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Poison-avoidance learning to food-related tactile stimuli: Avoidance of texture cues by rats

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Rats injected with lithium chloride after ingesting familiar food pellets presented in textured metal sleeves learned aversions to the sleeved food. In a choice between sleeved and unsleeved food, the aversions were evident following conditioning with toxicosis delayed as long as 120 min after exposure to the sleeved food (Experiment 1). Texture-specific aversions resulted from procedures in which rats were exposed to food in both rough- and smooth-textured sleeves but were injected with lithium only in conjunction with one of the textures (Experiments 2-4). This differential aversion learning occurred when lithium treatment was delayed 30 min after exposure to the sleeved food (Experiments 3 and 4) and was equally evident in rats conditioned and tested in total darkness or in normal room-level illumination (Experiment 4). However, differential texture aversion learning was not observed with 90- or 300-min delayed toxicosis (Experiment 3). The present experiments highlight the importance of tactile cues in the poison-avoidance learning of species that handle their food during the course of ingestion.

The investigation of poison-avoidance learning in the laboratory typically involves giving subjects access to a novel-flavored solution in a drinking tube and then injecting them with an aversive drug (see reviews by Domjan, 1980; Logue, 1979). This procedure results in avoidance of the novel-flavored solution and is viewed as a laboratory analogue of poison-avoidance learning in natural habitats. The implication is that animals outside the laboratory learn to avoid poisonous substances by associating the taste of such substances with aversive postingestional effects. However, this account of poison-avoidance learning may not be complete, because the typical laboratory experiment does not include a prominent aspect of the usual ingestive sequence. Presenting flavored solutions in a drinking tube does not allow animals to manipulate the ingested material with their forepaws during the course of ingestion.

In many species (rats, mice, squirrels, raccoons, cats, bears, and monkeys, to cite a few), the ingestive behavior sequence involves approaching the food, handling it with the forepaws, placing it in the mouth, and chewing and swallowing it. The taste of the food is experienced only at the end of the behavior sequence, when the food is taken in the mouth. Therefore, taste-aversion learning may be considered a mechanism of "last resort" in the avoidance of poisonous foods. Research has shown that animals can also learn aversions to visual and olfactory cues that are experienced earlier in the ingestive sequence (e.g., Galef & Osborne, 1978; Rusiniak, Hankins, Garcia, & Brett, 1979). In species that handle their food with their forepaws, another prominent nongustatory cue that is experienced prior to taste involves the tactile properties of the food. A conditioned aversion to the texture of food might disrupt consummatory behavior when the food is handled with the forepaws prior to its placement in the mouth. Conventional procedures used in the study of poison-avoidance learning have not encouraged investigation of the role of food-related tactile stimuli because such tactile stimuli are not experienced when a taste solution is presented in a drinking tube.

The present experiments were conducted to determine if rats can learn to reject food paired with aversive postingestional consequences on the basis of tactile stimuli. Highly familiar food was used so that the food would not have distinctive visual, olfactory, or gustatory features. The food pellets were provided with a distinctive texture by being placed in metal sleeves that had either a rough or a smooth outer surface. The animals held the sleeves with their front paws while gnawing out the food.

EXPERIMENT 1

We designed Experiment 1 to see if rats could be conditioned to avoid eating familiar food presented in textured metal sleeves. In addition, we were interested in determining whether such aversions could be conditioned with delayed toxicosis. Numerous studies have shown that ingestional aversion learning

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with taste stimuli can occur even if the toxicosis is delayed for an hour or more following exposure to the CS flavor (e.g., Revusky & Garcia, 1970). In the present study, independent groups of rats were injected with lithium 0, 30, 60, and 120 min after access to familiar food in novel metal sleeves.

Method

Twenty-seven female and 24 male experimentally naive young adult Sprague-Dawley rats were individually housed and adapted to a 23-h daily food-deprivation schedule. The rats were weighed every 2-4 days, and any animal that weighed less than 80% of its free-feeding weight was given a food supplement consisting of 3 g of food for each percentage point below its 80% weight. All food provided was Purina Lab Chow.

The conditioned stimulus consisted of pellets of Purina Lab Chow inserted into textured metal sleeves. The sleeves were made of a hard metal alloy and were 1 mm thick and 18-20 mm long and had an inner diameter of 16 mm. The food pellets were recessed 0-4 mm inside the ends of the metal sleeves so that the rats could not break off pieces of the food without holding the metal sleeves with their forepaws. Half of the sleeves had a smooth outer surface; the others had cross-hatched (knurled) bands cut into the surface to create a rough texture. Each rat was exposed to only one type of sleeve on all conditioning and test trials.

Texture-aversion conditioning was started 27 days after the beginning of the food-deprivation schedule. On conditioning days, each rat was given access to three sleeved food pellets for 15 min in the home cage. Each rat in Group 0 (five males, five females) received a 2.0% body weight ip injection of .15 M lithium chloride within 30 sec after the sleeved pellets were removed. Rats in Group 30 (five males, five females), Group 60 (five males, five females), and Group 120 (four males, six females) were injected with the same dose of lithium 30, 60, and 120 min, respectively, after the removal of the sleeved pellets from their cages. Rats in the control group (five males, six females) received their lithium injections approximately 24 h later. During the conditioning trials, five rats each in the 0, 30, 60, 120, and control groups were exposed to the rough-textured metal sleeves and the remaining rats were exposed to the smooth-textured sleeves.

Three conditioning trials were conducted with an intertrial interval of 3-4 days. On days between lithium injections, the animals were given their daily 1 h of access to food. When a rat weighed less than 80% of its free-feeding weight, the 1-h maintenance feeding was followed by the food supplement, as described above. On days when lithium injections were given, the 1-h maintenance food was omitted; however, the rats received the food supplement when necessary.

Six to 8 days after the last conditioning trial, the animals were given a choice test between food pellets in CS-textured metal sleeves and pellets presented without sleeves. Three sleeved and three unsleeved pellets were weighed and placed in each rat's home cage for 30 min following 23-24-h food deprivation. During the first 9 min, the rats were individually observed, and the amount of time they spent holding (touching with both front paws or with the mouth) each type of pellet was measured. At the end of the test session, the pellets were removed and weighed to obtain measures of the amount of each type of food that was eaten. (The intake measures were not corrected for spillage because the spillage from sleeved and unsleeved pellets could not be distinguished.)

Results

Preference for the sleeved food during the postconditioning test was measured in terms of both amount ingested and time spent holding the two types of food. An intake preference score was calculated for each rat by dividing the amount of sleeved food ingested by the total amount of food ingested during the 30-min test session and multiplying this ratio by 100. A time-holding preference score was calculated for each rat by dividing the amount of time spent holding the sleeved food by the total amount of time spent holding both types of food and multiplying this ratio by 100. The mean intake and time-holding preference measures are shown in Figure 1 for each group. The lowest preferences were evident in groups that were injected with lithium within 60 min after exposure to the sleeved food pellets during the conditioning trials. These rats evidenced close to zero preference for the sleeved food in terms of both response measures. Higher preferences were observed among rats in the 120-min delay and control groups. However, even the control group preferred the sleeved food far less than 50% in terms of both the intake and time-holding measures.

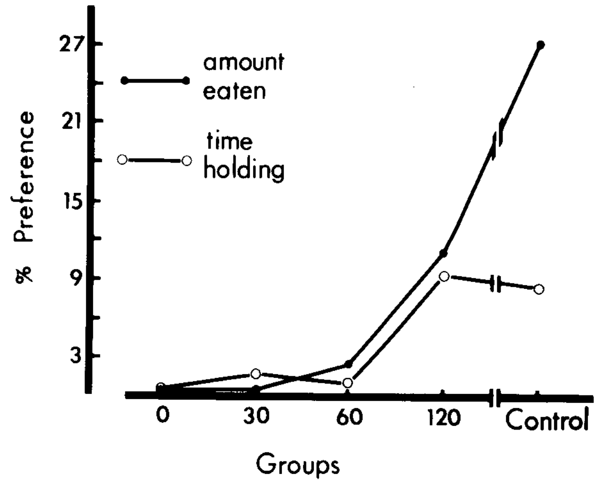

Figure 1. Mean percent preference (in terms of amount eaten and time-holding measures) for sleeved food pellets in a choice between sleeved and unsleeved food following conditioning with 0-, 30-, 60-, and 120-min delayed toxicosis in Experiment 1. (The control group had received toxicosis unpaired with access to sleeved food.)

A one-way analysis of variance of the intake preference scores indicated significant differences among the five groups [$F(4,46) = 12.93$, $p < .01$]. Subsequent comparisons with the Dunnett test ($p < .01$, two-tailed) showed that each of Groups 0, 30, 60, and 120 had significantly lower intake preference scores than did the control group. A one-way analysis of variance computed on the time-holding preference scores was not statistically significant [$F(4,46) = 1.62$, $p > .10$].

Discussion

The results of Experiment 1 demonstrate that rats can learn aversions to ingesting familiar food from textured metal sleeves. Furthermore, such learning can occur even if the aversive effects of ingestion are delayed for 120 min or more. In this respect, the present example of aversion learning to food in metal sleeves is similar to more common examples of taste-aversion learning.

Conditioned aversions to food in the metal sleeves were evident in a measure of preference for ingesting sleeved food rather than unsleeved food. However, measures of preference for holding the sleeved rather than unsleeved food did not provide evidence for aversion learning. This might have been due to a "floor effect," because even the control group had a mean preference of less than 10% for holding the sleeved food. Evidently, subjects were much less likely to maintain contact with the sleeved food than with the unsleeved food whether or not they received aversion conditioning.

The postconditioning test conducted in the present study involved a choice between sleeved and unsleeved food pellets. In other experiments, we tested rats with a choice between food in smooth- and rough-textured sleeves following the same type of conditioning that was used in Experiment 1. These studies indicated that conditioning procedures that do not involve a discrimination between smooth- and rough-textured metal sleeves do not result in texture-specific aversions. Following nondifferential conditioning, rats given a choice between smooth- and rough-textured metal sleeves evidenced comparable suppression of intake from both types of sleeves.

EXPERIMENT 2

Although subjects in Experiment 1 acquired an aversion to ingesting food from the metal sleeves, the procedures of Experiment 1 do not permit unambiguous interpretation of the cues that controlled the aversion behavior. The rats held the metal sleeves with their forepaws and gnawed out the food. In the process, they no doubt experienced the tactile features of the sleeves. However, they also may have tasted the metal. Therefore, conditioning may have occurred to the tactile, gustatory, or both aspects of the metal sleeves. Possible taste mediation of the conditioned aversions was minimized in Experiment 2. Experiment 2 was designed to see if rats could learn a discriminative aversion to food in smooth- vs. rough-textured metal sleeves. A discriminative aversion between the two metal sleeve textures cannot be mediated by gustatory or olfactory stimuli because the two types of sleeves were made of the same material.

Method

Fourteen experimentally naive male Sprague-Dawley rats were individually housed and adapted to a 23-h daily food deprivation schedule. The rats were weighed every 2-3 days throughout the experiment, and any animal that weighed less than 80% of its ad-lib weight was given a food supplement, as in Experiment 1.

Starting 19 days after the beginning of the food-deprivation schedule, the rats received differential aversion conditioning to the rough- and smooth-textured metal sleeves. On some days (+), three sleeved pellets of one texture were presented for 30 min. Ten minutes after the pellets were placed in the cages, the rats were briefly removed and received 2% body weight ip injections of .15 M lithium chloride. On these CS+ conditioning days, the animals were not given their daily maintenance access to food, but any rat that weighed less than 80% of its ad-lib weight was given the food supplement 1-2 h after the conditioning trial. On other days (−), the other type of sleeved food was presented in an identical procedure, except that no injections were administered. Following each CS− trial, the subjects received their daily 1-h maintenance access to food, and no food supplements were given. On yet other days (N), the subjects received only their daily 1-h food ration. Successive days of the experiment consisted of the following treatments: −+N−−N−+NN−−+N−−−−. For six rats, the rough-textured sleeves were used as the CS+ and smooth-textured sleeves were used as the CS−. For the remaining eight rats, the stimulus assignments were reversed. The food pellets protruded 6-9 mm from one end of the metal sleeves in this phase of the experiment. One to 2 days after the last CS− trial, the animals were given a choice between eating food from the CS+ and CS− sleeves. Three sleeved pellets of each type were placed in the cages for 30 min. Immediately following the test, the daily 1-h access to regular Lab Chow was provided, without a food supplement.

The first test session revealed only a weak discriminative aversion to eating food from the CS+ metal sleeves. Therefore, additional training was conducted with food pellets that were recessed 0-4 mm inside the metal sleeves to insure more extensive handling of the sleeves during the course of ingestion. The three treatments (+, −, and N) were administered in the following order: N−+NN−−. One to 2 days after the last CS− trial, the rats received a second 30-min choice test between food in the CS+ and CS− sleeves. The short food pellets were used during this test session.

Results and Discussion

The amount of time the rats were observed holding the CS+ and CS− sleeved pellets during the first 9 min of each choice test is presented in the top panel of Figure 2. The amount ingested from each type of sleeved food is shown in the bottom panel of Figure 2. During both test sessions, the rats spent less time holding the CS+ than the CS− sleeves and ate less from the CS+ sleeves than from the CS− sleeves. However, a greater differential response to the CS+ and CS− stimuli occurred during Test 2 than during Test 1.

Choice between the two types of sleeved food during the test sessions was evaluated as a ratio of the response to the CS+ stimulus divided by the sum of the response to both the CS+ and the CS− stimuli. This ratio has a value of .50 if the rats do not favor one stimulus over the other, and aversions to the CS+ are evidenced by values below .50. The mean ratio of the amount of time spent in contact with the two types of food during Test 1 was not significantly below .50 [mean = .391, $t(13) = 1.26$, $p > .20$]. However, a significant aversion to the CS+ sleeved pellets was evident in the ratio of amount ingested from each type of sleeve during Test 1 [mean = .332, $t(13) = 2.49$, $p < .05$]. During Test 2, both the time-holding and amount-ingested ratio scores were significantly below .50. The mean time-holding ratio score during Test 2 was .120 [$t(13) = 13.96$, $p < .01$], and the mean intake ratio score was .196 [$t(13) = 5.96$, $p < .01$].

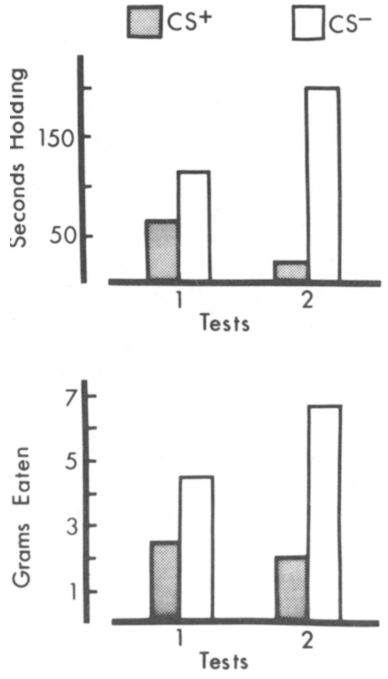

Figure 2. Mean amount of time rats spent holding food pellets in CS+ and CS− textured sleeves (top panel) and the mean amount they ate from each type of sleeved food (bottom panel) during Tests 1 and 2 of Experiment 2. (Discrimination training was continued between Tests 1 and 2.)

The present results indicate that rats are able to learn strong differential aversions to familiar food in smooth- vs. rough-textured sleeves. Because the CS+ and CS− sleeves were made of the same material and differed only in texture, the differential aversions observed could not have been mediated by gustatory stimuli. The present findings are consistent with the idea that rats are able to use differential tactile cues in avoiding foods that are followed by aversive postingestional consequences.

EXPERIMENT 3

In the differential conditioning procedure used in Experiment 2, rats received access to food in the CS+ sleeves for 30 min and were injected with lithium 10 min after the start of this stimulus exposure. Thus, the procedure did not involve a substantial delay between access to the CS+ sleeved food and lithium treatment. Experiment 3 was conducted to determine whether rats are able to learn differential aversions to familiar food in textured sleeves with delayed toxicosis. Independent groups received differential conditioning in which lithium treatment was delayed 30, 90, or 300 min after exposure to familiar food in the CS+ metal sleeves.

Method

Thirty-seven experimentally naive female rats were individually housed and adapted to a 23-h daily food-deprivation schedule. The rats were weighed every 2-4 days throughout the experiment, and any animal that weighed less than 80% of its free-feeding weight was given a food supplement, as in Experiment 1. Starting 25 days after the beginning of the food-deprivation procedure, the rats received food in rough- and smooth-textured sleeves. As in Experiment 1, short food pellets that did not protrude from the metal sleeves were used, forcing the rats to handle the sleeves extensively during the course of ingestion. On CS+ days, three food pellets in the CS+ sleeves were placed in each rat's cage for 15 min. Groups 30 (n = 13), 90 (n = 12), and 300 (n = 12) were injected with 3.0 meq/kg .15 M lithium chloride 30, 90, and 300 min after the end of the 15-min exposure, respectively. No other food was provided on CS+ days. On CS− days, three food pellets in the CS− sleeves were provided for 30 min. After this exposure, the rats received their daily 1-h access to unsleeved food pellets, followed by a food supplement when necessary. No injections were administered on CS− days. The sequence of treatment days was as follows: −+−−−+−−−+−−−. Rough-textured sleeves were used as the CS+ and smooth sleeves were used as the CS− for seven rats in Group 30 and six rats in each of Groups 90 and 300. The reverse stimulus assignments were made for the remaining six rats in each group.

One to 4 days after the last CS− trial, the animals were given a choice test in which three food pellets in rough sleeves and three food pellets in smooth sleeves were presented for 30 min. Further conditioning was conducted starting 3-6 days later. In addition to the CS+ and CS− days, on some days subjects received no special treatment (N) during this phase of the experiment. The order of treatments was −+−−−NNN+−−−. Starting 3-6 days after the end of the additional training, the animals received two choice tests with food pellets in the CS+ and CS− sleeves. These tests were conducted as was Test 1, with a 4-6 day interval between them.

Results

The amount of time rats spent holding the CS+ and CS− sleeved pellets during the first 9 min of the postconditioning choice tests is presented in Figure 3, and the amount of each type of sleeved food they ingested is presented in Figure 4. Groups 90 and 300 responded similarly to food in the CS+ and CS− metal sleeves during each test session. For these rats, a strong differential response to the two types of sleeved food was not evident in terms of either the time spent holding the two types of sleeved food or the amount of each type of food ingested. Only Group 30, which received a 30-min delay between exposure to food in the CS+ sleeves and subsequent lithium injections, showed an aversion to the CS+ sleeved food.

As in the previous experiments, choice between the two types of food was evaluated in terms of the ratio of the response to the CS+ stimulus divided by the sum of the response to both the CS+ and the CS− stimuli. The intake and time-holding ratio scores for each of Groups 90 and 300 were not significantly different from .50 on any test day [all $ts(11) < 2.00$, $ps > .05$]. Thus, no significant differential aversions to the CS+ sleeved pellets were observed in these two groups. In contrast, both the time-holding and intake ratio scores for Group 30 were significantly below .50 for both Test 1 and Test 2 [$ts(12) > 2.36$, $ps < .05$]. However this differential aversion to the CS+ sleeved food was extinguished by Test 3 [$ts(12) < 1.71$, $p > .05$].

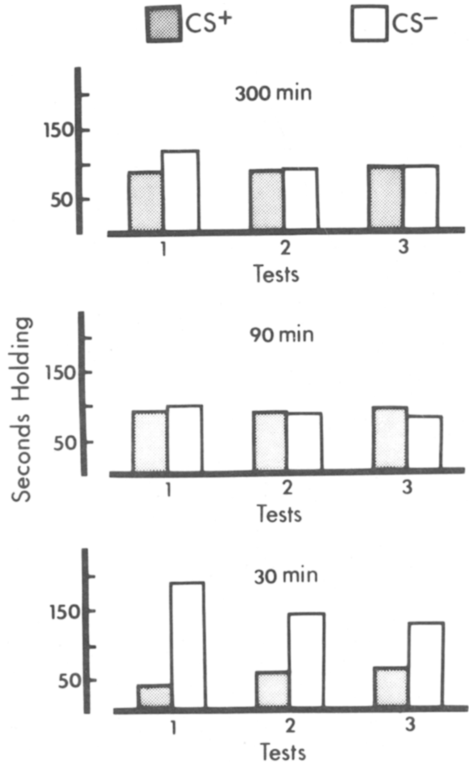

Figure 3. Mean amount of time rats spent holding food pellets in CS+ and CS− textured sleeves in Experiment 3 following discrimination training in which toxicosis was delayed 300 min (top panel), 90 min (middle panel), and 30 min (bottom panel) following access to CS+ sleeved food. (Discrimination training was continued between Tests 1 and 2.)

In addition to the preference measures, the total food intakes of Groups 30, 90, and 300 (corrected for spillage) were evaluated for each test day with one-way analyses of variance. No significant group differences in total food intake were found for any of the three test sessions [$Fs(2,34) < 1.57$, $ps > .10$]. Thus, the differential aversion learning evident in Group 30 was not accompanied by a suppression of total food intake in this group in comparison with subjects that were conditioned with longer delay intervals.

Discussion

The present results indicate that rats are able to learn discriminative aversions to the texture of metal sleeves with delayed toxicosis. However, the learning of a discrimination between smooth- and rough-textured sleeves required shorter CS-US intervals during conditioning than the learning of a discrimination between sleeved and unsleeved food. In Experiment 1, discrimination learning between sleeved and unsleeved food occurred with a 120-min delay between exposure to the sleeved food and subsequent lithium injection. In contrast, in the present study discriminative aversions to rough- vs. smooth-textured sleeves did not occur if the lithium treatment was delayed 90 min or more after exposure to the CS+ texture. Learning was evident only with 30-min delayed toxicosis during the conditioning trials.

The discrimination training procedure used in Experiments 2 and 3 (as well as in Experiment 4) involved less exposure to the CS+ than to the CS− texture prior to the test sessions. The fact that Groups 90 and 300 did not show a differential response to the two textures indicates that the relative novelty of the CS+ was not sufficient to produce aversions to it. The fact that Groups 90 and 300 did not acquire an aversion to the CS+ texture also indicates that prior lithium treatments did not invariably produce an aversion. Therefore, the aversions observed in Group 30 no doubt reflect an association between the CS+ texture and the delayed lithium treatments.

EXPERIMENT 4

Experiments 2 and 3 demonstrated that rats can acquire discriminative aversions to the specific texture of sleeves holding familiar food. Such dif-

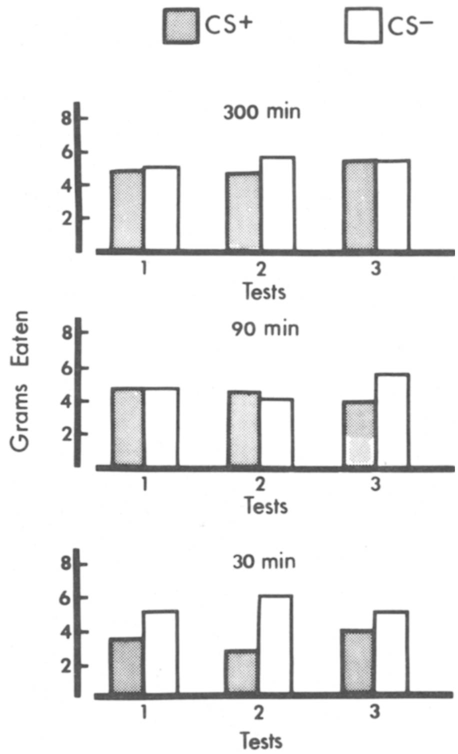

Figure 4. Mean amount ingested from food pellets in CS+ and CS− textured sleeves in Experiment 3 following discrimination training in which toxicosis was delayed 300 min (top panel), 90 min (middle panel), and 30 min (bottom panel) following access to CS+ sleeved food. (Discrimination training was continued between Tests 1 and 2.)

ferential aversions could not have occurred if the animals were responding on the basis of the taste of the metal sleeves, because the CS+ and CS− stimuli were made of the same material. Experiment 4 was designed to evaluate the possible contribution of visual cues to the discriminative aversion learning. All of the preceding experiments were conducted in normal room-level illumination. In Experiment 4, independent groups received discriminative aversion conditioning with delayed toxicosis in normal room-level illumination and in total darkness.

Method

The procedure was similar to that of Experiment 3 in all unspecified respects. Fourteen female and 13 male rats were used. Twenty-four days after the start of the food-deprivation schedule, each rat was assigned to one of two groups. Rats in Group Dark (7 females, 6 males) were transferred to a light-sealed room in which the overhead lights were on from 1:00 p.m. to 1:00 a.m. each day. Rats in Group Light remained in the original colony room, where the overhead lights were on from 8:00 a.m. to 8:00 p.m. daily. All rats received food in the middle of the morning each day. Therefore, rats in Group Dark were fed in the dark and rats in Group Light were fed when the overhead lights were on.

Starting 42 days after the initiation of the food-deprivation schedule, each day's procedure consisted of a CS+ trial (+), a CS− trial (−), or no special treatment (N). The three procedures were administered in the following order: −N−+NN−−−+−NN−−+−−NN−. On CS+ days, the animals received access to three food pellets in the CS+ metal sleeves for 15 min. Thirty minutes after the end of this stimulus exposure, each rat was injected with 3.0 meq/kg .15 M lithium chloride. On CS− days, animals received access to three food pellets in the CS− metal sleeves for 30 min and no injections were administered. Rough-textured sleeves were used as the CS+ and smooth sleeves were the CS− for six rats in Group Dark and seven rats in Group Light. Smooth sleeves were the CS+ and rough sleeves were the CS− for the remaining seven rats in each group. The two groups differed primarily in that all food and conditioned stimulus presentations took place in the presence of overhead illumination for Group Light and in total darkness for Group Dark. (The experimenter had practiced performing the procedures in total darkness before the beginning of the conditioning trials, using a system of tactile guides. A small red light was used for partial illumination when the lithium injections were given 30 min after the end of the stimulus presentations.)

One to 2 days after the last CS− trial, the rats were given a choice of eating food from the CS+ and CS− sleeves. A second, identical choice test was conducted 2 days later. Four to 5 days after this second test, each rat received three CS+ sleeved pellets for 30 min during the daily feeding period to promote extinction of the aversion to the CS+ stimulus. No CS− sleeved pellets or unsleeved pellets were provided during this session. [Data from the single-stimulus CS+ session are not presented because 16 of the 27 rats ran out of food before the end of the 30-min session. The number of rats that ate all of the food provided was not significantly different in the two groups ($\chi^2 = 2.98$, $p > .05$)]. One to 2 days after the single-stimulus test, a third choice test was conducted in the same way as the initial choice tests. On test days, the rats did not receive additional food; between test days, access to food was provided for 1 h each day, followed by a food supplement, as required by each rat's weight. All testing was conducted with overhead illumination for Group Light and in total darkness for Group Dark.

Results

Because all conditioning and test trials were conducted in total darkness for one group, measures of the amount of time rats spent holding each type of sleeved food were not obtained. The amount of food each group ingested from the CS+ and CS− sleeves is presented in Figure 5 for each of the three postconditioning choice tests. During each test session, the mean intake from the CS+ metal sleeves was less than intake from the CS− sleeves for both Group Light and Group Dark. As in the previous experiments, choice between the two types of sleeved food was measured in terms of the ratio of food ingested from the CS+ sleeves divided by the total amount of food ingested from both types of sleeves. These intake ratios were not significantly different for Groups Light and Dark during any of the three test sessions [$ts(25) < 1.00$, $p > .50$]. Because the two groups did not differ in terms of their preference for the CS+ vs. CS− sleeved food, the ratio scores for the two groups were combined for each choice test and compared with .50 to determine whether the animals acquired a significant aversion to the CS+ texture. The ratio scores were significantly below .50 for both Test 1 and Test 2 [$ts(26) = 3.00$ and 2.53, respectively, $ps < .05$]. However, the aversions were extinguished by Test 3 [$t(26) = 1.84$, $p > .05$].

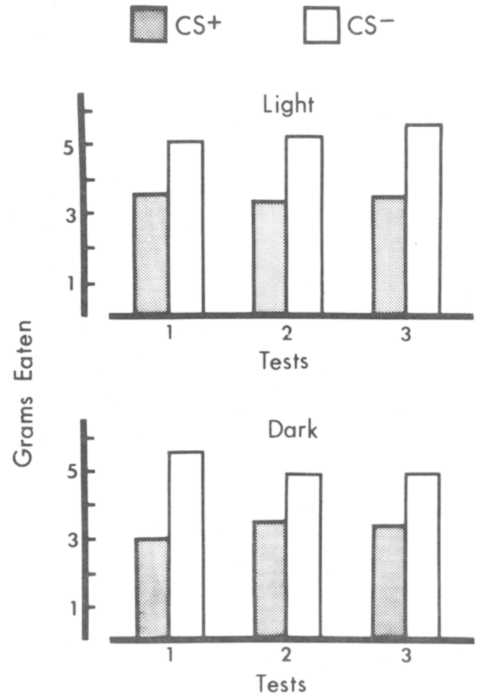

Figure 5. Mean amount ingested from food pellets in CS+ and CS− textured sleeves during choice Tests 1-3 in Experiment 4. Discrimination training and test sessions were conducted in normal illumination for Group Light (top panel) and in total darkness for Group Dark (bottom panel).

Discussion

The present findings confirm that rats can learn discriminative aversions to the texture of metal sleeves containing food and that such aversion learning is possible with toxicosis delayed at least 30 min after exposure to the CS+ stimulus. The present results also indicate that comparable discriminative learning occurs whether or not animals are conditioned and tested with overhead illumination. The absence of a difference between Groups Light and Dark demonstrates that visual cues are not necessary for the discriminative aversion learning. In addition, the comparable performance of the two groups provides further evidence consistent with the interpretation that tactile stimuli form the basis for the discriminative response to the two types of textured food sleeves.

GENERAL DISCUSSION

The present experiments demonstrate that rats are able to learn aversions to familiar food pellets presented in metal sleeves. In a choice test between sleeved and unsleeved food, the aversion learning was evident following conditioning with toxicosis delayed as long as 120 min after exposure to the sleeved food (Experiment 1). Texture-specific aversions resulted from procedures in which subjects were exposed to food in both rough- and smooth-textured sleeves but were injected with lithium only in conjunction with one of the textures (Experiments 2-4). This differential aversion learning occurred when lithium treatment was delayed 30 min after exposure to the sleeved food but not if toxicosis was delayed 90 min or more (Experiment 3). The texture-specific aversions conditioned with 30-min delayed toxicosis were equally evident in rats conditioned and tested in total darkness and rats conditioned and tested in normal room-level illumination (Experiment 4).

It is unlikely that the aversions observed in the present experiments were based on the taste or odor of the food provided. The food (Purina Lab Chow) was the only type of solid food the subjects had received prior to and during the experiment and was therefore highly familiar. Numerous studies have shown that taste-aversion learning is less likely with familiar than with novel flavored substances (e.g., Domjan, 1972; Revusky & Bedarf, 1967). In addition, all of the postconditioning tests involved a choice between pellets presented in one of two forms (sleeved or unsleeved, or in smooth- vs. rough-textured sleeves) that did not involve a modification of the food's taste. Therefore, a differential response could not have occurred because of an aversion to the taste of the food. The taste (or odor) of the metal sleeves may have had some role in the aversions observed in Experiment 1 because here the postconditioning test involved a choice between sleeved and unsleeved food. However, the texture-specific aversions observed in Experiments 2-4 cannot be explained in this way. The texture-specific aversions also cannot be explained by appeal to the visual features of the rough and smooth sleeves because the aversions were not attenuated when the subjects were conditioned and tested in total darkness. These considerations strongly support the conclusion that the rats learned an aversion to the tactile properties of the sleeved food pellets. Aversion learning to the texture of food was also entertained in a report by Martin and Lawrence (1979). However, the evidence they presented was much more indirect and might have been confounded with extinction and taste-aversion learning effects.

The present demonstration of texture-aversion learning increases the range of stimuli that have been successfully conditioned with poisoning. Studies comparing conditioning motivated by toxicosis and electric shock have emphasized that taste stimuli are selectively associated with toxicosis (e.g., Domjan & Wilson, 1972; Garcia & Koelling, 1966; Gemberling & Domjan, 1982; Miller & Domjan, 1981). However, this selective association of taste with toxicosis does not preclude the learning of aversions to other types of cues as well. Toxicosis-induced aversion learning in rats has been demonstrated with spatial, environmental cues (e.g., Krane, 1980), visual stimuli (Braveman, 1977; Galef & Osborne, 1978), olfactory stimuli (e.g., Rusiniak et al., 1979), the temperature of water (Nachman, 1970), cues of drinking from a cup (Revusky & Parker, 1976), and cues of drinking from spouts with large or small openings (Nachman, Rauschenberger, & Ashe, 1977).

The fact that rats are able to learn aversions to a variety of stimuli conditioned with toxicosis does not necessarily imply that all of these acquired aversions have the same role in poison-avoidance behavior. Ingestive behavior involves exposure to a variety of stimuli in a specific sequence. Ingestion takes place in a particular location, with the spatial and environmental cues of that location being experienced first. The rat then approaches the food and may be exposed to its visual and olfactory features. The food may then be manipulated by the front paws, providing tactile sensations. Finally, the food is taken in the mouth and provides orosensory tactile stimulation and gustatory sensations. Aversion learning to cues experienced at different stages may serve to interrupt the ingestive behavior sequence at different points. The present results demonstrate that tactile cues experienced during handling of the food prior to its placement in the mouth can become associated with delayed toxicosis and suppress subsequent handling and ingestion of the food.

The fact that tactile stimuli experienced 30 min or more prior to toxicosis can become conditioned presents a strong challenge to theories of long-delay learning. Such theories may be considered in two classes. Because most demonstrations of long-delay learning have employed taste stimuli, some theories have focused on special properties of gustatory stimulation in explaining long-delay learning (e.g., Krane & Wagner, 1975). Other theories have emphasized the importance of the absence of other conditionable stimuli during the delay interval (e.g., Revusky, 1977). (In the typical long-delay conditioning experiment, the conditioned stimulus flavor is the only gustatory cue explicitly presented prior to toxicosis.) Neither of these approaches predicts long-delay tactile aversion learning.

One particularly provocative aspect of the present experimental method was that no effort was made to limit the tactile experiences of subjects during the interval between exposure to the sleeved food pellets and subsequent delayed toxicosis. The rats no doubt experienced various tactile stimuli during the delay interval, including sensations provided by the cage walls and floor and sensations experienced during rearing and scratching. It is remarkable that these sources of tactile stimulation did not provide sufficient interference to prevent aversion learning to the texture of the food sleeves. Long-delay learning may have occurred because the intervening tactile stimuli were highly familiar. If this is true, placing the rats in a cage with novel floor and wall textures might disrupt the long-delay learning. Another possibility is that different memory systems exist for tactile stimuli experienced during the course of ingestion and tactile stimuli encountered during other activities. Perhaps the ingestive context serves to direct tactile information to a special ingestion-related memory mechanism in which the information is segregated from other tactile stimulation and stored long enough for association with delayed toxicosis (cf. Domjan, 1980). This hypothesis implies that tactile stimulation encountered in the absence of ingestion would not become as easily conditioned with toxicosis, even if other novel tactile sensations were minimized during the delay interval.

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