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Learning and nonlearned neophobia enhancement both contribute to the formation of illness-induced taste aversions by deer mice (*Peromyscus maniculatus bairdi*)

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An investigation was made of the occurrence of learned and nonlearned aversions in the acquisition of illness-induced taste aversions in mice of the genus *Peromyscus*. It was determined: (1) that illness following the ingestion of a novel flavor both produced aversions specific to that flavor and also enhanced neophobia directed toward novel flavors in general; (2) that the specific aversion and the enhanced neophobia appeared to be mediated by independent processes, with no indication that the enhanced neophobia was dependent upon the integrity of the specific aversion; and (3) that illness following the ingestion of familiar water produced enhanced neophobia, which did not appear to be mediated by an aversion to water. It was noted that the results were fundamentally in agreement with those previously obtained with laboratory rats, except that a demonstration of the independence between the two types of aversions has not yet been reported in those animals.

Although it seems well established that animals learn to avoid ingesting a particular flavor following a pairing of that flavor with illness (see an extensive literature indexed in Riley & Clarke, 1977), some findings have indicated that this aversion may, at least in part, derive from nonlearned mechanisms such as sensitization or neophobia enhancement (Carroll, Dinc, Levy, & Smith, 1975; Domjan, 1975; Mitchell, Kirschbaum, & Perry, 1975; Mitchell, Parker, & Johnson, 1976; Robbins, Note 1), and this in turn has stimulated an effort to assess the relative importance of these different processes (see, e.g., Bitterman, 1975, 1976; Garcia, 1978; Garcia, Hankins, & Rusiniak, 1976; Mitchell, 1978; Mitchell, Scott, & Mitchell, 1977; Revusky, 1977a, 1977b, 1978; Riley, 1978; Smith, 1978). Additionally, recent findings on laboratory rats have suggested that neophobia enhancement may be mediated by several different mechanisms: (1) true illness-induced novel-flavor sensitization [an apparently short-lived effect (Domjan, 1977a, 1977b)]; (2) generalization of a conditioned aversion to flavors exhibiting similar taste properties to the conditioned flavor (Domjan, 1975, 1977a; Nachman, 1963); and (3) generalization of a conditioned aversion to other flavors along a novelty dimension (Best & Batson, 1977; see also Revusky, Parker, Coombes, & Coombes, 1976).

Since the study of illness-induced aversions has led to a continuing discussion regarding the generality of the laws of learning, and since apparent taxon-specific differences have been obtained with this phenomenon (e.g., Wilcoxon, Dragoin, & Kral, 1971), it seems desirable that some attention be directed to the occurrence of learned and nonlearned illness-induced aversions in species other than the rat. This appears especially desirable, since at least one author (Mitchell, 1978) has alleged that the laboratory rat is inappropriate for such studies. However, in earlier studies with deer mice (*Peromyscus maniculatus bairdi*), I found that they learned taste aversions in much the same way as rats (Robbins, 1977b, 1978). Here I report four additional experiments involving taste aversions with deer mice, employing procedures similar to those used with rats.

The research reported in Experiment 1 represents a portion of the work carried out in partial fulfillment of the requirements for the doctoral degree under the direction of John A. King in the Department of Zoology at Michigan State University. Financial support for the research was provided in part by a predoctoral fellowship awarded by the National Science Foundation and by a teaching assistantship in the Biological Science Program at Michigan State University. Thanks are due to John A. King and Stephen C. Bromley and to the anonymous reviewers for their assistance in providing critical comments on the manuscript. Requests for reprints should be sent to Robert J. Robbins, Department of Zoology, Michigan State University, East Lansing, Michigan 48824.

EXPERIMENT 1

Mitchell, Parker, and Johnson (1976) found that rats given a LiCl injection after ingesting a novel almond-flavored solution subsequently showed equal aversions to the almond solution and to a different, maple-flavored solution. They interpreted this apparent lack of a generalization decrement as

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indicating that nonlearned processes were mediating the aversion. However, no independent measure demonstrating the discriminability of these tastes by rats was offered, thus rendering their interpretation tentative.

The design used here to determine the occurrence of generalization in deer mice was similar to that of Mitchell et al. However, taste-discriminability problems were reduced by using four distinctly different flavors: sweet (sucrose), salt (NaCl), sour (HCl), and bitter (quinine sulfate).

Method

The 96 subjects were experimentally naive adult (100-160 days of age) male and female *Peromyscus maniculatus bairdi* from the same stocks and reared and housed under the same conditions as described in Robbins (1978).

The four flavors were prepared fresh each day using room-temperature distilled water. The sucrose was a 20% w/v solution, the saline a .58% w/v solution, the HCl a .15% v/v solution of 37% reagent HCl, and the quinine a .049% w/v solution of quinine sulfate.

Since *Peromyscus* cannot tolerate restriction of fluid availability to short intervals every day, regular and reliable drinking patterns were produced by placing the subjects on the following schedule: On Day 0, the animals were removed from their colony cages, where water had been available ad lib, and were placed into their experimental cages. At 1300 h, their water was removed, beginning a 24-h deprivation. At 1300 h of Day 1, drinking tubes filled with water were placed on each cage, left for 20 min, then removed, and the amount consumed was recorded. Consumption was recorded to ±.1 ml by offering the fluid in 10-cc plastic syringes that had been modified into calibrated drinking tubes (Robbins, 1977a). Immediately following the recording of data, the tubes were refilled, replaced upon the cages, and left in position for approximately 24 h. At 1300 h on Day 2, the tubes were removed, beginning another 24-h deprivation, and the data were recorded. This alternation of fluid-availability/fluid-deprivation was continued throughout the experiment. The schedule provides a regular, postdeprivation, 20-min drinking period on every odd-numbered day, while providing 24-h periods of ad-lib water drinking, which conclude on every even-numbered day. The data from the pretreatment water-consumption days were analyzed to determine if by chance the groups differed in their baseline fluid consumption. They did not.

Water was presented to all of the animals according to this schedule for 8 days. On Day 8, each animal was weighed and assigned randomly to one of eight initial treatment categories. Each of these groups was assigned to have one of the four flavors paired with either a LiCl or a NaCl injection. On Day 9, each animal was offered its assigned flavor for 20 min and then injected (ip, 6.0 mEq/kg as 15 ml/kg of body weight of .4-M solution) with its assigned substance. On Day 11 (the pretest), to determine the degree of aversion shown to the training flavors, each group was tested for 20 min on the flavor it had received prior to injection. On Day 13 (the generalization test), each group was divided into three subgroups, with each subgroup tested for 20 min on a flavor other than the training flavor. (For example, the suc/Li group was subdivided into three subgroups tested on saline, HCl, and quinine, respectively.) On Day 15 (the posttest), all groups were retested for 20 min on the training flavor. Immediately after the 20-min drinking periods of Days 9, 11, and 13, water tubes were replaced on the cages and left in position for 24 h so that on Days 10, 12, and 14, 24-h water consumption was recorded.

Although this schedule delays the testing for a generalization decrement so that 3 days intervene between poisoning and testing (and thus might be an unsuitable design for laboratory rats—cf. Carroll et al., 1975), this should not bias the measurement of an unlearned aversion in *Peromyscus* since Robbins (Note 1) found no difference between the degree of enhanced neophobia shown by these animals when they were tested with 1 or with 3 intervening days.

Results and Discussion

Consumption of the flavored solutions differed among the saline-injected controls, reflecting the differing palatability of the flavors for deer mice. Since the present concern is with the extent of the learned aversions, the results for the LiCl-injected mice are shown in Figure 1 as a proportion of the mean consumption of controls drinking the same flavor (cf. Klein, Mikulka, Domato, & Hallstead, 1977; Nachman, Rauschenberger, & Ashe, 1977). Thus, a mean of 1.0 is expected for all groups in the absence of effects due to LiCl injection.

Independent t tests found that each group mean was significantly less than 1.0 on every trial [$t(11) > 2.98$, $p < .025$], indicating the occurrence of aversions. However, the aversions shown on the generalization test were significantly weaker than those on the pretest [$F(1,22) > 4.806$, $p < .05$] and than those on the posttest [$F(1,22) > 5.103$, $p < .05$] for all except the saline group.

Although analysis of variance found no differences among the four groups on the generalization test, significant differences were detected on both the

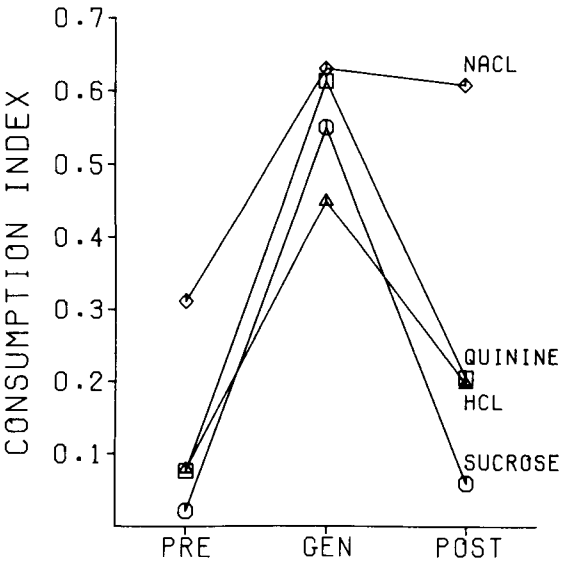

Figure 1. Mean consumption indices on the pre-, generalization, and posttests for the LiCl-injected groups in Experiment 1. The consumption index has been so defined (see text) that, in the absence of any injection effects, the expected mean is 1.0 for each group on every test. The pre- and posttests represent consumption of the flavor (indicated by the captions) previously paired with illness. The generalization test represents consumption of novel flavors other than that paired with illness.

pre- and posttests [$F(3,44) > 6.870$, $p < .001$], with subsequent multiple comparisons (Duncan's, 1955, multiple range test, $p < .01$) finding that the aversion to saline was significantly weaker than that to the other fluids. However, little meaning should be attached to this, since it may simply reflect a CS-concentration effect (Barker, 1976; Dragoin, 1971; Garcia, 1974) and no systematic effort was made to equate the salience of the four flavors.

The occurrence of significantly higher ratios on the generalization test demonstrates a generalization decrement. This is consistent with the hypothesis that learning is occurring and undermines the assertion of Mitchell et al. that "the absence of such a decrement ... argues against the primacy of associative factors" (Mitchell et al., 1976, p. 122).

However, the present results do show some peculiar patterns that might be interpreted as indicating that the aversions detected on the "generalization" trial may not be due to generalization of a learned aversion, but instead may be due to another, possibly independent, process. For example, consider that: (1) The animals poisoned after drinking saline showed a "generalized" aversion that was not significantly different from those shown by the other groups, even though the saline-drinking animals exhibited significantly weaker aversions to their training flavor; (2) there were no significant differences [$F(11,36) = .369$] on the generalization trial among any of the 12 subgroups produced by the double classification of training and generalization flavor. Thus, if it is assumed that the aversions on the generalization trial were in fact generalized learned aversions toward the training flavor, then these results require the conclusion that an aversion directed specifically toward one of the original flavors generalized equally toward each of the remaining three—a counter-intuitive result, given the differing nature of the flavors. Since these observations *suggest* (but certainly do not prove) the independent occurrence of a nonlearned, nongeneralized neophobia enhancement in these animals, the remaining experiments in this paper will present additional data bearing upon this issue.

EXPERIMENT 2

Although an earlier study using a design similar to that to be presented here reported finding no indication of enhanced neophobia in deer mice (Robbins, 1978, Experiment 4), it now appears that those results may have been misleading. Relatively few animals were used in each test group and the controls were injected with hypertonic saline. Work done subsequently has shown that hypertonic saline can induce aversions in deer mice (Robbins, Note 1), as it has been shown to do in rats (Andrews & Braveman, 1975). Since NaCl-induced aversions in the controls could mask weak LiCl-induced aversions in the noncontingently poisoned animals, this experiment replicated the earlier study, with the modifications that twice as many animals were used per group and the controls were given no injections.

Method

The 40 male and 40 female subjects were experimentally naive adult *P. m. bairdi*, as in the previous experiment. At the initiation of the experiment, the animals were housed individually in plastic laboratory cages and given water on the fluid schedule of Experiment 1 for 8 days. On Day 8, the animals were weighed and assigned randomly (with the restriction that each group be balanced by sex) to one of four treatment groups. On Day 9, the different treatment procedures were begun: Group 1 (S-Li) received a 20% w/v sucrose solution during the 20-min drinking period and then was immediately injected with 6.0 mEq/kg of a .4-M LiCl solution; Group 2 (W-Li) received water and then was similarly injected; Group 3 (S-No) received sucrose and then was handled but not injected; and Group 4 (W-No) received water and then was handled but not injected. After handling and injections, the animals were returned to their cages, where water was available for 24 h. On Day 10, the water drinking was recorded and the tubes removed. On Day 11, all groups were offered 20% sucrose solution during their 20-min drinking period. Following this, the experiment was terminated.

Results and Discussion

Figure 2 shows the results of the sucrose test on Day 11. Each group was significantly different from every other group [$F(3,76) = 31.790$, $p < .0001$; in all comparisons, $p < .05$ by Duncan's test]. This indicates that the following factors were operative: (1) Loss of neophobia with increased familiarity to the sucrose solution—Group S-No, which had been exposed to sucrose without contingent lithium prior to the test, exhibited a higher sucrose consumption than Group W-No, which had been similarly exposed to water; (2) dependence of the learned aversion to sucrose on prior consumption of sucrose preceding sickness—Group S-Li drank less sucrose than Group W-Li; (3) illness-enhanced neophobia—Group W-Li, which was subjected to lithium sickness without prior consumption of sucrose, exhibited an aversion to the sucrose in comparison with Group W-No.

Thus, it appears that the earlier report (Robbins, 1978) was in error and that a water/LiCl contingency can induce nonlearned aversions to sucrose in deer mice. Of course, it might be argued that the W-Li animals were showing a generalized learned aversion to water, but since similar results have been obtained with deer mice using a schedule that permits the animals' water drinking to return to baseline prior to testing for neophobia enhancement (Robbins, Note 1; also Experiment 3, below), this seems unlikely.

EXPERIMENT 3

Although the previous experiment suggested that illness can induce both learned and nonlearned taste aversions in deer mice, it did not determine whether

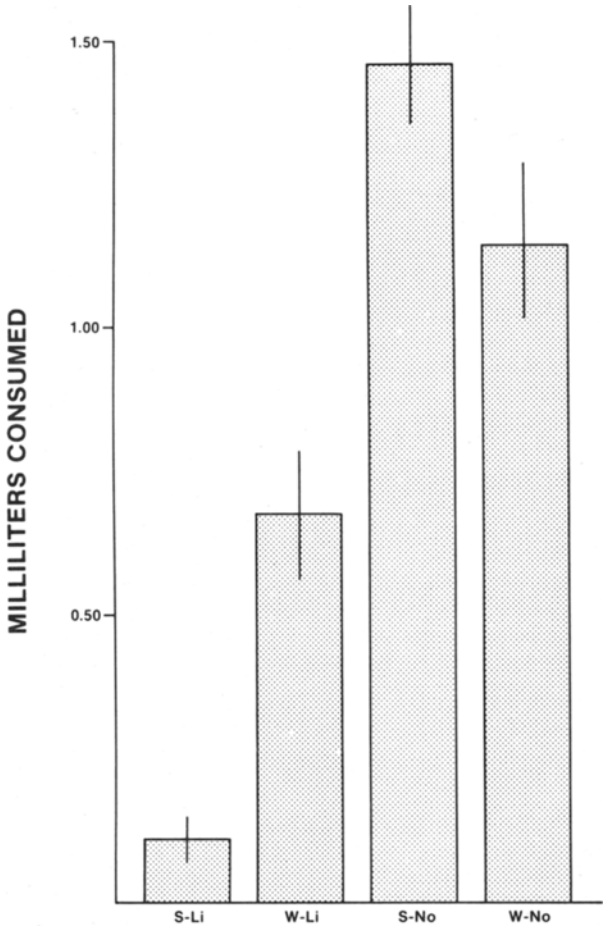

Figure 2. Mean sucrose consumption (±1 SE) on Day 11 of Experiment 2. The designations below the abscissa represent the treatments experienced by the groups on Day 9, as described in the text.

the S-Li group's acquisition of a learned aversion to sucrose would act to inhibit, facilitate, or not affect the simultaneous acquisition of enhanced neophobia to other novel flavors. This experiment addressed that issue by running a set of groups treated exactly as in the previous experiment, except that two 20-min test trials were administered, with the first trial employing a novel flavor other than sucrose. Since it is well established that learned taste aversions generalize to similarly flavored fluids (Nachman, 1963), dilute HCl was used in the first test to minimize flavor-similarity generalization.

Method

Eighty experimentally naive male and female adult *P. m. bairdi* were assigned randomly to groups and were treated exactly as were the groups in Experiment 2, except that on Day 11, the first 20-min trial following the sucrose/illness contingency, the animals were tested on a dilute HCl solution prepared as described in Experiment 1. After the 20-min test on HCl, all groups were given water for 24 h, then deprived for 24 h, and then tested on Day 13 with a 20-min exposure to sucrose solution. This extra test was to confirm the existence of greater suppression of sucrose consumption by the sucrose/lithium group in the event that this group did not show a greater suppression of HCl consumption.

Results and Discussion

Whenever animals are assigned randomly to groups, a chance arrangement may produce groups that show "significant" differences in consumption before any treatments are applied. Apparently, that occurred in this experiment, as analyses of variance found consistent, "significant" treatment effects on the water consumption trials prior to the administration of any different treatments. To eliminate any confounding of the results actually due to the treatments with this spurious effect, each animal's own baseline water consumption was used to standardize its drinking data into consumption indices defined as milliliters of fluid consumed by that animal on a given trial divided by the mean milliliters of water consumed by that animal on Days 3, 5, and 7. (Although this standardization renders these results imperfectly comparable to those of Experiments 2 and 4, the difference is not great, since performing a similar standardization on their data would, in effect, merely be dividing their means by a common constant, as in those experiments the groups did not differ on Days 3, 5, and 7.)

The results of the experiment are given in Figure 3. A day-by-day consideration of the figure follows:

Day 7 gives the mean consumption indices of 20-min water consumption on the last 20-min trial before the initiation of the treatment procedures. Analysis of variance found no differences due to treatments [$F(3,76) = 1.405$], indicating that the standardization was effective in eliminating spurious effects.

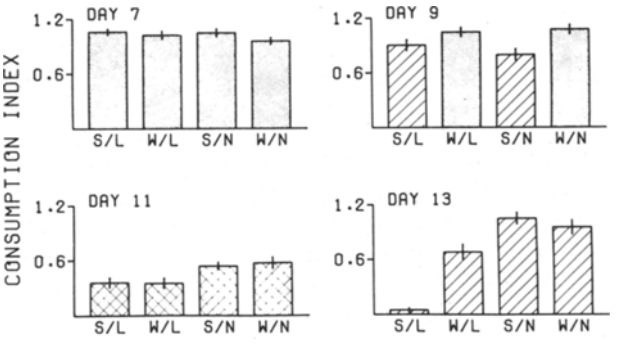

Figure 3. Mean fluid consumption (±1 SE) over four 20-min trials in Experiment 3. The stippled bars represent water consumption, the striped bars sucrose consumption, and the crosshatched bars dilute HCl consumption. Immediately after the 20-min drinking period of Day 9, Groups S/L and W/L were injected with LiCl solution and Groups S/N and W/N were handled but not injected. The means are expressed as consumption indices as defined in the text.

Day 9 gives the mean consumption indices of fluids just prior to injection. Analysis of variance shows a significant effect due to flavor [$F(3,76) = 5.539$, $p < .01$], indicating a neophobia response to the novel sucrose solution.

Day 11 gives the mean HCl consumption on the first 20-min trial after the flavor/illness contingencies of Day 9. Analysis of variance found a significant effect due to treatments [$F(3,76) = 5.026$, $p < .01$], indicating that aversions to HCl have been produced. Subsequent comparisons found that the W/L and S/L groups both differed from the noninjected groups but did not differ from each other.

Day 13 gives the mean sucrose consumption on the comparison trial. Analysis of variance found significant treatment effects [$F(3,76) = 47.547$, $p < .0001$], and subsequent comparisons found that the S/L group drank significantly less sucrose than did the W/L group, while the W/L animals drank less than the W/N group.

The lack of difference in the HCl consumption by the W/L and the S/L groups suggests that, for deer mice, the presence or absence of a learned aversion toward one novel flavor does not affect the degree of neophobia enhancement shown toward another novel flavor. This implies that the aversion to HCl shown on Day 11 reflect a true illness-induced sensitization rather than a learned aversion generalized along a novelty dimension. Although it might be suggested that the enhanced neophobia detected here and elsewhere in these experiments really represents a generalized aversion to drinking or to the texture or some other attribute of the fluids paired with illness, this is contradicted by the data of Days 12 and 13: On Day 12, the W/L group's water consumption had returned to baseline [its Day 12 water consumption did not differ from that of Day 8: $F(1,38) = .038$], yet on Day 13, Group W/L drank significantly less sucrose than did Group W/N. These results differ from those of Best and Batson (1977), who found that rats that had been made ill without having consumed a novel flavor did not show enhanced neophobia, provided their water consumption was permitted to return to baseline prior to testing.

The apparent lack of interaction between the learned aversion to sucrose and the aversion to HCl provides additional grounds for believing that the illness-induced processes of taste-aversion learning and neophobia enhancement may occur independently in deer mice. A more direct test of this independence will be provided in the next experiment.

EXPERIMENT 4

Sufficient preexposure to a flavor reduces or eliminates the single-trial formation of illness-induced aversions toward that flavor (Elkins, 1973; Fenwick, Mikulka, & Klein, 1975; Kalat & Rozin, 1973; Kiefer & Braun, 1977; Klein, Mikulka, & Hamel, 1976; Klein, Mikulka, Rochelle, & Blair, 1978; Mackay, 1974; McFarland, Kostas, & Drew, 1978; Mikulka & Klein, 1977; Robbins, 1979; Siegel, 1947; Vogel & Clody, 1972). This preexposure effect can be used to test the independence of neophobia enhancement and taste-aversion learning. For example, if the aversions to HCl and to sucrose produced by a sucrose/LiCl contingency are formed independently (and if there is no generalization between the flavors), preexposure to HCl should reduce the nonlearned aversion to HCl but should have no effect upon the acquisition of a learned aversion to sucrose. Similarly, preexposure to sucrose should affect the learned aversion to sucrose but not the nonlearned aversion to HCl.

This reasoning is equivalent to that previously employed in a study on rats (Best & Batson, 1977) in which aversions to vinegar were measured after a coffee/illness contingency.

Method

Fifty-four experimentally naive adult male and female *P. m. bairdi* were used as the subjects for this experiment. At the initiation of the experiment, the animals were housed individually in plastic laboratory cages and given water on the fluid schedule used in the previous experiments for 7 days. The animals were then assigned randomly to one of three treatment groups: Group 1 (N-P) was assigned to have no preexposure to either flavor prior to experiencing a sucrose/lithium contingency; Group 2 (H-P) was assigned to experience preexposure to dilute HCl prior to a sucrose/lithium contingency; and Group 3 (S-P) was assigned to experience preexposure to sucrose prior to a sucrose/lithium contingency. In the 24-h and 20-min trials of Days 8-16, Group 1 received only water, while Groups 2 and 3 received their assigned preexposure flavor. In the 20-min and 24-h trials of Days 17 and 18, all groups received water. On Day 19, all groups received sucrose during their 20-min drinking period, following which, all animals were injected with LiCl solution (ip, 6.0 mEq/kg of body weight). After injection, water tubes were replaced on all cages. On Day 20, the groups' 24-h water consumption was recorded. On Day 21, all groups were tested for 20 min on dilute HCl and then water tubes were placed on the cages. On Day 22, the groups' 24-h water consumption was recorded. On Day 23, all groups were tested for 20 min on sucrose. Following this, the experiment was terminated.

Noninjection controls were deliberately omitted, since the previous experiment (which employed such controls) had already demonstrated the occurrence of significant aversions both to HCl and to sucrose in animals treated similarly to those in Group 1 (N-P) above. As this experiment is intended only to measure the differing effects of the preexposure schedules upon animals receiving a sucrose/LiCl contingency, Group 1 was considered to provide an adequate standard against which the results of Groups 2 and 3 might be compared.

The flavored solutions were prepared in the same manner and in the same concentrations as in the previous experiments.

Results and Discussion

The results of this experiment (given as mean milliliters consumed) are shown in Figure 4. A day-by-day consideration of the figure follows:

Day 17 gives the mean water consumption during the last 20-min trial prior to the administration of the

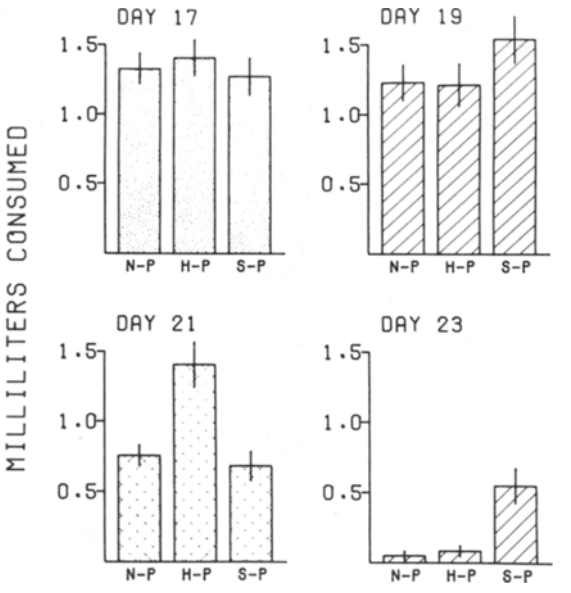

Figure 4. Mean fluid consumption (±1 SE) over four 20-min trials in Experiment 4. The stippled bars represent water consumption, the striped bars sucrose consumption and the cross-hatched bars dilute HCl consumption. Immediately following the 20-min drinking period of Day 19, all groups were injected with LiCl solution. Prior to Day 17, Group S-P had received preexposure to sucrose solution, Group H-P had received preexposure to HCl solution, and Group N-P had received no preexposure to either solution.

sucrose/lithium contingencies. Analysis of variance found no significant effect due to treatments [$F(2,51) = .297$], indicating that all groups were exhibiting equivalent baseline drinking.

Day 19 gives the mean sucrose consumption during the 20-min trial just prior to the injection of LiCl. Analysis of variance found no significant effect [$F(2,51) = 1.520$], despite the slightly greater drinking shown by the S-P group.

Day 21 gives the mean HCl consumption on the first 20-min trial following the sucrose/contingencies. Analysis of variance found significant effects due to treatments [$F(2,51) = 11.810$, $p < .0001$]. Subsequent comparisons found that Group H-P drank more than the other two groups, which did not differ from each other.

Day 23 gives the mean sucrose consumption on the final 20-min trial. Again, significant differences due to treatments were found [$F(2,51) = 13.447$, $p < .0001$]. Subsequent comparisons found that Group S-P drank more than the other two groups, which did not differ from each other.

Thus, it appears that HCl preexposure attenuated the enhanced neophobia shown toward HCl by the H-P group on Day 21, but had no effect upon that group's learned aversion to sucrose on Day 23, while the sucrose preexposure attenuated the S-P group's learned aversions to sucrose on Day 23, but had no effect upon that group's enhanced neophobia to HCl on Day 21.

These results suggest that the illness-induced processes of neophobia enhancement and taste-aversion learning are essentially independent in *Peromyscus*. This is not completely unanticipated in the rat literature, as Braveman and Jarvis (1978) have reported independence between neophobia (not enhanced neophobia) and taste-aversion learning.

The finding of independence is different from the results obtained by Best and Batson (1977), who found that rats given a coffee/illness contingency showed subsequent enhanced neophobia to vinegar, but that preexposing the rats to coffee prior to the coffee/illness contingency attenuated the vinegar aversion. From this, they concluded that the enhanced neophobia that they had detected "might best be characterized as instances of generalized aversions to the novelty of an ingestional stimulus" (p. 142). Of course, if Best and Batson's rats were generalizing from the coffee to the vinegar on a taste, not a novelty, dimension, their results would be expected and a taxon-specific difference would not be indicated.

Those authors tested for flavor generalization between coffee and vinegar by giving two nonpreexposed groups a coffee/illness contingency, then testing on vinegar, then extinguishing one group's coffee aversion, and then retesting both groups on vinegar. Finding no difference on the retest, they concluded that the animals were not generalizing on a flavor dimension. However, in their retest, both groups appeared to have lost their aversion to vinegar, as both drank as much as previously tested nonpoisoned animals (cf. Figures 3 and 4, Best & Batson, 1977, pp. 138-140). Consequently, their test for taste generalization does not appear to be conclusive, and a clear demonstration of a rat/deer-mouse difference cannot be claimed.

GENERAL DISCUSSION

Although the present results are similar to those previously reported with laboratory rats (in that illness has been found to induce learned aversions and enhanced neophobia in both species), two differences are suggested: (1) There may be a difference in the duration of enhanced neophobia in the two species. With rats, it appears that true illness-induced neophobia is a fairly short-lived phenomenon (Carroll et al., 1975; Domjan, 1977a, 1977b), with instances of illness-induced enhanced neophobia being observed several days after poisoning only in animals that experience a novel-flavor/illness contingency and then are tested on a different novel flavor while their aversion to the flavor paired with illness is presumably still intact (e.g., Best & Batson, 1977; Revusky et al., 1976). However, Experiment 3, above, found that deer

mice showed enhanced neophobia toward sucrose when tested 4 days after a water/illness contingency. Since these animals' water consumption had returned to baseline prior to the test on sucrose, it is difficult to argue that their enhanced neophobia was mediated by a learned aversion to water or to some of its attributes acquired during the water/illness pairing. (2) There may be a difference in the role of learned aversions in mediating neophobia enhancement in the animals. Best and Batson (1977) found a dependence between a learned aversion to one flavor and enhanced neophobia to another flavor, while the present studies found apparent independence between these phenomena in deer mice.

Although these differences seem fairly distinct, it would be premature to invoke the necessary involvement of taxon-specific differences, since procedural differences between the studies also exist: different flavors, drinking schedules, and doses of toxicant were employed. Of course, taxon-specific differences might be involved, and further work appears desirable. In particular, it would be interesting to determine how laboratory rats would behave if treated exactly as were the deer mice in Experiments 3 and 4 above.

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APPENDIX

Since these results have indicated the occurrence of both learning and neophobia enhancement, a determination of the relative contribution of these two processes to the aversion shown to the contingent flavor by animals poisoned after a flavor/illness pairing would be of interest. Although a quantitative analysis of this can be done, it does require that specific assumptions be made regarding the nature of the interaction between these processes. Performing the analysis under several different assumptions can provide an indication of the reliability of the relative measures obtained.

Table 1
Expected Mean Fluid Consumption During the Final Sucrose Test of the Different Treatment Groups of Experiments 2 and 3 Expressed as the Combination of the Different Factors Presumed to be Acting in Each Case

Group	Factors Contributing to Sucrose Consumption
(1) Sucrose/Lithium	M, N, ΔN_e, ΔN, L
(2) Water/Lithium	M, N, ΔN_e
(3) Sucrose/No	M, N, ΔN
(4) Water/No	M, N

Note–M = the species- and flavor-specific mean fluid consumption that would be expected in the absence of any modifying factors; N = the effect of neophobia upon novel fluid consumption during the animals' first contact with the solution (this value is presumably negative); ΔN = the change in consumption that occurs as the result of the attenuation of neophobia associated with the animals' second contact with the solution (this value is presumably positive); ΔN_e = the change in consumption (i.e., neophobia enhancement) brought about by the animals' experience of illness (this value is presumably negative); L = the change in sucrose consumption brought about through the animals' experience of a contingent pairing of illness with the ingestion of the flavor (i.e., learning) (this value is presumably negative).

To begin, the factors expected to influence the consumption of the different treatment groups must be identified (Table 1 provides this for the sucrose consumption on the test trial in Experiment 2), and then the assumptions can be made and the analysis undertaken. Three different assumptions will be considered here.

First, the processes might be mutually exclusive so that the acquisition of a learned aversion would completely block the occurrence of neophobia enhancement toward the same flavor. Quantitatively, this results in the simple assumption that all of the aversion shown toward sucrose by sucrose/LiCl animals is due to learning. While this assumption is not logically impossible, its likelihood is reduced by the demonstrated occurrence of enhanced neophobia toward other novel flavors in sucrose/LiCl animals.

Second, the processes might show simple arithmetic additivity. This assumption permits the direct calculation of unconfounded, quantitative estimates of the effects due to neophobia enhancement and to learning from appropriate comparisons among the means of the different groups. Since this is the same procedure as making linear contrasts in the analysis of variance, standard errors and significance can be attached to these estimates, as is illustrated in Table 2.

Table 2
Calculation and Determination of Significance of the Quantities ΔN_e, L, and L – ΔN_e From the Data of Experiment 2

Factors Estimated	Treatment Means and Their Multipliers: S/L .110	W/L .675	S/N 1.460	W/N 1.145	Contrast Value	Standard Error of Contrast	t(76)
ΔN_e	0	+1	0	−1	−.47	.1475	3.187*
L	+1	−1	−1	+1	−.88	.2086	4.219**
L – ΔN_e	+1	−2	−1	+2	−.41	.3298	1.243

Note–The technique of linear contrasts was used in the analysis of variance (cf. Snedecor & Cochran, 1967, p. 269). A comparison of these contrast vectors with the entries of Table 1 will verify that these contrasts do provide direct quantitative estimates of the contributions of neophobia enhancement and of learning in the acquisition of illness-induced taste aversions.
*$p < .05$ **$p < .01$

Under this assumption, the estimate of the effect due to learning is almost twice that for neophobia enhancement (although, with these data, the difference between them was not found to be significant).

Third, the process might be multiplicative, with learning and neophobia enhancement resulting in proportionate reductions of consumption. This assumption can be investigated by converting the raw data to logarithms and then performing the same manipulations as above. This analysis found that enhanced neophobia reduces consumption to 41% of baseline, while learning alone reduces consumption to 5% of baseline. Both effects are found to be significant and significantly different from each other [$F(1,76) > 5.870$, $p < .05$].

Under each of these three assumptions, the effect due to learning is greater than that due to neophobia enhancement. Although more complex assumptions might be offered that could reverse this result, anyone wishing to argue for the primacy of nonlearned effects would be obliged to formulate, then justify, those complex assumptions.

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