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suckled and while they were away from their dams (see also Kehoe and Blass, 1985). However, Pelchat and Brake also found that rejection was attenuated during suckling as compared to other, less natural contexts. Thus, there is an incomplete blockade of expression of rejection when the pup is at the nipple and it might be possible for a rat pup to express a lactose avoidance while suckling.

The results we have reviewed suggest a dissociation between the animal’s affective responses to food (liking) and its ingestive responses when on the nipple. A taste that will deter ingestion in a feeding/drinking situation has no effect or an attenuated effect on consumption while suckling.

There is some evidence for this affect–ingestion split in humans. Human infants make distinctive rejection faces in response to bitter tastes (Rosenstein and Oster, 1988; Steiner, 1979). But there is little evidence that bitter tastes suppress the young infant’s intake of solutions from a nipple (Desor et al., 1975). (This may also be interpreted as a difference in concentrations; the facial response studies used much stronger solutions.) There is also a relevant clinical finding. A few cases are on record of hospitalized infants that were mistakenly given bottles of hypertonic saline solutions instead of a sucrose-based formula for nursing (Finberg et al., 1963). Some infants ingested the solution readily, and died.

There are two sides to the findings we have reviewed in this section. They indicate protection against milk avoidance for the first part of nursing, but an end to this protection in just the period in which weaning begins. In this latter framework, the appearance of avoidance learning by rat pups on the nipple in the third week of life can be viewed as an adaptation to weaning, and is consistent with the hypothesis that lactose intolerance supports learning of milk rejection, and therefore plays a role in weaning.

3. Learned Preferences

The “nipple protection” effect has been demonstrated only for aversive aspects of food and nursing. In the first weeks of life, rat pups learn conditioned preferences for stimuli presented while suckling. For example, Gable and Henderson (1972) allowed rat pups free access, for the first 2 to 3 weeks of life, to suckling from a lactating female who was consuming a diet with a distinctive taste. When the pups were tested at weaning, they showed a
preference for their dam's diet over a novel diet. Brake (1981) exposed 11- to 14-day-old rat pups to a normally aversive orange odor while they were attached to the nipples of an anesthetized dam. Some pups received infusions of milk through an introral cannula while they sucked and others did not. Both groups of pups showed an increased preference for orange odor, but pups who received milk infusions while they sucked showed larger increases in preference.

There is no evidence for an attenuation of preferences which are learned during sucking as compared with preferences which are learned during feeding or drinking. However, the preferences that have been demonstrated are, in general, rather weak. The ability to form weak preferences is neither predicted nor denied by an adaptive approach, since it has both benefits and disadvantages. This ability allows the young mammal to learn something about the foods consumed by its parents, and thus may be beneficial after weaning. On the other hand, the same ability to learn preferences during sucking increases the chance of a stronger preference for milk, which may be maladaptive.

D. THE WEAKNESS OF POSITIVE AFFECTIVE LINKAGES TO FOOD IN NONHUMANS

We come now to some general features of mammals that have, as one effect, the reduction of the “attachment” to milk. Milk’s claim to such an attachment is dual: its association with repletion and nurturance, and its primacy as a food. We will deal with each in turn.

If generalist feeders, such as humans, rats, and pigs, confine their feeding to only a few foods, they take a considerable risk. The virtue of their broad acceptance of potential foods is the flexibility it provides in finding adequate food; shortages of specific foods, or the presence of a species that is a more efficient utilizer of a specific food, cause only minor disturbances to the generalist (Rozin, 1976b). Strong attachments to specific foods would blunt the generalist’s advantage and discourage it from its frequent exploration of new food possibilities.

The Asymmetry in Acquisition of Preferences and Avoidances

We have seen how aspects of the taste of milk, its gastrointestinal effects, and the insulated nature of the nursing situation conspire to make the milk preference less likely to occur in adulthood. But nonhuman generalists seem, in addition, to resist developing any strong acquired food preferences, in contrast to their ability to acquire food avoidances or aversions rapidly. This asymmetry is illustrated most clearly in studies of food preferences of laboratory rats. Acquired aversions are established rapidly, usually in one trial, and are typically strong and long lasting (Garcia et al., 1974; Rozin and Kalat, 1971; Domjan, 1980). Preferences are harder to demonstrate, and when they occur, they usually require a number of trials, are small in magnitude, and are relatively transitory (Capretta et al., 1973; Rozin and Kalat, 1971; Zahorik, 1979) [but see Booth (1982), for some exceptions and an argument against our claim].

Systemic “visceral” reinforcement, such as caloric repletion (Bolles et al., 1981; Booth et al., 1974; Holman, 1975; LeMagnen, 1981), recovery from illness (Garcia et al., 1967; Zahorik et al., 1974), or recovery from drug withdrawal (Parker et al., 1973; Zellner et al., 1985) can enhance preferences for associated foods. But, most strikingly, although the rat’s innate preference for sugar water is easily reversed after one contingent illness experience, its innate avoidance of bitter or irritant substances is extremely hard to reverse, even over many trials (e.g., Hilker et al., 1967; Rozin et al., 1979; but see Zellner et al., 1985).

There are only a few studies that have directly compared preference and avoidance acquisition. Seward and Greathouse (1973) report results favoring stronger negative conditioning, but no study has been able to find a way to equate convincingly the value of the positive and negative “USs” (this may not be possible).

Finally, although mere exposure seems to be a moderately effective means of producing food preferences in humans (e.g., Zajonc, 1968; Pliner, 1982), the effect is usually weak and transitory in most animal studies (e.g., Galef, 1977). The weakness of the exposure-preference link is most obvious in the laboratory rat’s limited allegiance to the chow that it has been raised on since weaning; it readily abandons this nutritive and reliable food source when any of a great variety of alternatives is offered.

There are indications that the same asymmetry (negative bias) exists in humans. Although one-trial taste aversions are frequent in humans (Carb and Stunkard, 1974; Logue et al., 1981; Pelchat and Rozin, 1982), their opposite, one-trial acquired preferences, are quite rare. Rozin (1986) collected experiences from 440 subjects on a questionnaire asking for recall of incidents in which likes or dislikes were created as a result of a single experience. In the domain of foods, 85 dislikes were described (taste aversions), but only 13 likes. Since people eat liked foods more frequently than disliked foods, there are more opportunities for them to acquire dislikes than likes, so that this finding does no conclusively argue for greater potency of negative learning.

We claim that in nonhuman generalist animals there is a resistance to acquiring strong attachments (preferences, likes) for foods. This makes adaptive sense. There is an urgency in avoiding dangerous foods, which could well be life threatening on a second experience, so a rapid and strong response is highly desirable. There is less urgency about acquiring preferences.
Furthermore, there are specific disadvantages, as discussed above, to heavy dependence on a single food.

E. The Absence of Food Imprinting or Primacy Effects in Mammals

A primacy effect means that all other things equal, if food A is experienced for a period of time before food B (periods can be minutes to months), there is a tendency to prefer food A to food B even if both foods are experienced for equal amounts of time. Food imprinting means that a food that was experienced during a “critical period” in an animal’s life will be liked better than an equally familiar food exposed at a time other than the critical period. Imprinting does not necessarily imply primacy. The critical period may occur at any time in an animal’s life. However, learning which occurs early in life is most relevant for our purposes. The critical period does not rule out learning at other times, but rather, it implies that learning will be particularly fast, robust, and persistent if it occurs within the critical period. Imprinting is usually especially resistant to reversal.

The adaptive arguments against imprinting and primacy in generalist animals overlap with those against strong acquired preferences by generalists. Given the instability of the food environment, especially across seasons, it is unlikely that a long-term fixation on foods present at any particular time in life would be desirable. The case for recognition of conspecifics, the traditional domain of imprinting, is just the opposite. We know of no evidence for imprinting on foods in mammals or other generalist vertebrates. But even in the absence of imprinting there might be a primacy effect that would favor foods encountered earlier in life. If this existed, milk might be highly preferred, among mammals. We do not claim that the lack of primacy or imprinting are specific adaptations to weaning. Imprinting and primacy are only present in specific domains (e.g., species recognition). Our claim is simply that the absence of such processes works to the advantage of weaning, even if this absence was not selected for in evolution.

We know of a few studies which demonstrate a primacy effect in nonmammalian vertebrates. Burghardt and Hess (1966) exposed hatchling snapping turtles to either horsemeat, guppy, or redworm for their first 12 meals and then exposed them to one of the other two foods for 12 feedings. The test involved a choice among the three foods. Out of 20 turtles, 16 preferred their first food. In a second study (Burghardt, 1967), hatchlings of the same species were offered single meals of horsemeat and worms 1 week apart. A choice test during the third week revealed a primacy effect in 20 of 25 turtles. Capretta (1969) exposed chicks to one of two colors of mash during their first 24 hours of life. The colors were then switched for the next 24 hours. When chicks were given a choice between the two colors, they preferred the color that they had experienced first.

Although a number of studies have tested for food primacy effects in mammals, none have demonstrated such an effect. Capretta and Rawls (1970) compared exposure to garlic flavor in young rats in the first 21 days of life (via mother’s milk) to exposure to garlic in drinking water during the first 5 postweaning days. Both procedures produced approximately equal modest increases in garlic preferences. Wurtman and Wurtman (1979) measured the effect of exposing rats of different ages to sugar on their later preference for sugar, and found no age effects. Bronson (1966) measured food intake in a choice situation and latency to consume food in a runway, using pellets as the baseline food and these same pellets inside gelatin capsules as the experimental food. Earlier exposure to the gelatin capsules (days 16–25) did not produce a greater preference for them than exposure for the same period later in life (days 33–42), with testing beginning at 48 or 100 days of age. None of these studies is or could be definitive; there may well be conditions under which primacy holds. Nonetheless, positive findings are lacking.

There is extensive evidence that early food experiences can affect later food preferences (e.g., Galef, 1977); for rats; Kuo (1976) and Wysocka (1981) for cats, but these studies do not explore whether early experience is more potent than later experience. Wysocka (1981) has discussed this issue at some length, and reviews both experimental and more anecdotal evidence. These preferences, which are acquired by infant mammals, may serve to ease the introduction of solid foods. The mechanism for these preferences, which tend to be weak and transient, seems to be familiarity [Galef (1977); see also Wysocka (1981), for a discussion of the role of parental factors in animal food preferences].

One might argue that the maladaptiveness of fixation on milk (by primacy or imprinting) is a reason (selection pressure) for the absence of these effects in mammals. (For imprinting, the milk “problem” could be “solved” by delaying the onset of the critical period until after weaning.) This may be true, but the weakness of these effects, and the meager evidence from nonmammalian generalists, suggest that more general ecological factors discourage such adaptations in generalists. Ironically, the best evidence to date for primacy and/or imprinting in mammals comes from milk; it is a highly palatable food to many laboratory animals and human domesticates (e.g., cats and dogs), and is one of the most palatable of all foods to adult humans in some cultures (e.g., Peryam et al., 1960; Rozin, 1976a).

III. Adaptations for Discovering Alternatives to Milk

We have described a set of adaptations (or processes, not specifically the product of natural selection) that might lead to weak preferences for milk, or perhaps to rejection of it. There is another side to weaning from milk: the exploitation of alternative food sources. The maturation of the young
and the mother’s behavior with respect to them provide increasing opportunities for feeding, and encourage a shift to solid foods. In the laboratory rat, this shift takes place over a 2-week period. Galef (1981) describes, for the rat in the period between 2.5 and 3.5 weeks of life, a set of events that all promote weaning: (1) the milk supply of the dam fails to meet the needs of her litter (days 16–18) (Thiels and Alberts, 1985); (2) solid food ingestion begins (day 17); (3) lactase deficiency appears (beginning in the third week); and (4) the ability to associate illness with cues experienced while suckling appears (between 15 and 20 days). In this same period, (5) the mother begins to reject her young or make herself less available for nursing and she is less likely to retrieve her pups (reviewed in Alberts and Gubernick, 1983); and (6) interactions between mother and offspring facilitate learning about solid foods, as the young learn what the mother and other adult rats eat and are exposed to these foods (Galef, 1977, 1985).

The latter point is of particular relevance, so we will discuss it briefly [it is well reviewed in Galef (1977, 1981, 1983)]. Rat pups become familiar with maternal foods by experiencing some of the food flavors in the mother's milk (Galef and Henderson, 1972; Galef and Sherry, 1973). Furthermore, by following the mother to feeding sites, weanling rats are exposed to both the locations and the chemical and other properties of the mother's foods (Galef and Heiber, 1976). Familiarity, or blunting of neophobia, encourages the weanlings to feed on these foods (Galef, 1977) [see Wywricka (1981), for some related observations and mechanisms in kittens].

The effect of these adaptations is to develop an alternative to milk at the very time when the mother's milk is failing, when the pup is losing its capacity to utilize the milk fully (lactase deficiency), when milk aversions become expressible, and perhaps when exposure to odors and flavors while nursing can influence later behavior (Galef, 1977; Melcer et al., 1985). This latter exposure effect is weak and transient (Galef, 1977), but it may be all the weanling needs to get started on appropriate foods.

We can only marvel at the exquisite articulation of these adaptations, though we should not really be surprised, given the vital importance of a smooth weaning for survival. We assume that the adaptations we have discussed, which are based largely on research on rats, hold to some degree among other mammals.

### IV. Milk as a Food for Humans

Humans differ from all other animals in that milk is often available as an adult food. There is not yet a satisfactory account of the history of milk as an adult food for humans. There is undoubtedly some linkage between early animal husbandry, an initial, minimal use of milk of domesticated animals, and later dairying and extensive milk use (see Simoons, 1969, 1970, 1978). Nonetheless, the great majority of the human race, like the rest of the mammals, are lactose malabsorbers (Harrison, 1975; Johnson et al., 1974; McCracken, 1971; Simoons, 1970, 1978). Many malabsorbers (e.g., in the Middle East and India) eat cultured milk products, in which the lactose is destroyed by microorganisms outside the body (or, in the case of yogurt, by lactase released in the gastrointestinal tract, as well (Kolars et al., 1984)). This is one of the many triumphs of culinary technology over biological limitations. Other groups, particularly the Chinese, reject milk and its derivatives.

The evidence is convincing that the capacity for lactose digestion and absorption in adulthood is produced by a single, dominant gene (Lisker et al., 1975; reviewed in Harrison, 1975; Simoons, 1978). The selection pressure for this was provided by the availability of milk from domesticates; this fits with the culture history of the lactose-tolerant groups (Simoons, 1970, 1978).

Humans stand out among the mammals in a number of regards with respect to their relations to milk. (1) Some humans can digest milk as adults [these are primarily people of Northern European stock and some scattered nomadic pastoral groups (Fig. 7). (2) Although lactose is not among the sugars most preferred by humans, one can infer that it tastes sweeter to humans than it

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**Fig. 7.** Percentage of individuals in several different populations who are lactose malabsorbers. The data were taken from a number of different sources (Kretchmer, 1972).
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V. Conclusions

The transition from milk and suckling to feeding and drinking, and from milk to other foods and fluids, is one of the major events in the development of mammals. It is assured by a wide set of overlapping adaptations in the physiology and behavior of both mother and offspring. We have described a set of adaptations and processes that might facilitate this transition: the lack of sweetness of lactose, the development of lactose intolerance as a possible source of milk avoidance, the nipple protection effect and its dissipation, the weakness of positive affective linkages, the absence of food imprinting or a primacy effect for foods, the drop in availability of the mother's milk, the decrease in availability and cooperativeness of the mother, and the interactions of mother and offspring that lead the offspring to become familiar with solid food sources. There is great redundancy here, as befits such an important transition. The adaptations we have discussed, and no doubt many others, illustrate Waddington's (1957) principle of canalization: the existence of multiple adaptations that, through redundancy, guarantee a certain course at important stages in development.

Finally, we see some, but not all, of the milk-weaning adaptations in our own species. The absence of some of them (particularly lactose malabsorption in adulthood) and the presence of strong social influences result in persistence of milk drinking and a high preference for milk among many adults in Western societies. But they are the exception. For the most part, the adaptations shared with other mammals for weaning from milk result in the fact that milk is not a preferred (or even acceptable) food for most adult human beings.

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References


Adaptations to Weaning from Milk


Note added in proof. It has just come to our attention that the relative unpalatability of milk sugar (lactose) among sugars is paralleled by peculiar properties of milk proteins (casein and lactalbumen) among proteins. In most cafeteria studies on food selection by rats (e.g., Richter et al., 1938), casein was the protein of choice. Some investigators [e.g., Scott, E. M. (1946)] self-selection of diet. I. Selection of purified components. *Journal of Nutrition* 31, 397-405 found that a substantial minority of rats failed to select adequate diets because they avoided casein, the only protein source. In recent study, Deutsch and Heinrichs (1988, A role for both neophilia and post-ingestive feedback in diet selection in protein deficient rats. *Neuroscience Abstracts*, in press) report an enhanced preference for protein that appears within a few minutes after a choice is presented to protein deficient rats. This substantial effect appeared for seven of the nine proteins tested. The two proteins on which the rats fail to show this striking effect are casein and lactalbumen. We do not know the origin of the special property; it is less unpalatability than failure to recognize these substances as protein. It is possible, as with lactose, that either special experiences during lactation or evolutionary selection of sensory properties of milk protein have rendered these two proteins anomalous and less desirable.