

ANNALS OF THE NEW YORK ACADEMY OF SCIENCES

*Volume 662*

**DEVELOPMENTAL PSYCHOBIOLOGY**

*Edited by Gerald Turkewitz*



*The New York Academy of Sciences  
New York, New York  
1992*

43. DAVIES, N. B. 1976. Parental care and the transition to independent feeding in the young spotted flycatcher (*Muscicapa striata*). *Behaviour* 59: 280-295.
44. MORENO, J. 1984. Parental care of fledged young, division of labor, and the development of foraging techniques in the northern wheatear (*Oenanthe oenanthe L.*). *Auk* 101(4): 741-752.
45. DAVIES, N. B. 1978. Parental meanness and offspring independence: an experiment with hand-reared great tits (*Parus major*). *Ibis* 120: 509-514.
46. STERN, J. M. & L. ROGERS. 1988. Experience with younger siblings facilitates maternal responsiveness in pubertal Norway rats. *Dev. Psychobiol.* 21: 575-589.
47. THIELS, E. & J. R. ALBERTS. 1985. Milk availability modulates weaning in the Norway rat (*Rattus norvegicus*). *J. Comp. Psychol.* 99(4): 447-456.
48. CROY, M. I. & R. N. HUGHES. 1991. The role of learning and memory in the feeding behaviour of the fifteen-spined stickleback, *Spinachia spinachia L.* *Anim. Behav.* 41(1): 149-159.

## Weaning from Mother's Milk to Solid Foods

### The Developmental Psychobiology of Self-Selection of Foods by Rats

BENNETT G. GALEF, JR.<sup>a</sup>

*Department of Psychology  
McMaster University  
Hamilton, Ontario L8S 4K1, Canada*

#### DIET SELECTION AS A PROBLEM IN DEVELOPMENT

Developmental psychobiologists have not been much involved in studies of how animals come to eat foods providing all of the varied nutrients needed for normal growth and development. The lack of attention paid by developmental psychobiologists to food selection is somewhat surprising, because choosing the right foods to eat poses one of the most severe challenges faced by juvenile animals in their struggle to survive.

For the first weeks or months following birth, all young mammals are sustained by mother's milk, a single, nutritionally adequate food. However, at some point in development, the needs of young outstrip either the energy-transducing capacity of their dam<sup>1</sup> or her willingness to invest additional resources in her offspring<sup>2</sup> and young mammals must then undertake the arduous task of finding a nutritionally adequate diet of solid foods. To survive, each weanling must select a balanced diet from among a plethora of substances—some beneficial, some harmless, and some dangerous—that it encounters in its attempt to find adequate rations.

Understanding how weaning animals manage this critical developmental transition from total dependence on mother's milk to self-maintenance on solid foods would seem a natural focus of attention for students of animal development. However, it has not proven so. Study of diet selection has been seen as a problem appropriate to regulatory physiologists rather than to developmental psychobiologists.

<sup>a</sup> Supported by grants from the Natural Sciences and Engineering Research Council of Canada and the McMaster University Research Board.

## IMPEDIMENTS TO STUDY OF DIET SELECTION AS A PROBLEM IN DEVELOPMENT

### *The Fragility of Weanlings*

Because of the vulnerability to stress of weanlings, regulatory physiologists interested in diet selection have generally adopted a strategy of extending young animals' dependence on others for their diet composition by weaning juveniles to a nutritionally adequate chow. Weaning from milk to chow maintains animals in a state of naiveté with respect to nutrient selection. Animals maintained on chow and faced for the first time, as adults, with a need to select foods for themselves have served as a model system for studying processes that normally occur in the course of weaning from mother's milk. The experimental convenience of adult animals as model systems has, however, obscured the importance of diet selection at weaning and, as I shall argue below, may have limited understanding of processes important in diet selection.

### ABSENCE OF A PROBLEM

Until recently, it was not apparent that there really was a problem of diet selection for developmental psychobiologists to address: Clara Davis was widely,<sup>3</sup> through inaccurately,<sup>4</sup> cited as having shown that human infants can compose an adequate diet by selecting items for themselves from a cafeteria of foods. Curt Richter and his coworkers<sup>5,6</sup> were generally believed to have demonstrated that rats in cafeteria feeding situations could self-select a balanced diet without difficulty. Richter,<sup>5</sup> Rozin,<sup>7</sup> Booth,<sup>8</sup> and others provided evidence of behavioral processes that would suffice to explain development of the adaptive patterns of dietary choice that Davis and Richter were said to have demonstrated. Nothing appeared to remain for developmental psychobiologists to study.

### A NEW APPROACH TO DIETARY SELF-SELECTION

My own interest in the problem of food selection at weaning arose from the realization that neither human infants<sup>4,9,10</sup> nor rats of any age<sup>9,10</sup> had been shown to be particularly adept at self-selecting an adequate diet from a cafeteria of foods. If, as recent reviews of the literature suggest,<sup>4,9,10</sup> (1) animals have great difficulty selecting a nutritionally adequate diet, and (2) selection of appropriate foods is a major problem facing all weanlings, then there is an important question for developmental psychobiologists to answer. How do weanlings succeed in making the life-threatening transition from mother's milk to solid foods?

## TWO EXPERIMENTAL PROCEDURES FOR STUDYING DIETARY SELF-SELECTION

### *Choosing a Diet*

In some studies of dietary self-selection, a subject is faced with an array of two or more foods only one of which is a nutritionally balanced diet containing, in proper proportion, all nutrients needed to sustain normal growth. In such situations, the subject's task is to focus its intake on the nutritionally balanced diet and reduce intake of deficient or imbalanced alternatives. The work of Harris *et al.*<sup>11</sup> and of Rozin<sup>12</sup> provides examples of experiments of this type.

### *Composing a Diet*

In other studies of dietary self-selection, subjects are presented with an array of foods no one of which is nutritionally adequate. In such situations, a subject must compose a balanced diet by eating a mixture of foods from the array presented to it. Richter's studies of total dietary self-selection are the best known experiments of this type.<sup>5,6,13</sup>

Although dietary generalists in natural habitat are probably more likely to face the problem of composing a diet than that of choosing a diet, my students and I began by studying diet choice, rather than diet composition, because evaluation of animals' performance in diet choice tasks is relatively straightforward; greater success can be defined as greater intake of the sole nutritionally adequate diet present. Criteria of success are not so easy to specify in diet-composition situations. Nevertheless, we have also begun to look at how animals come to compose nutritionally adequate diets, and I will mention our preliminary findings in this area at the end of the present chapter.

## DIET SELECTION: A CONTRIBUTION OF DEVELOPMENTAL PSYCHOBIOLOGY

As mentioned above, self-selection of foods has, historically, been considered a problem in regulatory physiology. Consequently, focus in studies of diet selection has been on how individual animals recognize internal deficiency states and alter either their behavior or physiology so as to redress any internal imbalance. Looking at selection of foods as a developmental problem suggests additional processes that might promote adaptive patterns of food choice in animals.

Infant animals are, obviously, not capable of independent life; they require social support to solve most of life's more pressing problems. For example, infant rats depend on their dams for sustenance and on both their

dams<sup>14</sup> and peers<sup>15</sup> for assistance in thermoregulation. One might, therefore, suspect that weaning rat pups might similarly depend on others for assistance in making the difficult transition from dependence on mother's milk to independent acquisition of a diet of solid foods.

By their very existence, adult rats demonstrate the adequacy of their food choices. For a weanling to choose an adequate diet, all it need do is learn to eat the food or foods that an adult is eating. Thus, there is a potential social (as well as a physiological) solution to the problem of diet choice. The social solution may be more salient from the perspective of a developmental psychobiologist, used to observing dependent infants, than from that of a regulatory physiologist, focused on physiological processes controlling the internal milieu.

## LABORATORY STUDIES OF SOCIAL INFLUENCE ON SELECTION OF FOODS

### *Demonstration of an Effect*

In our first experiment, we established rats of weaning age in individual cages (1 × 1 m), each containing four food bowls (see FIGURE 1).<sup>16</sup> Three of these four bowls contained diets (cinnamon-flavored diet: Diet Cin, cocoa-flavored diet: Diet Coc, or thyme-flavored diet: Diet Thy) that were both relatively palatable and relatively protein poor (4.4% protein by weight). The fourth bowl contained a diet (nutmeg-flavored diet: Diet Nut) that was both relatively rich in protein (17.5% protein by weight) and relatively unpalatable to rats. As can be seen in FIGURE 2, individual weanling rats maintained for

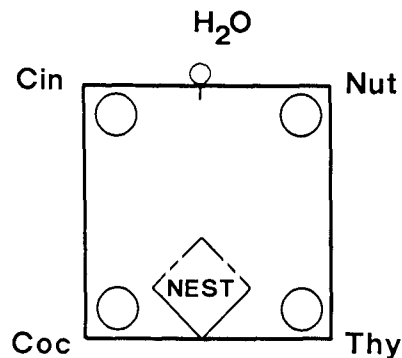


FIGURE 1. Overhead schematic of apparatus used in the first experiment. (Nut = nutmeg-flavored diet; Thy = thyme-flavored diet; Cin = cinnamon-flavored diet; Coc = cocoa-flavored diet). (From Reference 16. Copyright 1989 by the American Psychological Association. Reprinted by permission of publisher and authors.)

—|—  
.3 m

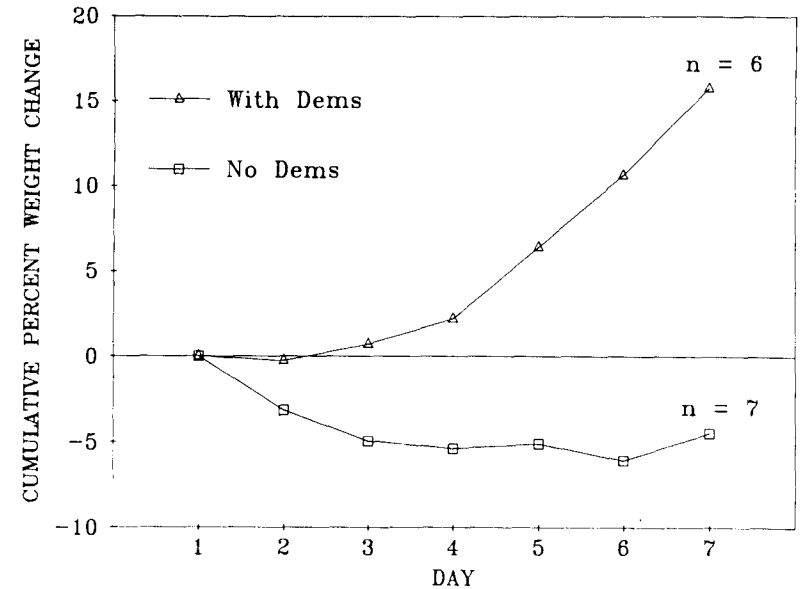


FIGURE 2. Mean cumulative percent weight change of weanling pups. (Dem = demonstrator.) (From Reference 16. Copyright 1989 by the American Psychological Association. Reprinted by permission of publisher and authors.)

6 days under such circumstances did very poorly, and were well on their way to a premature demise when, for ethical reasons, we terminated the experiment.

Weanling subjects in a second group each shared their respective enclosures with an adult rat trained to eat the protein-rich Diet Nut and to avoid eating protein-poor diets Cin, Coc, and Thy. As can also be seen in FIGURE 2, following a brief hiatus in growth, subjects that had access to social information thrived in the experimental situation.

### *Analysis of an Effect*

#### *Possibilities*

The results of the experiment described above raise more questions than they answer. In particular, they offer little clue as to how it is that the trained adult rats influenced the food choices of their juvenile cage mates. Results of previous studies of social influences on rats' food choices (see References 17-19 for reviews) provide evidence of several different ways in which food preferences of weanling rats can be modified by interaction with conspecifics: (1) Juvenile rats prefer to eat at locations where other rats are eating rather

than at locations where no other rats are to be found.<sup>20-22</sup> (2) Adult rats scent mark both feeding sites and foods they are exploiting thus increasing the attractiveness of those foods and feeding sites to conspecifics.<sup>23-25</sup> (3) After a naive rat interacts with a conspecific that has recently eaten some food, the naive rat exhibits a substantially enhanced preference for whatever food the conspecific with which it interacted has eaten.<sup>26-30</sup>

*Realities*

To investigate processes promoting adaptive food choice by weanling rats, we needed to gain control over the interactions of weanlings with adults. To that end, we placed weaning rats and their adult demonstrators in enclosures like that illustrated in overhead schematic in FIGURE 3. In these enclosures, a naive juvenile subject was separated from its adult demonstrator by a screen partition. Because adults could not eat from the food cups available to juveniles, we could measure directly intake of the foods available to each juvenile, and, because adults could not contact juveniles' food cups, adults could not scent mark either foods or feeding sites available to their cage mates. Last, and most important, by varying both the location and type food in the food cup on the adult's side of each enclosure, we could distinguish between effects of physical presence of an adult demonstrator in the vicinity of a food cup and effects of the smell of a food eaten by an adult on the food choices of juvenile subjects.

*Methods*

The arrangements of food cups used in the experiment are illustrated in FIGURE 4. Subjects assigned to the Same-Food, Same-Place group each

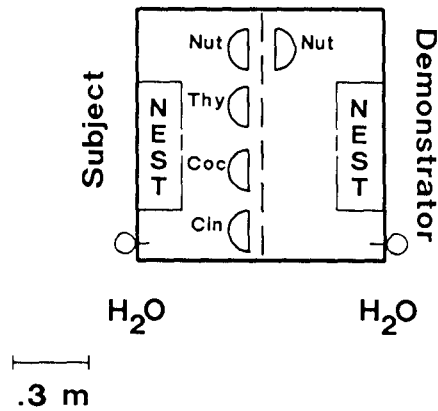


FIGURE 3. Overhead schematic of apparatus used to examine social effects on diet selection. See FIGURE 1 caption for abbreviations. (From Reference 16. Copyright 1989 by the American Psychological Association. Reprinted by permission of the publisher and authors.)

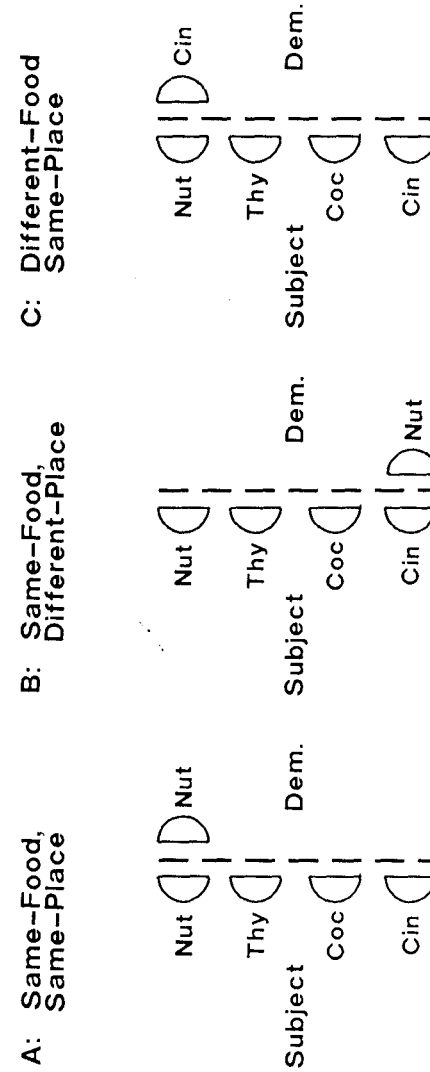


FIGURE 4. Overhead schematic of the positions and contents of food cups presented to subjects. (Nut = nutmeg-flavored diet; Cin = cinnamon-flavored diet; Thy = thyme-flavored diet; Coc = cocoa-flavored diet; and Dem = demonstrator. (From Reference 16. Copyright 1989 by the American Psychological Association. Reprinted by permission of publisher and authors.)

shared an apparatus with a demonstrator that had access to a single food cup containing Diet Nut and each demonstrator's food cup containing Diet Nut was placed directly across the screen partition from each subject's food cup containing Diet Nut (see FIGURE 4A). Subjects assigned to the Same-Food, Different-Place group interacted with a demonstrator rat eating Diet Nut from a food cup located directly across the screen partition from each subject's food cup containing Diet Cin (see FIGURE 4B). Last, subjects assigned to the Different-Food, Same-Place Group each shared an apparatus with a demonstrator rat eating Diet Cin directly across the screen partition from a subject's food cup containing Diet Nut (see FIGURE 4C). The experiment lasted 1 week, and during that week subjects and demonstrators were left undisturbed except for daily weighings of both food cups and subjects.

### Results

The main results of the second experiment are presented in FIGURE 5, which shows the mean amount of Diet Nut (the diet containing adequate protein) eaten by subjects. As can be seen in FIGURE 5, subjects in Same-Food,

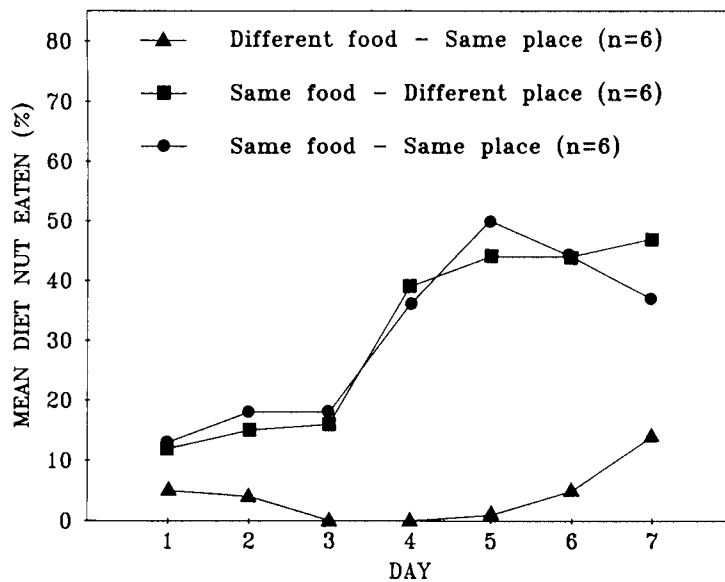


FIGURE 5. Mean amount of protein-adequate, nutmeg-flavored diet (Diet Nut) ingested as a percentage of total amount eaten by subjects in Same-Food, Same-Place (circles), Same-Food, Different-Place (squares), and Different-Food, Same-Place groups (triangles). (From Reference 16. Copyright 1989 by the American Psychological Association. Reprinted by permission of publisher and authors.)

Same-Place and Same-Food, Different-Place groups ate significantly more Diet Nut than did subjects in the Different-Food, Same-Place group and subjects assigned to Same-Food, Same-Place and Same-Food, Different-Place groups did not differ from one another in the amount of Diet Nut that they ate. This finding is consistent with the view that the flavor of the food that a demonstrator ate was more important than the location where it ate in influencing subjects' choices of foods.

It is, perhaps, worth noting in passing that, if the flavor of the food a demonstrator ate was the predominant factor biasing subjects' food selections, then subjects assigned to the Different-Food, Same-Place group [i.e., those subjects whose demonstrators ate Diet Cin (see Figure 3C)] should have exhibited an enhanced preference for Diet Cin, in comparison with subjects in the other two groups. As can be seen in FIGURE 6: (1) subjects in the Different-Food, Same-Place group did, in fact, eat a significantly greater percentage of Diet Cin from among the three available protein-poor diets than did subjects in either of the other two groups, and (2) subjects in the other two groups did not differ significantly from one another in their intake of Diet Cin.

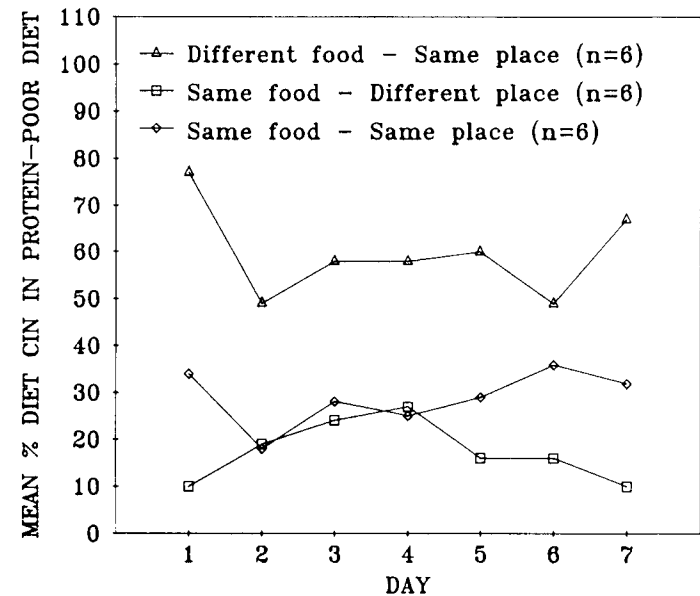


FIGURE 6. Mean amount of cinnamon-flavored diet (Diet Cin) ingested as a percentage of total amount of protein-poor, cinnamon-, cocoa-, and thyme-flavored diets eaten by three groups of subjects. (From Reference 16. Copyright 1989 by the American Psychological Association. Reprinted by permission of publisher and authors.)

## A CONUNDRUM

When considered in functional context, the ability of rats to bias conspecifics to eat foods that they have eaten poses something of a problem. Imagine two rats:  $\alpha$  and  $\beta$ .  $\alpha$  is a healthy individual that has been eating protein-rich food A;  $\beta$  has been subsisting on protein-poor food B and is malnourished. Following a brief period of interaction between  $\alpha$  and  $\beta$ ,  $\beta$ 's probability of eating nutritious food A should be increased, but then so should  $\alpha$ 's probability of eating substandard food B. Superficially, social influence appears of little use;  $\beta$ 's gain is  $\alpha$ 's loss.

More realistically, the long-term cost to the healthy  $\alpha$  of eating an inadequate food (which it could learn to avoid) is surely less than the long-term benefit to the sickly  $\beta$  of being induced to sample a nutritious food (which it could learn to eat). Still, one feels some unease at proposing a process inducing development of adaptive patterns of food selection that, of itself, has equal potential for good and ill.

If it were the case that healthy rats influenced conspecifics to eat foods that they were eating, while sickly rats influenced conspecifics to avoid foods that they were eating, then there would be no problem. However, evidence from several studies indicates that healthy and sickly demonstrators are equally effective in enhancing their respective observers' preferences for foods.<sup>31-33</sup> Rats develop preferences for, not aversions to, foods after interacting with either ill rats<sup>31-33</sup> or unconscious rats<sup>29</sup> that have eaten those foods. Consequently, differences in the response of observer rats to healthy and ill demonstrators do not appear to provide a solution to the conundrum.

The probability of socially acquired food preferences interfering with, rather than enhancing, adaptive food choices could also be reduced if the susceptibility of individual rats to social influence on their diet selection varied as a function of their internal states. For example, if rats that were doing well selecting foods (i.e., well-nourished rats) were relatively resistant to social influence on their food choices, while rats that were doing poorly selecting foods (i.e., malnourished or sickly rats) were relatively susceptible to social influence, then the immediate benefits of social influence would tend to be greater than the immediate costs.

### *An Experiment*

Determining whether deficient rats are more susceptible than replete rats to social influences on their food choices is not so straightforward a matter as it might appear at first glance. In particular, one cannot simply pair naive-deficient and naive-replete rats with demonstrators trained to select a nutritionally adequate food from among an array of foods and then see whether deficient subjects eat more nutritionally adequate food than do replete subjects.

First, and trivially, unless each subject is physically separated from its

respective demonstrator, there is no way to determine how much of each food was eaten by subjects and how much was eaten by their demonstrators. Second, and less trivially, deficient subjects might experience greater reward than replete subjects as a result of eating nutritionally adequate food. Consequently, deficient subjects might learn to select a nutritionally adequate food from an array of foods more rapidly than would replete subjects<sup>34</sup> even if deficient subjects were no more susceptible to social influences on their food choices than were replete subjects. Last, it is always possible that deprivation might cause changes in flavor preferences that only accidentally resulted in increased preference for a nutritionally adequate food.<sup>5</sup>

### *Methods*

Our experimental design<sup>35</sup> ensured that (1) both demonstrators and the subjects with which demonstrators were paired fed from separate feeding sites, (2) each of the foods among which replete and deficient subjects chose were equally ineffective in alleviating the deficiency state that had been induced in deprived subjects, and (3) there were no significant changes in the food preferences of subjects as a function of their deprivation states. Condition 1 was met by physically separating demonstrators from observers (see FIGURE 1B); condition 2 by providing subjects with four deficient foods to choose among (consequently they could not learn from postingestional consequences which food to eat), and condition 3 by examining the food choices of replete and deficient subjects in the absence of social influence.

The experiment was conducted in the apparatus illustrated in FIGURE 1B. Subjects chose among four protein-deficient diets (5% by weight casein) flavored with either cinnamon, cocoa, thyme, or nutmeg, and subjects were either protein replete or had been protein deprived for 7 days immediately before the start of the experiment.

### *Results*

The main results of the experiment are presented in FIGURE 7, which shows the mean amount of nutmeg-flavored diet (the diet eaten by demonstrator rats) eaten by subjects during the 7 days of the experiment. As would be expected on the basis of the results of the first two experiments described above, subjects interacting with demonstrators ate more of the relatively unpalatable nutmeg-flavored diet than did subjects without demonstrators. More important for the hypothesis under investigation here, there was a significant interaction between deprivation state and presence of a demonstrator in determining the amount of nutmeg-flavored diet eaten by subjects. Protein-deprived subjects with demonstrators ate significantly more nutmeg-flavored diet than did protein-replete subjects with demonstrators, while

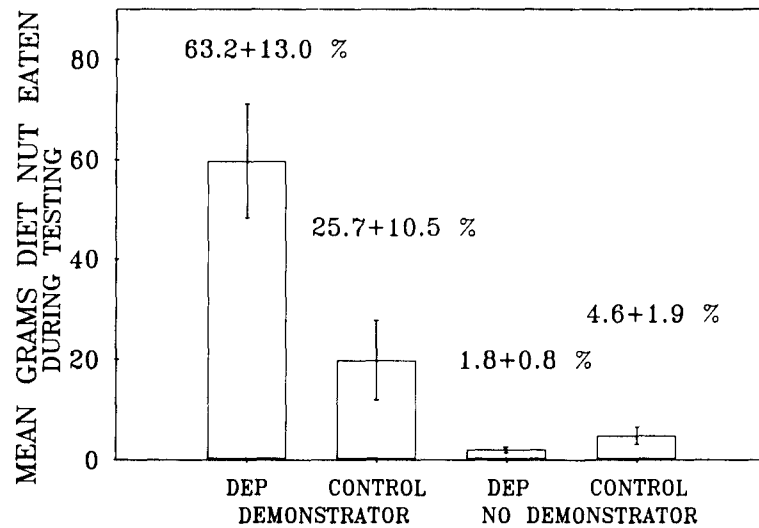


FIGURE 7. Mean total amount of protein-deficient nutmeg-flavored diet (Diet Nut) eaten during 7 days by subjects in each of four groups. Numbers above the histograms indicate the mean percent Diet Nut eaten during 7 days by subjects in each group. Flags =  $\pm 1$  standard error of the mean (SEM); Dep = deprived. From Reference 35. Copyright 1991 by the American Psychological Association. Reprinted by permission of publisher and authors.)

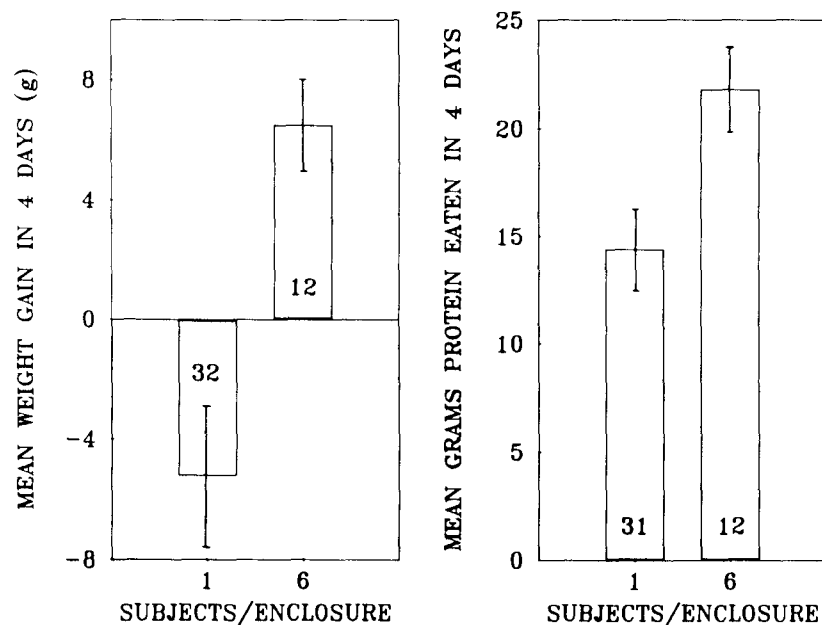


FIGURE 8. A: Mean cumulative weight change exhibited by subjects housed either individually or in groups of 6. B: Mean protein intake of subjects housed either individually or in groups of 6. Flags =  $\pm 1$  SEM.

protein-replete and protein-deprived subjects without demonstrators did not differ significantly in their intake of nutmeg-flavored diet. This last result indicates that protein deprivation affected the susceptibility of young rats to social influence, not their preference for protein.

### A Resolution

If the present laboratory experiments reflect difficulties weanling rats experience when attempting to choose an appropriate diet outside the laboratory, then weanlings are likely to get into serious nutritional trouble when they choose foods for themselves. As the physical condition of weanlings deteriorates, they should become increasingly susceptible to social influences on their food choices. On the other hand, healthy adults should be less influenced to select the inadequate rations of juveniles with which they interact. Thus, adults might induce juveniles to choose an adequate diet without seriously compromising the integrity of their own diet selection.

## SOCIAL INFLUENCES ON DIET COMPOSITION

My coworkers and I have only just started to explore the role of social influence in the weaning of rat pups living in environments where constructing a balanced diet requires composing an appropriate mixture of foods rather than choosing a single food. However, our early data are so surprising (and so promising), that they deserve some mention despite their preliminary nature.

In 1963, McDonald, Stern, and Hahn reported results of a study in which a group of 12 juvenile rats were placed together in an enclosure and the members of a second group of 12 juvenile rats were each placed in an individual cage.<sup>36</sup> All 24 animals had to compose a diet by eating from four containers which contained either casein, sugar, fat, or mineral mix (vitamins were provided in drinking water). McDonald *et al.* found that, although the isolated rats failed to gain weight, the rats living together in the group of 12 grew as rapidly as did control rats fed a nutritionally balanced chow.<sup>36</sup>

We have repeated McDonald *et al.*'s study using as subjects both individual juvenile rats ( $n = 12$ ) and juvenile rats in groups of six ( $n = 8$  groups). FIGURE 8 provides data describing both the rate of weight gain and protein intake of juvenile rats feeding either in isolation or in groups. As can be seen in FIGURE 8, individually housed rats ate less protein and grew more slowly than did rats housed in groups of six. In fact, isolated rats lost weight, while group-housed rats gained weight during their week in the test situation.

At the present time, we have no information as to how group living facilitates diet composition. However, whatever the mechanism, this social facilitation of food selection demonstrates a role of peer interaction in the



- tant foods: a laboratory investigation of the "information-centre" hypothesis. *Anim. Behav.* **31**: 748-758.
30. POSADAS-ANDREWS, A. & T. J. ROPER. 1983. Social transmission of food preferences in adult rats. *Anim. Behav.* **31**: 265-271.
  31. GALEF, B. G., JR., L. M. MCQUOID & E. E. WHISKIN. 1990. Further evidence that Norway rats do not socially transmit learned aversions to toxic baits. *Anim. Learn. Behav.* **18**: 199-205.
  32. GALEF, B. G., JR., S. W. WIGMORE & D. J. KENNETT. 1983. A failure to find socially mediated taste aversion learning in Norway rats (*R. norvegicus*). *J. Comp. Psychol.* **97**: 358-363.
  33. GROVER, C. A., J. S. KIXMILLER, C. A. ERICKSON, A. H. BECKER, S. F. DAVIS & G. B. NALLAN. 1988. The social transmission of information concerning aversively conditioned liquids. *Psychol. Rec.* **38**: 557-566.
  34. GIBSON, E. C. & D. A. BOOTH. 1986. Acquired protein appetite in rats: dependence on a protein-specific need state. *Experientia* **42**: 1003-1004.
  35. GALEF, B. G., JR., M. BECK & E. E. WHISKIN. 1991. Protein deficiency magnifies social influence on the food choices of Norway rats (*Rattus norvegicus*). *J. Comp. Psychol.* **105**: 55-59.
  36. McDONALD, D. G., J. A. STERN & W. W. HAHN. 1963. Effects of differential housing and stress on diet selection, water intake and body weight in the rat. *J. Appl. Physiol.* **18**: 937-942.
  37. GALEF, B. G., JR. 1991. Innovations in the study of social learning in animals: a developmental perspective. *In* *Developmental Psychobiology: New Methods and Changing Concepts*. H. N. Shair, G. A. Barr & M. A. Hofer, Eds.: 114-125. Oxford University Press. New York, NY.

## The Emergence of Behavioral Regulation during Fetal Development<sup>a</sup>

SCOTT R. ROBINSON AND  
WILLIAM P. SMOTHERMAN

*Laboratory for Perinatal Neuroethology  
Center for Developmental Psychobiology  
Department of Psychology  
Post Office Box 6000  
State University of New York at Binghamton  
Binghamton, New York 13902-6000*

The past decade has seen a renaissance of interest in prenatal behavior in fields that are dedicated to understanding brain-behavior relationships, such as psychobiology and behavioral neuroscience. The growth in fetal research has been accompanied by changes in the way prenatal development is viewed by many investigators. From the perspective of development, it has become manifest that newborn mammals exhibit sophisticated behavioral capacities within minutes or hours of birth, and that the mechanisms underlying this early behavioral organization must either appear *de novo* at the moment of birth, or extend their roots into the prenatal period.<sup>1</sup> From the perspective of understanding the neural control of behavior, the fetus provides a relatively simpler system in which to investigate the emergence of coordinated action and behavioral regulation.<sup>2</sup> Further, the simpler systems subserving fetal behavior are directly relevant and ultimately give rise to the behavioral complexity associated with the infant, juvenile, and adult mammal.

From the perspective of the experimenter, investigation of behavior during the fetal period also provides certain methodological advantages over early postnatal study. Newborn mammals, especially the offspring of altricial species with poorly developed motor skills at birth (e.g., rats and other Murid rodents), are highly dependent upon the behavior of the mother as a source of nutrition, water and salt balance, heat, and protection. Through their behavioral interactions, the mother and neonate form a dyadic relationship that is the ultimate source of behavioral and physiological regulation during the early postnatal period.<sup>3</sup> Consequently, experiments intended to

<sup>a</sup> The original research reported in this paper is supported by the National Institute of Child Health and Human Development (National Institutes of Health) grants HD 16102 and Research Career Development Award HD 00719 to WPS, and HD 28231 to SRR and WPS. WPS also is supported by the NATO Collaborative Research Grants Program (0551/90).