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Abstract

Rodents typically show conditioned aversions to substances previously associated with illness. Aversions can be observed when the tastant is presented in food, water and, for rats, when the tastant is smeared unilaterally on the animal's flank and ingested during autogrooming. Such results have important implications for rodent control. For that reason, others have investigated whether voles and mice continue to groom when tastants associated with sickness are smeared on their fur. Investigations have shown that grooming persists in the presence of the conditioned stimuli even though strong aversions are shown toward the same tastants in a drinking context. The question remains, however, whether conditioned aversions would be expressed in special situations. The present experiments clearly demonstrate that taste aversions can be observed during heterogrooming of a cagemate, but not during autogrooming of self. Such results suggest that social variables may modulate expression of conditioned taste aversions for some gregarious and/or communal species. Also, they are consistent with the notion that various species show specialized adaptive systems which may not obey conventional laws of learning.

Introduction

Rodents typically show conditioned taste aversions to substances previously associated with illness. Aversions can be demonstrated when the tastant is presented in food (Milgram, Krames & Alloway, 1977), water (Riley & Clarke, 1977) and, for rats, when the tastant is smeared unilaterally on the animal's flank and ingested while autogrooming (Reidinger & Beauchamp, submitted for publication). Taste aversions formed during grooming are robust and will transfer from the grooming context to other contexts, such as drinking. These results have important implications for rodent control and other workers have investigated whether voles (Geyer, Kornet & Reidinger, submitted for publication) and mice (Stewart, unpublished data) continue to groom when tastants are smeared on their fur. The investigations have shown that grooming does persist in the presence of conditioned stimuli even though strong aversions are shown toward the same tastants in a drinking context. Given the stereotypic quality of grooming (Fentress, 1977), such results reflect the possibility that voles (and mice) need to groom whenever a peripheral irritant is applied (Griswold, Borchelt, & Bensko, 1977; Fentress, 1977). The question remains, however, whether voles taste substances ingested from the fur while grooming, and if so, whether conditioned aversions would be expressed in some special situations.

In Experiment 1, taste aversions were induced after voles drank saccharin solution. To test whether the taste aversions affected ingestion of tastants while grooming, saccharin in CMC was placed on one flank and plain CMC on the other. In a manner analogous to a one versus two-choice drinking test, this procedure provided a more sensitive measure of tastant effects on grooming.

Method

Subjects. Ten male-female pairs of voles were used as subjects. These animals were laboratory-born from stock trapped near Beiglerville, Pennsylvania in 1972. Each pair of voles was housed and tested in a plastic shoe-box cage (27 cm long x 17 cm wide x 13 cm high). Animals were maintained under a 12/12 light-dark cycle and permitted ad lib access to alfalfa, peanuts, sunflower seeds and apple slices.

Procedure. Each pair of voles was adapted to handling and to a 14 hr water deprivation schedule. Then they were trained to drink water from a 10 ml syringe fitted with a sipper tube (Robbins, 1978). Training continued for three days. On the fourth day, the pairs of voles were separated for about two hours. One vole in each pair was selected randomly and allowed to drink 1 ml of 0.015 M sodium saccharin (.2% wt/vol in tapwater). Thirty minutes later, each of these voles was given an injection (ip) of either lithium chloride (LiCl: .51% wt/vol in distilled water) or distilled water as a control. Lithium-injected voles and their cagemates were subsequently referred to as group A while water-injected voles and their cagemates were referred to as group B. Sixty minutes after the injections, the pairs of voles in both groups were reunited in their home cages. On the next day (Day 5) and three and five days later, the injected vole in each pair was smeared with .5 ml of carboxymethylcellulose (CMC: 3.5% wt/vol in distilled water) and 0.15 M saccharin solution on one flank and .5 ml of CMC alone on the other. Counterbalancing was used to determine which side of each animal was smeared with saccharin and CMC. The cagemate of the injected vole in each pair was not smeared. Then, each pair of voles was observed for 15 minutes by two observers whose mean inter-rater reliability coefficient exceeded 0.95. Frequencies and durations of the following behaviors were scored on an Esterline-Angus event recorder for both members of each pair in both groups: (a) body washes (Bolles, 1960) of own left and right flank; (b) body washes of cagemate's left and right flank.

Results

Two-way analyses of variance (ANOVAs) and the Bonferroni post-hoc t-test (Games, 1977) were used to identify significant differences among means. While there was no difference ($p > .25$) between groups in the total amount of autogrooming and heterogrooming, the smeared injected animals in both groups groomed more than their cagemates ($F(1,19)=8.5$, $p < .05$) (See Appendix 1). While smeared injected voles in group A failed to groom one flank more than the other ($p > .25$), those in group B showed a slight but significant preference for grooming the flank smeared with saccharin ($p < .05$). Heterogrooming by cagemates of the smeared injected voles in both groups was greater in frequency and duration than autogrooming ($p < .05$) although it was not significantly differential, i.e., the saccharin-smeared flank was not pre-

ferred. There were no sex differences in autogrooming or heterogrooming on any of the test days ($p > .25$). Frequency and duration of grooming bouts were positively correlated in every instance.

Discussion

On the one hand, the results of Experiment 1 do not clearly demonstrate the existence of conditioned taste aversions during autogrooming for smeared voles injected with lithium (Group A). On the other hand, because voles given pairings of LiCl and saccharin showed no grooming preferences between the flank smeared with saccharin and the flank smeared with CMC alone while, smeared water-injected voles (Group B) did, suggest: (a) that the presence of conditioned taste aversions may have been masked by the rigid behavioral quality of autogrooming; or (b) that generalization to the grooming context was weak. Experiment 2 aimed to test these hypotheses.

Experiment 2

Introduction

Previous work (Geyer, et al., submitted for publication) and the results of Experiment 1 suggest that a vole whose partner is smeared with CMC heterogrooms more than it autogrooms. Such heterogrooming appears to be under the control of peripheral, social cues and might permit sensitive expression of conditioned taste aversion if the aversion readily generalized from the drinking to the grooming context. Experiment 2 investigated heterogrooming by voles toward cagemates after the former had been given pairings of LiCl and saccharin and the latter had been smeared with the conditioned stimulus on one flank and vehicle on the other.

Method

Subjects. Twenty-two male-female pairs of pine voles were used as subjects. The animals were experimentally naive, from the same stock as animals used in Experiment 1 and were housed and maintained as previously described.

Procedure. The procedure of Experiment 2 was identical to that of Experiment 1, except that the non-injected, rather than the injected, voles were smeared with saccharin and CMC. As before, voles injected with lithium were assigned to group A; the other injected voles were assigned to group B, and cagemates of each sort were assigned to the same group as their injected partners.

Results

Repeated measures ANOVAs and the Bonferroni procedure were used to isolate significant differences among means. As in Experiment 1, there were no differences ($p > .25$) between groups in the total amount of grooming (See Appendix 2). However, for both groups, heterogrooming (but not autogrooming) by injected voles was differential

($F(1,35)=34.8$, $p < .05$). Voles in Group A consistently groomed the flank of their partners smeared with CMC alone ($p < .05$) while voles in group B groomed the flank of their partners covered with saccharin CMC. Smeared voles groomed the flank covered with saccharin CMC regardless of whether their partners had been injected with LiCl or water ($p < .05$). Animals showed stronger preferences on some days than others ($F(3,160)=4.32$, $p < .05$), the strongest being on the second of the three test days ($p < .05$). By the third test, differential grooming by voles injected with LiCl or water had disappeared although differential behavior remained strong for the smeared uninjected voles in both groups ($p < .05$). There were no sex differences in autogrooming or heterogrooming on any of the test days ($p > .25$).

Discussion

Experiment 2 clearly demonstrated that voles will show conditioned aversions during heterogrooming towards substances smeared on a cage-mate's flanks. The positive correlations between the frequencies and durations of various grooming behaviors suggests that both measures give essentially the same information about the presence (or absence) of conditioned aversions. Together such results are consistent with the notion that heterogrooming is more controlled by situational or social cues than is autogrooming. The fact that aversions were strongest during the second preference test suggest that the animals were neophobic toward saccharin when it was first encountered during grooming.

General Discussion

Experiments 1 and 2 are consistent with previous findings that grooming is increased when substances are applied to the animal's fur. Likewise, the results are consistent with the notion that even if the substance would be rejected while feeding or drinking, autogrooming and therefore ingestion is largely unaffected (Reidinger & Beauchamp, unpublished data). However, the present studies demonstrate that heterogrooming is affected and animals reject substances smeared on the fur of conspecifics as they would if the substance was presented in water.

Grooming could offer an alternative means for presenting toxicants to pests and insuring ingestion of pharmacological amounts. The method of delivery has the advantage of not requiring animals to drink or eat poisoned water or food. The sole requirement is that the animals groom. The results of Experiment 1 provide support for the notion that ingestion of toxicants during autogrooming could be used in the control of vole populations to increase intake of otherwise avoided toxicants, perhaps administered through greased tubes (Fiedler, personal communication; Pank, personal communication) or tracking powders (Marsh, 1972). However, the finding in Experiment 2 that pine voles will show conditioned taste aversions during heterogrooming suggests that ingestion of toxicants will occur in pharmacological amounts when the animal is presented with substances on its own fur but

only in lesser amounts when one member of the colony is affected and groomed by other colony members. Thus, control of vole populations through measures similar to those used for vampire bat populations who show communal grooming is questionable (Thompson, Mitchell & Burns, 1972) and deserves further investigation.

Overall, the results of the present experiment suggest that social variables may modulate the expression of conditioned taste aversions for some social species. If so, then this is the first demonstration that social factors are important for modulating the plasticity of so-called fixed action patterns (Fentress, 1977). Moreover, the present demonstration that social factors are important for the expression of conditioned behaviors is consistent with suggestions by Rozin and Kalat (1971) and others that various species show specialized adaptive systems which may not obey the conventional laws of learning derived from typical laboratory studies of learning.

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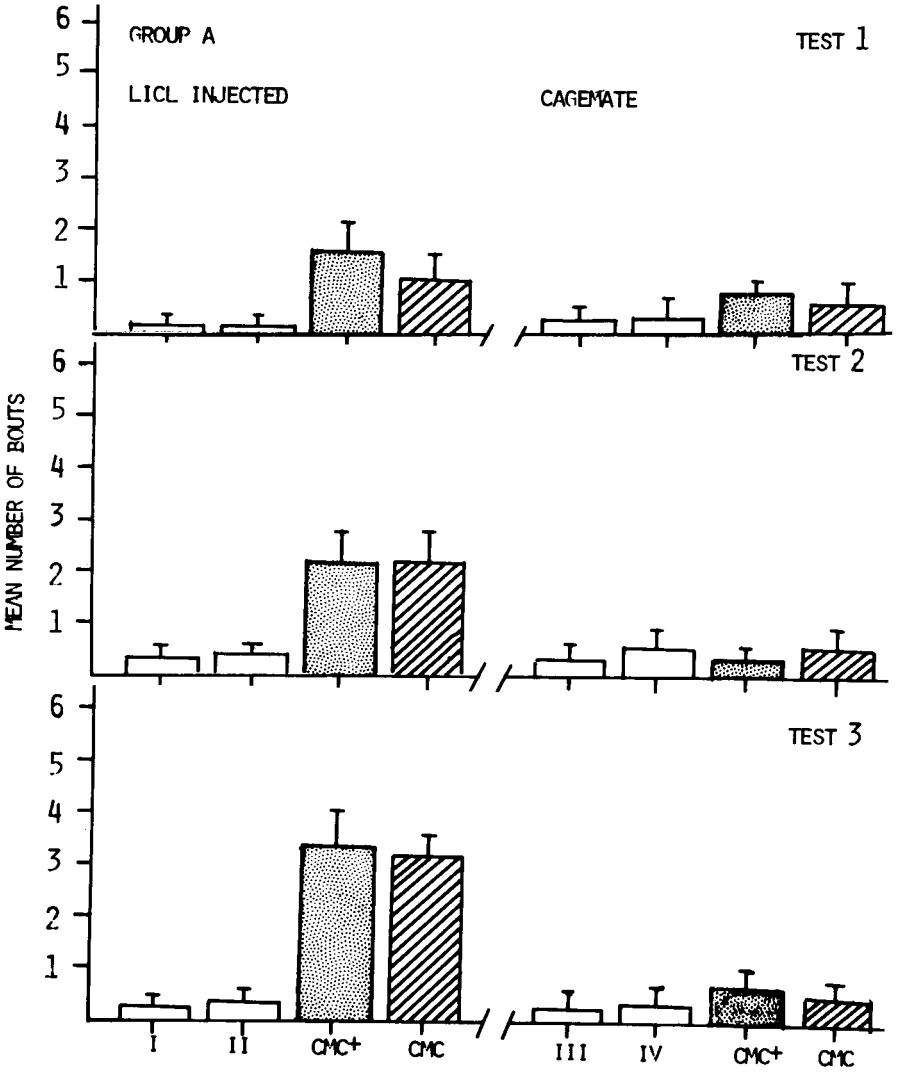
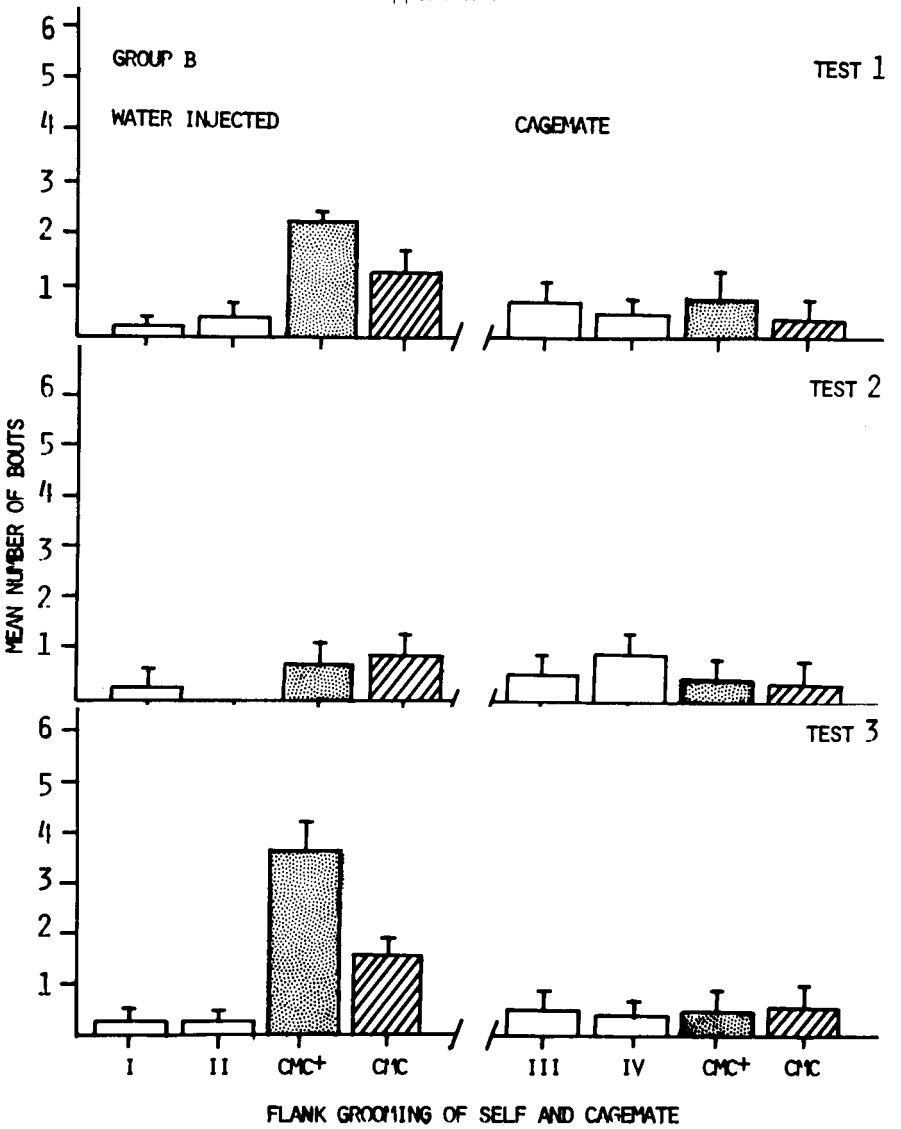
Appendix 1



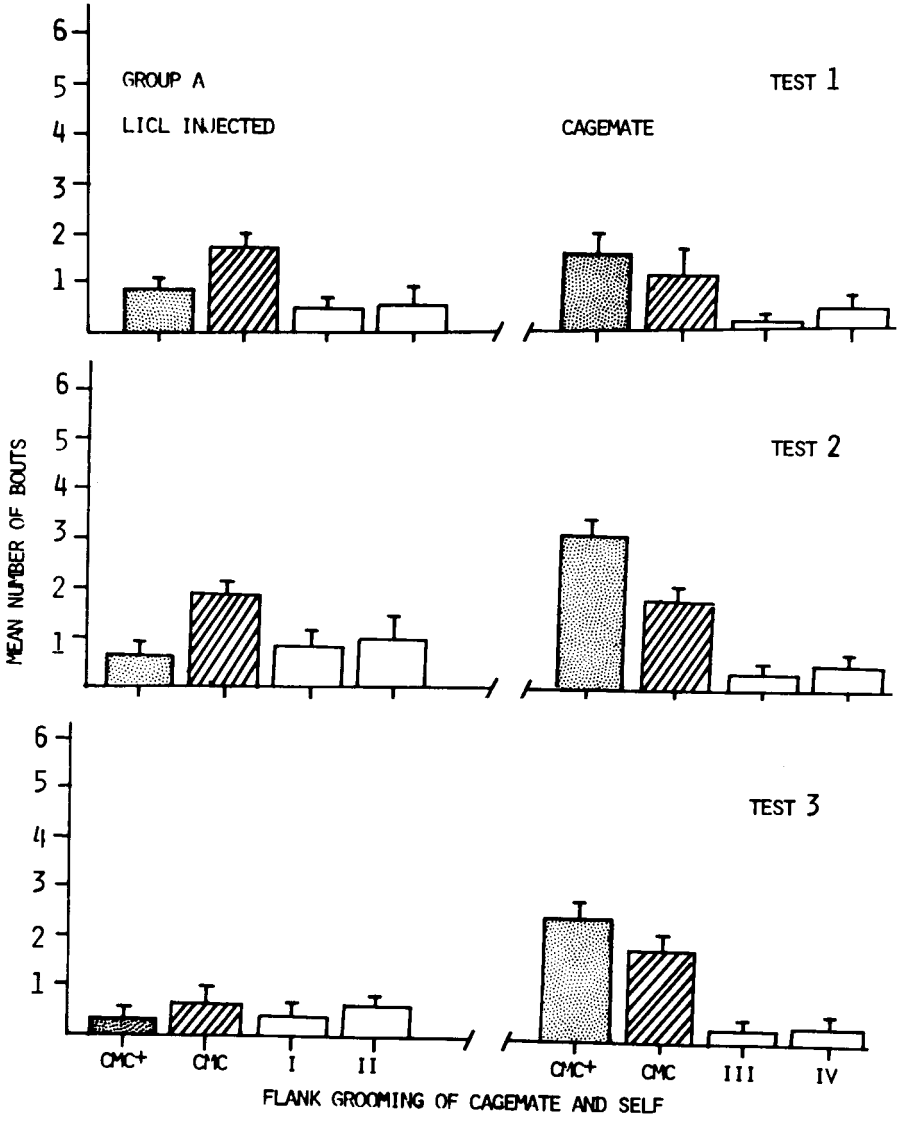
(Group A). (Left) LiCl-injected smeared voles do not show differential heterogrooming of cagemates (I,II) or autogrooming of themselves (CMC+, CMC). (Right) Cagemates of LiCl-injected voles do not show differential autogrooming (III,IV) or heterogrooming (CMC+, CMC). However, heterogrooming bouts were more frequent and for longer durations than autogrooming.

Appendix 1



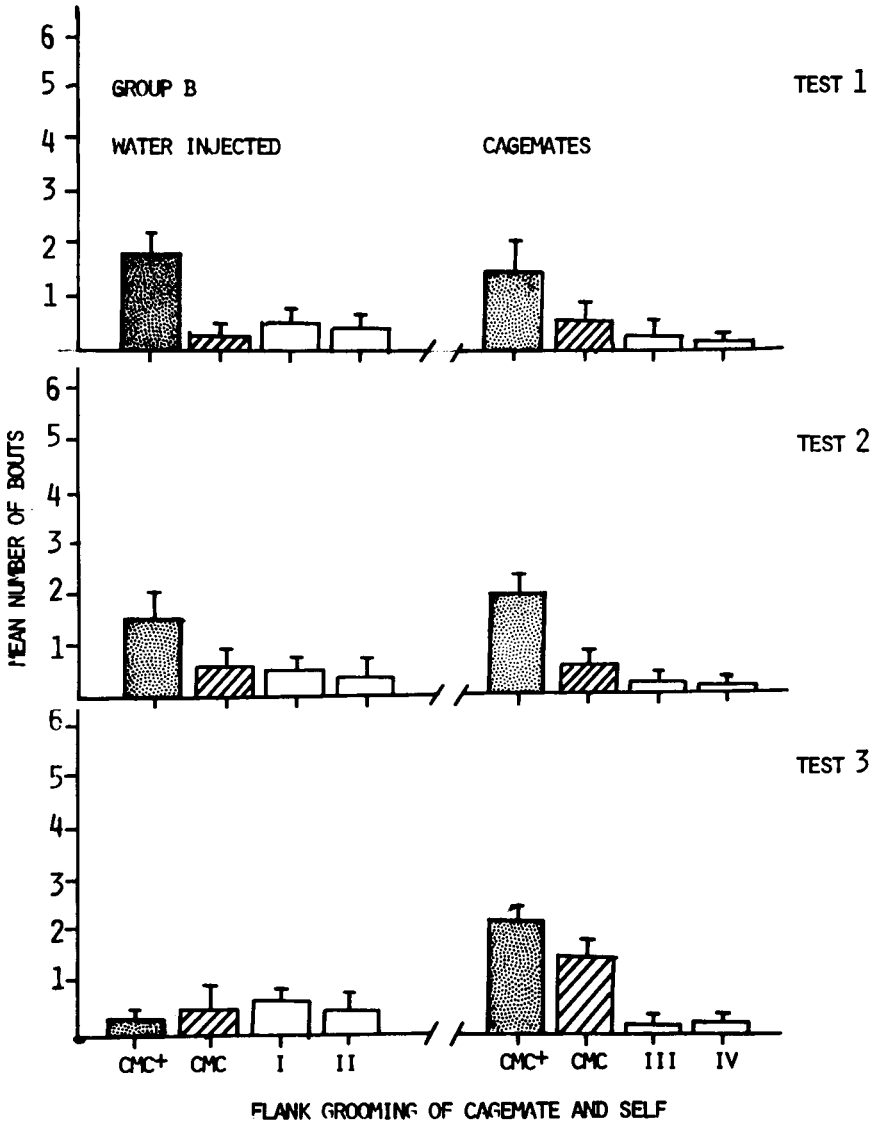
(Group B). (Left) Water-injected smeared animals do not show differential heterogrooming of cagemates (I,II) but do differentially autogroom their own flank smeared with saccharin CMC (CMC+). (Right) Cagemates of the injected smeared voles do not show differential autogrooming (III,IV) or heterogrooming (CMC+, CMC).

Appendix 2



(Group A). (Left) LiCl-injected voles show differential heterogrooming of cagemates' flanks smeared with CMC (CMC) and avoid the flank smeared with saccharin CMC (CMC+). They do not show differential autogrooming (I,II). (Right) Smeared cagemates of injected voles show differential autogrooming of the flank smeared with saccharin CMC (CMC+). They do not show differential heterogrooming of the injected voles' flanks (III,IV).

Appendix 2



(Group B). (Left) Water-injected voles heterogroom the flank of a cagemate smeared with saccharin CMC (CMC+) more than the flank smeared with CMC alone (CMC). No differential autogrooming by injected voles was observed (I,II). (Right) Non-injected smeared voles groom the saccharin CMC (CMC+) flank more than the flank smeared with CMC alone (CMC). No differential heterogrooming by these voles of the flanks of the injected voles was observed (III,IV).