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Effects of Caloric, Protein, and Sodium Deprivation on the Affiliative Behavior of Norway Rats (*Rattus norvegicus*)

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The tendency of food-deprived, protein-deprived, and sodium-deprived Norway rats (*Rattus norvegicus*) and their respective controls to affiliate with conspecifics deprived of either food, protein, or sodium was examined. The authors found that (a) independent of internal state, focal rats offered a forced choice between protein-deprived and protein-replete target rats spent more time near replete than deprived target rats; and (b) both food-deprived and sodium-deprived focal rats offered a forced choice between food-deprived and replete target rats spent less time near fasted rats than did well-fed and sodium-replete focal rats. The data indicate that (a) rats can distinguish both food-deprived and protein-deprived rats from replete rats and (b) the deprivation states of rats can affect their willingness to affiliate with deprived conspecifics.

The food choices of Norway rats can be influenced by interaction with conspecifics (for reviews, see Galef, 1982, 1996a). Although such social influences on rat foraging depend on several different behavioral processes (for review, see Galef, 1996b), most processes supporting social influence on foraging require animals to be close to one another if social biasing of feeding decisions is to occur. Consequently, choice of associates should play a role in determining the social influences to which individual rats are exposed, and thus the directions in which foraging decisions are socially biased.

In a recent paper, Krause, Hartmann, and Pritchard (1999) provided evidence that food-deprived zebra fish (*Danio rerio*) that were offered a simultaneous choice between shoals of well-fed and food-deprived conspecifics preferred to affiliate with well-fed shoals. Well-fed zebra fish, on the other hand, spent equal amounts of time in contact with well-fed and food-deprived shoals.

In the present article, we extend the work of Krause et al. (1999) to examine the relative preferences of nutrient-deprived and nutrient-replete Norway rats offered a forced choice between deprived and replete conspecifics. Decades of investigations of feeding behavior of mammals in general, and of Norway rats in particular, have provided techniques for inducing a range of deprivation states in rats (e.g., Stricker, 1990). Such techniques make possible the extension of Krause et al.'s (1999) studies not only to a mammalian species, but also to deprivation of specific nutrients, as well as of food in general.

In the experiments described below, we examined effects of caloric, sodium, and protein deprivation on affiliative preferences of Norway rats offered forced choices between conspecifics deprived of either food, sodium, or protein and their respective controls.

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General Method

Subjects

Female Long-Evans rats (*Rattus norvegicus*), purchased from Charles River Canada (St. Constant, Quebec), served as both focal and target subjects in the experiments described below. All rats were 6 to 7 weeks old when experiments started, and all served in other experiments under way in our laboratory after participating in the present experiment.

Apparatus

We conducted experiments in a floor enclosure, measuring 1.0 × 1.0 × 0.33 m, constructed of angle iron and hardware cloth (see Figure 1). A thin layer of wood-chip bedding covered the galvanized sheet metal floor of the enclosure.

Two 1/2-in. (1.27-cm) mesh hardware-cloth partitions divided the enclosure into three compartments. During the experiment, the central compartment, measuring 0.67 × 1.0 × 0.33 m, contained a focal rat, and each of the two outer compartments, each measuring 0.33 × 1.0 × 0.33 m, held a group of 3 target rats.

A 1-m-long strip of electrician's tape running parallel to the two hardware-cloth partitions at the midpoint of the roof of the central compartment facilitated observers' determination of which end compartment a focal rat was nearer at any moment. A video camera suspended directly above the tape recorded behavior of focal rats for later analysis.

Housing

Before the start of the experiment, we established pairs of focal rats and trios of target rats in shoe box cages (35.4 × 30.4 × 15.2 cm) and maintained them with ad libitum access to Purina Rodent Laboratory Chow 5001 and tap water.

Food deprivation. Twenty-four hr before the start of testing, we removed the Purina chow from the cages of subjects that were to be food deprived. We treated control rats that were not deprived of food identically to food-deprived rats except that the former had both food and water available ad libitum for the 24 hr preceding their participation in a test session.

Protein deprivation. Seven days before testing, we removed the maintenance diet from cages containing rats to be protein deprived and gave them ad libitum access to a food bowl containing a powdered diet with 3% protein content (Basal Mix for Adjusted Protein, Harlan Teklad, Madison,

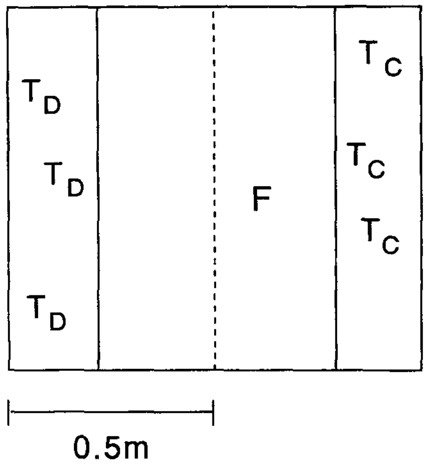

Figure 1. Overhead schematic of the apparatus. F = focal rat; T_D = deprived target rat; T_C = control target rat.

WI, Catalog Number TD86146, to which we added 3% by weight High Protein Casein, Catalog Number 160030, Harlan Teklad). We fed control rats Basal Mix for Adjusted Protein with sufficient High Protein Casein added to make a diet containing 20% protein, which is standard in rodent laboratory chows.

Sodium deprivation. We treated sodium-deprived rats in one of two ways. We either placed them in individual, stainless-steel hanging cages for 72 hr and provided them with ad libitum access to tap water and a sodium-free diet (Harlan Teklad, Catalog Number TD 170950) or left them in their home cages with access to a sodium-free diet. In the latter case, we provided rats with fresh cages every 24 hr to restrict their access to excreted sodium. In both cases, 48 hr after each rat had been placed on a salt-free diet, we injected it subcutaneously with 0.1 ml furosemide (Sabex, Boucherville, Quebec, Canada). Furosemide is a diuretic that, in combination with maintenance on a sodium-free diet, produces sodium deficiency in rats (Jalowiec, 1974). Control rats received the same treatment as did sodium-deprived rats except that for 3 days, control rats ate a sodium-free diet to which sufficient table salt had been added to make a diet containing 1.5% sodium chloride, the normal salt content of rat chow. Furosemide injection in combination with a sodium-replete diet does not produce sodium deficiency (Jalowiec, 1974).

Procedure

During testing, we first placed a group of 3 target rats in each end compartment and a focal rat in the central compartment of the apparatus. We then left all rats undisturbed for 20 min while we videotaped the behavior of focal rats.

The 3 target rats placed in one end compartment of the apparatus had all been deprived either of food, protein, or sodium; all 3 target rats simultaneously placed in the other end compartment of the apparatus were the control rats for the first group of target subjects.

Each set of 6 target rats participated in the experiment twice: once with a deprived focal rat and once with a control focal rat. We counterbalanced both the end compartment in which deprived and control target rats were held and the order in which we tested deprived and control focal rats.

To determine whether we had been successful in depriving our rats of protein and sodium, we (a) monitored the body weight of protein-deprived rats and their controls during the period of protein deprivation of the former rats, and (b) offered sodium-deprived rats and their controls a choice between a 3% saline solution and water for the 24 hr immediately following testing of affiliative behavior.

To determine interobserver reliability, two observers scored the amount of time focal rats spent closer to deprived rats in 10 randomly selected 20-min tapes.

Data Analysis

To examine effects of deprivation state of focal and target rats on affiliative preference, we used matched-pairs *t* tests, pairing those rats tested with the same groups of target rats, thus assuring independence of observations. Because we conducted experiments with rats in different deprivation states sequentially rather than simultaneously, only comparisons between deprived and control focal rats within each deprivation condition are, strictly speaking, appropriate for statistical comparison.

Experiment 1

In the first experiment, (a) focal rats that we had deprived of food for 24 hr and their controls chose between fasted target rats and their controls, (b) sodium-deprived focal rats and their controls chose between sodium-deprived target rats and their controls, and (c) protein-deprived focal rats and their controls chose between protein-deprived target rats and their controls.

Method

Subjects. Focal subjects were 104 rats. Of these, 40 were fasted rats and their controls, 32 were sodium-deprived rats and their controls, and 32 were protein-deprived rats and their controls. An additional 156 rats served as target subjects.

Apparatus and procedure. The apparatus and procedure were those described in the General Method.

Results

Our manipulations of both sodium and protein balance were successful. For example, during testing for preference between 3% saline solution and tap water, focal rats assigned to the sodium-deficient condition drank a mean (± *SEM*) of 38.8% (± 3.3) 3% saline solution, whereas sodium-replete controls drank only 13.5% (± 2.3) 3% saline solution: Student's *t* test, $t(30) = 6.29$, $p < .0001$. Protein-deprived focal rats lost an average 4.5% (± 2.0) of their initial body weight during the experiment, whereas focal rats maintained on protein-sufficient diet gained an average of 18.2% (± 1.3) of their initial body weight during the same period: $t(30) = 9.52$, $p < .0001$.

Examination of interobserver reliabilities in scoring from videotapes the number of seconds that focal rats spent closer to deprived than replete target rats revealed a highly significant correlation: Pearson's product moment correlation, $r(10) > .98$, $p < .0001$.

The main results of Experiment 1 are presented in Figure 2, which shows the mean number of seconds (out of 1,200) that focal rats assigned to food-, sodium-, and protein-deprived conditions and their controls spent closer to their respective deprived than control target rats (focal rats spent the remainder of each 1,200-s affiliative test closer to their control than deprived target rats).

As can be seen in Figure 2, (a) food-deprived focal rats spent significantly less time near fasted target rats than did replete focal rats: matched *t* test, $t(19) = 2.59$, $p < .02$; (b) sodium-deprived and sodium-replete focal rats did not differ in their tendency to affiliate with sodium-deprived and sodium-replete target rats,

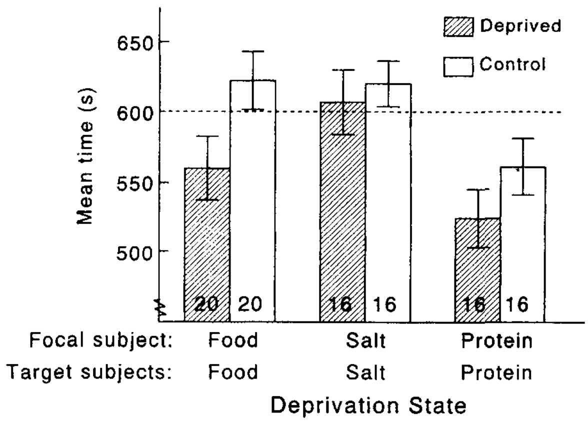

Figure 2. Mean number of seconds out of 1,200 that deprived focal rats and their respective controls spent closer to deprived than to replete target rats in Experiment 1. N = number of rats in deprived and in control conditions. Error bars = $\pm$ 1 *SEM.*

$t(15) = .48$, *ns*; and (c) protein-deprived and protein-replete focal rats did not differ in their tendency to affiliate with protein-deprived and protein-replete target rats, $t(15) = 1.70$, *ns*.

Twenty-six of the 16 protein-deprived focal rats and their 16 controls spent more time close to their protein-replete than their protein-deprived target subjects: binomial test, $q(32) = 6$, $p < .001$, whereas neither food-deprived nor sodium-deprived focal rats and their respective controls avoided their respective deprived target rats: binomial tests, both $ps > .30$.

Discussion

The results of Experiment 1 provide evidence, first, that rats can discriminate food-deprived from food-replete conspecifics and, second, that food deprivation affects rats' tendencies to affiliate with food-deprived and replete conspecifics. The results also provide evidence that rats are able to discriminate protein-deprived from protein-replete conspecifics.

Experiment 2

In Experiment 1, deprivation states of focal and target animals were confounded. Consequently, the data of Experiment 1 are not sufficient to determine whether effects seen in food-deprived focal rats but not in sodium-deprived focal rats reflected differences in deprivation states of focal or target rats or some interaction between the two. The same confound also makes it impossible to determine from the results of Experiment 1 whether protein-deprived target rats are aversive or whether something about maintenance on Basal Diet for Adjusted Protein makes focal rats avoid deprived animals generally. We undertook Experiment 2 to resolve these ambiguities.

Ideally, we would have examined all nine possible combinations of deprived and replete focal and target rats. However, practical constraints led us to examine only those groups that a priori seemed likely to prove most informative.

Method

Subjects. Focal subjects in Experiment 2 were 104 experimentally naive, female Long-Evans rats. Of these, 64 were food-deprived rats and their controls, and 40 were sodium-deprived rats and their controls. An additional 156 animals served as target rats: 60 food-deprived target rats and their controls, 48 sodium-deprived target rats and their controls, and 48 protein-deprived target rats and their controls.

Apparatus and procedure. The apparatus and procedures were the same as those described in the General Method except that in Experiment 2, (a) sodium-deprived and sodium-replete focal rats chose between food-deprived and replete target rats, and (b) food-deprived focal rats chose between both sodium-deprived and sodium-replete target rats and protein-deprived and protein-replete target rats.

Results and Discussion

The main results of Experiment 2 are presented in Figure 3, which shows the mean number of seconds out of 1,200 that focal rats assigned to the various conditions spent closer to deprived than to nondeprived target rats. Data from the three groups in Experiment 1 are included to facilitate comparisons.

As can be seen in the left panel of Figure 3, although sodium-deprived and sodium-replete focal rats responded differently to food-deprived and replete target rats, matched t test, $t(19) = 2.51$, $p < .02$, food-deprived and replete focal rats did not respond differently to sodium-deprived and sodium-replete target rats, paired t test, $t(15) = .36$, *ns*. These data are consistent with the view that, in Experiment 1, food-deprived target rats were more easily discriminated from their controls than were sodium-deprived target rats from their controls.

As can be seen in the right panel of Figure 3, food-deprived and replete focal rats failed to respond differently to protein-deprived and protein-replete target rats: matched t test, $t(15) = 0.14$, *ns*. Food-deprived focal rats and their controls, like protein-deprived focal rats and their controls in Experiment 1, tended to avoid protein-deprived target rats and remained closer to protein-replete target rats: binomial test, $q(32) = 10$, $p < .05$. On the other hand, only 32 of 64 focal rats choosing between either sodium-deficient and sodium-replete target rats, $q(64) = 32$, *ns*, and 48 of 102 focal rats choosing between fasted and replete target rats avoided deprived target subjects, $q(102) = 54$, *ns*. Protein-deprived rats but not sodium-deprived or food-deprived rats appear to be generally unattractive to conspecifics.

General Discussion

Taken together, the results of the two experiments reported above indicate that (a) food- and sodium-deprived focal rats and their respective controls can discriminate food-deprived from food-replete conspecifics; (b) both food-deprived and protein-deprived focal rats and their respective controls can discriminate protein-deprived from protein-replete conspecifics, and all avoid protein-deprived individuals; and (c) focal rats deprived of either sodium or food avoid food-deprived target rats more than do their respective controls. We conclude that Norway rats can discriminate food-deprived and protein-deprived rats from appropriate controls, and that, in rats, both food and sodium deprivation can affect the tendency to affiliate with deprived conspecifics.

Unfortunately, the pattern of preferences and avoidances revealed in the present data was not a simple one. Sodium deprivation caused rats to avoid food-deprived but not sodium-deprived conspecifics. Protein deprivation made rats generally unattractive

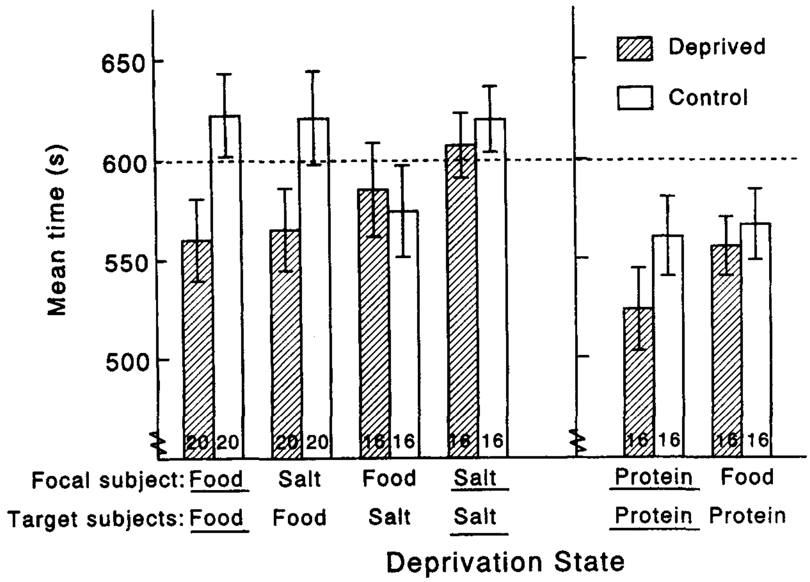

Figure 3. Mean number of seconds out of 1,200 that deprived focal rats and their respective controls spent closer to deprived than to replete target rats in Experiment 2. The data from Experiment 1 (underlined groups) are included to facilitate comparisons. N = number of rats in deprived and in control conditions. Error bars = ± 1 *SEM*.

to their fellows, but avoidance of protein-deprived target rats did not vary with the deprivation state of focal rats.

Of course, failure in the present experiments to have found effects (e.g., discrimination of sodium-deprived and sodium-replete target rats by sodium-deprived focal rats or a difference in the response of protein-deprived and protein-replete focal rats to protein-deprived and protein-replete conspecifics) cannot be taken as evidence that those effects do not occur. Different levels of deprivation or alternative measures of affiliation might have produced different outcomes. Consequently, the present results provide only a preliminary exploration of effects of deprivation state on affiliation, providing the first evidence of which we are aware that deprivation states of both focal and target subjects affect the affiliative behavior of Norway rats.

As mentioned earlier, Krause et al. (1999) have reported effects of food deprivation on affiliative behavior in zebra fish. These investigators also reported significant differences in the morphology of deprived and replete target subjects that may have been used by focal animals to select companions. We have not yet undertaken experiments to determine the stimuli that focal rats might use to distinguish deprived from replete conspecifics, but given the general importance of olfaction in the lives of Norway rats, we speculate that differences in the olfactory cues emitted by deprived and replete individuals may be important.

Because the deprivation state of both focal and target rats appears to affect the social choices of focal rats, and contact with others that have recently eaten influences subsequent food choice in rats (Galef, 1982, 1996a), it also seems likely that effects of deprivation state of both demonstrator and observer might influence the course of social learning about foods. For example, the present results indicate that food-deprived focal rats are more likely to contact replete than food-deprived target rats. Food-deprived focal rats should, therefore, be more likely than replete focal rats to acquire information about available foods socially.

We have previously reported that protein-deprived Norway rats are more strongly influenced by the food choices of replete conspecifics than are protein-replete Norway rats (Galef, Beck, & Whiskin, 1991). Such variance in the extent of social influences on food choice might have been predicted from the present results.

The results of the present experiments show that deprivation states of Norway rats influence their affiliative behavior. The generality of these results, the stimuli mediating them, and their possible effects on social biasing of food choice remain to be explored.

References

Galef, B. G., Jr. (1982). Studies of social learning in Norway rats: A brief review. *Developmental Psychobiology, 15,* 279–285.

Galef, B. G., Jr. (1996a). Social enhancement of food preferences in Norway rats: A brief review. In C. M. Heyes & B. G. Galef Jr. (Eds.), *Social learning and imitation: The roots of culture* (pp. 49–64). New York: Academic Press.

Galef, B. G., Jr. (1996b). Social influences on the food preferences and feeding behaviors of vertebrates. In E. D. Capaldi (Ed.), *Why we eat what we eat: The psychology of eating* (pp. 207–230). Washington, DC: American Psychological Association.

Galef, B. G., Jr., Beck, M., & Whiskin, E. E. (1991). Protein deficiency magnifies social influence on the food choices of Norway rats *(Rattus norvegicus). Journal of Comparative Psychology, 105,* 55–59.

Jalowiec, J. E. (1974). Sodium appetite elicited by furosemide: Effects of differential dietary maintenance. *Behavioral Biology, 10,* 313–327.

Krause, J., Hartmann, N., & Pritchard, V. L. (1999). The influence of nutritional state on shoal choice in zebrafish, *Danio rerio. Animal Behaviour, 57,* 771–775.

Stricker, E. (1990). *Handbook of neurobiology: Neurobiology of food and fluid intake.* New York: Plenum.

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