT scene and of projected developments in both CT and other types of systems, such as nuclear magnetic resonance (NMR).

Although it is barely 8 years since the first brain scanner was constructed, computed tomography is now relatively widely used and has been extensively demonstrated. At the present time this new system is operating in some 1000 hospitals throughout the world. The technique has successfully overcome many of the limitations which are inherent in conventional x-ray technology.

When we consider the capabilities of conventional x-ray methods, three main limitations become obvious. First, it is impossible to display within the framework of a two-dimensional x-ray picture all the information contained in the three-dimensional scene under view. Objects situated in depth—that is, in the third dimension—superimpose, causing confusion to the viewer.

Second, conventional x-rays cannot distinguish between soft tissues. In general, a radiogram differentiates only between bone and air, as in the lungs. Variations in soft tissues such as the liver and pancreas are not discernible at all, and certain other organs may be rendered visible only through the use of radiopaque dyes.

Third, when conventional x-ray methods are used, it is not possible to measure in a quantitative way the separate densities of the individual substances through which the x-ray has passed. The radiogram records the mean absorption by all the various tissues which the x-ray has penetrated. This is of little use for quantitative measurement.

Computed tomography, on the other hand, measures the attenuation of x-ray beams passing through sections of the body from hundreds of different angles, and then, from the evidence of these measurements, a computer is able to reconstruct pictures of the body's interior. Pictures are based on the separate examination of a series of contiguous cross sections, as though we looked at the body separated into a series of thin "slices." By doing so, we obtain virtually total three-dimensional information about the body.

However, the technique's most important feature is its enormously greater sensitivity. It allows soft tissue such as the liver and kidneys to be clearly differentiated, which radiographs cannot do. An example is shown in Fig. 1. It can also very accurately measure the values of x-ray absorption of tissues, thus enabling the nature of tissue to be studied.

These capabilities are of great benefit in the diagnosis of disease, but CT plays an additional role in the field of therapy by accurately locating a tumor, so indicating the area of the body to be irradiated, and by monitoring the progress of the treatment afterwards.

It may be of interest if I describe some of the early experiments that led up to

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The author is Senior Staff Scientist, Medical Systems Department, Central Research Laboratories, EMI, Middlesex, UB31HH, England. This article is the lecture he delivered in Stockholm on 8 December 1979 when he received the Nobel Prize in Physiology and Medicine, which he shared with Allan M. Cormack. The article is published here with permission from the Nobel Foundation and will also be included in the complete volume of *Les Prix Nobel en 1979* as well as in the series Nobel Lectures (in English) published by Elsevier Publishing Company, Amsterdam and New York. Dr. Cormack's lecture was published in the issue of 26 September.

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