

Learning as adaptation of the infant

Jeffrey R Alberts

Department of Psychology, Indiana University, Bloomington, Indiana, USA

Alberts JR. Learning as adaptation of the infant. *Acta Pædiatr* 1994;(Suppl 397):77–85. Stockholm. ISSN 0803–5326

The present report advocates an adaptive, ecological approach to the study of learning in infants. Concepts of developmental niche and ontogenetic adaptation are applied to early mammalian development. Within this conceptual framework, it is asserted that learning cannot be fully understood separately from a behaving body; that learning is a dimension of behavior and physiology. The role of learning in the development of ingestive behavior, especially suckling and the transition to solid food, is used to illustrate the potential of studying learning in development. These considerations are offered as examples of an alternative approach to the empirical study of learning by infants. The approach advocated herein can be applied to clinical issues: developmental adaptations evolved in contexts that differ from our modern environments. Exposure to contexts or contingencies that are evolutionarily unexpected may inadvertently create pathology. □ *Adaptation, learning nursing, ontogenetic adaptation, suckling, toxiphobia, weaning*

J Alberts, Department of Psychology, Indiana University, Bloomington, IN 47405, USA

Processes of learning and memory are fundamental to the formation and maintenance of living, behaving, adaptive beings. Learning and memory are also vital constituents of the psychological skeleton that supports and shapes the corpus of behavior comprising human individuals, families and cultures. It is natural for those of us concerned with the formation and early expression of behavior to inquire into the development of learning.

The present report is focused on learning by neonatal and immature organisms, primarily as seen in laboratory species. More specifically, I draw largely from research in the discipline of developmental psychobiology, with which I identify. It is hoped that this perspective may offer some of the benefits of novelty to an audience with pediatric interests and expertise, but which shares an involvement with the mysteries and challenges of organismic development and the workings of complex, living systems.

Briefly, development will be characterized as a sequence of transitions that display meaning in context – the context of a sequence of developmental habitats. That is, mammalian ontogeny invariably involves developmental habitats that include the uterus, the mother's body and lactational apparatus, and social cohorts of various types. Each of these habitats present specific types of challenges. The concept of ontogenetic adaptation is discussed as a foundation for a behavioral ecology of mammalian development.

One of the universal and unique processes in mammalian development is the transition from ingesting mother's milk early in life to independent feeding. I shall use the ontogeny of ingestion and the roles of

learning in it as the main avenue of exploration. This part of the report is used to integrate physiology, behavior and learning, always within the body and always with the body within a developmental habitat. It is hoped that this approach will inspire others to contemplate their work within analogous frameworks and possibly provide useful insights into the role of learning in development and the development of pathologies seen in clinical inquiries.

Learning is a property of a behaving body

I begin with a premise that is not traditional in the field of experimental psychology, namely that learning is not separable from a behaving body. Learning has no empirically accessible existence without a body. Such assertions contrast with venerable traditions in psychology, many of which are based on a pursuit of principles and laws of learning that are guided by the implicit view that learning exists as a separate process.

I am more interested in the challenge of integrating learning as a dimension of the integrated physiology and behavior of a living system. This view requires that behavior is the primary substrate of study and that learning is seen as one of its properties. This approach is instigated by the conviction that learning does not have an independent existence (1). Thus I am obliged to discuss the development of behavior if I am to discuss the development of learning. Likewise, to examine learning in an infant it is essential to place learning in the context of an infant's behavior, in other words, to embody it.

It follows that our domain *must* include the behaving body. Indeed, to place myself at risk of being provocative but wrong, I will assert the general thesis that *learning does not develop, bodies develop*. As the body develops so does its behavior and, as a property of behavior, learning will change during ontogenesis. Thus in the following sections of this report, I will describe early learning as “embodied” in newborn and developing mammals. It is necessary to place these behaving organisms in a context and for this I extend the biological context of my approach and invoke certain ecological constructs selected to lend some generality to our conceptualization of behavior during development.

More specifically, I will draw selectively on aspects of bodies and behavior that pertain to a fundamental aspect of life, ingestion. Although ingestion changes during development, it is nonetheless maintained continuously, for it is part of the underlying support of life processes.

Ontogenetic adaptation as the foundation for a behavioral ecology of mammalian development

Ontogenetic adaptation is an ecological concept, derived from a perspective that seeks to unify development and evolution (2, 3) and that places the development and the developing animal in a functional context. This

context is the animal’s niche. The concept of ontogenetic adaptation directs our attention to specialized responses of the organism to specific environmental challenges. More generally, the idea of ontogenetic adaptation suggests that each state of development is a form of completeness, rather than an approximation of the final adult goal. This contrasts sharply with a century-old, general view that developmental traits are essentially precursors or antecedents of adult characteristics (4). The evolutionary basis of ontogenetic adaptation introduces the tenet that natural selection can operate on each point in development (5).

Alberts & Cramer (2) discussed the distinction between habitat and niche. Habitat was defined as an environment, definable in terms of standard contextual parameters, such as temperature, luminance, chemical composition, spatial location, and so forth. In this sense, an organism’s habitat is its *address*—where it lives. A niche, in contrast, was defined as an organism’s adapted life in that environment, how it adjusts, utilizes, responds and copes. In this sense the niche is the organism’s *occupation*—how it earns its living. Habitat and niche, address and occupation, can be applied usefully to developmental trajectories and may help us to appreciate some of the elegance inherent in the concept of ontogenetic adaptation.

Along these lines, consider Fig. 1 as a visual outline of the behavioral ecology of development for one mammalian species, the Norway rat (*Rattus norvegicus*). Development can be viewed as occurring in a sequence

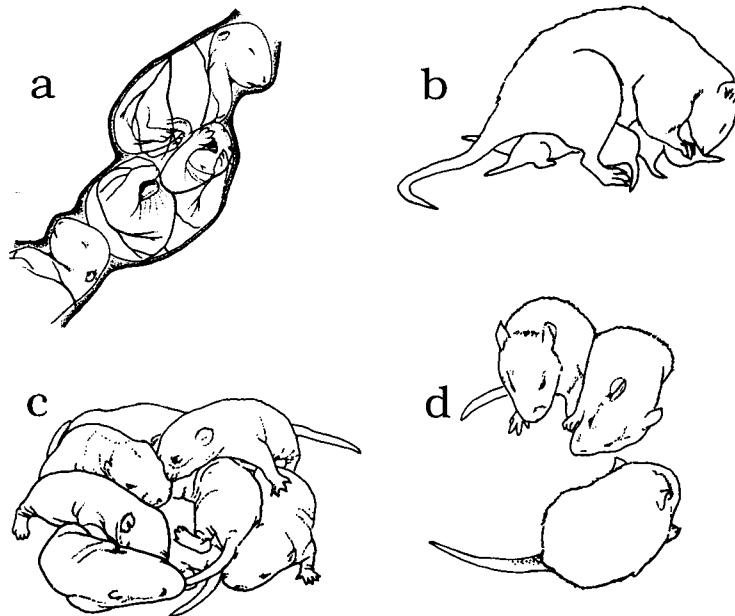


Fig. 1. Four habitats experienced by Norway rats during their development: (a) the uterus during prenatal development; (b) the mother’s external body is a major part of the offspring’s environment during early postnatal life; (c) the huddle of littermates increasingly serves as habitat as the dam spends more time away; and (d) the coterie of littermates with which the pup interacts as weaning approaches and they prepare to leave the nest (see (2) for further discussion).

of habitats, each of which presents a specific and unique set of characteristics and challenges. In Fig. 1, the first such habitat is the uterus. Next in the sequence is the mother's body, characterized by the challenge of finding a nipple and extracting milk from it. For offspring of species such as the Norway rat, which produce litters of multiple offspring, the next developmental habitat is the huddle of siblings. In rat, for instance, the mother spends increasing amounts of time away from the nest as the young develop. In the absence of the dam, it is the nest and the other littermates that constitute the young's immediate environment. Thus we have described the huddle as a developmental habitat for the infant rat.

The fourth habitat shown in Fig. 1 illustrates the young pup's social coterie as habitat. This stage is marked by an expanding social world.

During the transitional stages depicted in Fig. 1, the infant should not be viewed primarily as an incomplete version of the adult. Instead, we view development as a sequence of adaptive stages during which the developing organism displays a succession of stages of completeness. During the fetal phase, for example, the conceptus is uniquely organized (adapted) for life in the uterus. Feeding is accomplished through the umbilicus, as is breathing and excretion. No adult or postnatal organism is capable of such feats. The newborn rat displays its own profile of specializations. It orients towards sources of heat and directs its movements at crevices and surfaces in a manner that brings its mouth in contact with a nipple. Nipple contact then releases a set of appetitive movements that culminate in apprehension of the nipple. The oral grasp involves the establishment of a salivary seal around the nipple, which is then drawn deep into the oral cavity under negative pressure generated by the pup's mouth. Suckling movements, which are myographically distinct from other oral movements associated with ingestion (i.e. chewing and lapping) are then exhibited.

The suckling activities of the pups are prominent during the second and third stages of life, depicted in Fig. 1. The drawing in Fig. 1d shows a typical social scene among weanling age mates, as they play with a piece of food. Depicted here is an aspect of the process of shifting to solid food from an exclusive diet of mother's milk. The weaning transition is a major developmental milestone and we will examine some of its varied dimensions in the life of the rat.

We can now consider complex adaptive behavior in development and try to recognize the roles of learning in these processes.

Development of ingestion: physiology and behavior, including learning

Almost immediately upon leaving the uterine habitat, that is, soon after birth, the newborn must become an

oral ingestor. In addition, the newborn must "forage" for a nipple. In order to suckle, the neonate must find one of its mother's 12 nipples, that are distributed in a spatial array on the mother's ventral surface.

Much is now known about the way in which the behavior of the newborn rat is activated to accomplish the relatively astounding feat of beginning to search around a new, three-dimensional world, negotiating new surfaces, temperatures, textures and chemical cues, "recognizing" a nipple, apprehending it and beginning to suckle.

Just as the pup's early behavior shows specializations for finding, grasping and sucking on a teat, the infant's gastrointestinal system is structurally specialized for the digestion and absorption of milk. Subsequently, during weaning, the intestinal epithelium loses its adaptations for the liquid diet of infancy and simultaneously acquires the epithelial adaptations for adult ingestion. Figure 2 is a composite based on separate studies of age-related digestive enzyme changes in the rat. I selected these data because they show biochemical modifications in the rat's mouth, stomach, pancreas and intestine. A dramatically coherent pattern is readily apparent: the age-related changes in enzyme levels are tightly correlated. Specifically, the intestinal enzyme lactase, which is important for the breakdown and absorption of lactose, the major carbohydrate in mother's milk, shows a sudden and precipitous decline beginning around day 15, just prior to the onset of weaning (6, 7). It has been suggested that this decrease in intestinal lactase renders mother's milk less utilizable and thus contributes to the accretion of a net energy deficit in the pup (8, 9) and accelerates incorporation of additional nutrient sources into the diet (7). Coincident with this decline in milk-related digestion is a coordinate surge in the digestive mechanisms that assist in the utilization of a solid-food diet (see also (10)). These changes appear simultaneously in the pup's mouth, stomach, pancreas and intestine. This physiological profile is a stunning example of an adaptive shift that corresponds to changes in ingestive niche.

The beautifully synchronized pattern of physiological changes seen in Fig. 2 results from a multitude of organizational factors. In some cases it appears that nutritive stimuli regulate the maintenance and shifts in physiology. The enzymes are affected by substrate. As the substrate changes (e.g. from milk to solid food), the enzymes change in response. Interestingly, this can be seen as a pattern in which behavior "drives" physiology. Alternatively, there are other cases in which the physiological changes are insensitive to substrate and are regulated instead by another physiological factor. Thyroid hormones, for example, can initiate or accelerate gastrointestinal developments. These physiological changes, in turn, have been hypothesized to "drive" behavior.

One goal for enriched conceptualizations of learning, I believe, is to be able to integrate learning into such

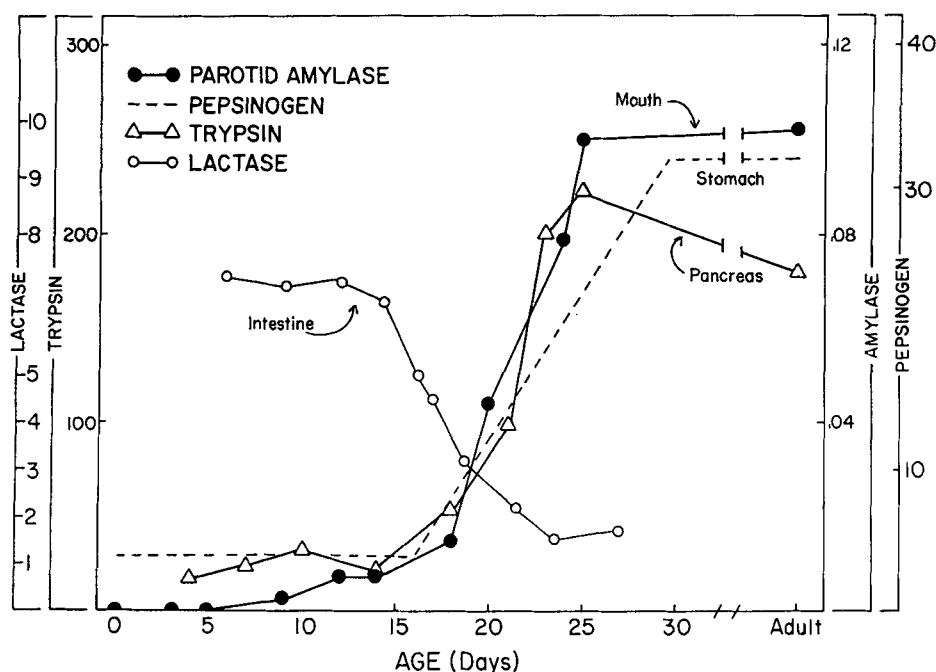


Fig. 2. An overview of selected physiological developments relevant to ingestive behavior and physiology, as measured in the stomach, intestine and pancreas (see (1) for references to source materials for this figure).

multi-levelled views of the animal. It would seem rather absurd to strive to abstract out of the physiological picture of Fig. 2 just the salivary or pancreatic changes. Instead, our appreciation of these changes is enhanced by their integration with changes in other aspects of the animal's body. Why should this be less true for learning? Indeed, why should this be less true for any aspect of the animal's behavior?

We now turn our attention to the development of ingestive behavior and consider some of the recent findings that may guide and illuminate our considerations of the roles of learning in behavioral and physiological development.

Suckling as an expression of early learning

Suckling is a *congenital* behavior. That is, it is present at birth. It is crucial to emphasize, however, that congenital is not synonymous with innate (11, 12). That is, congenital simply means "present at birth" but it does not denote an "innate" quality or a specific type of genetic basis. The organization of suckling in newborn rats illustrates well how a vital, adaptive, stereotyped neonatal behavior is congenital, but not rigidly specified. It has been found that olfactory cues are critical for exciting a newborn pup to seek and find a nipple. If the pup is deprived of its sense of smell, it will not nurse and dies (13), even if it is placed in contact with a lactating rat. Similarly, a pup with an intact sense of smell will not nurse if the nipples of its mother have been thoroughly washed. Moreover, if the

condensate of the wash that was removed from the dam's ventrum is re-applied, suckling is re-instated. Together, this suite of results indicates the existence of olfactory cues that are essential for the activation and expression of suckling in the newborn rat.

Interestingly, it appears that the critical cue for suckling, namely the olfactory stimulus, is *learned* by the infant rat. Pedersen & Blass (14) came to this exciting conclusion after gathering suggestive evidence that the chemical, dimethyldisulfide (DMDS) may be the odorant that they were removing and replacing in the wash-and-paint experiments. DMDS is a natural molecule, present in amniotic fluid, among other places, well known for its odoriferous qualities. One possibility is that the presence of DMDS in the uterine environment during fetal life is integrated into the pup's development and is thus part of an experience that guides its subsequent behavior. If true, it follows that other molecules, if present in the amniotic fluid, might also be effective in guiding neonatal behavior. Such a result would indicate that this "odor recognition" by the newborn is based on learning.

Pedersen & Blass (15) introduced a novel chemical cue, citral, into the amniotic fluid of late gestation rats. These pups were thus exposed to citral, in utero, for the final days of gestation. They then were delivered by cesarean section. At the time of delivery, still in the presence of the citral-laced amniotic fluid, the pups were stimulated with a small paint brush to replicate the vigorous cleaning and licking normally provided by the rat dam after delivery (16). These

citral-exposed pups displayed the normal, species-typical sequence of behavioral arousal and scanning movements along the dam's ventrum as pups had shown to natural odors and to DMDs applied to a washed ventrum. This exciting finding reveals how learning can be embedded within the melange of stimuli that comprise a natural context. The uterine environment supplies the cue that will be learned. Additional analyses by Pedersen & Blass suggest that the uterine environment and the mother's licking behavior during and immediately after delivery may also make necessary contributions to the learning process.

In the vocabulary of learning theory, it appears that both the conditioned stimulus (CS) (an odor CS in this case) and the unconditioned stimulus (US) (presumed to be some form of tactile US) occur at appropriate levels and in effective sequence during the natural course of gestation and delivery. It is useful to remember that our appreciation of these natural stimuli and events is based entirely on the ability and the proclivity of the fetus to perceive, respond and integrate the stimuli into coherent, long-lasting, functional patterns of behavior. Discussion of the developmental neurobiology of the fetal rat olfactory system is beyond the scope of the present essay, but it should be noted that this developmental phenomenon has provided a valuable guide to neurobiological investigations, which are beginning to define the necessary and sufficient substrates for this stunning form of early learning.

Although there is compelling evidence that suckling is essentially organized at the time of birth, there are additional lines of evidence that experience plays an additional role in the behavior, that of *maintenance*. That is, unless a pup actively suckles during its early life, this behavior will disappear from its repertoire and seems to become unavailable, as though its potential is lost also. This surprising finding emerged from Hall's well known studies of intragastric feeding of rat pups (17). By installing an intragastric cannula directly into the stomach of a newborn pup and solving myriad technical problems associated with the maintenance of the fragile neonates, Hall was able to rear rat pups in isolation from all other conspecifics. Because these pups were fed intragastrically, they took no oral sustenance and hence did not nurse. Such pups grew at reasonable rates and showed remarkably normal behavioral development. Onset of feeding of solid food was essentially normal. Curiously, however, if these pups were given the opportunity to suckle after a week of not suckling, the congenital, stereotyped, species-typical act of suckling was not emitted. Apparently, this previously prepotent act requires experience and expression for its maintenance. It is curiously experience-dependent. Although formed before and at the time of birth, and vital for survival, suckling is a remarkably fragile and transient behavior (see also (18)).

Not only is the survival or maintenance of suckling dependent on experience, but the "microstructure" of suckling behavior can be shaped by experience. Brake et al. (19) made electromyographic (EMG) recordings of digastric (jaw) muscles and described different types of suckling patterns. They used an intraoral cannula to deliver milk according to different schedules to the mouths of pups that were attached to the nipples of an anesthetized dam. They found that receipt of milk and the schedule of milk delivery can modify subsequent nipple attachment, sucking behavior, and the topography of the sucking patterns, thus demonstrating a novel form of conditioning.

A particularly dramatic demonstration of learning that can affect early ingestive behavior is a study of appetitive conditioning in one-day-old rats (20). Neonates were equipped with an intraoral cannula through which milk could be infused. These newborns learned to press either of two overhead paddles made discriminable with different spice scents. This phenomenon provides additional evidence that food-getting behaviors are readily modifiable in the infant. Other similar types of findings have been obtained with classical conditioning paradigms in which olfactory cues are paired with intraoral infusions of milk. The results of such tests show that olfactory and auditory stimuli can evoke stereotyped food-related responses from pups (21, 22).

Weaning as ontogenetic adaptation

Weaning, the transition from dependence on mother's milk to independent ingestion of solid food, is one of the great commonalities of mammalian development. Through the process of weaning, the infant leaves the niche of infancy and enters a new realm of independence. To accomplish the transition or transitions, the developing mammal undergoes a melange of histological, enzymatic, hormonal and behavioral changes, some of which were mentioned earlier. The behavioral changes involved in weaning are no less profound than the renowned physiological ones, yet little attention has been afforded to behavior. Preliminary analyses of behavioral aspects of weaning are quite exciting and learning has been implicated at several points in the process.

Rat pups that have never eaten or sampled solid food nevertheless can learn about the properties of food. Studies of initial food selection—the pup's first bite—show that rats initially select the same diet eaten by their mother during lactation. Milk carries cues that the pup can recognize in food, and these cues guide their initial food selections (23). Galef (23) scrutinized the problem of how the weanling pup chooses safe (non-poisonous) foods and avoids ingesting dangerous ones. The results of these studies show that pups have a strong tendency to follow adults to the colony's feeding sites, where they begin to eat the same foods that the

adults are eating. Thus the pups can benefit directly from the adults' prior experiences. It was shown, however, that the pups do not learn to avoid a food that the adults avoid; instead they learn to feed on the same, safe foods that adults consume.

In another recent set of experiments, rat pups were reared in cages that permitted access to food by the mother but not the pups. These pups lived solely on mother's milk. At 22 days of age or more, these food-naïve pups were offered brief (2-h) periods of access to two dietary concoctions which were similar in texture, consistency and palatability, but were either calorically void or contained carbohydrate (1 kcal/g). Each diet was sweetened with saccharin and contained a distinctive, artificial, food odor. After sampling each substance, pups rapidly formed a preference for the "food" (caloric diet). Moreover, in another test, pups continued to eat the calorie-paired flavor even as part of an acaloric mixture, thus showing evidence of associative learning in early food recognition (24).

With this background in mind, we were understandably perplexed to find that pre-weanling rats showed no evidence of learning a taste toxiphobia when a novel milk-borne CS was delivered during a nursing episode and paired with a lithium chloride injection (25). We refer to this absence of aversion as *blockade of toxiphobia*. The results of numerous analyses indicated that the key difference between our findings and those from the numerous other studies in which pups

displayed robust toxiphobia, was that pups displaying the blockade were engaged in nutritive suckling during training. In other words, pups that were behaviorally involved in their niche on the mother's body (suckling) displayed this dramatic blockade.

In a typical procedure (Fig. 3), pups were equipped with a tongue cannula through which the flavored-milk CS could be delivered, giving experimental control over the quantity, timing, and placement of the CS delivery to a freely moving rat. Pups aged 10–22 days were given oral infusions, via the tongue cannula, of geraniol-flavored milk (the CS) while suckling the nipple of an anesthetized dam, or while in the presence of the dam but not suckling (i.e. off-nipple). Anesthesia eliminated variations in maternal behavior from affecting the results and, importantly, prevented milk let-down (26). Animals were injected with lithium chloride or saline following milk delivery. Then on either day 22 or 24, pups were given a choice between three diets, one of which (diet G) contained the flavor CS. Toxiphobia is shown by suppressed intake of diet G relative to the two other test diets (familiar, safe purina rat chow and a novel diet created by mixing the chow with acetophenone).

Figure 4 summarizes the results of the food preference test. Older, weanling pups (21–22 days old) injected with lithium chloride avoided diet G, whether or not the milk CS was delivered while nursing or off-nipple (right panel). In contrast, the younger,

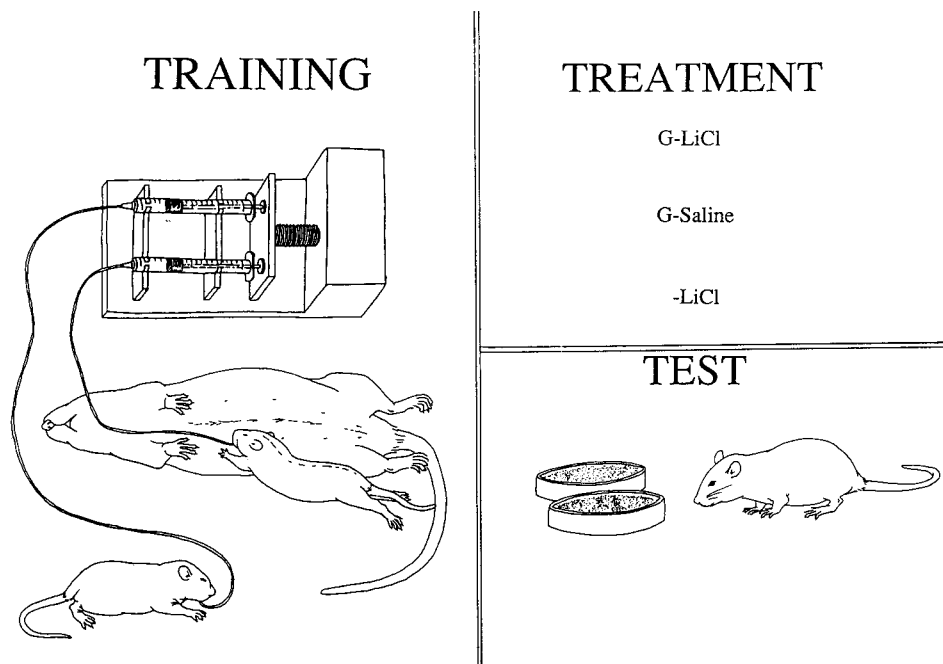


Fig. 3. Outline of experimental procedure used for some experiments on the blockade of toxiphobia by suckling (e.g. (24, 30)). Pups received identical rations of flavored milk (G = geraniol flavoring) through an intraoral cannula while attached to a nipple of an anesthetized dam or while nearby but not suckling. After training they were treated with a non-lethal toxin (LiCl) or saline; another control group received the toxin only. Pups were subsequently given food preference tests using powdered chows, including one laced with geraniol.

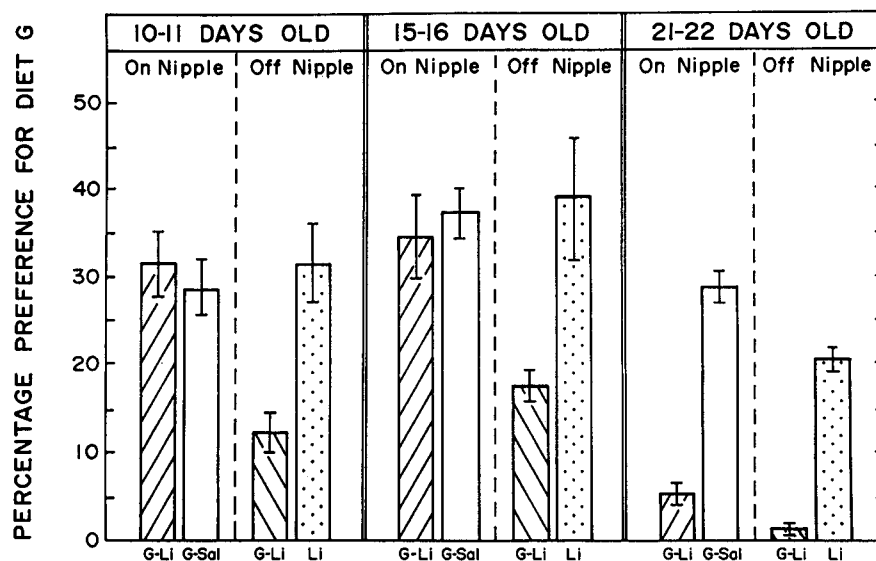


Fig. 4. Preferences for a flavored diet (G) in pups given a three-choice food test at weaning. During training (conducted at the ages displayed along the tops of the panels), pups received oral infusions of flavored milk either while attached or not attached to the nipple of an anesthetized dam.

pre-weaning pups that received the CS while suckling did not show toxiphobia to diet G (Fig. 4, left and middle panels). Pre-weanlings trained identically, but not while suckling (i.e. off-nipple), exhibited robust, single-trial conditioned aversions to diet G, as seen in the middle and left panels of Fig. 4.

Thus conditioned taste aversions *in the preweaning* rat are apparently blocked by suckling. This blockade is absent in weanlings, even when the conditioning procedures are conducted while suckling. Thus the blockade of nursing-related toxiphobia disappears by 20 days of age. Weanling pups displayed clear aversions to food containing the CS experienced while nursing. Although rat pups do not acquire nursing-related taste aversions in a nursing context, it is clear that neonatal rats learn other types of contingencies while nursing (27) and that the suckling act itself, even without nutritive consequences, is rewarding (28, 29).

We have examined this fascinating phenomenon in a variety of ways. The interested reader can consult other reports and papers to learn more about the parameters and possible mechanisms that have been investigated (1, 30).

For the purposes of the present discussion, however, I would like to relate one part of an experimental approach that was designed to address the *blockade of toxiphobia as ontogenetic adaptation*. From the perspective of ontogenetic adaptation, we can appreciate a variety of morphological and physiological changes that co-occur with entry into different ingestive niches during development. It is possible to view behavior, and especially *learned aspects of behavior*, in the same adaptive context. This approach, although

feasible, has not been broadly pursued and remains an important, but under-utilized avenue to integrating learning into a more complete biological framework. Moreover, I believe that our perspective on newborn behavior and its development would be enhanced by application of this approach.

The blockade phenomenon is divisible into two aspects. First is the blockade itself, namely the lack of toxiphobia exhibited by young pups (less than 20 days of age) that receive the taste-illness pairing during a nursing episode. The second significant aspect is the absence of the blockade in pups older than 20 days that receive the identical CS-UCS pairings while they suckle.

As an ecological construct, the perspective of ontogenetic adaptation does not emphasize age-related changes per se, although time-linked developmental milestones can be valuable clues in the early stages of such work. The adaptive perspective directs our attention towards contextual changes that typically occur during development. In the case of the blockade phenomenon, we were struck by the correlation between weaning and the transitional change in the blockade. Specifically, we noted that the blockade was intact in pre-weaning pups (<20 days) and disappeared as they grew older. In terms of the pup's ontogenetic niches, the blockade operates while the infant lives as an obligate suckler and subsists in the ingestive niche where mother's milk is the sole nutritive source. By the third postnatal week, the rat pup has entered the next niche, the weaning niche, in which there are available sources of nutrients other than mother's milk.

From an evolutionary perspective, we might expect some learning strategies to change during development

as different niches are encountered. While the infant rat inhabits a feeding niche in which it is an obligate suckler, there are no possible benefits to be gained from learning or expressing an aversion to a maternally associated ingestive cue. The costs of avoiding nursing-relating stimuli, of course, are great. At this stage, the pre-weanling might even be "protected" from acquiring or expressing aversions to maternal food cues. The weanling, in contrast, inhabits a niche in which it can acquire and utilize nutritive resources in addition to mother's milk. The weanling possesses the behavioral and physiological adaptations for consumption of such foods. In this sense, then, the weanling can "afford" to avoid mother's milk.

Although we have identified some of the parameters that are necessary and sufficient to obtain the blockade of toxiphobia, it is not apparent how pups younger than 20 days do not become toxiphobic while suckling, whereas pups just a few days older show suckling-related aversions under identical circumstances. We can reject explanations involving limited sensory, learning or memory abilities in pups less than 20 days old. Pups in the various littermate control groups learned and demonstrated clear aversions, as long as they were not suckling during training.

We therefore conclude that the nursing-related blockade of toxiphobia and the dissolution of this blockade are two learning strategies. These strategies alter the manner in which information is integrated and the way in which the learning is expressed. Pups alter their strategies as part of an overall pattern of adaptation to two different ingestive niches. Specifically, the blockade of toxiphobia while nursing is an ontogenetic adaptation related to the ingestive niche occupied by the infant rat. It is significant that the developmental dissolution of the blockade of learning by nursing coincides with reduction in the maternal milk supply and the weanling pup's exploitation of alternative nutritional sources.

We imposed a delay on weaning by denying pups access to food and water sources other than mother's milk. Delayed weaning was accomplished in specially constructed cages that allowed mothers, but not pups, access to food and water. Pups were trained on day 26 in the standard taste aversion procedures and aversion learning was assessed in a three-choice food test on day 29 (31).

We found that 26-day-old pups without prior experience with food (delayed weaning) did not demonstrate a taste aversion to a suckling-related cue that had been paired with toxicosis. The delayed weaning procedure did not interfere with the pup's ability to learn and remember the taste aversion because delayed-weaning pups trained identically, but not while suckling, displayed aversions to diet G. Normally weaned animals displayed taste aversion learning in both on-nipple and off-nipple conditions. The apparent blockade of learning by delayed weaning pups was eliminated by

giving pups just 4 h experience with solid food 2–3 days prior to training (31).

Weanling pups reared exclusively on mother's milk thus provided no evidence of learning a conditioned taste aversion in a nursing context. On the basis of these data, we could not determine if delayed weaning produced pups that failed to acquire conditioned taste aversions while nursing or failed to express the conditioned taste aversion. Thus the issue of learning versus performance appeared. If delayed-weaning pups failed to learn an aversion while suckling, then pups exposed to food after being trained should not show aversions to diet G. If, however, experience with non-maternal food resources permits the expression of a previously learned conditioned aversion acquired while nursing, then delayed-weaning pups exposed to food after training on nipple should subsequently avoid food containing the flavor CS (diet G). Indeed, we found that a brief, 4-h exposure to food two days after training on nipple resulted in aversions to diet G (31). Thus a short period of ingestion, even after taste aversion conditioning, appears to eliminate the blockade.

Delayed-weaning pups trained while nursing learn aversions to the flavored milk CS but fail to express the aversion unless they experience food. Because experience with food either several days prior to training or after training can turn off the blockade, we must conclude that the blockade by nursing is related to failure to express rather than to acquire the learned association.

The view of learning that is at the core of this interpretation differs from the traditional approaches and perspectives portrayed earlier in this report. The perspective of ontogenetic adaptation used here was an asset in illuminating the possibility of new hypotheses to test. It is highly unlikely that we would have conceptualized the experiments on delayed weaning and others in this series (24) without this perspective. Again, these experiments, unlike so many others in the area of early learning, were not formulated to study learning per se, but were designed to study the developing animal and the formative course of its behavioral organization during the discontinuities of early life.

Conclusions

To embody learning involves relinquishing the putative benefits of separating an abstract process (learning) from the body which, through its behavior, is the manifestation of learning. Any lost benefits are more than compensated for by gains in ability to recognize learning in its various functional manifestations. These "functional manifestations" are adaptations and those that appear and disappear with infancy are initial candidates for consideration as *ontogenetic adaptations*.

Perspectives that incorporate concepts of ontogenetic adaptation, whether morphological, neural or

behavioral, are likely to be ecologically oriented. Ecological orientations require the presence of behaving, interacting bodies that change over time, so there is fit between many developmental and ecological constructs. Learning is treated in this report as part of the body's action and development. It can be driven or regulated by experience but, like other elements in bodily function, it is carried by physical development. In this sense, I have suggested the idea that learning does not develop, but bodies develop.

The present report featured analyses of early learning that were made possible or that make more sense by use of an ecological framework. The animal's natural environment, which tends to change sequentially during early development, requires significant modifications in morphology, physiology and behavior. These adaptive modifications can be seen as the template of development. Learning changes along with and like other such bodily characteristics.

Clearly and irrefutably, fetuses, neonates and infants learn. Investigations that concluded otherwise were probably aimed at forms of behavior that were inappropriate for age or context. Types of learning and the roles of learning change at each point in development.

This perspective has potential value for some clinical concerns. Many of the sequential adaptations that constitute development were selected for (evolved) in contexts that differ from our modern environments. To the extent that we place infants in environments that differ from their evolutionary niches, there is increasing potential for malleable processes to become redirected or variably regulated. It would seem particularly likely that experience-sensitive mechanisms (e.g. learning) could incorporate stimuli, responses or contingencies that are evolutionarily unexpected and that some new patterns might constitute pathology. Only with increased sensitivity to learning in the developing body will we be able to recognize how development, parent-infant interactions and environmental regulations can shape development into forms that present health or malfunction.

References

1. Alberts JR. Early learning and ontogenetic adaption. In: Krasnegor NA, Blass EM, Hofer MA, Smotherman WP eds Perinatal Development: A Psychobiological Perspective. New York: Academic Press, 1987:11-37
2. Alberts JR, Cramer CP. Ecology and experience: Sources of means and meaning of developmental change. In: Blass EM ed Handbook of Behavioral Neurobiology. New York: Plenum Publishing, 1988:1-39
3. Gould SJ. Ontogeny and Phylogeny. Cambridge: Belknap Press, 1977
4. Oppenheim RW. Cell death of motoneurons in the chick embryo spinal cord: 7. Motoneurons prevented from dying in the embryo persist after hatching. Dev Biol 1984;101:35-59
5. Williams GC. Adaptation and Natural Selection. Princeton: Princeton University Press, 1966
6. Galef BG. Social effects in the weaning of domestic rat pups. J Comp Physiol Psychol 1971;75:358-62
7. Thiels E, Alberts JR. Milk availability modulates weaning in the Norway rat (*Rattus norvegicus*). J Comp Psychol 1985;99:447-56
8. Lieberman M, Lieberman D. Lactose deficiency: A genetic mechanism which regulates the time of weaning. Am Naturalist 1978;112:625
9. Rozin P. The selection of food by rats, humans, and other animals. In: Rosenblatt J, Hinde RA, Bees C, Shaw E eds Advances in the Study of Behavior. New York: Academic Press, 1976:21-76
10. Heird WC, ed. Nutritional Needs of the Six to Twelve Month Old Infant, vol. 2. New York: Raven Press, 1991
11. Alberts JR. Ontogeny of social recognition; An essay in mechanism and metaphor in behavioral development. In: Gollin ES ed Comparative Development of Adaptive Skills: Evolutionary implications. Hillsdale, NJ: L Erlbaum Assoc, 1984:65-99
12. Arnold SJ. The microevolution of feeding behavior. In: Kamil E, Sargent T eds Foraging Behavior: Ecological, Ethological and Psychological Approaches. New York: Garland Press, 1980: 409-53
13. Alberts JR. Olfactory contributions to behavioral development in rodents. In: Doty RL ed Mammalian Olfaction, Reproductive Processes, and Behavior. New York: Academic Press, 1976:67-93
14. Pedersen PE, Blass EM. Olfactory control over suckling in albino rats. In: Aslin RN, Alberts JR, Peterson MR ed Development of Perception. New York: Academic Press, 1981:359-81
15. Pedersen PE, Blass EM. Prenatal and postnatal determinants of the 1st suckling episode in albino rats. Dev Psychobiol 1982;15:349-55
16. Ronca AE, Lamkin CA, Alberts JR. Maternal contributions to sensory experience in the fetal and newborn rat (*Rattus norvegicus*). J Comp Psychol 1993;107:61-74
17. Hall WG. Weaning and growth of artificially reared rats. Science 1975;190:1313-15
18. Hall WG. What we know and don't know about the development of independent ingestion in rats. Appetite 1985;6:333-56
19. Brake SC, Sager DJ, Sullivan R, Hofer MA. The role of intraoral and gastrointestinal cues in the control of sucking and milk consumption in rat pups. Dev Psychobiol 1982;15:529-41
20. Johanson IB, Hall WG. Appetitive learning in 1-day-old rat pups. Science 1979;205:419-21
21. Johanson IB, Teicher MH. Classical conditioning of an odor preference in 3-day-old rats. Behav Neural Biol 1980;29:132-6
22. Rudy JW, Hyson RL. Consummatory response conditioning to an auditory stimulus in neonatal rats. Behav Neural Biol 1982;34:209-14
23. Galef BG. Development of olfactory control of feeding-site selection in rat pups. J Comp Physiol Psychol 1981;95:615-22
24. Melcer T, Alberts JR. Early weaning does not accelerate the expression of nursing-related taste aversions. Dev Psychobiol 1985;19:375-82
25. Martin LT, Alberts JR. Taste aversions to mother's milk: The age-related role of nursing in acquisition and expression of a learned association. J Comp Physiol Psychol 1979;93:430-45
26. Lincol DW, Hill A, Wakerly JB. The milk-injection reflex of the rat; An intermittent function not abolished by surgical levels of anesthesia. J Endocrinol 1973;57:459-76
27. Brake SC. Suckling rats learn a preference for a novel olfactory stimulus paired with milk delivery. Science 1981;211:506-7
28. Amsel A, Burdette DR, Letz R. Appetitive learning, patterned alternation, and extinction in 10-day-old rats with non-lactating suckling as reward. Nature 1976;262:816-8
29. Kenny JT, Blass EM. Suckling as an incentive to instrumental conditioning in preweanling rats. Science 1977;196:898-9
30. Alberts JR, Gubernick DJ. Early learning as ontogenetic adaptation for ingestion by rats. Learn Motiv 1984;15:334-59
31. Gubernick DJ, Alberts JR. A specialization of taste aversion learning during suckling and its weaning-associated transformation. Dev Psychobiol 1984;17:613-28