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Potentiation of taste and extract stimuli in conditioned flavor preference learning

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In these experiments, we investigated the nature of potentiation in the conditioned flavor preference paradigm. Almond and banana extracts, which have strong odor components, were combined with salt and saccharin (liked tastes; Experiment 1) or quinine and citric acid (disliked tastes; Experiment 2) in a flavor preference procedure that mixed these solutions with a caloric reinforcer (polycose). The results showed that liked tastes potentiated preference conditioning to extracts (Experiment 1), whereas extracts potentiated preference conditioning to disliked tastes (Experiment 2). In both experiments, the presumably less liked stimulus (i.e., the extract in Experiment 1 and the disliked taste in Experiment 2) was the potentiated cue.

Rusiniak, Hankins, Garcia, and Brett (1979) found that almond-scented water produced only a weak aversion when followed by illness, whereas saccharin water produced a strong aversion. Thus, conditioning to taste produced a stronger aversion than did conditioning to extract. However, when the extract and taste cues were combined (almond-scented saccharin water), a strong aversion was formed to the extract as well. This phenomenon has been termed *potentiation*. Although not all investigators have replicated this phenomenon (e.g., Bouton & Whiting, 1982; Mikulka, Pitts, & Philput, 1982; Privitera & Capaldi, 2006; Rosellini & Lashley, 1986), when potentiation is observed, taste reliably potentiates an aversion to an extract (e.g., Durlach & Rescorla, 1980; Palmerino, Rusiniak, & Garcia, 1980; Rusiniak et al., 1979; Rusiniak, Palmerino, Rice, Forthman, & Garcia, 1982), and with few exceptions (Slotnick, Westbrook, & Darling, 1997), this finding is asymmetrical—that is, extract does not potentiate learning about taste (Durlach et al., 1980; Palmerino et al., 1980). At present, little is known about potentiation from preference procedures.

In preference conditioning, a flavor that is paired with an already preferred flavor will come to be preferred (Holman, 1975), and a flavor that is paired with calories will also come to be preferred (Capaldi, Campbell, Sheffer, & Bradford, 1987). In preference potentiation learning (unlike in aversion conditioning), conditioning has been observed to extracts that is stronger than or equal to that to tastes. For example, Holder (1991) tested for potentiation in preference conditioning, using extracts presented on disks and taste stimuli presented in bottles. This study failed to show potentiation (or overshadowing) of an extract by taste in conditioned flavor preference learning in which sucrose was used as a positive reinforcer. Instead, he found that conditioning to taste and extract was as strong following taste-alone and extract-alone conditioning as it was following taste+extract compound conditioning. Capaldi and Hunter (1994) mixed extract solutions in bottles for consumption, using a similar design, and also failed to find evidence for potentiation.

Both of these studies used sucrose as the unconditioned stimulus. To increase the power of detecting an effect in the present study, we used polycose as a reinforcer, which evidence suggests is a stronger reinforcer than is sucrose (Ackroff, Manza, & Sclafani, 1993). Also, the sweet taste of sucrose may have complicated the interaction of taste and extract in previous studies. Extracts potentiated in the aversion paradigm were used in the present study (almond and banana, as used by Durlach & Rescorla, 1980). In this exploratory study, we hoped that using these same stimuli would increase the sensitivity for detecting potentiation in preference conditioning. The aim was to determine whether potentiation could be obtained in preference conditioning.

EXPERIMENT 1

In Experiment 1, we mixed extract cues with *liked* tastes, as in previous studies in which potentiation in preference conditioning has been investigated (Capaldi, Hunter, & Lyn, 1997; Holder, 1991). Also, we used polycose as the reinforcer, with subjects receiving either 2% or 20% concentration. These concentration differences have produced conditioned preferences in previous experiments (Capaldi et al., 1997; Lucas, Azzara, & Sclafani, 1998). The measure of conditioned preference was greater consumption of a cue that had been paired with 20% polycose than of a cue that had been paired with 2% polycose. Potentiation of extract by taste would be shown by greater preference for an extract that had been paired with 20% polycose than for

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an extract that had been paired with 2% polycose when the extracts had been mixed with tastes in training than when they had been given alone. Potentiation of taste by an extract would be shown by a greater preference for a taste that had been paired with 20% polycose than for a taste that had been paired with 2% polycose when the tastes had been mixed with extracts in training than when the tastes were given alone.

Method

Subjects. The subjects were 40 naive, male Sprague–Dawley rats from Harlan Co. (Indianapolis, IN). They were 73 days old upon arrival and 76 days old at the start of deprivation.

Materials and Apparatus. Solutions were presented in 50-ml Nalgene centrifuge tubes with rubber stoppers and metal spouts. Taste stimuli were 0.2% NaCl w/v and 0.06% saccharin; odorous stimuli were 1% banana extract or 1% almond extract (McCormick's brand). All the stimuli were presented in 40 ml of distilled water, which also contained either a 2% or a 20% polycose reinforcer purchased from Ross Laboratories (Columbus, OH). The rats were trained and tested in their home cages. A 12:12-h light:dark cycle was always in effect, with lights on at 6:00 a.m.

Procedure. Ad lib water was present throughout the experiment in clear plastic bottles mounted to the right of the food hopper on each cage front. On Day 1, all food was removed from the cages. On Days 2–11, the rats were fed 14 g each day at 9:00 a.m., and during training (which was at 9:30 a.m.), they were fed at 1:00 p.m. The 40 subjects were divided randomly into four groups of 10 subjects each. Group Taste was trained with the taste stimuli (salt and saccharin), one stimulus given with 20% polycose and the other with 2% polycose. Group Extract was trained with the extracts (banana and almond), one stimulus given with 20% polycose and the other with 2% polycose. Group Taste/Extract–Taste, and Group Taste/Extract–Extract were trained with the tastes and extracts, one taste–extract combination given with 20% polycose and the other with 2% polycose. All flavors and reinforcers were mixed in compound and were presented in bottles for ingestion in training.

Training. There were 10 days of training beginning on Day 12. On an ABABABABAB schedule, the rats in each group received five daily sessions of a flavor cue paired with 20% polycose solution on A Days, alternated with five daily sessions of a flavor cue paired with 2% polycose solution on B Days. In training, 40 ml of solution were presented for 10 min each day. All stimuli were counterbalanced: For half of Group Taste, salt was associated with 20% polycose and saccharin was associated with 2% polycose, and the other half received the reverse pairings; for half of Group Extract, almond was associated with 20% polycose and banana with 2% polycose, and the other half had the reverse pairings. For each taste/extract group, 5 rats received almond+saccharin mixed in 20% polycose and banana+salt in 2% polycose, 5 received banana+saccharin mixed in 20% polycose and almond+salt in 2% polycose, 5 received almond+saccharin mixed in 2% polycose and banana+salt in 20% polycose, and 5 received banana+saccharin mixed in 2% polycose and almond+salt in 20% polycose.

Testing. There were 4 days of testing beginning the day following training. Each test lasted 4 h. In testing, Group Taste and Group Taste/Extract–Taste received a two-bottle test between the two taste stimuli presented in bottles, Group Extract and Group Taste/Extract–Extract received a two-bottle test between the two extract stimuli also presented in bottles for ingestion. In testing, half the taste/extract subjects were randomly assigned to receive an extract; half were randomly assigned to receive a taste. At least 2 subjects from each taste/extract counterbalancing assignment were assigned to receive a taste, and at least 2 were assigned to receive an extract in testing. For all the rats, the left tube was placed into each cage and was moved briefly so the rat would approach and contact the tube; then the right tube was inserted and moved briefly so the rat would also contact this tube. Positions of the tubes were reversed between tests.

Data analyses. In training, an ANOVA included groups, pairing, and blocks of days (a block consisted of one 20% polycose day + one 2% polycose day) as factors. In test, an ANOVA included training stimulus (groups trained with one stimulus vs. groups trained with two stimuli), testing stimulus (whether the subjects received a taste or an extract in test), pairing (paired with 2% polycose vs. paired with 20% polycose in training), and days as factors.

Preference was defined as greater consumption of the 20%-polycose-associated solution than of the 2%-polycose-associated solution, indicated by a significant main effect of pairing. In test, *taste-mediated extract potentiation* was defined as a significantly greater preference for an extract following compound training (i.e., Group Taste/Extract–Extract) than following single-element training (i.e., Group Extract). Similarly, *extract-mediated taste potentiation* was defined as a significantly greater preference for a taste following compound training (i.e., Group Taste/Extract–Taste) than following single-element training (i.e., Group Taste). Consumption in test was compared only between groups receiving the same solutions (either extract or taste) at test. The possibility of potentiation was indicated by a significant pairing × groups interaction. If this interaction was significant, the difference in consumption between 2%- and 20%-polycose-paired solutions was taken for each group, and Newman–Keuls tests were conducted on these difference scores between groups.

Results

Training. All the groups acquired a preference to the taste or extract cue associated with the larger reinforcer [i.e., 20% polycose; $F(2,37) = 3.48$, $p < .05$], and the strength of this preference varied by group [$F(2,37) = 4.00$, $p < .03$; see Table 1]. Newman–Keuls tests showed that the preference was largest for Group Taste, reflecting a larger difference in consumption between the 20%-polycose- and 2%-polycose-paired taste solutions for Group Taste, as compared with all the other groups ($p < .01$). The tastes used in this experiment are innately preferred by rats, which likely explains why the subjects expressed significantly greater liking for these tastes in training. The difference due to each additional factor in the analysis was significant [pairing, $F(1,37) = 52.54$, $p < .001$; blocks $F(4,148) = 69.53$, $p < .001$]. No additional effects were significant.

Testing. Taste-mediated extract potentiation was evident in the subjects tested with an extract following taste+extract training; there was no evidence for extract-mediated taste potentiation (Table 2). As is shown in Table 2, all the subjects expressed a preference for the 20% polycose-associated solution [$F(1,36) = 12.41$, $p < .001$], and the strength of this preference varied by group

Table 1
Mean Amount Consumed (in Milliliters) of Each Solution by Each Group in Training (Collapsed Across Days) in Experiment 1

	Flavor Paired With	
Group	20% Polycose	2% Polycose
Extract	5.00±0.9	1.58±0.5
Taste	9.22±1.1	1.26±0.4
Taste/extract	5.51±0.8	1.74±0.7

Note—All values are given as the mean plus or minus the standard error of the mean.

Table 2
Mean Amount Consumed (in Milliliters) in Two-Bottle Preference Testing Between the Stimuli That Had Been Associated With 20% Polycose or 2% Polycose in Training (Collapsed Across Days) in Experiment 1

Training Stimulus	Testing Stimulus	Flavor Associated With	
		20% Polycose	2% Polycose
Taste	taste	6.33±0.9	0.93±0.2
Extract	extract	3.65±0.7	1.35±0.4
Taste/extract	taste	7.18±1.0	1.78±0.7
Taste/extract	extract	6.55±1.0	1.20±0.3

Note—All values are given as the mean plus or minus the standard error of the mean.

[$F(1,36) = 12.68$, $p < .01$]. Subsequent Newman–Keuls tests showed that the subjects trained with a taste/extract compound expressed a significantly larger preference for the extract associated with 20% polycose in test, as compared with a group receiving extract alone training, ($p < .01$), whereas groups tested for a preference to the taste (i.e., Group Taste and Group Taste/Extract–Taste) did not differ. Thus, training with the taste/extract compound potentiated a preference to the extract in Group Taste/Extract–Extract, as compared with Group Extract, but training with the taste/extract compound did not affect preference to the taste, as compared with Group Taste.

Also, when the strength of taste-mediated extract potentiation was compared for subjects receiving saccharin versus salt as the taste cue, there was only a main effect of pairing [with polycose; $F(1,36) = 4.79$, $p < .05$]. There was no interaction between pairing and salt versus saccharin ($F < 1$). Thus, the strength of taste-mediated extract potentiation was significant with both saccharin and salt. Overall, the subjects in Group Extract consumed the least amount of solution at test ($p < .05$). No additional effects were significant.

Discussion

This experiment demonstrates that liked tastes potentiate preferences to extract stimuli and that this is an asymmetrical relationship—that is, extracts do not potentiate conditioning to liked tastes. This is rather surprising, since odor extracts are considered a stronger cue for preference conditioning than is taste (Capaldi & Hunter, 1994). In aversion conditioning, tastes potentiate conditioning to odor, but odor is considered a weaker cue than is taste in aversion conditioning, generally speaking. One possible explanation may be that this effect is due to the additive contribution of extract → taste learning for the compound conditioned groups. Thus, the stronger preference expressed in Group Taste/Extract–Extract could have been mediated by both extract → polycose and extract → taste–polycose associations, whereas only an extract → polycose association supported the preference expressed by Group Extract. Of course extract–taste conditioning also affects the cue associated with 2% polycose. Thus, without additional assumptions, extract–taste associations cannot explain a greater preference for the extract/taste compound group.

Also, although extract–taste conditioning could affect preference for the extract for subjects receiving saccharin as the taste cue (Holman, 1975), this is likely not so for those receiving salt (McCaughey & Scott, 1998). Liking for salt is dependent on a subject's need for sodium (Symonds, Hall, & Bailey, 2002; Tordoff & Coldwell, 2002), so that preferences for salt are absent in sodium-replete rats (Clark & Bernstein, 2006; Coldwell & Tordoff, 1993). Since the subjects were not sodium deprived in Experiment 1, an extract → salt association should not have contributed to the extract → polycose preference association observed in Experiment 1. Because the role of any extract–taste conditioned preferences was unclear in Experiment 1, in Experiment 2 we sought to minimize any enhancement of consumption due to this factor by using disliked tastes.

EXPERIMENT 2

To eliminate the contribution of positive flavor → taste associations in the potentiation of flavor preferences, we used initially disliked tastes in Experiment 2. By using disliked tastes, any associations with tastes would be predicted to *decrease* consumption, not increase it. Therefore, we can be more confident that any preferences (or *increased* consumption) observed in this experiment were primarily mediated by associations with polycose, not taste.

Method

All methods, procedures, and data analyses were the same as those in Experiment 1, except for the taste stimuli used. In Experiment 2, saccharin and salt were replaced with 0.031% citric acid (sour taste) and 0.00396% quinine hydrochloride hydrate (bitter taste). All the subjects were 40 naive, male Sprague–Dawley rats that were the same as those described in Experiment 1.

Results

Training. An overall preference for the taste or extract cue associated with the larger reinforcer (i.e., 20% polycose) was shown by a significant main effect of pairing [$F(2,37) = 4.12$, $p < .03$], and the strength of this preference varied by group [$F(2,37) = 4.00$, $p < .03$; see Table 3]. Newman–Keuls tests showed that the preference was largest for Group Extract, reflecting a larger difference in consumption between the 20%-polycose- and the 2%-polycose-paired solutions for Group Extract, as compared with all the other groups ($p < .05$). The rats innately

Table 3
Mean Amount Consumed (in Milliliters) of Each Solution by Each Group in Training (Collapsed Across Days) in Experiment 2

Group	Flavor Paired With	
	20% Polycose	2% Polycose
Extract	5.37±1.0	2.03±0.7
Taste	2.49±0.8	0.98±0.4
Taste/extract	3.00±0.9	1.14±0.5

Note—All values are given as the mean plus or minus the standard error of the mean.

Table 4
Mean Amount Consumed (in Milliliters) in Two-Bottle Preference Testing Between the Stimuli That Had Been Associated With 20% Polycose or 2% Polycose in Training (Collapsed Across Days) in Experiment 2

Training Stimulus	Testing Stimulus	Flavor Associated With	
		20% Polycose	2% Polycose
Taste	taste	2.93±0.7	1.01±0.6
Extract	extract	4.65±0.8	1.44±0.4
Taste/extract	taste	4.20±0.8	1.66±0.5
Taste/extract	extract	5.25±1.0	1.53±0.6

Note—All values are given as the mean plus or minus the standard error of the mean.

disliked the tastes used in this experiment, which likely explains why the subjects expressed significantly lower consumption of these tastes in training. The difference due to each additional factor in the analysis was significant [pairing, $F(1,37) = 18.33$, $p < .001$; blocks, $F(4,148) = 9.76$, $p < .001$]. No additional effects were significant.

Testing. Potentiation was evident in the subjects tested with a taste following taste+extract training, but not in the subjects tested with an extract. As is shown in Table 4, all the subjects expressed a preference for the 20%-polycose-associated solution [$F(1,36) = 4.12$, $p < .05$], and the strength of this preference varied by group [$F(1,36) = 8.38$, $p < .01$]. Subsequent simple effects tests showed that the subjects trained with a taste/extract compound expressed a significantly larger preference for the taste associated with 20% polycose in test, as compared with a group receiving taste-alone training ($p < .01$). Groups tested for a preference to the extract (i.e., Group Extract and Group Taste/Extract–Extract) did not differ. Thus, training with the taste/extract compound potentiated a preference to the taste (extract-mediated taste potentiation), not the extract. No additional effects were significant.

GENERAL DISCUSSION

The results from Experiment 2 showed potentiation, as in Experiment 1, but in the opposite direction. In Experiment 1, a liked taste potentiated a preference to an extract; in Experiment 2, an extract potentiated a preference to a disliked taste. In training in Experiment 1, the difference in consumption between the 20% polycose solution and the 2% polycose solution was greatest for the taste groups; in Experiment 2, this difference was greatest for the extract groups. The pattern of results across both experiments suggests that differences in training are greater when solutions are liked, mixing a liked taste in with polycose enhanced the difference in consumption between 20% and 2% polycose, as compared with the plain extract. Mixing a disliked taste in with the polycose reduced the difference in consumption between the 20% and the 2% polycose. Potentiation also varied with liking. The findings in Experiment 1 suggest that liked tastes can potentiate preferences for relatively neutral odor extracts, whereas Experiment 2 showed that the same odor extracts can potentiate preferences for disliked tastes. This indicates that an effective potentiating cue can be any cue that is more liked, relative to the conditioned cue (ranked from most to least liked). Thus, a liked taste potentiated a preference to a neutral odor extract, which potentiated a preference to a disliked taste (ranking: liked taste > extract > disliked taste).

On the basis of these findings, future experiments should consider using tastes that differ in preference ranking and consider whether this effect is dependent on the type of reinforcer used. Previous studies have used sucrose as a reinforcer, whereas we used polycose. One unique feature of flavor preference potentiation is that the reinforcer is mixed with the conditioned stimuli. The presence of the highly liked sweet taste of sucrose in all solutions in previous studies may have minimized the effects of taste cues shown here. If potentiation were at least partially dependent on the salience or strength of reinforcement, it would be important to determine how relatively reinforcing these solutions were when mixed with conditioned stimuli. In addition, the potential for potentiation to be dependent on the unique interaction of specific combinations of flavor stimuli and reinforcers (when these solutions are mixed together) would appear to be most consistent with unique stimulus (Rescorla, 1973) or configural (Pearce, 2002) interpretations, which describe the potential changes in stimulus salience that can occur when two or more flavor stimuli are mixed together. In all, these experiments provide evidence for successful potentiation of conditioned flavor preferences, using both liked and disliked tastes, that should bolster future investigations into the effectiveness of this preference-learning paradigm.

AUTHOR NOTE

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