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In 2 experiments, access to a 0.15% saccharin solution was followed on alternating days by access to a 32% sucrose solution and the same saccharin solution. In Experiment 1, rats increased both intake of and preference for a flavored saccharin solution that predicted sucrose, but neither effect was found using a predictive odor cue alone. Experiment 2 replicated the predictive flavor results but showed suppression of saccharin intake when environmental cues predicted sucrose. When both flavor and environment predicted sucrose, saccharin intake did not change, but preference for the predictive flavor increased. Discriminative taste cues appear to facilitate the development of preference conditioning, but environmental cues favor negative anticipatory contrast effects. Also, preference conditioning and contrast may develop concurrently and compete for expression.

Flavor cues, particularly tastes, appear to be readily linked to systemic consequences related to a food's biological value. For example, it is widely known that flavor aversions develop when malaise follows the ingestion of a novel-flavored food (see Domjan, 1980, for a summary). Animals learn these aversions even when delays of 1 hr or more occur between experience of the flavor and the onset of malaise. Furthermore, flavors appear to be more readily associated with malaise than are environmental stimuli.

It is perhaps less widely appreciated that robust flavor preferences can develop when flavors are followed by positive systemic consequences, such as relief from caloric deprivation (Booth, 1985; Fedorchak & Bolles, 1987; Methel & Bolles, 1984, 1988) or recovery from thiamine deficiency (Zahorik & Maier, 1969; Zahorik, Maier, & Pies, 1974). There is also evidence that these positive systemic consequences can support conditioning over long delays (Capaldi, Campbell, Sheffer, & Bradford, 1987; Elizalde & Sclafani, 1988; Holman, 1975a).

Although evidence for the conditioning of flavor preference with caloric consequences is widespread, the determinants still are not completely understood. Conditioning sometimes fails to occur (see Simbayi, Boakes, & Burton, 1986). Elizalde and Sclafani (1988) showed that the conditioning of a predictive flavor across a delay may be blocked by inadvertent conditioning to distinctive flavors that accompany the ingestion of the caloric consequence.

In addition, in many cases, following one food with another appears to result in negative anticipatory contrast rather than positive conditioning. In negative anticipatory contrast, subjects show a decrease rather than an increase in the consumption of the first food (e.g., Flaherty & Checke, 1982; Flaherty & Rowan, 1986; Lucas, Gawley, & Timberlake, 1988) and an apparent reduction in preference for that food (Capaldi et al., 1987). It is not yet clear which procedures lead to negative contrast and which procedures facilitate intake of the first food (Lucas, Timberlake, Gawley, & Drew, 1990).

Recently, Capaldi, Sheffer, and Pulley (1989) speculated that negative anticipatory contrast and preference conditioning may occur in the same paradigm, producing opposing effects on intake that may cancel each other. That is, the final preference for a flavor may depend on an algebraic sum of the positive associations that are based on conditioning and the negative evaluations that are based on contrast. They used this hypothesis to account for a number of anomalous results. For example, the finding that higher concentrations of a sucrose reinforcer sometimes conditioned less preference than lower concentrations presumably occurred because the higher sucrose concentrations also resulted in stronger negative contrast effects that reduced the resultant preference.

The present experiments attempted to establish anticipatory contrast and preference conditioning in the same paradigm and to determine how different cue types affected the development of each. We used a within-subjects training procedure to assess contrast (Flaherty & Rowan, 1985) and followed training with a simultaneous-choice test to measure preference. Within this design, we varied the type of cues used to predict the second food. The data support the conclusion that preference conditioning and negative anticipatory contrast can develop concurrently. However, the results show that distinctive flavors facilitate the development of preference conditioning but distinctive environmental cues facilitate the development of negative anticipatory contrast. The results suggest that flavor plays a special role in preference conditioning with caloric consequences.
Experiment 1

When a 0.15% saccharin solution is followed, after a short delay, by a highly preferred 32% sucrose solution, intake of the saccharin solution is suppressed in comparison with that of a control that receives only saccharin, or receives saccharin followed by a less preferred solution (e.g., 4% sucrose or more saccharin, Flaherty & Checke, 1982; Flaherty & Rowan, 1986; Lucas et al., 1988). This suppression of saccharin preceding a highly preferred second food has been attributed to a contrast effect resulting from the comparison of the saccharin with the more preferred sucrose. Flaherty & Rowan (1985) showed that anticipatory contrast effects could be obtained also with a within-subjects procedure if the saccharin-sucrose pairings were presented in one setting, and the saccharin-saccharin pairings were presented in a different setting.

There are several reasons to think, though, that the effect of flavors as discriminative cues may be different. First, flavor is very important in the learning of conditioned aversions. Also, considerable data suggest that simultaneous flavor–sucrose pairings result in flavor preferences (e.g., Mehiel & Bolles, 1988) rather than negative contrast. However, if the emphasis in the sequential-presentation paradigm is on the comparison of the flavor–saccharin taste with sucrose rather than on the predictive relation, a negative contrast effect on saccharin intake may well occur.

To test these possibilities in the present experiment, we used the within-subjects design of Flaherty and Rowan (1985), but with flavor (taste plus related odor) as the discriminative cue. We added to this design a simultaneous-choice test between the cues at the end of acquisition. Because odors appeared to be important components of the discriminative contexts used by Flaherty and Rowan (1985), we also included a group using an external odor, but not taste, as the discriminative cue. This group was included on the assumption that preferences that are based on external odors may not condition as readily as preferences that are based on taste plus related odor (Domjan, 1973; Durlach & Rescorla, 1980; Garcia & Rusiniak, 1980; Rusiniak, Hankins, Garcia, & Brett, 1979). For all groups, the delay between the end of the first intake period and the start of the second was 15 s.

Method

Subjects

The subjects were 20 naive female Sprague-Dawley albino rats. They were 90–120 days old at the start of the study. Individual weights ranged from 240–300 g ad libitum. The animal colony was maintained on a 12-hr light–dark cycle. Water was available continuously in the home cages.

Approximately 8 days before the beginning of training, the subjects were isolated in individual cages and their daily food was restricted (7 g per day) until each subject was reduced to 85% of its ad libitum body weight and thereafter was maintained at this weight.

Apparatus and Procedure

The apparatus and general procedure were described in detail previously (Lucas et al., 1988) and are presented here in brief. Air in the training rooms was exhausted to the outside to prevent odors from lingering and contaminating subsequent conditions. A standard cage rack on wheels was modified so that the animals' home cages could be placed in the rack and the animals could be transported in groups of 10 to the training room. On each day the rat was weighed, and its cage was moved to the modified rack. After all rats in a group were weighed, the rack was transported to the experimental room, where the rats were left for a 10-min accommodation period.

At the end of the 10-min accommodation, 10 ml of 0.15% saccharin solution were placed into the rat's cage and left there for 5 min. All solutions were presented in 50-ml glass beakers that were tilted to 40° by a metal holder. After the 5-min access period, the saccharin was removed, and a 15-s delay period began. At the end of the delay period, a second solution was presented in the rat's cage for 5 min. After removal of the second solution, the rats were left in the experimental room for 10 min (while the solutions were measured) and then returned to the colony. A daily feeding of Purina Lab Chow, sufficient to maintain each subject at 85% body weight, was provided 90 min after the end of each training session.

Test solutions. Solutions were mixed at 3-day intervals and were kept refrigerated at 4 °C until they were measured out each day. The solutions were approximately 18 °C when presented. A 0.15% saccharin solution was mixed from a commercially available 2.33% stock solution (Pillsbury “Sweet-10”) by dilution with tap water. We mixed a 32% sucrose solution by weight (sucrose/sucrose + water) from commercially available sugar and tap water. We mixed flavored and odor solutions of the 0.15% saccharin by adding approximately 0.20% orange- or grape-flavored Kool-Aid unsweetened soft drink mix (General Foods) to the saccharin solution (one 4-g package per 2,000 ml of saccharin solution).

Pretraining. All subjects were pretrained for 4 days with unflavored 0.15% saccharin solution presented in both the first and second feeding periods. We then assigned subjects to one of two groups equated for saccharin intake.

Training. Two training cues were used. In the flavor group, a flavored 0.15% saccharin solution was presented as the first food. For half of these subjects, the orange flavor was presented on odd days; for the other half, grape was presented on odd days. The second food on odd days was always 32% sucrose. On even days, the alternate flavored saccharin solution was presented as the first food and was followed by unflavored 0.15% saccharin.

Subjects in the odor group were treated exactly like those in the flavor group, except that the orange- and grape-flavored solutions were placed in shallow dishes (8 cm diameter) on the rack 5 cm directly below the wire mesh floor of each cage. Unflavored 0.15% saccharin solution was placed in the drinking wells. These subjects were therefore exposed to the odor of the respective flavor solutions each day, but not to the taste. To avoid intermixing odors, the counterbalanced subgroups for each flavor and odor were run separately. Each training condition lasted for 16 days (i.e., for eight alternating 2-day blocks).

Simultaneous-choice test. On the day after the last day of training, the subjects in both groups were brought to the experimental room and were presented with the two flavored solutions simultaneously for 10 min. For those subjects in the odor group, this was their first exposure to the flavors mixed with the saccharin solution.

Results and Discussion

The mean intake of the 0.15% saccharin solutions in the first feeding period, across 2-day blocks, is shown in Figure 1. A preliminary analysis found no significant differences for the subgroups within either the flavor or odor conditions, so these subgroups were combined. The top figure shows the
Figure 1. Mean intake of 0.15% saccharin in the first daily presentation period across 2-day training blocks in Experiment 1. (Subjects trained with flavor cues mixed with the 0.15% saccharin are shown in the top panel. Subjects trained with the odor of the same cues present but not mixed with the saccharin are shown in the bottom panel. Squares represent intake on odd days when sucrose was predicted. Circles represent intake on even days when unflavored saccharin was predicted. Test data are the mean amount of 0.15% saccharin consumed during a 10-min simultaneous choice between the two flavored saccharin solutions.)

Subsequent contrast tests showed that this interaction occurred because there was a significant effect of consequence on saccharin intake in the flavor group, $F(1, 18) = 48.2, p < .01$, but no significant effect of consequence on saccharin intake for the odor group, $F(1, 18) = 1.47, p > .10$.

Although the subjects in the odor group displayed an active interest in the odors when they were presented each day, they showed little evidence of discriminating between the two odors in terms of their saccharin intake. If anything, there was a slight trend toward more saccharin intake in the presence of the odor that predicted sucrose. These rats did not suppress saccharin intake in anticipation of sucrose.

We conducted a separate ANOVA on the saccharin intake on the simultaneous-choice test day to assess differences in flavor preference. This analysis revealed a significant difference in saccharin intake between the two cue types (flavor or odor), $F(1, 18) = 28.5, p < .01$. This effect occurred because the subjects in the odor group consumed less of the flavored solutions during the test, presumably because the taste was novel. The analysis also revealed a significant effect of consequence (saccharin or sucrose) on saccharin intake, $F(1, 18) = 8.70, p < .01$, and a significant Cue × Consequence interaction, $F(1, 18) = 13.1, p < .01$. Again, subsequent contrast tests showed that this interaction occurred because there was a significant effect of consequence on saccharin intake in the flavor group, $F(1, 18) = 21.6, p < .01$. That is, the subjects that received the flavor cues (taste plus odor) showed a strong preference for the flavor that predicted sucrose. However, no significant effect of consequence on saccharin intake was obtained for the odor group, $F(1, 18) = .22, p > .10$, indicating that subjects in the odor group did not develop a flavor preference.

Finally, it may be worth pointing out that differences in group effects on intake of the initial solution are not due to differences in intake of the second solution. Rats took in more sucrose than saccharin as the second solution, 8.4 ml versus 4.1 ml, $F(1, 41) = 218.7, p < .01$, but with no differential effects of condition.

In summary, we obtained no evidence of a within-subjects negative anticipatory contrast effect when either flavor or odor was used as a discriminative cue. Instead, subjects trained with flavors consumed more of the flavored saccharin that predicted sucrose and displayed a distinct preference for that flavor in simultaneous flavor comparisons. However, subjects trained with the odors did not differ in their consumption of saccharin on days when sucrose or saccharin was predicted, and they showed no preference in simultaneous flavor comparisons. This latter finding shows that odors alone were less effective than taste plus odor in conditioning preferences.

Experiment 2

The failure to obtain a negative anticipatory contrast effect with flavors in Experiment 1 led us to examine more closely the successful within-subjects contrast procedure used by Flaherty and Rowan (1985). In that study, the authors used a number of environmental cues to create clearly distinct training environments. One environment involved dim light, a tone, and white noise; the alternate environment involved...
bright light, a clicking sound, and the odor of menthol. In effect, the discriminative cues used by Flaherty and Rowan (1985) may have been more appropriate for learning about the location in which the different foods were found than for learning about the consequences of their consumption.

In the present study, we attempted to determine whether preference conditioning and negative contrast develop differently when flavors predict the second food as opposed to when nonflavor environmental cues predict the second food. For this reason we trained subjects in two distinct rooms. One room was distinguished by dim light, a lilac fragrance, and a 1000-Hz tone. The alternate room was distinguished by bright light, menthol odor, and the sound of a fan. For one group, these unique room cues predicted whether the subjects would receive sucrose or saccharin in the second feeding period. For a second group, a “redundant” flavor cue (grape or cherry) accompanied the room cues and also predicted the second food. For a third group, the flavors alone predicted the second food.

Method

Subjects

The subjects were 44 naive female Sprague-Dawley albino rats selected and housed as in Experiment 1.

Apparatus and Procedure

The same equipment and general procedures described in Experiment 1 were used, with the following additions. As in the previous study, the delay between the end of the first feeding period and the start of the second was 15 s. However, two different training rooms were used to maximize the different environmental cues, and a third room was used for testing. The three rooms differed in lighting, odor, and sound.

The dim, lilac, tone room was dimly illuminated by a 25-W red incandescent bulb located about 1 m from the cage rack. The odor of the room was made distinctive by releasing a 2-s spray of a lilac-scented aerosol immediately before the rats were placed in the room each day. A 1000-Hz tone was constantly sounded in this room.

The bright, menthol, fan room was brightly illuminated by overhead fluorescent bulbs. The odor of the room was made distinctive by spreading approximately 1 g of mentholated ointment (Mentholatum) on a paper towel located approximately 1 m from the cage rack immediately before the rats were placed in the room each day. A white-noise sound from a noisy exhaust fan located about 3 m from the test rack was continuously present in this room.

The neutral test room was moderately illuminated by a 40-W white incandescent bulb. Distinctive odor or sound cues were not presented in this room.

Test solutions. The 0.15% saccharin and 32% sucrose solutions were mixed as in Experiment 1. The flavored solutions were approximately 0.20% solutions of grape or cherry Kool-Aid mixed in 0.15% saccharin.

Pretraining. All subjects were pretrained for 4 days with unflavored 0.15% saccharin solution presented in both the first and second feeding periods. The subjects were then assigned to one of three groups equated for saccharin intake.

Training. Three training procedures were used, depending on what type of cues reliably predicted the second feeding period. The predictive cue types and the number of subjects per group were (a) room cues, n = 12, (b) room plus flavor, n = 12, and (c) flavor alone, n = 20. The training procedure remained in effect for 32 sessions (16 alternating 2-day blocks). For subjects trained with the room cues, 0.15% saccharin was always followed by 32% sucrose in one room and by 0.15% saccharin in the alternate room. The type of second food alternated across days. The order of presentation and the room that predicted sucrose or saccharin were counterbalanced within the group.

The subjects trained with the room and redundant flavor cues were treated exactly like those trained with the room cue alone except that a unique flavor (grape or cherry) was mixed in the 0.15% saccharin solution. For half the subjects, grape was redundant with the dim, lilac, tone cues, and cherry was redundant with the bright, menthol, fan cues. For the remaining subjects, the flavor–room combinations were reversed.

For subjects trained with the flavors, one flavor was presented on days that 32% sucrose followed saccharin, and the alternate flavor was presented on days that 0.15% saccharin followed as the second food. For half of these subjects, cherry preceded sucrose and grape preceded saccharin. For the remaining subjects, the combination was reversed. Half the subjects in each flavor combination were trained in the dim, lilac, tone room, the other half in the bright, menthol, fan room.

Simultaneous-choice test. On the day after the last day of training, the subjects in each group were brought to the neutral test room and presented with the two flavored 0.15% saccharin solutions simultaneously for 5 min.

Results and Discussion

A preliminary analysis found no significant differences between the counterbalanced flavor and room subgroups in the redundant cue condition or between the counterbalanced flavor subgroups in the flavor alone condition, so the data were combined within each set of subgroups. The mean intake of the saccharin solution during the first feeding period is shown across training blocks in Figure 2 for each of the three training conditions. The two lines represent saccharin intake for days on which saccharin preceded sucrose (squares), and for alternate days on which saccharin was followed by a second saccharin solution (circles). Note that the intake on saccharin–saccharin days was similar across all three groups. But on days that saccharin preceded sucrose, the performance of the groups differed considerably. Saccharin intake was suppressed for the group in which room cues predicted the sucrose, but saccharin intake was facilitated for the group in which flavors predicted sucrose. However, for the group in which both flavor and room cues predicted sucrose, there was no clear difference in saccharin intake on alternate days.

To assess the differences in saccharin intake that developed during training in more detail, we calculated the mean saccharin intake for the first feeding period during the last two blocks of training, and we performed an ANOVA comparing these measures between groups and within conditions. The results of this analysis revealed a significant effect of cue type (room, room plus flavor, or flavor) on saccharin intake, F(2, 41) = 5.64, p < .01, indicating that total saccharin intake differed among the three groups. There was, though, no significant overall difference of the consequence (sucrose or saccharin), F(1, 41) = 0.58, p > .10, because the magnitude
Figure 2. Mean intake of 0.15% saccharin in the first daily presentation period for each of the three groups in Experiment 2 across 2-day training blocks. (The squares indicate saccharin intake in the presence of cues predicting sucrose as the second food. The circles indicate saccharin intake in the presence of cues predicting unflavored saccharin. Test data are the mean amount of 0.15% saccharin consumed during a 5-min simultaneous choice between the flavored saccharin solutions. Rm = room; F = flavor.)

of facilitation and suppression effects canceled each other. However, there was a significant Cue X Consequence interaction, $F(2, 41) = 26.3, p < .01$.

Subsequent contrast tests confirmed that saccharin intake on sucrose days was significantly suppressed below that on saccharin–saccharin days in the group trained with predictive room cues, $F(1, 41) = 16.2, p < .01$; significantly facilitated in the group trained with predictive flavors, $F(1, 41) = 34.4, p < .01$; but not significantly different in the group trained with redundant flavor and room cues, $F(1, 41) = 3.06, p > .05$. These data imply that when flavor and room cues were presented together, the combination resulted in conflicting motivational tendencies that effectively canceled each other (cf. Capaldi et al., 1989).

We conducted a separate ANOVA on the saccharin intake on the simultaneous-choice test to assess differences in flavor preference. This analysis revealed a marginal overall effect of cue type (room, room plus flavor, or flavor) on saccharin intake, $F(2, 41) = 3.17, .05 < p < .10$. However, there was a significant overall difference between consequence conditions (sucrose or saccharin), $F(1, 41) = 21.3, p < .01$, and there was a significant Cue X Consequence interaction, $F(2, 41) = 6.52, p < .01$. Subsequent contrast tests confirmed that these latter findings resulted from a distinct preference for the flavor that preceded sucrose. This preference developed in both groups that received flavors, $F(1, 41) = 33.4, p < .01$, for the group trained with predictive flavors and $F(1, 41) = 9.22, p < .01$, for the group trained with redundant flavor and room cues. As expected, no flavor preference was observed for the group trained with the predictive room cues alone, $F(1, 41) = .01, p > .10$. Finally, as in Experiment 1, the intake of sucrose was approximately twice that of saccharin as the second food, and there were no effects of condition.

General Discussion

The present results show that the type of predictive cue used in training is an important determinant of whether negative anticipatory contrast or preference conditioning develops when one food is followed by another. These results are consistent with the suggestion of Capaldi et al. (1989) that negative contrast and preference conditioning may develop concurrently and produce opposing effects (see also Williams, 1990).

In both the experiments, the use of predictive flavors (tastes and odor combinations) led to the conditioning of preference, but negative contrast developed when predictive environmental cues were used. In Experiment 1, we found no evidence for negative contrast with either predictive odors or flavors. But predictive flavors led to preference conditioning.

In Experiment 2, we found negative contrast when room cues alone predicted sucrose. At the same time, we found a facilitation of intake of the saccharin flavor predicting sucrose as well as a preference for its flavor. When both types of cue were predictive, though, we found a preference for the flavor predicting sucrose but did not obtain a facilitation of saccharin intake.

Our results with odors were somewhat surprising. Because odors were apparently important components of the discrim-
inative contexts used successfully by Flaherty and Rowan (1985) to produce within-subjects negative contrast (see also our Experiment 2), we assumed that odor alone would be a sufficiently strong environmental cue to support negative contrast. However, we found no evidence of negative anticipatory contrast effects with olfactory cues in Experiment 1, and the data gave no suggestion that negative contrast would have developed with more training. However, odors did not lead to preference conditioning either. The absence of conditioning effects with odors may simply indicate that the odors we used were not salient cues. However, this seems unlikely. The two odors were easily recognized and discriminated by human observers, who generally are far less sensitive to odor than rats. It was clear by their sniffing behavior that our rats readily attended to the odors when they were presented.

Still, there may be differences in odor quality that make some odors more effective flavor cues than others (cf. Elizalde & Sclafani, 1988). Also, odors may serve as either environmental or flavor cues, with accompanying cues determining the direction of learning. For example, tastes appear to potentiate the use of odors as flavor cues in taste aversion learning (Domjan, 1973; Durlach & Rescorla, 1980; Garcia & Rusiniak, 1980; Rusiniak et al., 1979). Perhaps a similar potentiation of odor cues develops with the conditioning of caloric consequences. From this perspective it would be interesting to determine whether coincident environmental cues facilitate the recognition of odors as nonflavor cues.

The present results have implications for how negative anticipatory contrast develops. Because we used a within-subjects training procedure, it was necessary for our rats to attend to a particular aspect of the stimulus environment to discriminate what food would follow. Using this procedure, our results showed that environmental cues, rather than tastes, were important for the development of negative anticipatory contrast. These data imply that in the more typical between-subjects training procedure, the rats may attend more to the event of presenting the predictive saccharin solution than to its taste. This suggests that procedures that enhance attention to the flavor of the first solution would be likely to interfere with the development of negative anticipatory contrast (see Lucas et al., 1990).

In many ways these findings are reminiscent of the findings of selective association of flavor cues in toxicity conditioning (Garcia & Koelling, 1966). Our rats appeared to learn differently when flavors predicted subsequent foods than when environmental cues predicted the same foods. It is tempting to conclude that selective associations of tastes with caloric consequences and of environmental cues with other consequences might account for the differences in saccharin consumption that we found. Such differences in associability would imply evolved differences in the type of cues that animals use to learn about the location and availability of a food (e.g., nonflavor environmental cues) versus those cues that animals use to learn about the consequences of ingesting a food (e.g., flavors). There is supporting evidence that a food’s appetitive value and its consummatory value can differ (Holman, 1975b). For example, learning an aversion to ingesting a particular prey item does not guarantee that a predator will not continue to capture and kill similar prey (Garcia, Clarke, & Hankins, 1973; Gustavson, Garcia, Hankins, & Rusiniak, 1974).

Whether the current results depend on selective associations of taste with caloric consequences remains to be determined. However, our data suggest there is a difference in how rats respond to tastes versus environmental cues that predict positive caloric consequences. These findings, together with previous work demonstrating conditioned preferences across long delays (Capaldi et al., 1987; Elizalde & Sclafani, 1988; Holman, 1975a), argue that it may be worthwhile to consider the conditioning of flavor preferences as a positive counterpart to taste aversion learning.

References


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