Preference Behaviour and Chemoreception

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choices as you imply certainly can be modulated due to postingestional factors. As to the relation of all this to feeding strategies, I am not sure It could be that as the tree becomes increasingly defoliated and changes both in physical appearance and chemical appearance it affects ongoing predation by the squirrels.

Galef

Have you considered the possibility that the feeding behavior of the squirrels alters the chemistry of the pine tree to the squirrels own advantage? The destruction of the tree might inhibit terpene production, for example, thus rendering its twigs more palatable.

Capretta

We have done little to date in looking at the "response" of the tree to predation. In a section of our chapter entitled "Long-term responses of trees to predation by squirrels", we do consider the coevolutionary implications of this plant-animal interaction. Though we have concentrated on the squirrel's role in this interaction, it would be wise to monitor trees for change in some of their chemistry due to different degrees of feeding related defoliation (slight, moderate and severe). We do say in the chapter that "It is reasonable to suspect that increased defoliation leads to decreased photosynthetic activity, and as a consequence there would follow a reduction in the nutritional value of inner bark of heavily browsed trees".

Galef

It is possible that the difference in results reported by Mugford and Kuo is the consequence of many different strains of dog. After all, wild rats are highly neophobic while domestic rats are only mildly neophobic even though both are strains of the specis R.norvegicus.

Social transmission of learned diet preferences in wild rats[1]

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Abstract

When a colony of adult wild rats is trained to avoid one of two available diets, as a result of that diet's previous association with poison, pups born tc the colony eat only the diet which the adults of their colony are eating. Following isolation from the adults, pups continue to avoid ingesting other diets.

Adults influence pups' initial choice of diet in three ways: (1) by depositing olfactory cues near a feeding site, (2) by being physically present at a feeding site, and (3) in the case of dams, by transmitting flavor cues in their milk which reflect the flavor of their diet and affect pup diet choice at weaning. Once pups become familiar with cues associated with the diet to which their colony introduced them, they avoid other diets because of their novelty. Such socially mediated transmission of feeding patterns facilitates pups' transfer of feeding from milk to solid food by reducing the time needed by pups to locate foods in the environment and the probability that they will ingest toxic foods.

INTRODUCTION

It is a commonplace observation that the members of any species exhibit a tendency to select similar foods for ingestion. It seems reasonable to propose, as did P.T. Young (1968), that such species-typical food preferences are determined, at least in part, by genetically encoded and transmitted propensities to experience some gustatory sensations as more pleasurable than others. In other words, the physiological systems underlying affective response to various tastes may be considered an evolved species-typical characteristic, presumably promoting efficient utilization of food resources by species members in their natural habitat.

Even the existence of genetically influenced consistencies in the flavor preference hierarchy of members of a species does not preclude the possibility that experiential factors may produce differences in the dietary preferences of conspecific individuals. It is, for example, well established that animals which have experienced aversive gastro-intestinal events in association with the ingestion of a normally preferred food will subsequently exhibit a profound aversion to that food (Garcia, Hankins & Rusiniak, 1974). Conversely there is preliminary evidence that animals, which have a history in adolescence of prolonged ingestion of normally non-preferred food items may show a preference for these foods when subsequently offered them in a choice situation. Kuo (1967), for example, reared puppies on soybeans and other vegetables for the first 6 months of life and found that, when grown, these pups refused to take any meat, eggs, milk or fish and preferred vegetable to animal foods generally.

Examination of the feeding patterns of subpopulations of various species in their natural habitats, also frequently reveals consistent differences in the dietary selection patterns of members of different subpopulations. The causes of such differences in food preference exhibited by members of natural populations, living in uncontrolled environments are difficult to ascertain. However, a number of field workers have reported observations suggesting that in order to understand subpopulation differences in food selection it is necessary to take into account, among other things, the social context in which feeding behavior occurs. This is the case because patterns of food resource utilization may be traditional within a subpopulation and may be socially transmitted from individual to individual and from one generation to another within a given subpopulation. For example, Hinde and Fisher (1951) have reported that a variety of species of British birds have acquired the habit of removing the caps of milk bottles and eating cream from the surface of the milk. The fact that many birds in some localities, and none in other areas, where similar milk bottles are available, have acquired the milk bottle opening behavior suggests a social transmission of this behavior from individual to individual in those localities where it is common. In laboratory situations, an observer will not normally see the effects of such social processes on diet selection, unless he or she intentionally looks for them, because most experimental paradigms are explicitly arranged to keep the behavior of individual subjects independent of one another. However, examples of differences in feeding patterns which seem to require explanation in terms of the intraspecific social context in which feeding occurs are not uncommon in the reports of naturalists (See Galef, 1976, for further examples).

There is reason to believe that social influences on feeding behavior in mammals and birds are particularly important during the weaning of fledging process (Galef, 1977). The young of a species are ignorant of the location of nutritious foodstuffs to be found in the vicinity of the site where they are reared and have to go looking for such foods at a time when they are particularly vulnerable to environmental stress. The adults which reared them have, of course, learned the identity and location of necessary foods during their own explorations in the area where they rear their young. It would clearly be advantageous to the young, and therefore, to the reproductive advantage of their parents, if the young could be directed to available foods by adults. The ability of the young to acquire such information from adults would better prepare them for life in the particular area in which they must achieve independence of their parents.

The genetically encoded palatability preferences typical of a species, are only adaptive in terms of the mean properties of that species' ecological niche (Williams, 1966). It is behavioral plasticity which enables the individual to adapt to the special demands of the particular micro-habitat in which that individual is located. Social transmission processes could serve to reduce the cost to the individual, (in terms of both the energy and risk involved in the usual sort of trial and error learning) in discovering the distribution of resources within its own particular ecological situation.

SOCIAL FACTORS AND THE FOOD PREFERENCES OF WILD RATS

In the case of wild rats, which have been the major focus of my own work on social transmission processes, the ability of individuals to influence one another's feeding patterns might be particularly important at weaning. During weaning young rats, in addition to lacking information about the location and identity of needed foods, also lack the information necessary to protect themselves from poisons which may have been introduced into their environment. Poison avoidance mechanisms in individual rats generally depend on recognition of a potential food as novel (Galef & Clark, 1971). To the weanling rat, all solid foods are novel, so the weanling is in particular need of information if it is to avoid ingesting human introduced toxic baits.

There is, in fact, field data suggesting that the social transmission of feeding preferences from adult to young rats is a real phenomenon, serving to protect the young from potentially noxious foods in the environment. Fritz Von Steiniger (1950), reported that if a given poison bait is used in one area for an extended period of time, despite initial success, with the rats eating large amounts of the poison bait and dying in large numbers, later acceptance of the bait is very poor. Steiniger noted, in particular, that the offspring of animals surviving initial poisoning reject the bait without ever sampling it themselves. He attributed this poison avoidance by naive young rats to the behavior of experienced individuals which, he believed, dissuaded the inexperienced young from ingesting the poisoned food.

For the past several years, my students and I have been examining the social interactions of both wild and domesticated rats during weaning, under controlled conditions, seeking mechanisms whereby the social transmission of diet selection might proceed. In our basic experimental paradigm (Galef & Clark, 1971) colonies consisting of two male and four female wild rats were established in 1 x 2 m enclosures containing four wooden nest boxes. Water was continuously available and food was presented to the colony for 3 hr/day in two ceramic food bowls located approximately .9 m apart. Each of these bowls contained one of two nutritionally adequate diets (referred to below as Diets A and B[2]), each discriminable from the other in color, texture, taste and smell.

The adult members of a number of colonies were trained to eat either Diet A or Diet B and to avoid the other diet by introducing sub-lethal doses of poison (lithium chloride) into the samples of one of the diets offered to a colony during daily 3-hr feeding periods. Under these conditions, our wild rats rapidly learned to avoid ingesting the poisoned diet and continued to avoid it for some weeks, even when subsequently

offered the once poisoned diet free from lithium chloride contamination.

The experiment proper began when litters of pups born to colony members left their nest-sites to feed on solid food for the first time. We observed the adults and pups throughout daily 3-hr feeding periods on closed-circuit television and recorded the number of times the pups approached to within 10 cm of each food bowl and the number of times they ate from each food bowl containing an uncontaminated portion of either Diet A or Diet B.

After the pups had been feeding on solid food for a number of days, they were transferred to a new enclosure, where, without the adults of their colony, they were again offered the choice of uncontaminated samples of Diets A and B for 9 hr/day. The amount of each diet eaten by the pups in this situation was determined by weighing food bowls before and after each feeding session.

The results of these experiments are presented in Figures 1-2. Figure 1a presents data describing the feeding behavior of a typical litter of wild rat pups born to a colony trained to avoid ingesting Diet A, while Figure 1b presents data describing the feeding behavior of a litter of pups born to a colony trained to avoid ingesting Diet B. As is clear from comparison of the data presented in Figures 1a and 1b, the learned feeding preferences of adult colony members profoundly affected the feeding preferences of their young. In the presence of adults of their colony, pups ingested only the diet that the adults were eating. Furthermore, as shown in Figure 2, the learned dietary preferences of the adults continued to affect the feeding preferences of their young for 8 to 10 days following transfer of the pups to enclosures separate from the adult colony. Pups removed from colonies eating Diet A continued to eat Diet A while those removed from colonies eating Diet B continued to prefer that diet even in the absence of adults.

Taken together, these observations demonstrate that adult rats can, in some fashion, lead their offspring to feed solely on a safe diet in an environment containing food known by the adults to have been poisoned, thereby allowing the young to avoid ingesting potentially noxious foods. The data also show that the food preferences learned in the presence of the adults continues to affect the feeding behavior of the pups for some time following their removal from direct adult influence.

MECHANISMS FOR SOCIAL TRANSMISSION OF DIET PREFERENCES

Although I'm not going to describe the relevant experiments in any detail the results of further studies in my laboratory indicate that, as a

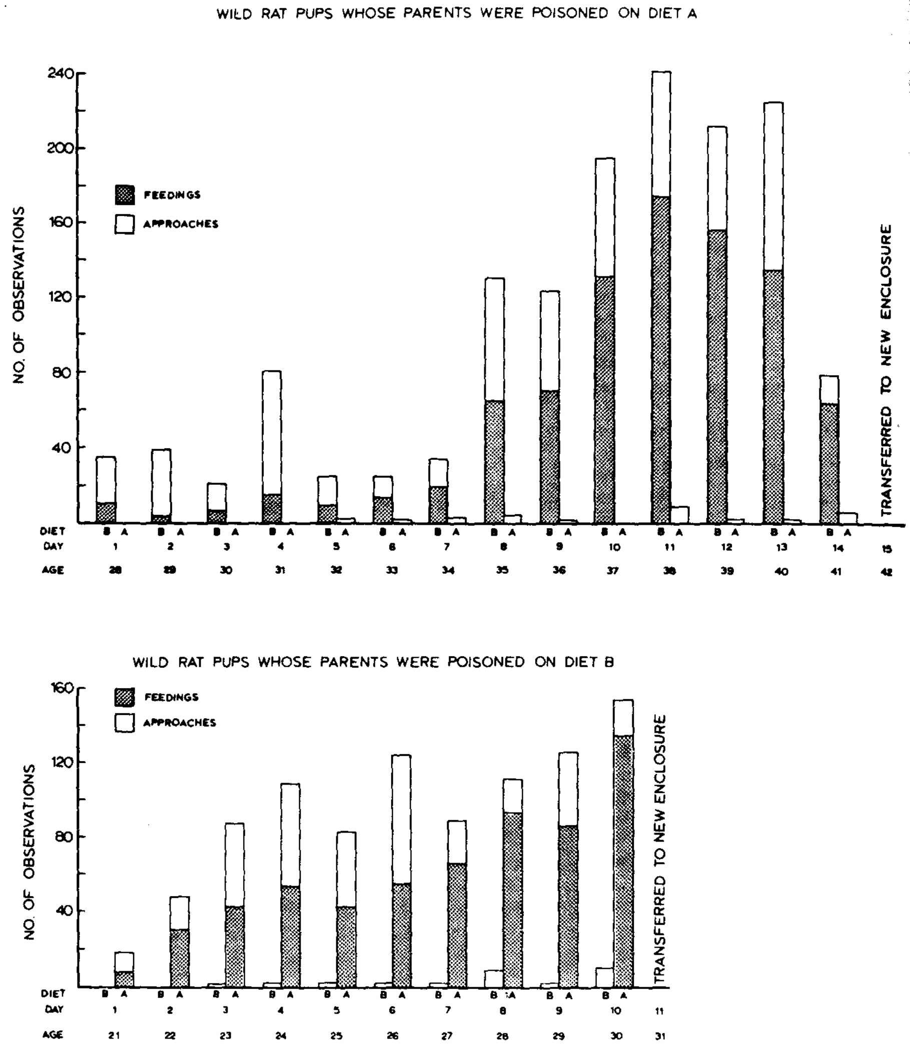

Figure 1. Number of observed approaches to and feedings upon Diets A and B by wild rat pups whose parents had been poisoned on either Diet A or Diet B.

result of interaction with the adults of their colony, rat pups learn to eat the diet which the adults of their colony are eating rather than to avoid the diet which the adults of their colony are avoiding (Galef & Clark, 1971). Furthermore, we have evidence of three ways in which adult rats can induce their young to wean to a given food.

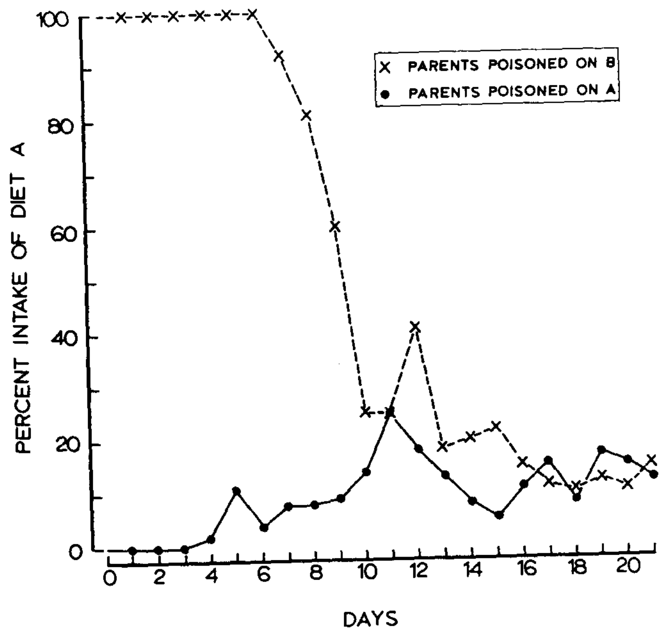

Figure 2. Amount of Diet A eaten, as a percentage of total intake of Diets A and B, by pups following removal to a new enclosure isolated from adults.

First, Mertice Clark and I (Galef & Clark, 1971, 1972) have found that the physical presence of adults at a feeding site attracts pups to that feeding site and markedly increases the probability of young rats initiating weaning on the foodstuff located at that site. This approach response on the part of the pups is in large measure mediated by visual cues.

Second, Linda Heiber and I (Galef & Heiber, 1976) have found that adult rats deposit residual olfactory cues in areas which they visit and that these olfactory cues bias weaning pups' choice of area for exploration and initiation of feeding. Pups prefer to explore and eat in an area soiled by conspecifics rather than in a clean area.

In addition to being able to influence pups' choice of feeding site, the mother of a litter of rats can also directly influence pups' dietary preference. David Sherry and I (Galef & Henderson, 1972; Galef & Sherry, 1973) have found that the milk of a lactating female rat contains cues directly reflecting the flavor of her diet and, at weaning, pups will exhibit a preference for a diet of the same flavor as the diet which their mother has been eating during lactation.

More recently Michael Leon and I (Leon, Galef, & Behse, 1977) have undertaken a series of investigations which suggest to me that there is a single mechanism underlying all three of these ways in which adults influence the food choice of young. Leon and I exposed young rats daily, from age 3 to 19 days, for 3 hr/day, to the odor of peppermint extract by placing the pups in individual cages and pumping in air which had passed over a dish containing peppermint extract. Control pups were treated identically except that the air stream entering their cages was uncontaminated. On day 20 each pup was placed individually in a food choice apparatus for 24 hr and its intake of each of two available diets was determined by weighing. The two diets presented to the pups had the same base: one diet was the base mixed with peppermint extract and one the base mixed with lemon extract.

Figure 3 indicates the amount of peppermint- and lemon-flavored diets eaten by control and peppermint pre-exposed individuals. As is clear from examination of the figure, the control pups exhibited a strong preference for the lemon flavored diet, presumably reflecting sensory-affective palatability hierarchies of the sort P.T. Young described. To the contrary, peppermint-odor pre-exposed pups exhibited a preference for peppermint-flavored diet. These data indicate that weaning pups prefer a diet of familiar smell, and that this familiarity produced preference is sufficient to overcome a considerable sensory-affective bias.

I would like to propose that the three mechanisms described briefly above (1) transfer of flavor cues in mother's milk, (2) the deposition residual olfactory cues, and (3) a tendency of pups to approach adults at a feeding site are just three ways in which adult rats are able to influence their young to become familiar with the properties of one diet rather than another. Because pups exhibit a preference for a familiar diet when selecting foods for ingestion, anything which an adult does to increase pup familiarity with the cues associated with a given diet will increase pup ingestion of that diet. Thus, in general terms, I believe one can understand the initial preference of pups for the diet which the adults of the colony are exploiting as a result of an enhanced familiarity with that diet consequent upon social interaction with adult colony members.

ROLE OF NEOPHOBIA IN THE MAINTENANCE OF DIET PREFERENCES

Of course there is more to the phenomenon described above than a simple pup preference at the time of initiation of feeding for the diet which adult colony members are eating. Not only do weanling wild rat pups

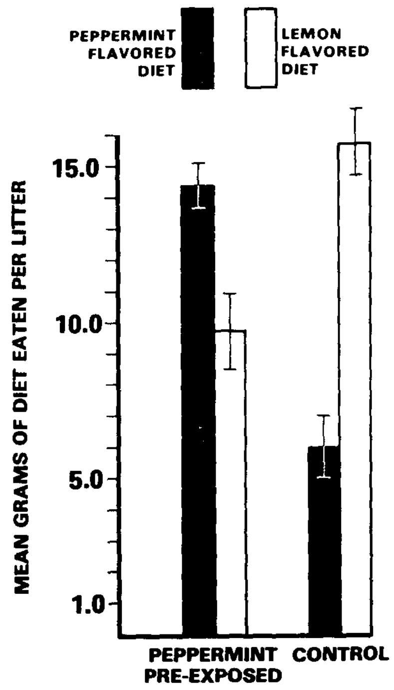

Figure 3. Mean grams of peppermint- and lemon-flavored base diet eaten by litters of pups pre-exposed to either peppermint odor or a clean air stream.

begin feeding on the solid food which the adults of their colony are eating, they continue to ingest only that diet so long as they were with the adults and continue to show the effects of interaction with the adults for some 8 to 10 days after removal from direct adult influence. An obvious question concerns the cause of the continuance of the pups' apparent preference for the diet to which the adults have introduced them.

I would like to propose a three-stage process to describe the entire phenomenon: initiation of feeding by wild rat pups on the adult diet and continued avoidance of the adult avoided diet by pups in isolation. First, as indicated above, adult wild rats can bring their young to initiate feeding on one diet rather than another. Second, I would suggest, that pups, as a result of ingesting the diet to which the adults have introduced them, increase their familiarity with its taste and smell and, third, that they then avoid alternative diets because of the relative novelty of those alternative diets. Wild rats have been described by Barnett (1958), Rozin (1968) and others as strongly neophobic; they show a strong tendency to avoid novel foods or other novel objects in the environment. It is at least conceivable that such neophobia is responsible for continued avoidance by pups of alternative diets once the pups have become familiar with the diet which the adults of their colony are eating.

If, in fact, neophobia is, at least in part, responsible for continued avoidance by wild rat pups of the adult-avoided diet, then one would expect domesticated rat pups, which are at best only mildly neophobic in comparison with wild rat pups (Barnett, 1958, Rozin, 1968) to behave quite differently from wild pups in our basic experiment. Domesticated rat pups might initially follow adults to the diet which the adults were trained to eat, but the pups should then transfer feeding to the adult avoided alternative diet at the time when neophobia becomes responsible for continued avoidance on the part of wild rat pups. Figure 4 reports typical

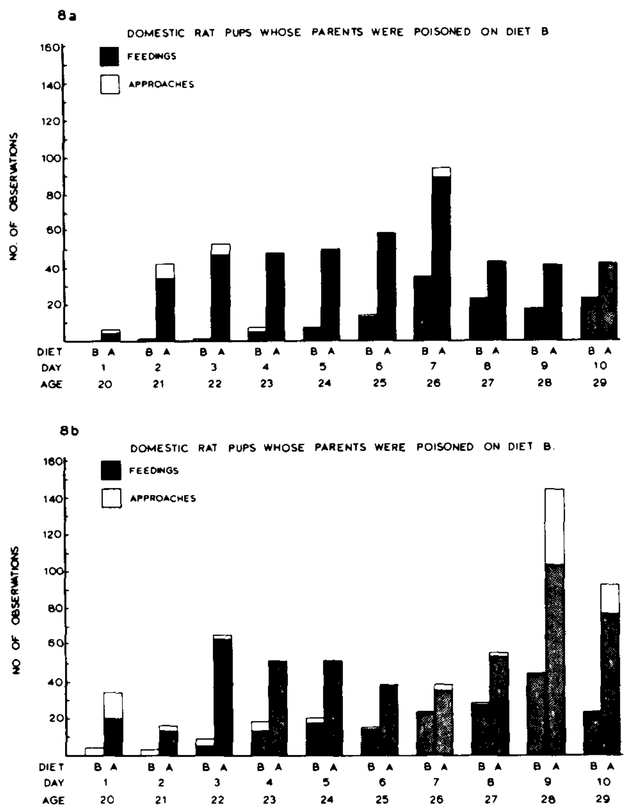

Figure 4. Number of observed approaches to and feedings upon Diets A and B by domesticated rat pups whose parents had been poisoned on Diet B.

data describing the feeding behavior of two of a number of litters of domesticated (Long-Evans) rat pups we've run in our basic experiment. As is evident from examination of the figure, domesticated pups, although initially feeding on the same diet as the adults of their colony, begin to eat the adult-avoided alternative diet after some 3 to 5 days (Galef & Clark, 1971). Thus the comparative data are consistent with the hypothesis that the extreme neophobia of wild rat pups is responsible for the maintenance of their avoidance of diets other than those introduced to the pups by the adults of their colony.

The results of other experiments support the same conclusion: (1) If wild rat pups are force-fed, at a time other than during the 3-hr colony feeding period, samples of the diet which the adults of their colony have been trained to avoid, the pups initiate feeding on the colony-avoided diet during colony feeding periods 1 to 3 days later (Clark & Galef, 1972). (2) If the adult colony is trained to avoid one feeding site rather than another (using electric shock) and the same diet is present at both feeding sites, wild rat pups transfer feeding to the adult-avoided feeding site 5 or 6 days following their initiation of feeding on solid food (Galef & Clark, 1972). Both of these findings are consistent with the view that it is the novelty of alternative diets which keeps wild rat pups feeding at adult utilized feeding sites and eating diets to which adults introduced them.

Thus the example which I've been discussing, the transmission of adult rat feeding preferences to their young, depends both on an ability of adults to bias the young toward experience of a specific food as a result of social interaction and on an independent predisposition on the part of the young to respond differently to a food once experienced than to other foods not introduced to them by adults and, hence, not familiar.

CONCLUSION

If one looks more broadly at the development of the range of behaviors in which social transmission processes appear to play a role, the same pattern emerges with considerable regularity. Experienced individuals introduce naive ones, via any of a variety of mechanisms, to one of a class of stimuli to which the young might have been introduced and the young individuals thereafter respond in a special way to that particular stimulus (Galef, 1976).

The means of introduction clearly varies considerably from species to species. Hogan (1966), for example, has shown that mother hens use a special food-call to attract their young to a feeding site and a food-calling hen can induce her chicks to ingest objects, such as mealworms, which they would otherwise avoid. According to Ewer (1963) a meerkat (Suricata suricatta) female with weanling young will run to and fro in front of her offspring holding some food in her mouth, evoking a food-snatching response in her kits and thus inducing the kits to ingest foods such as bananas, which they would normally ignore. As described above, wild rats by their simple presence at a food-site can induce pups to feed there on a relatively unpalatable diet. Maintenance of the transmitted behavior may depend either on reinforcement contingent on engaging in the pattern of behavior in question or a predisposition to behave in a certain way toward some stimulus once it has been experienced.

In conclusion, it seems clear that young animals may be strongly influenced in their diet selection as a result of interactions with conspecifics which render particular substances familiar to the neonates. Such social transmission of feeding patterns may be an important element in the adaptation of rat pups, facilitating the pups' transfer of feeding from milk to solid food both by reducing the time needed by young rats to locate necessary nutrients in the environment and by reducing the probability that weanlings will ingest poison foods which the adults of their colony have already learned to avoid. The observed socially transmitted feeding preference is the result both of social interaction and the reluctance of wild rats to ingest unfamiliar substances.

NOTES

1. The research reported here was supported by grants from the National Research Council of Canada and the McMaster University Research Board.

2. Diet A was powdered Purina Laboratory Chow and Diet B a sucrose and and casein based diet. Both wild and domesticated rats normally strongly prefer Diet B to Diet A.

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DISCUSSION

Rozin

Is there any evidence that the rat's earliest foods (your diets A or B) have any special status (e.g. resistance to poisoning, preference under stress) after the diets have achieved "control level" palatability in your experiments?

Galef

In response to your question, I'm sorry to have to admit that I don't have the data to allow me to answer it. I'll let you know in a few months how the relevant experiment comes out.

Rozin

The absence of strong-long lasting preferences for "pre-weaning" foods in rats might be a consequence, in an adaptive sense, of the mammalian condition. Milk is the first food. It would be maladaptive to search for it post-weaning: it isn't available in the world, and isn't fully digestible for the adult rat. So long-lasting early food attachments would be maladaptive. They may also be more generally maladaptive for any omnivore or general herbivore. The question now becomes, why are humans different? Why do they seem to develop strong attachments to early foods of life (including milk, but also native cuisines)? Might this have something to do with lactose tolerance in humans?

Galef

As to this question, I suspect that the absence of long-lasting preferences in rats and their presence in man reflects fundamental differences in feeding strategies rather than differences in lactose tolerance between the two species. While rats engage in oral exploration of their environment throughout life, gnawing and ingesting samples of most of the objects with which they come in contact, man does not. Humans depend, in large measure, on cultural processes in the selection of food stuffs. So it seems likely that every individual rat is able to discover for itself whatever is edible in its environment and can and should be ready to shift its feeding preferences to exploit new sources of nutrition which become available as the result of oral exploration. Because the average human does not engage in sampling behavior which would enable him or her to discover new foods, a relatively greater dependence on past experience in the selection of food items is not really unexpected. Obviously the preceding comments are very speculative and very nearly circular but I think they may be relevant.

Capretta

What if you poison the rats after they recover from the serially transmitted aversion; do they show more or less an aversion than they did previously, and is it more or less long-lasting?

Galef

We haven't examined that question directly, but given that the pups don't directly learn aversions as a result of interaction with adults, but rather avoid novel diets as a result of learning to eat those diets to which adults introduce them, I don't think that one would see much effect of social avoidance learning on toxicosis induced aversions.

Den Otter

Is there a sensitive period, in other words, must the animals learn their preference for a diet within a certain number of days after birth?

Galef

Social effects on diet selection are far more pronounced in juvenile than adult rats. Adults seem to select food for ingestion more or less independently of the behavior of adult conspecifics. So there is a resticted period during which social transmission of food preferences is likely to occur, though food preferences can be established throughout life by means other than social ones.

Capretta

How long-lived was the peppermint effect in your experiment?

Galef

The effects of exposure to an arbitrary odorant on diet selection in domestic rat pups tends to be relatively short-lived, on the order of 24 hr. We have, however found effects of peppermint exposure on other aspects of pup behavior i.e. approach to an odor source, that last for weeks.

Learned changes in preferences for chemical stimuli: asymmetrical effects of positive and negative consequences, and species differences in learning

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Abstract

It has often proved convenient to consider some chemoreception preferences to have been "built in" by natural selection and other preferences to have been "learned" in the course of an individual organism's experiences with its environment. While adaptive responses to chemical cues can arise through the collective evolutionary experience of a species or through the learning experiences of species members, these two routes to adaptive chemoreception preferences are not independent. Many preference behaviors reflect interactions between evolutionary and individual experience. Preferences for chemicals occupying different points in a "built in" preference hierarchy may not be equally easy to modify through learning, and evolutionary constraints on a species' learning mechanisms may determine the nature of the chemical cues species members learn about in their natural habitat.