

Flavor Avoidance Expressed in Grooming by Pine Voles (*Microtus Pinetorum*): Importance of Context and Hormonal Factors

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MASON, J. R., R. F. REIDINGER, JR. AND Y. KATZ. Flavor avoidance expressed in grooming by pine voles (*Microtus pinetorum*): Importance of context and hormonal factors. *PHYSIOL BEHAV* 35(6) 979-983, 1985.—Pine voles (*Microtus pinetorum*) were given sipper tubes containing saccharin solution, and after drinking, were injected with 0.15 M LiCl. Subsequently, two-sipper tests were given to assure the presence of conditioned flavor avoidance (CFA), and then animals were presented with saccharin in carboxymethyl-cellulose on their own fur (autogrooming), or on the fur of cagemates (allogrooming). CFA was expressed in two-sipper tests, and during allogrooming of material from a cagemate's fur, but not during autogrooming. Failure to express CFA during autogrooming was associated with high circulating levels of corticosterone and cortisol, steroids implicated in behavioral arousal. These results are consistent with previous work showing that rats and mice will ingest flavors while grooming that they would otherwise avoid. We speculate that our findings provide a plausible explanation for the successful use of grooming to increase the ingestion of unpalatable toxicants.

Grooming Conditioned avoidance Flavor Voles Corticosterone Rodent control

RODENTS show conditioned flavor avoidance (CFA) of substances associated with illness [24]. Avoidance is observable when the flavor is presented in food [20] or water [24], but it is not expressed in autogrooming of flavored material applied bilaterally to the flanks of rats (*Rattus norvegicus*, laboratory strain; [23]), mice (*Peromyscus leucopus*; Stewart, unpublished observation) or voles (*Microtus pinetorum*, *Microtus pennsylvanicus*, [10,11]). Robust CFA is acquired, at least by *R. norvegicus*, however, during autogrooming, and is expressed in contexts such as drinking [23].

Given the stereotypy of grooming in other contexts [1, 3, 4], one possibility is that rodents, and mammals such as vampire bats (*Desmodus rotundus*, [30]), are predisposed to groom whenever aversive materials are applied to the fur [7, 10, 13]. This possibility is consistent with evidence suggesting that expression of CFA is suppressed during the performance of relatively stereotyped, or essentially unlearned, behavioral sequences, such as sexual behavior [17], mouse-killing by rats [2], and schedule-induced polydipsia [25]. Conceivably, however, CFA might be expressed in grooming under special circumstances. The present experiment was designed to assess (1) whether CFA would be detected in autogrooming in a two-choice situation potentially

more sensitive [6] than the one-choice methods previously employed [10, 11, 23]; (2) whether CFA would be expressed in special contexts (e.g., allogrooming) if not in autogrooming; and (3) whether physiological (i.e., hormonal) correlates might exist for the suppression of CFA in the autogrooming context. For this final purpose, blood levels of various steroids were assayed. Particular attention was paid to cortisol and corticosterone, since corticosteroids have been implicated as mediating factors in CFA (e.g., [27]), and as indicators of stress in rats and mice [21].

METHOD

Subjects

Thirty experimentally naive male/female pairs of adult pine voles (*Microtus pinetorum*) were randomly selected from laboratory-born stock trapped near Beiglerville, PA in 1972. These rodents were selected for study because they are colonial [8], and because they spontaneously exhibit high levels of autogrooming and allogrooming ([10,11], personal observation). Each pair was housed and tested in a plastic cage (27 cm long × 17 cm wide × 18 cm high). Animals were maintained under a 12/12 light-dark cycle, and permitted free

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TABLE 1

MEAN DRINKING (ml \pm STANDARD ERRORS OF THE MEANS) OF SACCHARIN SOLUTION AND DISTILLED WATER BY S+ VOLES DURING TWO-SIPPER TESTS

	0.15 M Saccharin	Distilled Water
Group EXP		
S+	<u>0.5 \pm 0.2</u>	<u>1.8 \pm 0.1</u>
Group CTR-1		
S+	<u>2.2 \pm 0.2</u>	<u>1.0 \pm 0.3</u>

Significantly different means are underlined ($p < 0.05$).

access to alfalfa, peanuts, sunflower seeds, and apple slices, except as described below. Male/female pairs (rather than same sex pairs) were used to minimize the potential of serious agonistic encounters between cagemates. The gonadal state of males (i.e., scrotal or abdominal) was not examined, but none of the females became pregnant during the course of the experiment.

Procedure

The pairs of voles were randomly assigned to three groups ($n=10$ pairs/group). All groups were adapted to a daily 17 hr (1100–0800 hr) water deprivation period [10], and trained to drink from a 10 ml syringe fitted with a sipper tube [10,11]. Training continued for three days. On the fourth day, the voles in each pair were separated for about 2 hr (0800–1000 hr), and placed in clean cages without access to food.

For Group EXP, one (S+) member of each pair was selected (5 males and 5 females), and given 1 ml of aqueous 0.15 M sodium saccharin to drink. The other (S-) member of each pair was given 1 ml of distilled water. Thirty minutes later, both members were given intraperitoneal injections of aqueous 0.12 M lithium chloride (LiCl, approximately 100 mg/kg). After another 60 minutes, the pairs were reunited in their home cages, and given food and water ad lib.

Treatment of Group CTR-1 was identical to that of Group EXP, except that neither vole in any pair was injected. Ninety minutes after fluid presentations, CTR-1 voles were returned to their home cages. Group CTR-2 pairs received neither saccharin nor injections. Both members of each pair were given 1 ml of distilled water to drink, and were returned to their home cages after 90 minutes.

On the day following treatment, S+ voles in Groups EXP and CTR-1 were given two-sipper preference tests between 0.15 M saccharin in aqueous solution and distilled water to assess whether conditioning had occurred. Two days after treatment, saccharin CMC and plain CMC were applied to the flanks of S+ voles in half the Group EXP and CTR-1 pairs. S- voles in the other 5 pairs in each group received an identical treatment. The frequency and duration of allogrooming (i.e., body washes; [1, 3, 4]) by each animal of its own left and right flank, and the frequency and duration of allogrooming (i.e., body washes) of the cagemate's left and right flanks, were recorded for both members of each EXP and CTR-1 pair. Test sessions were 15 minutes in duration, and grooming bouts were scored by 2 observers whose mean inter-rater reliability exceeded 0.95. Immediately after test-

TABLE 2

MEAN FREQUENCY AND DURATION OF SACCHARIN CMC VERSUS PLAIN CMC GROOMING (\pm STANDARD ERRORS OF THE MEANS) BY EXP AND CTR-1 VOLES

	Frequency		Duration	
	Saccharin CMC	Plain CMC	Saccharin CMC	Plain CMC
	Group EXP			
S+ autogr.	0.8 \pm 0.3	1.0 \pm 0.2	7.4 \pm 0.5	9.2 \pm 0.3
S+ allogr.	<u>0.4 \pm 0.2</u>	<u>1.3 \pm 0.3</u>	10.6 \pm 4.8	17.2 \pm 2.3
S- autogr.	2.1 \pm 0.6	1.3 \pm 0.5	8.8 \pm 1.4	9.7 \pm 3.6
S- allogr.	<u>3.5 \pm 0.2</u>	<u>1.2 \pm 0.2</u>	<u>12.4 \pm 3.1</u>	<u>5.1 \pm 2.3</u>
	Group CTR-1			
S+ autogr.	1.1 \pm 0.3	1.8 \pm 0.6	7.3 \pm 0.2	8.7 \pm 1.3
S+ allogr.	<u>10.6 \pm 1.7</u>	<u>7.1 \pm 0.1</u>	<u>15.8 \pm 1.0</u>	<u>5.3 \pm 0.2</u>
S- autogr.	12.2 \pm 0.6	10.8 \pm 2.3	13.4 \pm 0.3	13.2 \pm 0.4
S- allogr.	<u>5.6 \pm 0.3</u>	<u>2.1 \pm 0.1</u>	<u>10.6 \pm 0.4</u>	<u>5.5 \pm 1.7</u>

EXP S+ voles expressed CFA in allogrooming. EXP S- voles and CTR-1 S+ and S- voles expressed saccharin preferences in allogrooming. Otherwise, there were no significant differences.

Significantly different means underlined ($p < 0.05$).

ing, all voles in both groups were decapitated and 0.5 ml of trunk blood was collected from each animal into heparinized tubes. Group CTR-2 animals were also sacrificed, and their blood collected, to provide baseline data.

Steroid Extraction and Separation

Blood samples were centrifuged (2500 \times g) for 30 minutes at 4°C and ensuing plasma aliquots were transferred into 16 \times 125 mm screw-capped, teflon lined tubes. Plasma samples were extracted once with 10 ml peroxide-free, acid-washed diethyl ether, and once with 10 ml light petroleum ether (38–56°C). The combined extracts from each sample were dried in a 50°C sand bath with a gentle stream of nitrogen, and fractionated on a 2.5 g (8 ml) Sephadex LH-20 column, eluted with a mixture of (freshly redistilled) chloroform: *n*-heptane: methanol: water, 500:500:75:3 [32]. The glass columns (8-mm i.d.; acid-washed) and polyethylene fittings (QSH Practi-Columns, Isolab, Akron, OH) were treated for 1 hr with 1% trichloromethyl silane (Aldrich Chemical Co.) in chloroform prior to packing. Material eluted from the columns was dried and taken up in 1.0 ml steroid radioimmunoassay (RIA) buffer (0.1 M Na phosphate in saline, pH 6.9, containing 0.1% gelatin and 0.01% thimerosal).

Steroid Radioimmunoassay

All determinations were done on precoded samples whose identity was unknown to the investigator involved with the analytical procedures. Aliquots of the samples in steroid RIA buffer were analyzed in specific RIA systems. The following antibodies and tritiated steroids were used: (1) rabbit antiprogestosterone-11 α -hemisuccinyl-bovine serum albumin (BSA) and [1,2,6,7-³H]progesterone, 89 Ci/mmol; (2) rabbit antiandrostenedione-7 α -carboxyethyl-thioether-BSA and [1,2,6,7-³H]androstenedione, 114 Ci/mmol; (3)

TABLE 3
MEAN STEROID LEVELS (ng/ml PLASMA \pm STANDARD ERRORS OF THE MEANS) IN BLOOD SAMPLES FROM VOLES

Steroids (ng/ml)	Group EXP Allo-CS	Group CTR-1 Allo-Contr.	Group EXP Auto-CS	Group CTR-1 Auto-Contr.	Group CTR-2 Handling Contr.
Androstenedione	0.44 \pm 0.36	0.79 \pm 0.34	1.25 \pm 0.70	1.10 \pm 0.64	0.55 \pm 0.34
Progesterone	0.78 \pm 0.18	1.60 \pm 1.50	1.13 \pm 0.33	0.98 \pm 0.22	0.60 \pm 0.08
Testosterone	1.11 \pm 0.88	1.08 \pm 0.41	1.23 \pm 1.10	0.93 \pm 0.40	0.99 \pm 0.33
5 α -dihydrotestosterone	0.66 \pm 0.52	0.53 \pm 0.36	1.53 \pm 0.45	0.60 \pm 0.22	1.43 \pm 0.58
Estrone	0.22 \pm 0.21	1.01 \pm 0.52	1.69 \pm 1.62	1.10 \pm 0.84	0.58 \pm 0.29
Corticosterone	30.70 \pm 7.30	46.00 \pm 19.50	<u>99.40 \pm 27.60</u>	39.80 \pm 13.00	36.90 \pm 9.80
Estradiol	0.02 \pm 0.01	0.01 \pm 0.01	<u>0.20 \pm 0.20</u>	0.11 \pm 0.05	0.04 \pm 0.03
Cortisol	13.90 \pm 4.50	15.10 \pm 4.60	<u>33.80 \pm 4.60</u>	13.60 \pm 7.34	18.50 \pm 5.90

One member of each EXP pair was given CFA to 0.15 M saccharin (CS). CTR-1 pairs were given a control treatment in which neither vole in any pair was injected, but one member of each was given saccharin. CTR-2 animals were given neither saccharin nor injections. Autogrooming S+ voles in Group EXP had significantly higher levels of corticosterone and cortisol ($p < 0.05$) than did any of the other voles. Otherwise, there were no significant differences.

Significantly different means are underlined ($p < 0.05$).

rabbit antitestosterone-7 α -carboxymethyl-thioether-BSA and [1,2,6,7,16,17-³H]testosterone, 150 Ci/mmol; (4) rabbit anti-5 α -dihydro testosterone-1 α -carboxyethyl-thioether-BSA and [1,2,4,5,6,7,16,17-³H] 5 α -dihydrotestosterone, 190 Ci/mmol; (5) rabbit antiestrone-6-(0-carboxymethyl)-oxime-BSA and [2,4,6,7-³H] estrone, 85 Ci/mmol; (6) rabbit anti corticosterone-21-hemisuccinyl-thyroglobulin and [1,2,6,7-³H] corticosterone, 89 Ci/mmol; (7) rabbit antiestradiol-17 β -6(0-carboxy-methyl)-oxime BSA and [2,4,6,7,16,17-³H]estradiol-17 β , 152 Ci/mmol; (8) rabbit anticortisol-21-hemisuccinyl-thyroglobulin and [1,2,6,7-³H] hydrocortisone, 93 Ci/mmol. All the antibodies were produced by Miles-Yeda. Rehovoth, Israel, except for antiestradiol, which was a gift of Dr. D. T. Armstrong, London, Ontario, Canada; the tritiated steroids were purchased from New England Nuclear, Boston, MA, or Amersham, Arlington Heights, IL, and were purified before use (on the Sephadex LH-20 columns).

Dextran-coated charcoal methodology was used to separate bound from free steroids in the RIA tubes. Centrifuged supernatants were counted for radioactivity in ACS II aqueous scintillation cocktail (Amersham, Arlington Heights, IL), using a Packard Instruments liquid scintillation spectrometer Model 2425, and were fully corrected for quenching. Data reduction was performed on a Hewlett-Packard 9815A/9721A desktop computer, using log-logit transformations. For assay validation, see Katz *et al.* [18].

Analysis

A two-way analysis of variance (ANOVA) with repeated measures on the second factor was used to assess saccharin consumption by EXP and CTR-1 S+ voles in two-sipper tests. The independent factor was groups (2 levels), while the repeated factor was saccharin versus distilled water (2 levels).

Separate three-way ANOVAs with repeated measures on one factor were used to assess flavor-directed grooming and the grooming of plain unsmeared fur. The first independent factor in each analysis was subgroup (e.g., smeared EXP S+ voles versus smeared EXP S- voles versus smeared CTR-1 S+ voles versus smeared CTR-1 S- voles). The second fac-

tor was grooming (i.e., autogrooming versus allogrooming) by the members of each subgroup. The repeated factor was either (1) grooming of saccharin CMC versus plain CMC, or (2) grooming of left or right side. Subsequently, Bonferroni post-hoc *t*-tests [9] were used to identify significant differences among means.

Analyses were performed to investigate sex differences in drinking and grooming, but no significant differences were obtained ($p > 0.25$). For this reason, the results of these analyses are not presented below.

A two-way ANOVA with repeated measures on the second factor was used to assess plasma steroid data. The independent factor in the analysis was groups (6 levels; 3 groups \times 2 animals/pair), while the repeated factor was steroids (androstenedione, progesterone, testosterone, 5 α -dihydrotestosterone, estrone, corticosterone, estradiol, cortisol). Tukey *b* post-hoc tests [31] were used to isolate significant differences among the means ($p < 0.05$).

RESULTS

Two-Sipper Tests

There were no overall differences between EXP and CTR-1 S+ voles in drinking ($p > 0.25$), or in overall consumption of saccharin versus distilled water ($p > 0.15$). However, the two-way interaction was significant, $F(1,18)=7.2$, $p < 0.001$, and Bonferroni tests revealed that EXP S+ voles consumed significantly less saccharin than distilled water ($p < 0.05$; Table 1). Conversely, CTR-1 S+ voles (exposed to saccharin but not injected) consumed relatively more saccharin ($p < 0.05$).

Grooming Tests

There were no differences in autogrooming or allogrooming in the absence of saccharin and CMC smeared on the fur ($ps > 0.25$). However, when the frequency or duration of flavor-directed grooming was examined, there were significant three-way interactions among subgroups, autogrooming versus allogrooming of stimuli, and saccharin CMC versus plain CMC ($F_s(3,32)=5.5, 4.9, ps < 0.01$, respectively). There were no other significant effects.

Post-hoc tests revealed that both EXP S+ and CTR-1 S+ voles exhibited longer bouts of allogrooming than autogrooming ($p < 0.05$; Table 2). CTR-1 S+ voles also exhibited more frequent bouts of allogrooming ($p < 0.05$). CTR-1 S- voles exhibited relatively more frequent and longer bouts of autogrooming ($p < 0.05$), while EXP S- voles exhibited no significant differences ($p > 0.10$).

When grooming of saccharin CMC versus plain CMC was examined, EXP S+ voles showed fewer and shorter bouts of allogrooming directed toward flanks smeared with saccharin CMC ($p < 0.05$). Conversely, EXP S- voles, and CTR-1 S+ and S- voles, exhibited more frequent and longer bouts of grooming directed toward the flanks of cagemates smeared with saccharin CMC ($p < 0.05$). Otherwise, there were no significant differences ($p > 0.10$).

Steroid Radioimmunoassay

There were significant differences in assayed steroid levels among groups, $F(11,48)=4.9$, $p < 0.01$ (Table 3), and post-hoc tests indicated that autogrooming EXP S+ voles had significantly higher blood levels of corticosterone and cortisol ($p < 0.05$, Table 3) than did the animals in any other subgroup. Otherwise, there were no significant differences ($p > 0.25$).

DISCUSSION

The findings of the present experiment are consistent with work demonstrating that expression of CFA is suppressed during autogrooming ([10, 11, 23], Stewart, unpublished observations). Such suppression is robust, and occurs regardless of whether material is applied bilaterally in one-choice tests as in previous work ([10, 11, 23], Stewart, unpublished observations), or unilaterally in two-choice tests as in the present experiment. The results also permit the conclusion that flavor preferences are suppressed during autogrooming. Together, these observations support the hypothesis that autogrooming, as an essentially unlearned and stereotypic behavior, is more persistent than learned behaviors such as CFA [12], and that it may even mask the expression of other essentially unlearned behaviors, such as flavor preference for saccharin. Allogrooming, in contrast to autogrooming, is less stereotypic, insofar as both CFA and flavor preferences are exhibited during its performance.

Whether or not rodents are predisposed to autogroom

aversive materials as a function of endogenous hormonal factors remains unclear. However, CFA suppression during autogrooming in the present experiment was associated with high circulating levels of cortisol and corticosterone. The latter is well-documented as an indicator of stress in rats and mice [21]. Also, several previous studies of CFA and corticosteroids have suggested that, in single-choice tests, elevated pituitary and adrenal hormone levels in rats may be due to stress-evoked conflict produced by a single-bottle design, rather than to learning, per se [14, 15, 22, 28]. We speculate that EXP S+ voles detected the aversive flavor of saccharin during autogrooming. Detection would be stressful and conflict-producing, presuming that rodents are predisposed to autogroom. If detection is stressful, then it would elicit corticosteroid production and/or release, and that, in turn, might lead to greater behavioral arousal. Because stressed rats show increased autogrooming [5], the high levels of corticosteroids may have elicited further autogrooming, and additional experience with the aversive flavor.

From the view of rodent control, the present findings have several implications. First, the results suggest that voles, like other rodents (e.g., [23]), and mammals such as vampire bats [30], will ingest materials while grooming that they would not ingest while feeding or drinking. As such, grooming appears to represent a weakness in flavor-mediated defenses against dietary poisoning, such as neophobia, unlearned food avoidance, and CFA. This weakness appears not to be due to an inability to detect a material while grooming, as suggested by high corticosteroid levels in autogrooming EXP S+ voles and CFA by allogrooming EXP S+ voles (see also [23]). Rather, the weakness appears due to a repression of CFA. As such, our findings provide a plausible explanation for the successful use of grooming behavior to increase ingestion of unpalatable toxicants, as when tracking dusts and powders are employed in rodent control [19,26].

Our findings also imply a departure from current rodent control methods that dictate that poisoned baits must be palatable to pest species (e.g., [29]). Grooming could provide one means of delivering a control compound to rodent pests regardless of the compound's palatability or potential for causing bait-shyness. We speculate that grooming in the presence of an unpalatable flavor is a robust phenomenon not sufficiently exploited with current practices in rodent control.

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