EARLY SOCIAL ISOLATION AND INFORMATION TRANSMISSION IN RATS

CONSPECIFIC INFLUENCES ON DIET CHOICE IN THE NORWAY RAT (Rattus norvegius): THE ROLE OF EARLY SOCIAL ISOLATION

By

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A Thesis

Submitted to the School of Graduate Studies
in Partial Fulfilment of the Requirements
for the Degree
Master of Science

McMaster University

Master of Science (1993)
(Psychology)

McMaster University
Hamilton, Ontario

Title: Conspecific Influences on Diet Choice in Norway Rats (Rattus norvegicus): The Role of Early Social Isolation

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NUMBER OF PAGES: vii, 50

ABSTRACT

There is a large literature discussing social influences on diet choices in rats. However, the ontogeny of social influences on diet choices is poorly understood. Early experiences have dramatic affects on the development and expression of future behaviors.

The present research investigates whether early social experience altered the susceptibility to social influences on diet choices in juvenile Norway rats (R. norvegicus). Interactions with dam and siblings between parturition and weaning are prominent features of early rats development. It was hypothesized social behavior developed during this period and rearing pups in social isolation would disrupt the development of normal social behaviors.

Conspecifics influence the diet preferences of others by socially interacting. The first experiment investigated whether demonstrators could influence diet choices of rats with no social experience. In terms of diet preferences, demonstrators influenced both normally reared rats and rats reared in social isolation.

Interactions with conspecifics and exposure to diet odors without social contexts influenced the diet choices of 21 day old pups. Only interactions with conspecifics influenced diet choices of 28 day old rats. Rearing rats in social isolation may delay the onset of social specificity and the results of experiment 1 may have been the product of two different mechanisms. The second experiment investigated whether rats reared in social isolation attended to socially specific cues or to general olfactory cues. Exposure to flavored diets in a non-social context did not influence diet choices of rats reared in social isolation or normally-reared rats. Thus early social interactions do not appear to be necessary for demonstrator rats to influence the diet choices of other rats.

ACKNOWLEDGEMENTS

I found myself in a quandary when trying to decide who I was going to acknowledge and how I was going to acknowledge them. I did not want a boring list of names and their contributions. Each person made quite unique and equally important contributions to the completion of my Masters Degree. So, I decided that the best way for me to show my appreciation and gratitude for each of these people was write a short allegory.

I would like to thank my undergraduate friends, Dave Erikson and Jennifer Etter, for daring me to fly. I would like to thank my committee members, Jeff Galef, Martin Daly and Dave Rollo, for giving me the tools to build my wings. Dr. Galef took in a raw, enthusiatic dreamer, planted my feet firmly on the ground, taught me to be pragmatic, and to start from the ground up. Martin taught me that without a theory of how to birds do it, my dream of flight would remain just that, a dream. Dave's ever eager input fuelled my excitement for flying and, as each version of my wings crashed and burned, he offered helpful alternatives.

I also would like to thank my lab mates, Laurel McQuoid and Elaine Whisken, for helping me use the tools I was given. Laurel taught me how to use some of the more intricate tools while Elaine was forever telling me where to find them.

When times were tough and I despaired about ever building my wings, Phil Higham and Tom Eissenburg were there. Phil was always there, helping me fly while skeptics mocked me. Tom, with our latenight all veggie pizza from 527-1111, gave me strength during those all night work sessions. Finally, I would like to thank Janine Jennings, who was there during the final days before my first flight, helping me fine tune my wings and ensure that, when the time came, my explosion into flight would be controlled.

TABLE OF CONTENTS

Page

Introduction

Social Learning about Foods by Rats

Rats are social animals, living in a system of burrows from which they emerge to forage for food and to which they return between foraging bouts (Calhoun, 1962). Within the burrows, gregariousness is a prominent aspect of the behavior of rats and each rat spends a large amount of time in close proximity to others of its species.

Living socially can involve costs. For example, rats living in groups often have their food stolen by other group members (Whishaw & Tomie, 1987). However, potential benefits of sociality tend to outweigh potential costs (Galef, 1982). An increased ability to avoid toxic diets is one such benefit. Wild rats do not evaluate unfamiliar diets independently (Beck, Hitchcock, & Galef, 1988). They neither eat one unfamiliar diet at a time nor pause for extended periods of time between meals of different unfamiliar foods. Should a rat become ill, determining the diet responsible for illness becomes difficult. Interacting with conspecifics, and learning what they have eaten, provides an alternative to independent trial and error learning for the identification of potential toxins (Galef, 1986).

Further, food resources used by rats tend to be scarce or distributed in patches. Living colonially can benefit foragers in three ways. First, unsuccessful foragers can directly follow successful foragers to food sites (Galef, Mischinger & Malenfant, 1987; Horn, 1968). Second, living socially allows rats to make use of residual olfactory cues left by prior foragers at food sites (Galef & Heiber, 1976; Laland & Plotkin, 1991). Finally, rats can benefit by interacting at nest sites and gathering information about distant food sources (Strupp & Levitsky, 1984; Galef & Wigmore, 1983; Galef, Kennett, Wigmore, 1984; Myhal & Fleming, 1990; Galef & Whiskin, 1992).

Deposits of urine and feces around feeding sites are attractive to other rats (Galef & Heiber, 1976; Laland & Plotkin, 1991) and the attractiveness of these substances increases the probability that naive rats will feed at particular locations. Toxic or unpalatable foods are less likely to be revisited by rats. Consequently, such foods have fewer residual cues deposited near them. The presence of attractive markers decreases the probability that naive conspecifics will feed on toxic foods. Thus, although rats do not actively transmit learned aversions to conspecifics (Galef, McQuoid & Whiskin, 1990; Galef, Wigmore & Kennett, 1983; Grover et al., 1988), the presence of residual cues effectively serves the same function. Rats eat foods that other rats eat rather than avoiding foods that other rats avoid (Galef, 1985).

Social interactions affect many aspects of diet choice in rats. They influence the diets to which rats develop aversions (Galef, 1989, 1987,1986). Social interactions also promote preferences for unpalatable diets (Galef, 1989; Dib, 1990) and increase the magnitude of preferences for palatable diets (Beck & Galef, 1989).

Laboratory rats show aversions to foods associated with illness (Green & Garcia, 1971). However, interacting with rats that ate a particular diet reduces the likelihood of developing an aversion to that diet

(Galef, 1989, 1987,1986). This reduced likelihood of aversion learning is observed even if there are 7-8 days between the initial social interaction and the subsequent diet choice (Galef, 1987). After social interactions, rats will exhibit preferences for diets previously associated with illness (Galef, 1985).

Naive rats will come to prefer unpalatable diets to more palatable diets after interacting with conspecifics that have eaten the unpalatable diet (Galef, 1989; Dib, 1990). When given a choice between a piquant diet (one containing Cayenne pepper) and another diet, rats eat the nonpiquant diet (Dib, 1990). Yet, after only two or three interactions with demonstrators that ate a piquant diet, rats exhibit preferences for such diets. Further, these preferences last for long periods of time (Galef, 1989). Rats with no opportunity to socially interact require extensive habituation (over 2 weeks) before they prefer a piquant diet to plain rat chow (Dib, 1990). That so few interactions have such an immediate and long lasting effect on the diet choices of rats demonstrates the powerful influence that conspecifics have on the diet choices of other members in the group.

Given that social interactions can reverse previous learned aversions it is not surprising that they also magnify preferences for foods associated with recovery from nutrient deficiency. Rats prefer diets that have distinctive positive associations and do not develop aversions to these foods (Buskist et al., 1982; Beck & Galef, 1989). Social interactions magnify this effect (Galef, Beck & Whiskin, 1991), possibly by reducing the associability between a diet and its negative consequences (Galef, 1987).

The presence of olfactory cues in a social context plays an important role in determining diet choices in rats (Galef & Wigmore, 1983). Rats are capable of quite subtle distinctions among different olfactory cues. Naive observer rats prefer a diet eaten by their demonstrators over totally unfamiliar diets even if the demonstrators ate several different diets during a single foraging episode (Galef & Whiskin, 1992). Naive observer rats will also prefer a diet eaten by their demonstrators even if they interact with several conspecifics that ate different diets (Galef, 1983; Galef, Attenborough & Whiskin, 1990). However, simple exposure to a diet, and hence its olfactory characteristics, is insufficient to cause this preference (Galef, Kennett, & Stein, 1985). The diet choices of rats are influenced only if the olfactory cues are imbedded within a social context (Galef & Wigmore, 1983; Baker & Booth, 1989).

While the mechanism of how conspecifics influence the diet choice of others is well understood, the ontogenetic origin of this mechanism is not (but see Galef, 1981). Early developmental conditions play a significant role in the final form of adult behaviors (Bronstein, 1989). Ontogenetic experiences can serve several different functions. First, experiences during development may serve a facilitative function, regulating development of future characteristics. Second, they may serve a maintenance function, where continued exposure to stimuli serves to maintain the presence of behavioral or morphological characteristics. Finally, experience may serve an inductive function, setting the stage for the development of future adaptations. Inductive experiences provide the animal with necessary experiences, ensuring development of characteristics that would not appear if the inductive experiences were not present (Gottlieb, 1976).

Processes of Behavioral Development

All developing organisms share a number of developmental characteristics. They exhibit growth, such as cell growth and division, and an increase in the complexity and organization of behavioral and morphological characteristics (Brooks & Wiley, 1988). Further, development tends toward definite end states (e.g.,a discrete organ) with the developmental pathways being canalized. Canalization buffers the developmental system against environmental and genetic perturbations (Waddington, 1942). Finally, during development, organisms usually pass through sensitive periods where some experiences have a greater influence on the organism than at other times (Hess, 1973).

There are three general ways to characterize canalization. Some theories emphasize the role of the genome (Waddington, 1942). Other theories emphasize the importance of the environment (Kuo, 1976) and yet other others emphasize the importance of interactions between genome and environment (Schneirla, 1957; Lehrman, 1953; Gottlieb, 1991a).

Two fundamental observations served as the basis for emphasizing the role of genes in the control of development. First, embryological tissues are distinct, not masses of material that gradually merge into one another. Similarly, it is possible to guide tissues into a number of distinct pathways, but it is difficult to induce tissues to differentiate into intermediate forms lying between two normal possibilities. Second, wild-type populations (which presumably have large amounts of genetic variability) have more robust phenotypes than inbred populations. These observations suggested both that phenotypic development is buffered against minor environmental variation and that genotype was capable of absorbing a certain amount of genetic variation (Waddington, 1968).

Waddington proposed that there were a limited number of developmental pathways, which he called “creods”. Creods are self-stabilizing time trajectories of change in multi-component systems (Waddington, 1971). The term creod was intended to convey the idea that development followed particular pathways. These pathways were capable of compensating for disturbing influences and restoring normal developmental outcomes during later stages of the developmental process. Development was seen as a homeorhetic process, following a stable course through time.

Waddington (1957), visually represented creods in terms of an epigenetic landscape. He described the landscape as a tilted, undulating surface, consisting of a system of hills and valleys. Within this landscape, earlier points in development were higher than later points in development. The valleys represented stable developmental pathways and the hills represented unstable plateaus. The top edge of the surface represented different cytoplasmic states in various parts of the egg, and the lower edge of the surface represented such end points as an eye, a spinal cord or some other completed morphological characteristic. The essential point of this metaphor was to demonstrate that trajectories of development, starting at the top of the surface, tended to converge toward particular discrete end points regardless of individual variations in the trajectories between the top and the bottom of the surface.

A second aspect of this model that deserves some attention is the ease with which it makes possible visualization of deviations from normal developmental trajectories. If a ball, travelling down the epigenetic landscape, is pushed slightly off its normal course, it travels up the slopes of the valley. If the push is large enough the ball leaves its current trajectory and falls into another valley or pathway. If the push is insufficient to alter the trajectory in this way, the ball rolls back into its valley and continues along its original trajectory.

Waddington believed that the genome contained all information necessary to guide development. However, he required a mechanism to explain how acquired adaptive characteristics became controlled by the genome. Clearly, animals were capable of responding to external stimuli via developmental reactions. For example, the application of friction to the skin produced calluses. However, in other instances calluses were present at birth. Waddington (1942) proposed that environmentally adaptive characters become assimilated into the genome and canalized, by the process of natural selection, such that calluses of the proper thickness and spatial location were present at birth.

In Waddington's model, the environment modified the existing developmental path (i.e., friction on skin surfaces produced calluses). In ancestral populations this modification was tied closely to the intensity of the environmental stimulus. More friction produced larger calluses. Over generations, natural selection readjusted the reactivity of the skin, producing thickening of the skin from normally occurring stimulus intensities. Then, via the process of canalization, the reactivity of the skin became decoupled from the intensity of the environmental stimulus. The magnitude of the skin's response becomes disproportionate compared to the magnitude of the external stimulus. Above a stimulus threshold, organisms exhibited the complete optimal response. As the response became canalized, the environment came to act as a switch, turning on relevant genes to produce an adaptive phenotype. However, decoupling the reactivity from the stimulus intensity meant that relevant genes became sensitive to stimuli other than the normal environmental stimulus (Waddington, 1942). Many stimuli were capable of acting as switches. As the developmental response became canalized, the genome gained control of the developmental response and acted as the switch, irrespective of environmental conditions.

Waddington (1953) experimentally established that a characteristic that had originally been environmentally acquired could become assimilated into the genetic makeup of a population. Groups of Drosophila melanogastor pupae, exposed to 40 ^{O}C, exhibited an increase in the frequency of crossveinless wings as adults. Over many generations, adults came to exhibit crossveinless wings even in the absence of the original environmental stimulus. The genetic assimilation of control for the development of the phenotype depended upon continual selective pressure both to increase the frequency of the phenotype and to stabilize its development.

Another theoretical interpretation, proposed by Kuo, emphasized the importance of environmental influences in normal developmental processes . This interpretation viewed canalization as a broad principle where initial conditions allowed a great range of possible behaviors. Only a few of the potential behaviors (usually species-typical behaviors) were actually realized. Kuo demonstrated the broad range of available phenotypes by rearing dogs (normally carnivorous) on herbivorous diets. As adults, they refused to eat meat when offered a choice between a herbivorous diet and a carnivorous diet (Kuo, 1976). Pups born to bitches reared on herbivorous diets also refused to eat meat. Kuo repeated these experiments using cats, mynahs, jays, robins, and thrushes and found similar results.

As development progresses, earlier experiences begin to act as constraints on future behaviors, reducing both their range and plasticity. Examples of decreased behavioral plasticity include song learning in birds and diet breadth in mice. Marler & Peters (1982) found that juvenile male swamp sparrows had song repertoires 4-5 times larger than adult males. Similarly, Gray & Tardif (1979) demonstrated that the range of diets eaten by mice (Peromyscus) decreased as they grew older.

The decrease in plasticity was to be understood in terms of an individual's particular developmental experiences - biochemical, physiological, and anatomical as well as environmental experiences. Kuo believed that no two individuals experienced the same history, and that variability in behavior was a manifestation of differences in individual history. Apparent behavioral similarities among animals, such as similarities in particular motor sequences, resulted from morphological characteristics that tended to experience plasticity reduction earlier than behavioral characteristics. This limited the number of potential solutions to the challenges faced by individuals.

Both Waddington's and Kuo's interpretations have face-validity (Gottlieb, 1991a). It is easy to visualize Waddington's epigenetic landscape, and to appreciate Kuo's assertion that an individual's actions will be shaped by its unique developmental experiences. However, both approaches contain serious weaknesses. The fundamental problem with the view that each new environment has a different effect on developmental outcome is that it is essentially non-predictive. The outcome cannot be specified prior to actual empirical investigation, beyond predicting that two outcomes will differ from each other (Gottlieb, 1991a). Waddington's epigenetic landscape metaphor experiences similar difficulties. The concept is easy to visualize, but it lacks any empirical content and therefore provides few concrete hypotheses about processes involved in development (Gottlieb, 1991a).

Waddington's explanation of how genes regulated development also contains serious deficiencies. Waddington hypothesized that the elementary chemical processes taking place during development were the result of specifications at single gene loci and that there were many individually distinct genes. Individual genes acted in concert, forming gene batteries, coordinating the development of large masses of tissues. The activities of specific genes were controlled by products of regulatory genes or gene batteries, serving as feedback loops (Waddington, 1968). Regulatory genes were specific to particular genes and reactive with external factors that modified that specificity. In a simplistic example, gene A produced substance A' that regulated gene B that produced substance B' that controlled the activity of gene A.

The difficulty with this mechanism arises from gene B reacting with external factors. Interaction of Gene B with external factors alters the activity of gene A such that gene A produces a range of gene products (Oyama, 1985). This represents a degenerative relationship. The elements in one set (the genome) map onto many elements in another set (gene products). Further, more than one gene or gene battery can produce the same gene product (Oyama, 1985). This represents an ambiguous relationship. Many different elements in one set (the genome) map onto one element in another set (gene products). Thus, Waddington's description of the genetic mechanism is both degenerate and ambiguous, making predictions difficult.

The final class of developmental theories emphasizes the interaction between the genome and the environment (Gottlieb, 1991a; Schneirla, 1957). It is the continuous interaction between intraorganic developmental processes and the effects of extrinsic conditions that causes development (Schneirla, 1957).

From an interactionist perspective the environment also has the potential of acting as a canalizing force. For example, Mallard ducklings (Anas platyrhynchos), exposed to mallard contact calls, develop appropriate species-specific perceptual preferences (Gottlieb, 1991b). Ducklings without exposure to contact calls respond to the maternal call of other species. Thus, exposure to environmental cues influences expression of a supposedly hard-wired phenomenon.

Developmental theories that emphasize interactions between genes and environment are not uniform in their approach. Approaches put forward by Schneirla (1957) and Lehrman (1953) had similar problems to those proposed by Waddington (1942) and Kuo (1976). Such approaches had good explanatory power, but little predictive power (Gottlieb 1991a). However, recent developments in hierarchical theory may make the generation of specific testable hypotheses possible.

It is possible to organize biological systems into a hierarchy of different functional levels, such as DNA, cytoplasm, organs, organisms, and environment (Brooks & Wiley, 1988). The cause of development is the relationship between the components, not the components themselves (Gottlieb, 1991a). For example, spontaneously hypertensive rat pups (SHR) suckled and reared by SHR females are also hypertensive. When normal females rear SHR pups the pups do not develop hypertension. Normal rat pups do not develop hypertension, regardless of whether they are reared by SHR or normal females (Myers, Brunelli, Shair, & Hofer, 1989; Myers, Brunelli, Squire, Shindeldecker, & Hofer, 1989) Therefore, although SHR pups differ genetically from normal rat pups, hypertension is the result of an interaction between the genome of SHR pups and the rearing environment provided by a SHR dam. It is not an inevitable outcome from the fact that they are genetically and physiologically different from normal rats.

Hierarchical systems tend to have a degree of autonomy at each level (Eldridge, 1985; Gottlieb, 1991a). The processes occurring at one level are independent of processes that occur at another level. Generally, the products of processes immediately below and above the level of interest have the largest impact on the focus level. Hence, for the sake of convenience, hierarchies are generally formulated in terms of a triad. Lower levels produce necessary constituents for processes at the focal level (the level that the investigator is examining). In other words, lower levels determine the initiating conditions of focal processes (Salthe, 1985). Upper levels establish boundary conditions within which focal levels operate. The boundary conditions govern or control focal level processes (Salthe, 1985). Different levels interact via products produced at each level. Processes at the focal level use products produced by initiating and boundary levels, but the processes themselves do not interact with each other.

An important characteristic of interactions between levels is their bidirectionality. The principle of bidirectionality allows levels above the genome, such as cell cytoplasm to influence the functioning DNA-protein transcription processes (Grouse, Schrier, Letendre & Nelson, 1980). Ho (1984) demonstrated that environmental events altered female egg cell cytoplasm such that the interaction between the nuclear genes and the cytoplasm produced a different phenotype. There was no alteration of the allele frequencies in the gene pool, yet there was an alteration in phenotype.

While it is generally accepted that development involves endogenous and exogenous factors interacting dynamically over time, these factors do not exert equal pressure on development at every moment. Organisms generally proceed through different developmental phases where many structures and functions are especially susceptible to particular experiences (Bronstein, 1989). Exposure or lack of exposure to these experiences exerts definite influences on future characteristics, both behavioral and morphological.

Early exposure to conspecific adult bird song is important to many species of song birds. Young fail to sing the species-specific adult song unless they hear this song within a narrow time window. For instance, young swamp sparrows (Melospiza georgiana) require exposure to adult song between 10 and 50 days of age, otherwise they will not sing the species-typical song as adults. During this sensitive period, young song birds learn all the song elements required for species-typical adult song. Song elements presented outside of this sensitive period are not learned nearly as well as those presented within the sensitive period, if at all (Marler & Peters, 1987). Deafened or auditorally isolated young only sing isolated notes or rudimentary songs as adults (Gould, 1982; Marler & Waser, 1977). Further, young tend to learn conspecific songs over heterospecific songs (Marler & Peters, 1987; Price, 1979). Thus it appears that many species of song birds have specific, narrowly defined temporal windows within which to learn basic song patterns (Price, 1979; Gould, 1982).

Visual imprinting in fowl is another example of a narrowly defined window of opportunity. In the case of imprinting, exposure to visual cues has a large impact on behavior. Spalding (1873) observed that chicks hatched in the absence of a hen followed any moving object presented to them in the first few days after hatching, but not later.

Sensitive periods are not necessarily clearly demarcated with definite onset or offset times. Often, there is a gradual rise and decay of susceptibility (Bronstein, 1989). Song birds are capable of learning the songs of other species (Baptista & Petrinovich, 1984; Eales, 1987; Petrinovich, 1985; Todt, Hultsch, & Heinke, 1980) and learning new song elements outside of the sensitive period described (Eales, 1987; Kroodsma & Pickert, 1980; Graves, 1972; Baptista, 1974), if they are exposed to live tutors rather than tutor tapes. Male zebra finches (Taeniopygia guttata) reared with live Bengalese finch tutors (Lonchurs striata) both learn Bengalese mating songs (Eales, 1987) and prefer female Bengalese finches to female zebra finches (ten Cate, Los & Schilperoord, 1984).

There is also no requirement for sensitive periods to occur early in an organism's life cycle (Bornstein, 1989). Some species of birds become sensitive to adult songs as they approach adulthood. Indigo Buntings (Passerina cyanea) learn the general feature of their species' song from their respective fathers, but fine tune their songs by mimicking the songs of surrounding males after becoming adults (Payne, 1981). Also, adult Saddlebacks (Philesturnus carunculatus) alter their songs as adults to more closely match those of their neighbors (Jenkins, 1978).

Even within a single species there are differences between the characteristics of sensitive periods. Female cowbirds are capable of discriminating between songs of at least two different subspecies of cowbirds. Females prefer consubspecific mating songs over heterosubspecific mating songs songs, even if they have been reared listening to tapes of heterosubspecific mating songs (Eastzer, King & West, 1985; King & West, 1983). The finding that female cowbirds prefer the mating songs of consubspecifics supports the hypothesis that female cowbirds have an innate preference for these songs. However, mating songs of male cowbirds are malleable. Males that join the flock can discriminate between local songs that are effective and ineffective in releasing copulatory reponses in females (West & King, 1986). Males of both subspecies are capable of copying effective songs of either their own or other subspecies (West & King, 1986). Male cowbirds also modify their songs in response to nonvocal feedback from females (West & King,1985; King & West, 1983). Juvenile males, housed with heterosubspecific females, develop distinctively different song repetoires from juvenile males housed with consubspecific females (West & King,1985). The ability of males to alter their song in response to local feedback from both males and females suggests that song learning in male cowbirds is more flexible than was originally thought (West, King & Harrocks, 1983). The ability of males to modifiy their songs also effectively nullifies any predisposition of females to mate with consubspecifics. Male cowbirds sing the songs that females like to hear, limiting the role of any innate behavior in mate selection. Thus, even brood parasites, such as the cowbird, exhibit considerable flexibility when it comes to song learning.

Finally, the development of functional characteristics such as imprinting, involves susceptibility to multiple cues and experiences. Both auditory cues and visual cues influence imprinting (Johnston & Gottlieb, 1985). Mallard ducklings prevented from hearing mallard contact calls prior to hatching (either their own or from sources external to the egg) develop preferences for extraspecific maternal calls over mallard maternal calls. Ducklings exposed to contact calls prenatally do not respond to extraspecific maternal calls (Gottlieb, 1991b). Peking ducklings and domestic chicks tend to visually imprint on the first model they are exposed to after training, but only if test models are silent (Johnston & Gottlieb, 1985; Johnson, Bolhuis & Horn, 1985). When models contain both visual and auditory components, chicks attend more to the auditory component than the visual component (Graves, 1973).

Perinatal and postnatal experiences also affect imprinting (Miller & Blaich, 1984; Kovach, 1987; Gottlieb, 1991b). Quail chicks (Coturnix coturnix japonica), exposed either to quail or to blue jay calls prior to hatching, follow a model after hatching more readily than chicks incubated in auditory isolation (Ewing, Ewing & Vanderweele, 1975). Domestic mallard ducklings show similar perinatal influences. Normally, ducklings respond to mallard alarm calls by freezing (Miller & Blaich, 1984). However, ducklings that are not exposed to auditory stimulation prior to hatching are not responsive to mallard alarm calls (Miller & Blaich, 1984; Kovach, 1987). Mallard ducklings preferred model mallards over model red hens only if reared socially with at least two other conspecifics (Lickliter, & Gottlieb, 1985). Ducklings socially reared with other species of birds do not exhibit preferences for mallard models (Lickliter & Gottlieb, 1988).

Development of Feeding in Rats

Diet choices in rats also exhibit sensitivities to early developmental influences. As I discussed earlier, the presence of olfactory cues in the context of social interactions influences the diet choices of naive rats. Thus, both olfactory cues and social interactions can play important roles in development of food preferences.

Olfactory cues also play an important role in suckling behavior and social attachment to dams,. Unless appropriate olfactory cues are present on a dam's nipples, neonatal rats do not attach and suckle. After parturition, females spread amniotic fluids over their nipples, leaving residual scents that facilitate nipple attachment by their pups. Washing nipples and replacing the scents deposited by the dam with odors not present in amniotic fluid reduces the probability of nipple attachment by pups (Pederson, Williams & Blass, 1982). Furthermore, bulbectomized pups do not attach to nipples, rapidly lose weight and die (Risser & Slotnick, 1987). Thus, appropriate olfactory cues are critical if young are to be reared successfully.

Neonatal rats prefer their own dam's scent. Pups, reared by females that did not produce maternal pheromones, did not approach pheromones produced by normal females (Leon, Galef, & Behse, 1977). In addition, pups exposed to an arbitrary odor in the presence of maternal pheromones show long-term enhanced preferences for that odor. Pups exposed to an odor in the absence of maternal pheromones show rapid attenuation of their preference (Galef, 1982). Thus, maternal scents can have long term effects on a pup's behavior.

The transition from a liquid diet to a diet of solid food is a critical time for weanling rats. The dam exerts considerable influence on the initial diet choices of weanlings in a number of ways. It is during lactation that pups experience dietary cues in a social context. The taste of a dam's milk is influenced by her diet and this taste is transmitted to her pups. This first experience influences initial diet choices of weanlings. Weanling pups tend to prefer diets corresponding to foods eaten by their dam during lactation (Galef & Henderson, 1972; Galef & Sherry, 1973; Levine, Bronstein, 1976; Bronstein, & Crockett, 1976a; Bronstein, & Crockett, 1976b; Galef, 1982; Morris & Anderson, 1986; Terry & Johanson, 1987).

Young rats must do more than select safe foods. They also must select safe feeding sites. Juvenile rats strongly affiliate with adult rats on their initial foraging trips (Galef, 1978; Calhoun, 1962). Furthermore, during these initial feeding forays, weanlings are more hesitant to transfer feeding from familiar diets to novel diets than are adults (Galef, 1977). Thus, the affinity that rats have for each other plays an important role during weaning.

Early experiences clearly have a potentially profound impact on diet choices and foraging behaviors in young rats. Infant rats are altricial and heavily dependent on their dam until weaning. This dependence involves both close social contact with the dam for approximately 21 days and exposure to taste, olfactory, auditory and tactile stimuli in a social context. Thus, given the importance of olfactory cues and the intimate social interactions between infant rats and their dam, it is possible that this early period represents a sensitive period serving a facilitative or inductive function. If this hypothesis is correct, disrupting the normal developmental experiences may be sufficient to alter the canalized pathway. I hypothesized that demonstrator rats will not influence the diet choice of juvenile rats reared in social isolation since shortly after birth. Rats reared in social isolation would not have had the requisite experience of having olfactory cues presented in a social context.

EXPERIMENT 1

Methods

Subjects

Sixty Long-Evans rats participated in this experiment. Thirty subjects served as observers, thirty as demonstrators. All were born in the vivarium of the McMaster University Psychology Department (Hamilton, Ontario) to breeding stock aquired from Charles River Canada (St. Constant, Quebec).

Fifteen observers (those assigned to the isolation-reared group) were taken from their dams 36-48 hours after birth. Each pup was anesthetized with ether and implanted with a chronic gastric cannula, using methods described by Hall (1975). To maintain each pup in visual and tactile isolation, it was placed in a polystyrene cup floating in a constant-temperature bath (Hall, 1975), and fed an enriched milk formula (Diaz, 1991) through its cannula. Each pup's cannula was removed when it was 18 days old, and the pups were then placed individually in small, shoe-box cages (27.5 x 17.5 x 12.5 cm), to maintain their visual and tactile isolation. The pups were gradually weaned from a mash of powdered Purina Rodent Laboratory Chow #5001 and water to dry, powdered Purina chow and, finally, to pellets of Purina chow.

Fifteen other observers (those assigned to the control condition) were reared by their dams in the normal manner. Litters of pups assigned to the control condition were culled to 10 pups 1-4 days after birth and weaned when they were 21 days old. After weaning pups in control litters were placed in polycarbonate shoe-box cages (37 x 30 x 17 cm) with 3-4 same-sex littermates. Pups had ad-lib access to water and pellets of Purina Rodent Laboratory Chow #5001. The cages were housed in a humidity- and temperature-controlled colony room illuminated on a 12:12-hr light/dark cycle.

The 30 demonstrators were reared in the same manner as the observers assigned to the control condition. They were 7-10 days older than the observers in this experiment.

Apparatus

Each observer was housed and tested in a 42.5 x 24 x 27.5 cm wire-mesh hanging cage (Wahmann Co., Baltimore, Md.). A hardware-cloth screen (1.25 cm mesh) partitioned each cage into two compartments of equal size. Each demonstrator was housed in a 36 x 18 x 18 cm wire-mesh hanging cage (Wahmann Co., Baltimore, Md.). We presented food to subjects in semicircular food cups (10 cm diameter) hung from the wire mesh walls of the hanging cages.

Procedure

Observers, assigned to both isolation-reared and control groups, were randomly divided into two groups. One half the observers in each group interacted with demonstrators fed Purina Rodent Laboratory Chow #5001 adulterated with 1% (wt/wt) ground anise (Diet ANI), the other half interacted with demonstrators fed Purina Rodent Laboratory Chow #5001 adulterated with 2.4% (wt/wt) Marjoram (Diet MAR).

The experiment began when observers were 42 days old. Observers in both conditions experienced the same four step procedure.

Step 1. Demonstrators were introduced into their cages and placed on a 23 hr food-deprivation schedule for 2 days. They were offered ad-lib Purina chow daily for 1 hr. Each observer was placed into one compartment of a large hanging cage and allowed to become familiar with the experimental apparatus. Observers had ad-lib access to pellets of Purina chow. Both demonstrators and observers had ad-lib access to water.

Step 2. After a third 23 hr period of food deprivation, demonstrators were offered a weighed food dish containing one of two flavored diets for 1 hr. Fifteen demonstrators were offered Diet ANI, the remaining fifteen demonstrators were offered Diet MAR. Observers had their pellets removed at this time.

Step 3. One demonstrator was placed in the unoccupied compartment of each observer's cage. The two rats were left to interact for 1 hr.

Step 4. After 1 hr, demonstrators were removed from the experiment. Observers were then offered both Diet ANI and Diet MAR in weighed food cups for 22 hrs. The cups were counter-balanced for position within each group.

At the end of the 22-hr feeding period the amount of Diet ANI and Diet MAR eaten by each observer was determined. We then calculated: (1) the percentage of each observer's total intake that was Diet ANI and (2) the percentage of each observer's total intake that corresponded to its demonstrator's diet.

Results and Discussion

The primary results of Experiment 1 are illustrated in Figure 1, which shows the mean amount (± SE) of Diet ANI eaten, as a percentage of total intake, during the 22-hr test period by observers whose demonstrators ate either Diet ANI or Diet MAR.

Insert Figure 1 about here

Normally-reared observers ate an average of 85.8% (± 4.2) Diet ANI when their demonstrators ate Diet ANI and an average of 32.5% (± 6.8) Diet ANI when their demonstrators ate Diet MAR. The figure clearly shows, and statistical tests confirm, that normally-reared observers ingested a greater percentage of the diet corresponding to their demonstrator's diet (Mann-Whitney $\underline{U} = 0$, $\underline{p} = .0006$) than of the alternative diet.

Observers reared in isolation ate an average of 58.1% (±7.8) Diet ANI when their demonstrators ate Diet ANI and an average of 25.3% (± 5.4) Diet ANI when their demonstrators ate Diet MAR. A Mann-Whitney U test revealed that observers reared in isolation also exhibited a significantly enhanced preference for the diet of their respective demonstrators ($\underline{U} = 7$, $\underline{p} = .0075$).

Figure 1. Mean amount of Diet ANI eaten, as a percent of total amount eaten, by observers (reared normally or in social isloation) whose demonstrators had eaten either anise- or marjoram-flavored diet. Error bars indicate ± 1 SE.

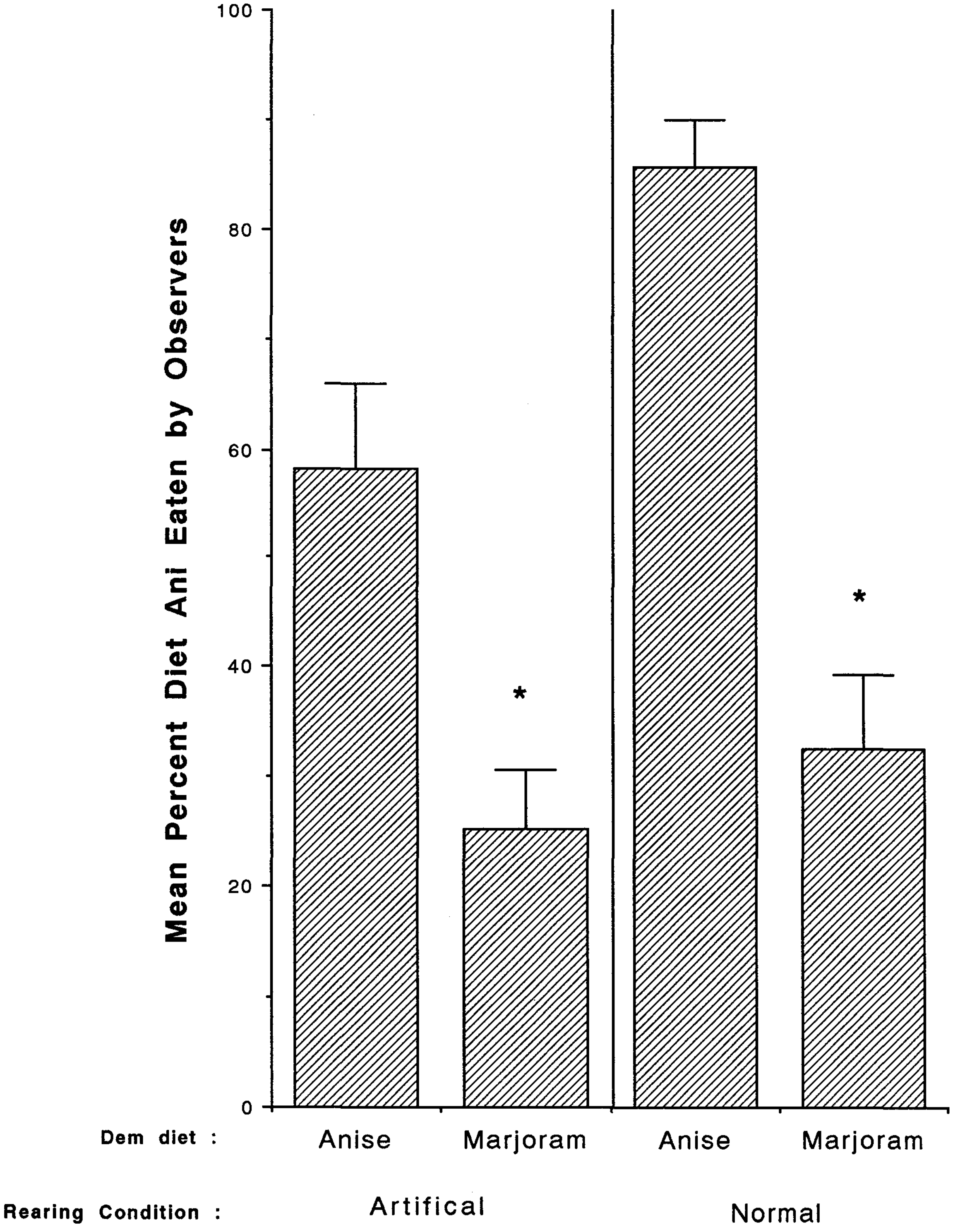

Mean Percent Diet Ani Eaten by Observers
100
80
60
40
20
0
*
*
Dem diet :
Anise
Marjoram
Anise
Marjoram
Rearing Condition :
Artifical
Normal

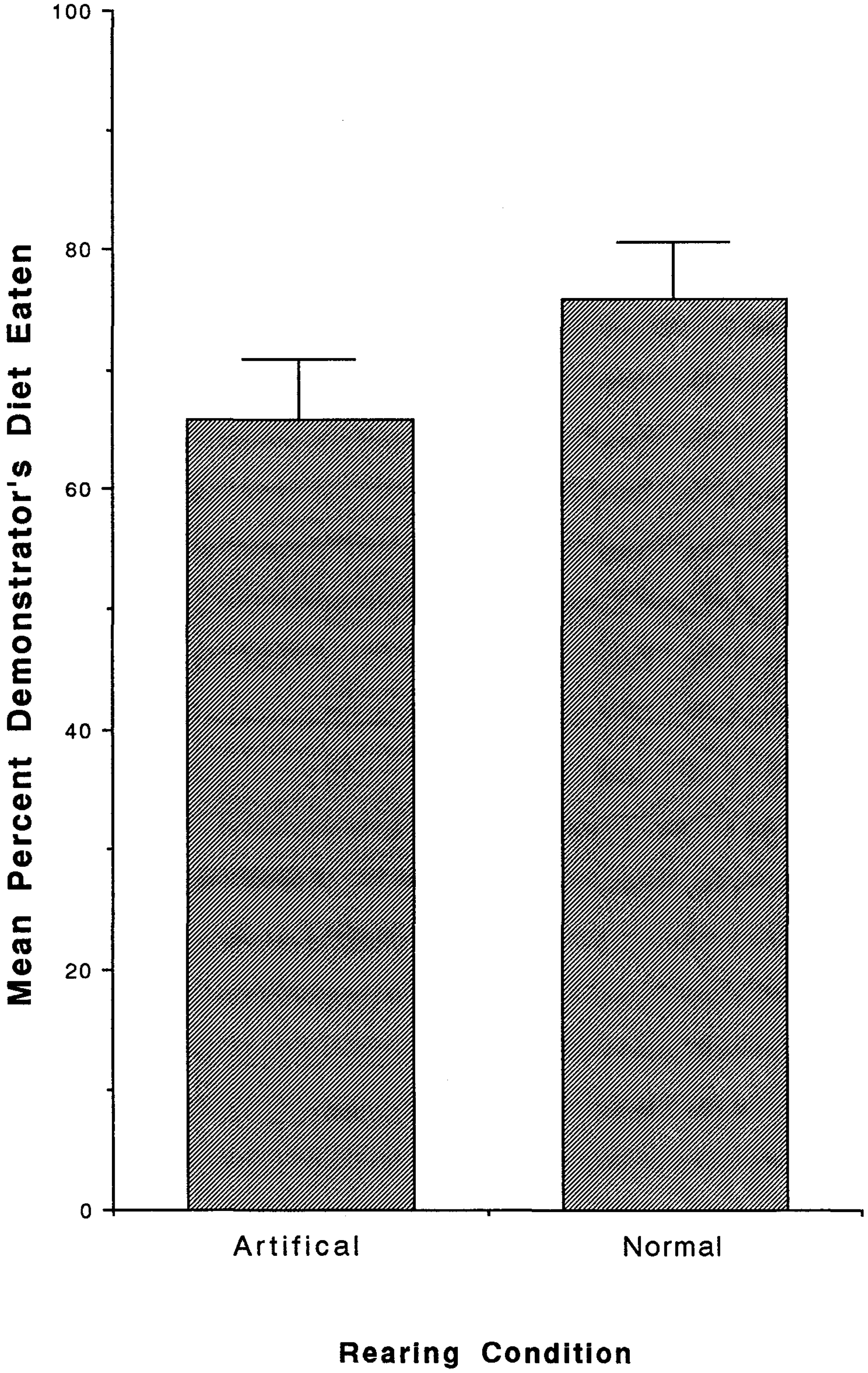
Figure 2 shows the mean percentage (± SE) of total intake by the isolation reared and control groups, that corresponded to their respective demonstrators' diets.

Insert Figure 2 about here

Normally-reared observers ate a mean of 76% (± 4.7) of their demonstrators' diets and observers reared in isolation ate an average of 65.8% (± 5.2) of their demonstrators' diets. Isolation-reared observers and normally-reared observers did not differ significantly in the mean percent of total intake that corresponded with the demonstrator's diet ($t_{2\text{-tail}}(28) = 1.46$, $p = .1565$).

These data suggest that both normally-reared rats and rats reared in isolation preferred their demonstrator's diet to a novel flavored diet and were similarly susceptible to demonstrator cues. Rats reared in isolation did not exhibit any demonstrable decrement in their susceptibility to social influences.

Figure 2. Mean amount of demonstrator's diet eaten, as a percent of total amount eaten, by observers reared normally or in social islation, irrespective of demonstrator's diet. Error bars indicate ± 1 SE.


Mean Percent Demonstrator's Diet Eaten
100
80
60
40
20
0
Artifical
Normal
Rearing Condition

EXPERIMENT 2

Introduction

The previous experiment demonstrated that demonstrators influence the diet choices of rats reared in social isolation. This supports the hypothesis that social interactions influence the diet choices of rats. However, until approximately 28 days of age, the familiarity of the odor also influences diet choices (Galef & Kennett, 1987). After this age, familiarity no longer influences diet choices Rearing rats in social isolation may extend the time that familiarity with an odor influences diet selection. The diet preferences exhibited by rats reared in social isolation may have been due to the familiarity of the odor and not from social interactions with conspecifics.

Galef, Kennett & Stein (1985) demonstrated that the diet choices of normally reared rats are not influenced by the familiarity of an odor. If rearing rats in social isolation does extend the period where olfactory familiarity influences diet choice, then rats exposed to a diet prior to a 22 hr choice should exhibit preferences for that diet. Normally reared rats should not exhibit a preference for any diet. If rats reared in social isolation do not exhibit a preference, this would support the hypothesis that the same mechanism is operating for rats reared both normally and in social isolation.

Methods

Subjects

Twenty-eight Long-Evans rats, born in the vivarium of the McMaster University Psychology Department (Hamilton, Ontario), participated in this experiment. Fourteen subjects were reared and maintained in the manner described in the Methods of Experiment 1 for isolation-reared subjects . The fourteen subjects assigned to the control condition were reared and maintained in the manner described in the Methods of Experiment 1 for control subjects.

Apparatus

The apparatus was the same apparatus used in Experiment 1.

Procedure

The procedure used in Experiment 2 was similar to that of Experiment 1 except the observers did not interact with demonstrators. Instead, observers were exposed, for 30 min, to a 10-cm diameter, semicircular stainless-steel dish containing either Diet ANI or Diet MAR during Step 3. The dishes were placed in the same compartment as the observer, maximizing subject's simple exposure to the diets.

Results and Discussion

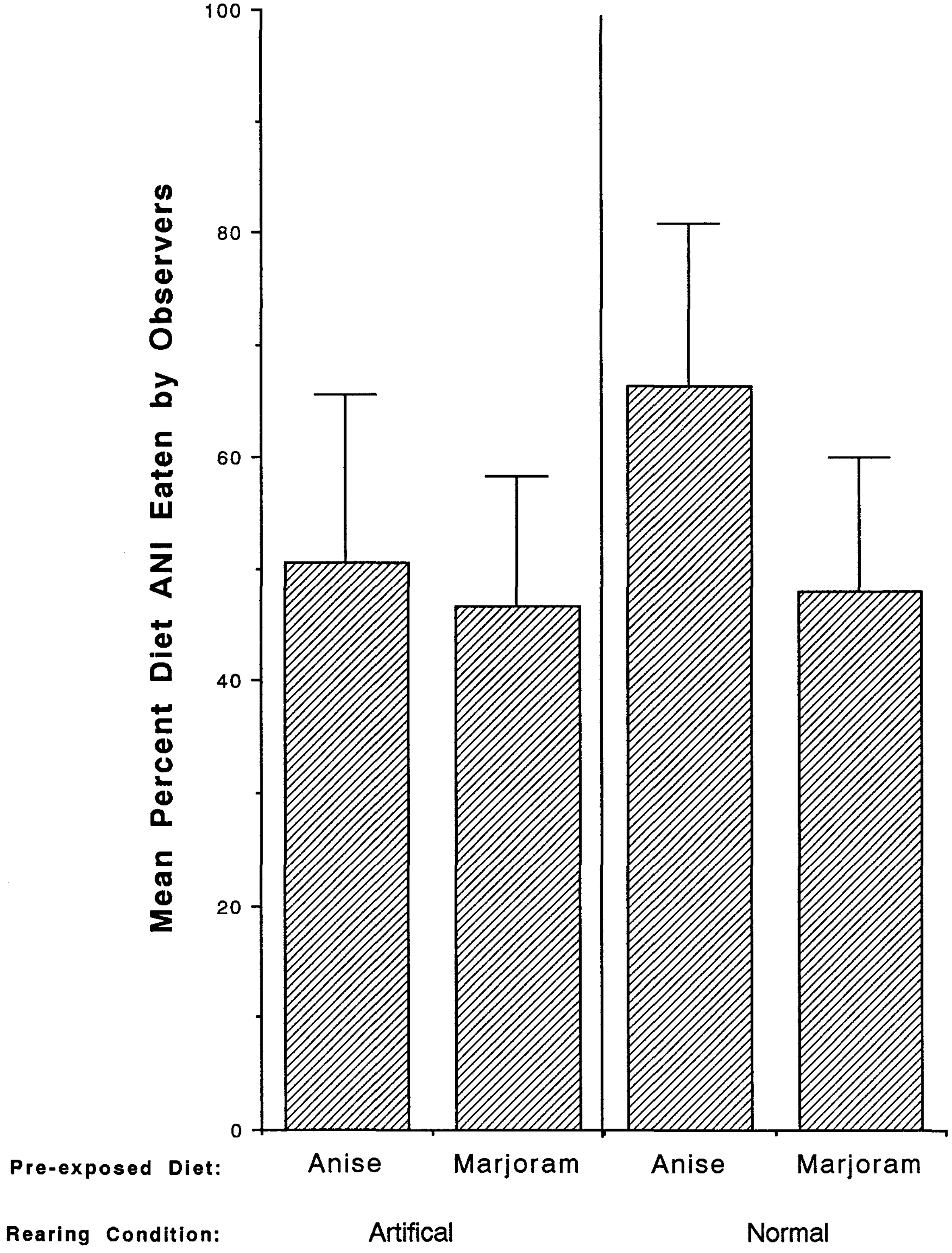
The primary results of Experiment 2 are illustrated in Figure 3. This figure shows the mean amount (±SE) of Diet ANI eaten, as a percentage of total intake, during the 22-hour test period by observers exposed to either Diet ANI or Diet MAR.

Insert Figure 3 about here

Normally-reared rats ate an average of 66.4% (±14.4) Diet ANI when exposed to Diet ANI prior to the test period and an average of 47.9% (±12.9) Diet ANI when exposed to Diet MAR prior to the test period. Rats reared in isolation ate an average of 50.4% (±15.1) Diet ANI when exposed to Diet ANI prior to the test period and an average of 46.6% (±11.6) Diet MAR when exposed to Diet MAR prior to the test period.

A 2-way analysis of variance was performed using rearing condition and the diet rats were exposed to prior to the test period as independent variables. The dependent variable was % Diet ANI eaten by the subjects. There was no significant difference between the percentage of Diet ANI and Diet MAR eaten ($F(1,24) = 0.674$, $p = .4197$). Approximately equal amounts of Diet ANI and Diet MAR were eaten by both isolation-reared rats and normally-reared rats. There was no significant difference between rearing conditions ($F(1,24) = 0.409$, $p = .5288$). Rats reared in isolation ate approximately the same percentage of Diet ANI as rats reared normally. Finally, there was no significant interaction of rearing condition and diet flavor ($F(1,24) = 0.295$, $p = .5918$).

Figure 3. Mean amount of Diet ANI eaten, as a percent of total amount eaten, by observers (reared normally or in social isloation) pre-exposed to either anise- or marjoram-flavored diets, in the absence of a demonstrator. Error bars indicate ± 1 SE.


Mean Percent Diet ANI Eaten by Observers
100
80
60
40
20
0
Pre-exposed Diet:
Anise
Marjoram
Anise
Marjoram
Rearing Condition:
Artifical
Normal

These results suggest that the preference for the demonstrator's diet exhibited by both normally-reared rats and rats reared in isolation seen in Experiment 1 is not due to simple familiarity with the smell or taste of the diet. Thus, we are able to eliminate the possibility that rats reared in isolation exhibited a preference for their demonstators' respective diets because they were familiar with the scent of the diet. Simple exposure to the diet did not induce a preference for that diet.

General Discussion

The present research investigated whether the period between parturition and weaning represented a sensitive period during which social interactions between a dam and her pups served a facilitative or inductive function, enabling young rats to develop the ability to exchange information concerning distant food sites. The diet choices of observer rats reared normally and in social isolation were similar in both experiments we conducted. Both groups of observers preferred their demonstrators' diets. Also, exposure to a diet, in the absence of a demonstrator, did not influence the diet preferences of either observers reared normally or in social isolation. These results suggest that social interactions with dams and siblings between birth and weaning is not necessary for development of a susceptibility to social influences on diet choice.

One of the hypotheses tested by these experiments was that interactions with a dam were important in socially influencing diet choices of juvenile rats. The presence of olfactory, tactile, and taste cues represented important physical characteristics affecting the development of this phenomenon. Rats reared in social isolation did not have the opportunity to engage in these interactions, yet diets eaten by demonstrators influenced their diet choices. Thus, if social development is susceptible to the presence or absence of specific experiences, the structural characteristics are quite different from song learning and imprinting and probably do not involve dam-sibling interactions.

There are other scenarios that could result in diet choices being socially influenced. While I could discuss potential factors that may have influenced the results of these experiments and present evidence to suggest why they probably did not , I believe it is more productive to focus on processes that could actually affect the social influence of diet choice.

Adult social behaviors may arise from normal perceptual development. Normal perceptual development can serve an inductive function, allowing normal behavioral development. For instance, homing behavior in rat pups normally increases, until approximately day 14, and then decreases. Prematurely opening the eyes of rat pups disrupts normal perceptual development. Pups with prematurely opened eyes continue to exhibit increases in homing behavior (Kenny and Turkewitz, 1986). Removing distinctive visual cues in the nest eliminates this difference. Similarly, it is possible to disrupt huddling behavior in rats. Until approximately day 15, pups attend primarily to thermal cues. After day 15 they become more selective, preferring conspecifics over surrogates with similar tactile and thermal properties. Making pups anosmic eliminates preferences for conspecifics and thermal cues are once again primary determinants of huddling (Alberts & Brunjes, 1978).

Altering normal perceptual development, via addition or removal of a sensory modality during a particular developmental stage, changes the specificity of that behavior and its functional success (Alberts & Brunjes, 1978). Galef and Kennett (1987) found that odors presented in social and in nonsocial contexts influenced diet choice in 21 day old rats. Odors presented in a non social context did not influence diet choice, when rats were tested at 28 days old. Olfactory cues influence diet choice prior to weaning, but the specificity of a social context on diet choice occurs after weaning. Thus, much like huddling and homing behaviors, there is continuity in the expression of the behavior but a change in the variables that regulate its specifity.

Prior to birth, neonatal rats have fully developed (Santacana, Heredia & Valverde, 1992; Marchand & Belanger, 1991) and functional (Pederson, Stewart, Greer & Shepherd, 1983) olfactory bulbs. Perhaps normal development serves a maintainence function where exposure to multiple olfactory cues maintains normal olfactory development. Therefore, one approach may be to rear rat pups in a single odor environment. If during normal development, olfactory cues can serve as discriminative stimuli then each olfactory cue may carry differential informational values. For instance, the dam's olfactory signature is different from another adult's olfactory signature and odors of different foods may differentially indicate safety or toxicity. In a single odor environment olfactory cues cannot serve as discriminative cues and rat pups may no longer attend to olfactory cues. In an environment where olfactory cues can serve as discriminative cues, rats reared in a single-odor environment may continue to ignore these cues, especially if other useful discriminative cues are available.

The presentation of specific appropriate sensory experiences also affects the structure or function of behavior. Sensitive periods tend to have stimulus-specific parameters. Male song birds use auditory cues to attract and induce females to copulate. The presence of inappropriate or absence of appropriate auditory cues during development adversely affects their ability to successfully reproduce. A similar argument applies to imprinting. Domestic chicks do not imprint to appropriate visual models when presented with visual cues that are not species-typical . The experiments in this thesis explicitly removed social interactions from the developmental process. However, demonstrator rats did influence the diet choices of rats reared in social isolation. This suggests that social interaction with dams is not the relevant parameter affecting normal social development.

The experiments in this thesis explicitly removed social interactions from the developmental process. Social behavior may assist individual rats in making safe diet choice decisions. Rats are neophobic (Galef, 1970; Barnett, 1958). When given a choice between a food they have ingested previously and a novel food, rats tend to prefer the familiar food. A rat, presented with two novel diets, is unable to determine the safety of either diet. However, the smell of another rat's breath is highly correlated with actual ingestion of food, perhaps indicating diet safety. Thus, interacting with a rat that had eaten one of those diets is a secondary source of information that observer rats can use to evaluate the probable safety of the diet. The observer has no personal experience with either diet but knowledge that other rats ate the diet may be sufficient. In other words interacting with a demonstrator makes the diet familiar to the observer rat. Observers should not exhibit a preference for a particular diet if they interact with demonstrators that ate both choices prior to interacting with observers. This interpretation would also predict that obervers should not prefer diets eaten by demonstrators if they previously ingested the alternate diet. Both diets should be eaten in approximately equal amounts.

In summary, prior social experience does not appear to be necessary for demonstrators to influence the diet choices of conspecifics. The results were discussed in terms of the possibility that there was a sensitive period, where disruptions of normal developmental pathways would eliminate this effect.

The sensitive periods of song learning and imprinting appear to have different structural characteristics than social influences on diet choice. These differences were discussed and the possible role of social interactions on diet choice was also discussed. These two experiments are certainly not definitive. However, they do suggest directions for further research.

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