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Taste + odor interactions in compound aversion conditioning

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In three experiments with rats, taste + odor interactions in compound aversion conditioning were investigated. In Experiment 1, two odors (0.02% almond and 0.02% orange) were compared on single-element odor aversions, taste (denatonium) potentiated odor aversions, and potentiated odor aversions following taste extinction. Although no odor differences were seen following single-element conditioning, both types of potentiated orange odor aversions were stronger than their almond odor counterparts. These data show that odors of similar conditionability are differentially potentiated by the same taste. To determine whether these differences were due to unique perceptual representations, the effects of elemental extinction or compound extinction on aversions to the compound were investigated in Experiments 2 and 3. In Experiment 2, orange odor extinction weakened responding to the compound significantly more than taste extinction did. In contrast, almond odor extinction and taste extinction produced similar decrements in responding to the compound in Experiment 3. These results suggest that the perceptual representation of these specific taste + odor compounds are different, and they are discussed in regard to configural and within-compound association accounts of potentiation.

Flavor aversion learning is a common classical conditioning paradigm in which learning occurs rapidly, often involving only a single conditioned-stimulus–unconditioned-stimulus (CS–US) pairing. A typical experimental example involves an organism such as a rat consuming a novel flavor (CS), followed by an emetic (US), which produces illness (unconditioned response, or UR). Upon subsequent presentation of the novel flavor, the rat demonstrates an unwillingness to consume the flavor (conditioned response, or CR).

One reason why flavor aversion learning has been a popular means of studying associative learning is that it produces outcomes that differ from other types of classical conditioning. For example, in a simultaneous compound conditioning situation (AX+) with a salient CS A and a less salient CS X, the two stimuli compete to acquire associative strength, and the more salient CS A garners more associative strength and elicits a stronger CR than does CS X. Thus, the presence of CS A is said to *overshadow* learning to CS X (Pavlov, 1927, pp. 269–270). Because overshadowing is observed in most classical conditioning paradigms, overshadowing and the general concept of *cue competition* have been incorporated into most formal models of associative learning (e.g., Pearce & Hall, 1980; Rescorla & Wagner, 1972). However, when compound aversion conditioning is conducted with a strong taste and a weak odor, overshadowing of the odor by the taste may not occur. Instead, in many cases, the CR to the odor is strengthened, as compared with controls receiving only the odor, followed by illness. For example, Rusiniak, Hankins, Garcia, and Brett (1979) showed that following compound conditioning with 0.1% saccharin and 2% almond (AL) odor, the odor aversion was significantly stronger, relative to controls. This phenomenon has been termed *taste-mediated odor potentiation*. Since the work of Rusiniak et al., taste-mediated odor potentiation has been demonstrated numerous times (e.g., Bouton, Jones, McPhillips, & Swartzentruber, 1986; Coburn, Garcia, Kiefer, & Rusiniak, 1984; Droungas & LoLordo, 1991; Durlach & Rescorla, 1980; Holder & Garcia, 1987; Slotnick, Westbrook, & Darling, 1997).

Because most formal models of classical conditioning do not accommodate potentiation, new models have been proposed to explain this phenomenon. The within-compound association model proposed by Durlach and Rescorla in 1980 is the theoretical interpretation of potentiation that has garnered the most empirical support (for a review, see Batsell & Blankenship, 2003). The within-compound association model accounts for potentiation on the basis of the associations formed between the taste, the odor, and the illness-producing US. Specifically, three associations are formed during taste + odor compound conditioning. Direct associations form between taste → illness and odor → illness, and an indirect within-compound association forms between taste ↔

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odor. To explain odor potentiation, after compound conditioning, presentation of the odor activates the odor aversion directly through the odor → illness association and indirectly through the odor → taste → illness association. Thus, activation of these multiple associations produces a stronger CR than that produced by controls that have only the direct odor → illness association.

According to the within-compound association model, the strength of the potentiated odor aversion is related directly to the strength of the taste aversion. Therefore, the primary means of testing the within-compound association model has been to conduct odor + taste compound conditioning, postconditioning taste extinction, and testing of the potentiated odor aversion. For example, in a within-subjects design, Durlach and Rescorla (1980) demonstrated that postconditioning taste extinction significantly weakened the aversion to the odor that was conditioned in compound with that taste. They inferred that taste extinction had eliminated the direct taste → illness association and, therefore, the indirect odor → taste → illness association. Thus, odor presentation could activate only the direct odor → illness association, and as a result, the odor aversion was weakened. In general, the majority of the studies in which the taste extinction procedure has been used to investigate potentiation have obtained results that are consistent with the within-compound association model (e.g., Batsell, Paschall, Gleason, & Batson, 2001; Durlach & Rescorla, 1980; Westbrook, Homewood, Horn, & Clarke, 1983); however, a few studies have produced contradictory results (Droungas & LoLordo, 1991; Lett, 1984).

In a recent report from our lab, an inflation procedure was used to confirm that the strength of the taste aversion influences the strength of the potentiated odor aversion (Batsell, Trost, Cochran, Blankenship, & Batson, 2003). Just as postconditioning taste extinction devalues the taste → illness association, postconditioning taste inflation involves presenting an additional taste–illness pairing to strengthen the taste → illness association. If a within-compound association is present, the additional taste–illness pairing should strengthen the potentiated odor aversion, relative to controls that received only taste + odor compound conditioning. In these AX+/A+ studies, we demonstrated that following compound conditioning (AX+), postconditioning inflation (A+) of one element (CS A) increased the CR to the other element (CS X). For example, during AX+ conditioning, the bitter taste denatonium saccharide (DEN) was paired with AL odor and followed by the emetic lithium chloride (LiCl). Then, in A+ conditioning, DEN was paired with LiCl. During testing, the AX+/A+ group showed an increased AL aversion, relative to groups that received AX+ or X+ conditioning. This increased aversion to CS X is consistent with the within-compound association model. Additional studies suggested that the within-compound association is bidirectional: Postconditioning inflation of the taste increased the odor aversion (Experiments 1 and 2), and postconditioning inflation of the odor increased the taste aversion (Experiments 3 and 4). Moreover, Batsell et al. (2003) showed that the inflation effect was specific to conditioning of the cue that was used in compound conditioning. In Experiments 2 and 4, use of an AX+/B+ design showed the stimulus specificity of the inflation manipulation, because conditioning to CS X was not affected when a novel stimulus (CS B) received the inflation treatment. For example, in Experiment 4, even though CS A and CS B were similar concentrations of different odors (0.02% AL odor solution and 0.02% orange [ORG] odor solution), an increased CR to the taste was recorded only if its odor associate from AX+ conditioning was inflated. Overall, each of the four experiments reported by Batsell et al. (2003) provided support for the formation of within-compound associations during taste + odor compound conditioning.

Serendipitously, in a follow-up test of our inflation research, we observed that potentiated AL odor aversions and potentiated ORG odor aversions were differentially affected by taste extinction. Following compound conditioning (ORG + DEN conditioning or AL + DEN conditioning) and DEN extinction, the potentiated ORG odor aversion was significantly stronger than the potentiated AL odor aversion. This difference was surprising because we had chosen these two odors on the basis of pilot work that had shown that they produced odor aversions of equal strength.[1] Thus, these data suggest that the strength of potentiated odor aversions may depend on the unique interaction of specific tastes and odors. Moreover, this outcome is of importance because it contradicts a prediction derived from the within-compound association model: If two odors of similar salience are paired with the same taste, this should result in potentiated odor aversions of similar strength. This prediction is based on the premise that the increased responding observed to the potentiated odor is contributed by the indirect taste–illness association. Therefore, two odors that have equivalent odor–illness associations and equivalent taste–illness associations should result in equivalent potentiated odor aversions. It should be noted that there is another possible interpretation of the differences to the potentiated ORG and AL odors following taste extinction, and this alternative interpretation would be consistent with the within-compound association model. Namely, if taste extinction was less effective in the ORG condition, the indirect ORG odor → taste → illness association may have been stronger relative to the indirect AL odor → taste → illness association, and this resulted in the stronger ORG odor aversion.

The present research was initiated to determine whether two odors of equal concentration are differentially susceptible to potentiation by the same taste. If single-element odor conditioning of AL odor and ORG odor solutions produces aversions of similar strength, but conditioning of each odor in compound with the DEN taste results in differential odor aversions, this outcome would suggest that taste + odor interactions influence potentiation, and

it would demonstrate a limitation of the within-compound association model. Because the initial evidence for taste + odor interactions originated from research that used a taste extinction procedure—and the effects of taste extinction may have been the factor that produced the differential responding to the odors—a related purpose of this research was to determine whether potentiated AL and ORG odor aversions are differentially sensitive to the effects of postconditioning taste extinction. The within-compound association model may be supported if differences in the strength of the potentiated odor aversions are observed only after taste extinction or can be attributed to corresponding differences in taste aversions.

EXPERIMENT 1

Method

Subjects and Materials. Sixty-four experimentally naive male albino rats (*Rattus norvegicus*; weight range, 300–415 g) of Holtzman strain were purchased from Harlan Sprague Dawley as subjects. All the rats were housed individually in standard hanging cages (Unifab Corporation, Kalamazoo, MI) and were maintained on a 12:12-h light:dark cycle beginning at 0700 h. The rats had free access to lab Rat Chow (Kaytee Forti-Diet, Chilton, WI). Two weeks prior to the experiment, the rats were placed on a water deprivation schedule consisting of 20-min access to 40 ml of room temperature tap water daily at 1000 h. All fluids were presented in 50-ml plastic drinking tubes with rubber ball bearing stoppers. Liquid consumption was measured to the nearest 0.1 g by comparing the weights of the tubes before and after drinking. All intakes were recorded to the nearest 0.1 g, and we assumed that 1 g = 1 ml. Intakes served to match the subjects into groups.

Table 1 shows the eight groups that were designated according to their treatments. Groups A+ (n = 7 rats) and O+ (n = 7 rats) received single-element odor aversion conditioning. Groups A+/D− (n = 5 rats) and O+/D− (n = 6 rats) received single-element conditioning followed by DEN extinction. Groups DA+ (n = 10 rats) and DO+ (n = 10 rats) received taste + odor compound conditioning. Groups DA+/D− (n = 10 rats) and DO+/D− (n = 9 rats) received compound conditioning followed by DEN extinction. The group mean water intakes ranged from 19.0 to 19.3 ml.

The odor stimuli were solutions of 0.02% Adam's AL extract (Adams Extract, Austin, TX [0.2 cc extract/L of room temperature tap water]) and 0.02% pure ORG extract (Flavorganics, Newark, NJ [0.2 cc extract/L of room temperature tap water]). Previous research has confirmed that a 1% AL odor solution is mediated by its odor properties, not by it taste properties (Rusiniak et al., 1979). The taste stimulus was a 0.01% solution of DEN (0.1 g dissolved in 1 L of room-temperature tap water; Atomergic Chemetals Corporation, Farmingdale, NY). The compound conditioning fluid was a mixture of DEN + AL (0.1 g of DEN and 0.2 cc of AL extract mixed in 1 L of water) or a mixture of DEN + ORG (0.1 g of DEN and 0.2 cc of ORG extract mixed in 1 L of water). The emetic was an isotonic 0.15-M solution of LiCl (12 mg/kg body weight), which was administered via intraperitoneal injection. This concentration of LiCl is the same as that used in many previous investigations of compound conditioning (cf. Batsell & Batson, 1999).

Table 1
Design of Experiment 1

Group	Conditioning	Extinction	Testing
A+	AL–LiCl	Water	AL; DEN
O+	ORG–LiCl	Water	ORG; DEN
A+/D−	AL–LiCl	DEN	AL; DEN
O+/D−	ORG–LiCl	DEN	ORG; DEN
DA+	AL + DEN–LiCl	Water	AL; DEN
DO+	ORG + DEN–LiCl	Water	ORG; DEN
DA+/D−	AL + DEN–LiCl	DEN	AL; DEN
DO+/D−	ORG + DEN–LiCl	DEN	ORG; DEN

Note—AL, 0.02% almond odor solution; ORG, 0.02% orange odor solution; DEN, 0.01% denatonium saccharide solution; LiCl, 0.15 M lithium chloride solution.

Procedure. To allow for comparison with previous experiments from our lab, all experimental procedures occurred in the familiar home cages. The experiment consisted of a 1-day conditioning phase, a 5-day extinction phase, and a 4-day testing phase. The procedures were conducted at 1000 h.

Conditioning was conducted on Day 1. Groups A+ and A+/D− received 10-min access to 10 ml of AL odor solution, and Groups O+ and O+/D− received 10-min access to 10 ml of ORG odor solution. Groups DA+/D− and DA+ received 10-min access to 10 ml of the DEN + AL solution, Groups DO+/D− and DO+ received 10-min access to 10 ml of the DEN + ORG solution. On removal of its drinking tube, each rat received LiCl-induced toxicosis (CS–US interval = 0 min). All the rats received 20-min access to water 4 h later. Day 2 was a recovery day in which all the rats received 20-min access to water at 1000 h.

DEN extinction occurred on Days 3–7. Groups DA+/D−, DO+/D−, A+/D−, and O+/D− received 20-min access to 40 ml of DEN each day. Groups DA+, DO+, A+, and O+ received 20-min access to 40 ml of water. To prevent any dehydration due to low DEN consumption across these trials, all the rats were given their daily water access 4 h after each DEN exposure.

The test phase was conducted on Days 8–11. On Days 8 and 9, Groups A+, A+/D−, DA+, and DA+/D− received a one-bottle test in which the rats were given 20-min access to AL solution. Likewise, Groups O+, O+/D−, DO+, and DO+/D− received 20-min access to ORG solution. A single-bottle test was used because previous research had shown this testing method to be superior to a two-bottle test in detecting aversions of differential strength (Batsell & Best, 1993). Day 10 was a water recovery day. A single DEN test in which all the groups received 20-min access to DEN was conducted on Day 11.

Data analysis. DEN extinction data were analyzed with a 2 × 2 × 5 mixed analysis of variance (ANOVA) with type of odor (AL vs. ORG), type of conditioning (single element vs. compound), and trials (1–5) as factors in order to determine whether there were differences between AL and ORG groups during DEN extinction. Three 2 × 2 × 2 factorial ANOVAs with odor, type of conditioning, and type of extinction (DEN extinction vs. no extinction) were conducted on the intakes from the first odor test, the second odor test, and the taste test. Because we were uncertain whether the triple interaction would occur, two planned comparisons (t tests) were set prior to the experiment. A comparison of Groups A+ and O+ was conducted to determine whether the single-element odor aversions differed, and a comparison of Groups DA+ and DO+ was conducted to determine whether the potentiated odor aversions differed. The statistical significance criterion was set at .05 for all the analyses.

Results and Discussion

Conditioning. During the conditioning, all the groups drank similar amounts: Group DA+/D− drank 7.0 ml and Group DA+ drank 6.2 ml of the DEN + AL solution. Group DO+/D− drank 5.7 ml and Group DO+ drank 5.1 ml of the DEN + ORG solution. Group A+/D− drank 7.8 ml and Group A+ drank 8.6 ml of the AL solution, and Group O+/D− and Group O+ both drank 8.3 ml of the ORG solution. Due to a procedural error, there were 8 animals in Group A+ and 6 animals in Group O+.

Extinction. Figure 1 shows the mean DEN intakes across the five extinction trials. As can be seen, some group differences in DEN intake were evident during the initial trials. As compared with the single-element odor groups, groups that received taste + odor during conditioning (DA+/D− and DO+/D−) showed reduced DEN consumption. After five trials, however, all the groups were drinking similar amounts of DEN. Mean intakes for the final extinction trial were as follows: DA+/D−, 17.4 ml; DO+/D−, 16.8 ml; A+/D−, 16.8 ml; and O+/D−, 18.1 ml.

A 2 × 2 × 5 mixed ANOVA was performed for the DEN extinction groups with odor, conditioning, and trials as factors. There was a significant conditioning effect [$F(1,26) = 9.2$], whereby single-element groups drank significantly more DEN than compound groups did. This was expected, due to DEN conditioning for the compound groups. The trial effect was also significant [$F(4,104) = 33.3$], whereby intakes increased over subsequent trials. There was no significant effect of odor [$F(1,26) < 1$], signifying that DEN consumption was equivalent for both AL groups and ORG groups. No interactions for factors were statistically significant [odor × conditioning, $F(1,26) < 1$; odor × extinction, $F(4,104) < 1$; conditioning × extinction, $F(4,104) = 2.2$; and odor × conditioning × extinction, $F(4,104) < 1$].

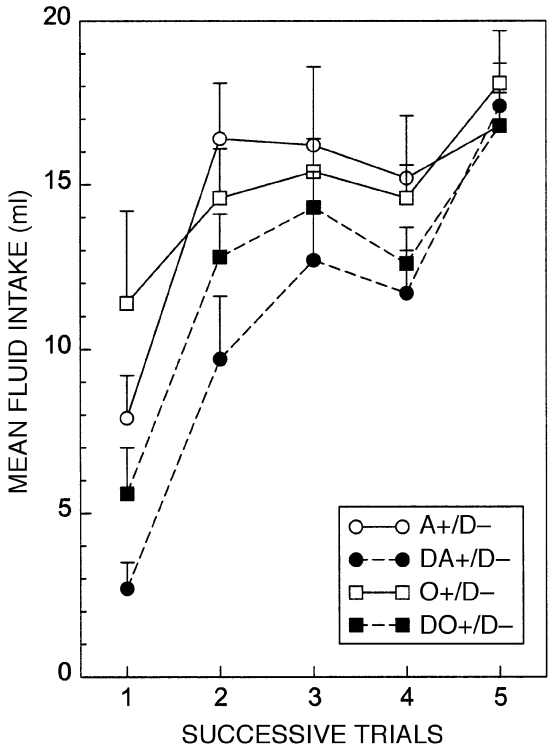

Figure 1. Mean (+*SE*) denatonium saccharide solution (DEN) intake in milliliters across the five extinction trials in Experiment 1. Prior to DEN extinction, Group A+/D− received an AL–LiCl pairing, Group O+/D− received an ORG–LiCl pairing, Group DA+/D− received an AL + DEN–LiCl pairing, and Group DO+/D− received an ORG + DEN–LiCl pairing. AL, 0.02% almond odor solution; ORG, 0.02% orange odor solution.

Odor testing. Figure 2 shows the mean AL odor solution and the mean ORG odor solution consumed on Odor Test 1. There are three notable features depicted in Figure 2. First, there is a pronounced effect of DEN extinction for the groups that received compound conditioning: Group DA+/D− drank much more AL odor solution than Group DA+ did, and Group DO+/D− drank much more ORG odor solution than Group DO+ did. Second, a comparison of Groups A+ and O+ shows that they drank similar amounts of their respective solutions. Third, differences were evident between the compound conditioning groups: Group DO+ drank less of the ORG odor solution than Group DA+ drank of the AL odor solution.

A 2 × 2 × 2 factorial ANOVA conducted on the Test 1 intakes, with odor, conditioning, and extinction as factors, confirmed these interpretations. The extinction effect was significant [$F(1,56) = 14.8$], and the extinction × conditioning interaction was significant [$F(1,56) = 10.3$]. This significant interaction was explored further with an analysis of simple effects, using the overall error term. The simple effects analyses confirmed that there was no effect of conditioning within the extinction groups ($F < 1$) but that there was a significant effect of conditioning in the no-extinction groups [$F(1,56) = 14.7$]. The latter difference demonstrates the significant potentiation effect in the no-extinction condition in which the taste + odor groups drank less odor solution than the single-element odor groups. Furthermore, there was no effect of extinction on the single-element groups ($F < 1$), but there was a significant effect of extinction on the taste + odor groups [$F(1,56) = 32.4$]. Following compound conditioning, DEN extinction increased consumption of both odor solutions: Group DA+/D− drank more AL odor solution than Group DA+ did, and Group DO+/D− drank more ORG odor solution than Group DO+ did.

The effect of odor was significant [$F(1,56) = 7.5$]. Although the conditioning effect did not surpass the statistical criterion [$F(1,56) = 3.8$, $p = .06$], the odor × conditioning interaction was significant [$F(1,56) = 5.4$]. There was no effect of odor within the single-element groups ($F < 1$), but there was a significant effect of odor in the taste + odor groups [$F(1,56) = 16.6$]. The two planned comparisons clarified the differences in the no-extinction groups. There was no significant difference in odor solution consumption between the single-element odor conditioning groups (Group A+ = Group O+). There was, however, a significant difference in odor solution consumption between the compound conditioning groups: Group DA+ drank significantly more odor solution than Group DO+ did. Thus, these comparisons indicate that single-element conditioning of these odors produces aversions of similar strength but that compound conditioning results in potentiated odor aversions of differential strength. Finally, the odor × extinction interaction [$F(1,56) = 3.4$] and the odor × conditioning × extinction interaction [$F(1,56) < 1$] were not significant.

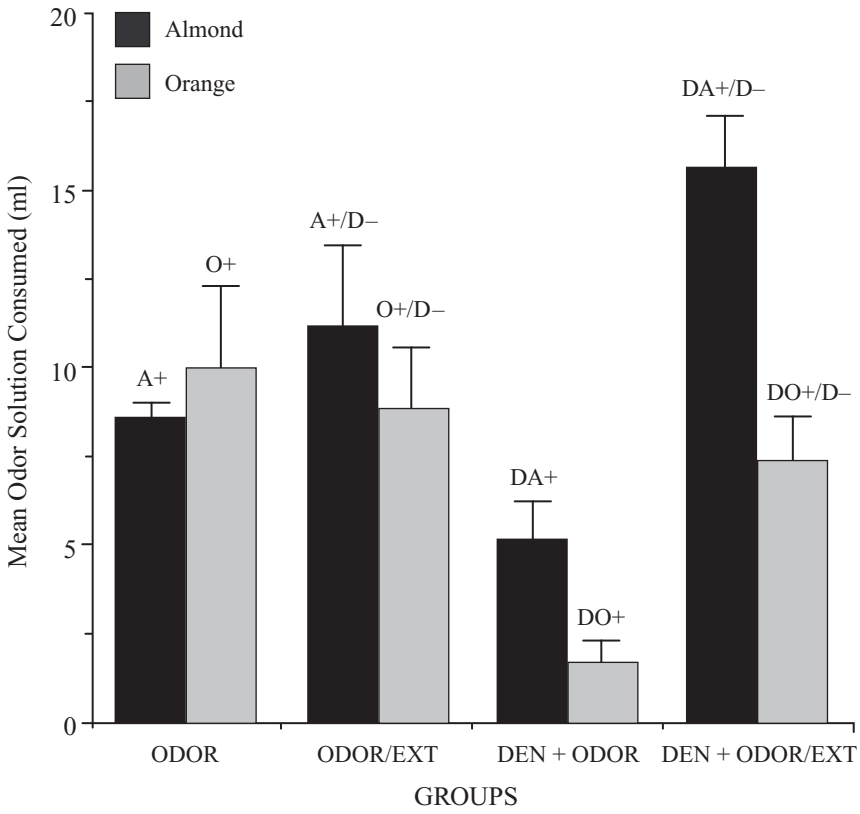

Figure 2. Mean (+*SE*) almond (AL) odor solution intake and orange (ORG) odor solution intake in milliliters on Odor Test 1 in Experiment 1. Group A+ received an AL–LiCl pairing, and Group O+ received an ORG–LiCl pairing. Group A+/D− received an AL–LiCl pairing followed by five denatonium saccharide (DEN) solution extinction trials. Group O+/D− received an ORG–LiCl pairing followed by five DEN extinction trials. Group DA+ received an AL + DEN–LiCl pairing, and Group DO+ received an ORG + DEN–LiCl pairing. Group DA+/D− received an AL + DEN–LiCl pairing followed by five DEN extinction trials. Group DO+/D− received an ORG + DEN–LiCl pairing followed by five DEN extinction trials.

On the second odor test, all the groups' intakes increased due to extinction of the odor aversions. All the groups drank similar amounts except Group DO+, whose consumption remained low (M = 7.9 ml). The means were as follows: Group DA+/D− drank 18.0 ml, Group DO+/D− drank 14.1 ml, Group DA+ drank 15.7 ml, Group A+/D− drank 15.9 ml, Group O+/D− drank 14.8 ml, Group A+ drank 17.1 ml, and Group O+ drank 15.1 ml. A 2 × 2 × 2 factorial ANOVA with odor, conditioning, and extinction as factors revealed a significant odor effect [$F(1,56) = 9.4$] and a significant conditioning × extinction interaction [$F(1,56) = 4.3$]. The conditioning effect within the no-extinction condition remained significant ($F = 7.1$), as did the extinction effect in the taste + odor conditioning groups ($F = 8.2$). These significant effects appear to have been driven by the potentiated ORG odor aversion in Group DO+. Indeed, the planned comparisons on the second odor test replicated the group differences observed during the initial test. Finally, no other main effects or interactions were significant.

This experiment was conducted to determine whether aversions to AL odor and ORG odor differed following single-element conditioning, compound conditioning with DEN, and compound conditioning with and extinction of DEN. The results of the single-element odor groups suggest there are no differences between AL conditioning and ORG conditioning. The data show that potentiated ORG odor aversions were stronger than potentiated AL odor aversions, both following DEN extinction and without DEN extinction. Therefore, the hypothesis that ORG odor may be resistant to the effects of taste extinction is wrong. Instead, the data clearly show that when AL and ORG odors are conditioned in compound with DEN, potentiation occurs, but it is stronger with ORG + DEN. Thus, it appears that ORG and DEN interact in a unique way to produce the stronger CR to ORG than the CR to AL produced by AL + DEN conditioning.

Taste testing. Figure 3 shows the mean DEN intakes during the taste test. Single-element groups that had no prior DEN exposure (Groups A+ and O+) drank similar

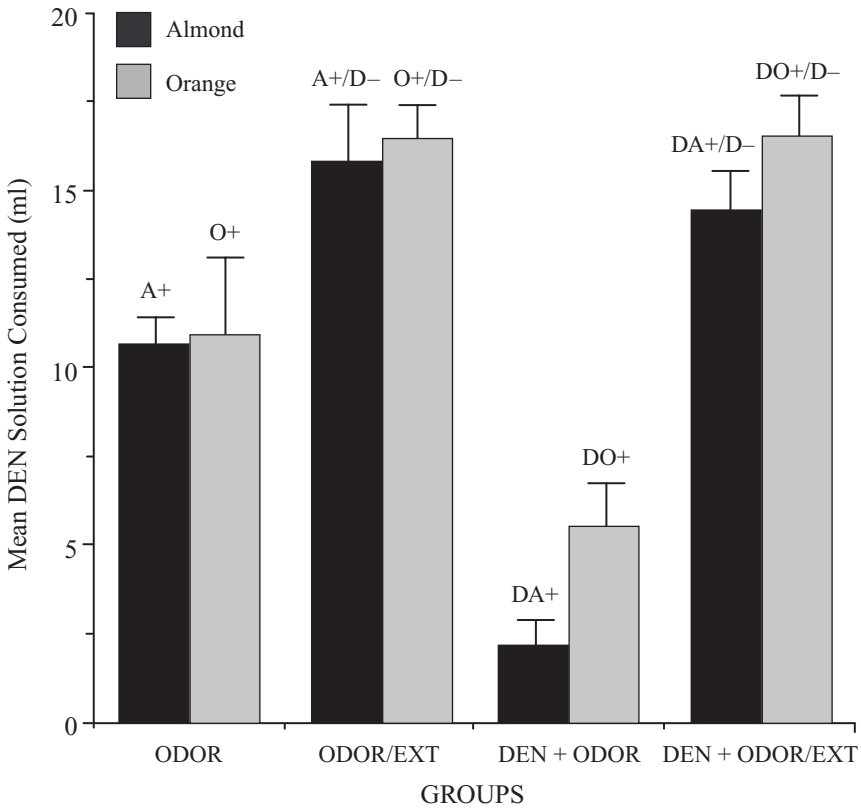

Figure 3. Mean (+*SE*) denatonium saccharide solution (DEN) intake in milliliters in Experiment 1. Group A+ received an AL–LiCl pairing, and Group O+ received an ORG–LiCl pairing. Group A+/D− received an AL–LiCl pairing followed by five DEN extinction trials. Group O+/D− received an ORG–LiCl pairing followed by five DEN extinction trials. Group DA+ received an AL + DEN–LiCl pairing and Group DO+ received an ORG + DEN–LiCl pairing. Group DA+/D− received an AL + DEN–LiCl pairing followed by five DEN extinction trials. Group DO+/D− received an ORG + DEN–LiCl pairing followed by five DEN extinction trials. AL, 0.02% almond odor solution; ORG, 0.02% orange odor solution.

amounts, and single-element groups that had received nonreinforced DEN exposure (Groups A+/D− and O+/D−) drank similar amounts. It appears that neophobia of the novel DEN was responsible for the lower DEN consumption in Groups A+ and O+, as compared with Groups A+/D− and O+/D−. The compound conditioning groups, however, showed differential DEN consumption: The groups that had been conditioned with AL drank less than the groups conditioned with ORG, and in particular, Group DA+ drank less than Group DO+.

To determine whether there were differences in DEN consumption, a 2 × 2 × 2 factorial ANOVA was performed with odor, conditioning, and extinction as factors. As was expected, the groups that received DEN extinction drank significantly more DEN than the no-extinction groups [$F(1,56) = 99.7$]. There was also a predicted conditioning effect [$F(1,56) = 19.2$], whereby the single-element groups drank significantly more than the compound groups. The only statistically significant interaction was for conditioning × extinction [$F(1,56) = 13.6$]. Simple effects analyses confirmed that there were no differences in DEN consumption across the extinction groups ($F < 1$) but that there were differences in DEN consumption across the no-extinction groups [$F(1,56) = 35.9$]. As was expected, the compound conditioning groups (Groups DA+ and DO+), which had DEN during conditioning, drank significantly less than the single-element groups (Groups A+ and O+), which had not experienced DEN. The planned comparisons confirmed that Group DA+ drank significantly less DEN than Group DO+ did, but no differences in DEN consumption were seen between Groups A+ and O+. No other main effects or interactions were significant.

Taken together, the odor and taste results of Experiment 1 point to the unique interactions between tastes and odors in compound aversion conditioning. Although the results following the extinction manipulation are consistent with the within-compound association model, the odor and taste results of Groups DA+ and DO+ do not fit well with this model. According to the within-compound association approach, the strong CR to a potentiated odor is produced by the direct odor → US associ-

ation and the indirect odor → taste → US association. Therefore, if one infers from the results of Groups O+ and A+ that the direct ORG → US association and AL → US association are of equal strength, the differences in responding between Groups DA+ and DO+ must be due to the indirect odor → taste → US pathway. Specifically, the DEN → US association should be stronger in Group DO+ to produce the stronger CR to ORG. The taste test reveals that this was not the case. In fact, it is notable that even though a robust DEN aversion was present in Group DA+, Group DA+ had a very weak AL aversion on the second odor test.

Even though the within-compound association model cannot account for the results of Experiment 1, an alternative elemental approach could still accommodate the differences in taste-potentiated odors. For example, in consideration of the results of Groups DA+ and DO+, if one assumes that DEN masked the presence of AL odor more than DEN masks ORG odor, the salience of AL in compound could be weaker than the salience of ORG in compound. Then, according to compound-conditioning rules similar to those of the Rescorla–Wagner model, this difference in odor salience could account for the differences in responding to the potentiated odor aversions. This interpretation, however, is problematic when one considers the differences in DEN consumption between Groups DA+ and DO+. Although an elemental model would predict that a more salient odor cue (e.g., ORG) should produce greater DEN overshadowing than a less salient odor cue (e.g., AL), elemental models of associative learning do not predict one-trial overshadowing (for a review, see Pearce & Bouton, 2001). Instead, an elemental model would predict equivalent DEN aversions in Groups DA+ and DO+ following a single conditioning trial. Because reliable differences in DEN consumption were observed between these groups following a single taste + odor conditioning trial, it appears that this alternative elemental interpretation is not plausible.

The demonstration that potentiation is influenced by specific taste + odor interactions is anticipated by a configural account of potentiation. In 1981, Rescorla proposed an alternative conception of potentiation in terms of a *configuration* of the taste and odor into a unitary stimulus. Because this unitary stimulus would be made up of two stimuli, its salience would be greater than the salience of each stimulus. During testing of one of the elements (e.g., odor), the rat would confuse the odor for the compound, and a strong CR would be recorded. The strength of the CR to the odor would reflect the generalization decrement from the taste + odor compound to that specific odor, which would be greater than the CR in the odor-alone control group. If this configural approach is applied to the results of Experiment 1, one might surmise that the generalization from the ORG + DEN compound to ORG is greater than the generalization from the AL + DEN compound to AL.

There are various advantages to adopting a configural approach to explain potentiation. First, a configural model such as that of Pearce (2002) can account for both competitive conditioning (i.e., overshadowing) and synergistic conditioning (i.e., potentiation) through the same mechanism. Following compound conditioning, responding to either element of the compound is mediated by stimulus generalization from the compound. If the generalization from the compound to the element is strong, the resulting aversion will be stronger than the single-element conditioning (i.e., potentiation). However, if the generalization from the compound to the element is weak, the resulting aversion will be weaker than single-element conditioning (i.e., overshadowing). Although many researchers have discounted the role of generalization in producing taste-mediated potentiation (e.g., Bowman, Batsell, & Best, 1992), in those studies, only generalization from the taste to the odor, not that from the compound to the odor, was looked at. Second, a configural account of potentiation is consistent with many of the conditions that have been shown to be necessary for the production of potentiation, such as mode of stimulus presentation and the *salience rule* (for a more extensive review of the conditions that produce potentiation, see Batsell & Blankenship, 2003). For example, numerous studies have confirmed that potentiation occurs only when the cues are presented simultaneously (e.g., Batsell et al., 2001; Holder & Garcia, 1987; Kucharski & Spear, 1985), rather than sequentially. Although the requirement for simultaneous presentation of stimuli is not unique to the configural approach, evidence of potentiation with sequential stimulus presentation would be inconsistent with the configural account of potentiation. Also, it has been noted that potentiation appears to follow a salience rule, in which potentiation is observed when a strong stimulus is paired with a weaker stimulus (e.g., Bouton et al., 1986; Slotnick et al., 1997). The salience rule is compatible with a configural account because the stimuli concentrations must be presented in a specific combination for the cues to be configured into a unitary stimulus.

Even though the configural account can accommodate many of the findings in the potentiation literature, there has been only one empirical assessment of configural associations in potentiation. In 1985, Kucharski and Spear investigated conditioning of a two-taste compound with preweanling rats and adult rats. They showed that in preweanling rats, nonreinforced exposure to one element of the compound did not affect the aversion to the compound. That is, groups that received compound conditioning (sucrose + coffee) followed by brief extinction of an element (either sucrose or coffee) retained an aversion to the compound. In terms of the configural association model, Kucharski and Spear argued that the extinction phase helped the rats discriminate the extinguished taste from the compound stimulus. Thus, the compound was still aversive during the testing phase. Furthermore, Kucharski and Spear showed that the preweanling rats that had experienced extinction of the compound drank more of the compound during testing than did the rats

that experienced separate extinction of both elements of the compound. The configural association model explains this as well, in that an organism perceives the compound not as a summation of the elements that make up the compound, but as an entirely separate stimulus in itself. Unfortunately, when Kucharski and Spear tested similar manipulations in adult rats, they did not find statistically significant evidence in support of a configural interpretation.

Experiments 2 and 3 were designed to test the concept of taste + odor interactions and predictions derived from a configural account of potentiation. First, if taste + odor interactions were the source of the differences in potentiated ORG and AL odor aversions in Experiment 1, this could be confirmed by examining the effects of element extinction on the aversion to the compound. In other words, if the ORG + DEN compound is perceived by the rat as being more similar to the ORG component than to the DEN component, ORG extinction should reduce the CR to the compound more than DEN extinction does. On the other hand, if the AL + DEN compound is perceived by the rat to be equally made up of the two components, DEN extinction and AL extinction should produce similar effects. Second, similar to the procedures of Kucharski and Spear (1985), testing of the compound can occur following extinction of the separate elements or the compound. According to the configural association model of Pearce (2002), extinction of the separate elements of the compound should have less of an effect on responding to the compound, relative to the extinction of the compound cue. These two predictions were tested in Experiments 2 and 3: Experiment 2 tested interactions of ORG + DEN, and Experiment 3 tested interactions of AL + DEN.

EXPERIMENT 2

Method

Subjects, Materials, and Procedure. Forty-seven experimentally naive male rats (weight range, 290–350 g) of the same strain and supplier as those in Experiment 1 served as subjects. All housing, feeding, and water deprivation manipulations were the same as those described in the previous experiment. The stimuli (DEN, ORG, DEN + ORG, and LiCl) were the same concentrations as those used in Experiment 1. All conditioning, extinction, and testing manipulations occurred at 1000 h in the rats' home cages. The 47 rats were matched to one of five groups on the basis of their mean water intakes for a 7-day period prior to conditioning. Group means ranged from 18.5 to 18.9 ml. Groups T−, O−, and OT− each had 10 rats, Group O−/T− had 9 rats, and Group W− had 8 rats.

Table 2 shows the five groups designated according to their extinction treatments. Conditioning was conducted on Day 1. All the rats received the same conditioning treatment consisting of 10-min access to 10 ml of the DEN + ORG solution. Immediately after removal of the drinking tube, each rat received a LiCl injection. Day 2 was a water replacement day.

Extinction occurred on Days 3–7. To facilitate comparison of results across experiments, we chose to use the same extinction procedure as that utilized in Experiment 1 (20-min daily access across 5 days). One additional advantage of this procedure was that it allowed for detection of group differences across the extinction period. It should be noted that Kucharski and Spear (1985) used a different extinction method in which rats were given very brief exposures (cf. 10 exposures to 2 ml of the extinguished taste across 5 days).

Table 2
Design of Experiment 2

Group	Conditioning	Extinction	Testing
T−	DEN + ORG	DEN	DEN + ORG
O−	DEN + ORG	ORG	DEN + ORG
OT−	DEN + ORG	DEN + ORG	DEN + ORG
O−/T−	DEN + ORG	DEN // ORG	DEN + ORG
W−	DEN + ORG	Water	DEN + ORG

Note—ORG, 0.02% orange odor solution; DEN, 0.01% denatonium saccharide solution.

Five extinction trials were conducted consisting of 20-min access to 30 ml of the respective solution. Group OT− received the ORG + DEN compound, Group O− received ORG odor solution, Group T− received DEN, and Group W− received water on each extinction trial. Group O−/T− received separate, consecutive 10-min odor exposure and 10-min taste exposure, counterbalanced across 4 days. In other words, on Extinction Trial 1, half of Group O−/T− had 10-min access to ORG odor solution, followed immediately by 10-min access to DEN. The other half of Group O−/T− had 10-min access to DEN, followed by 10-min access to ORG odor solution. The rats given ORG followed by DEN on Trial 1 were given DEN followed by ORG on Extinction Trial 2, and vice versa. Counterbalancing was repeated on Extinction Trials 3 and 4. The use of this procedure provided a convenient within-subjects analysis of the generalization of the DEN + ORG compound to DEN and ORG. As will be noted in the Results and Discussion section, because ORG consumption was significantly lower than DEN consumption across the first four trials, the counterbalancing procedure was discontinued on the fifth extinction trial. On the fifth trial, the rats in Group O−/T− were given 10-min access to ORG odor solution before 10-min access to DEN, in order to equate DEN and ORG consumption before compound testing.

Testing occurred on Day 8. All the groups were tested with the ORG + DEN compound. Testing consisted of a single-bottle test of 20-min access to 30 ml of the compound solution.

Data analysis. A 5 × 5 mixed ANOVA was performed with groups and trials as factors to determine the effects of extinction. Also, a 2 × 4 within-subjects ANOVA with modality (odor or taste) and extinction trials as factors was used to determine whether modality played a significant role in extinction in Group O−/T−. A one-way ANOVA was conducted on the test intakes of the five groups to determine differences in consumption levels of the ORG + DEN compound.

Results and Discussion

Conditioning. During conditioning, all the groups drank similar amounts of the ORG + DEN compound. Mean intakes were as follows: Group OT− drank 7.7 ml, Group O− drank 6.8 ml, Group T− drank 7.4 ml, Group O−/T− drank 6.5 ml, and Group W− drank 7.5 ml.

Extinction. Figure 4 shows the mean fluid intakes over the five extinction trials. As expected, Group OT− showed the same extinction trend as the other extinction groups, but this trend progressed at lower consumption levels. That is, it showed the strongest aversion on all trials. Groups O−/T−, O−, and T− showed similar consumption levels relative to each other across trials, and thus, showed similar extinction patterns. Group W− showed a consistent water intake across the five trials.

In order to determine the effects of extinction, a 5 × 5 mixed ANOVA was performed with groups and trials as

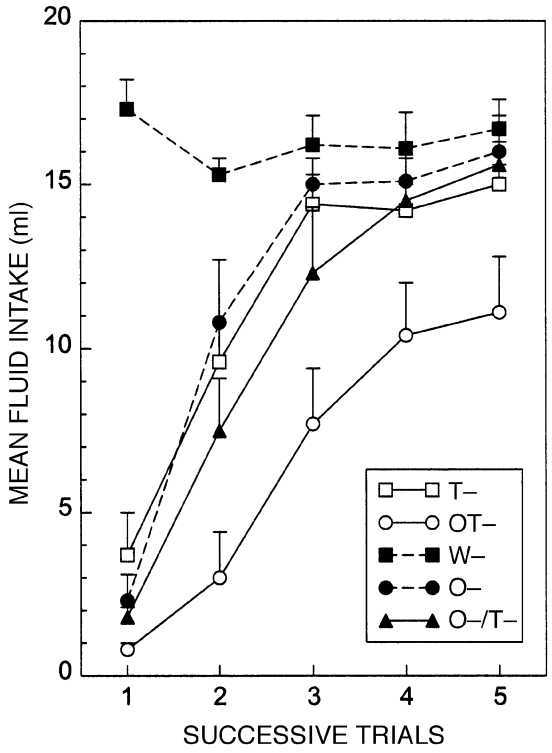

Figure 4. Mean (+*SE*) fluid intake in milliliters across the five extinction trials in Experiment 2. All the groups received an ORG + DEN–LiCl pairing before extinction. During extinction, Group W− received water, Group O− received ORG odor solution, Group T− received DEN solution, and Group OT− received the ORG + DEN compound solution. Group O−/T− received counterbalanced presentations of ORG odor solution and DEN solution. DEN, denatonium saccharide solution; ORG, 0.02% orange odor solution.

factors. This ANOVA yielded a significant group effect [$F(4,40) = 14.8$], a significant trials effect [$F(4,160) = 107.4$], and a significant groups × trials interaction [$F(16,160) = 8.8$]. Separate one-way ANOVAs were conducted for each extinction trial in order to determine relative differences in consumption between groups on each trial. On Trial 1, the group effect was significant [$F(4,40) = 66.4$]. Student Newman–Keuls tests revealed that Group W− differed from all the other groups and that Group OT− was significantly different from Group T−. On Trial 2, the group effect was significant [$F(4,40) = 8.5$]; subsequent SNK tests revealed that Group W− differed from all the other groups and that Group T− and Group O− differed from Group OT−. On Trial 3, the group effect was significant [$F(4,40) = 4.5$]. SNK tests revealed that Group W− differed from all the other groups and that Group OT− differed from all other groups except Group O−/T−. The group effects on Trials 4 and 5 were not significant [$F(4,40) = 1.2$ and $F(4,40) = 2.1$, respectively].

The extinction trials of Group O−/T− provided an interesting within-subjects comparison of ORG and DEN following compound conditioning. Because ORG and DEN were presented in a counterbalanced order over the first four extinction trials, these trials were analyzed. A 2 × 4 ANOVA with stimulus (ORG vs. DEN) and trials as factors confirmed significant effects of stimulus [$F(1,16) = 7.9$] and trials [$F(3,48) = 9.6$]; the stimulus × trials interaction was not significant [$F(3,48) = 1.5$]. In terms of the significant stimulus effect, mean ORG consumption ($M = 2.8$ ml) was significantly less than mean DEN consumption ($M = 6.2$ ml), suggesting that the ORG component of the compound was more aversive than the DEN component. That is, the rat may have perceived the ORG odor solution to be more perceptually similar to the ORG + DEN compound than was DEN.

Testing. Figure 5 shows the mean ORG + DEN fluid intakes of the five groups. It can be seen that Group W− consumed the least, Group T− consumed a moderate amount, and Groups O−, O−/T−, and OT− drank similar high amounts of the compound. A one-way ANOVA conducted on the intakes revealed a significant group effect [$F(4,44) = 25.8$]. SNK tests showed that Group W− was significantly different from all the other groups. Furthermore, Group T− drank significantly less than Groups O−/T−, O−, and OT−. The comparatively low consumption level of Group T− is informative. Because the compound aversion was weakened less by DEN extinction, relative to ORG extinction, it suggests that the odor may be the more identifiable component of the compound. This conclusion is bolstered by the observation that the compound aversion in Group O− was similar to the compound aversion in Group OT−. Indeed, both of these results are consistent with the extinction results of Group O−/T−, which demonstrated a stronger aversion to the ORG component following DEN + ORG conditioning.

The other comparison of note was between Groups OT− and O−/T−: There was no significant difference in consumption of the compound between these groups. On the basis of the configural model and previous results with preweanling rats from Kucharski and Spear (1985), Group OT− was predicted to show greater consumption than Group O−/T−. Although reliable differences between Groups OT− and O−/T− may be obscured by a ceiling effect produced by the extensive extinction used in the present study, our data are consistent with the results from adult rats reported by Kucharski and Spear.

The results of Experiment 2 indicate that the ORG odor component, not the DEN taste, is more perceptually similar to the ORG + DEN compound. This interpretation is consistent with the results of Experiment 1 that showed that ORG conditioned in compound with DEN was more aversive than AL conditioned in compound with DEN. Extrapolating from the AL results of Experiment 1, it was predicted that rats would be less likely to "confuse" AL with the AL + DEN compound. Therefore, AL extinction would be less effective in reducing the CR to the compound, relative to compound extinction.

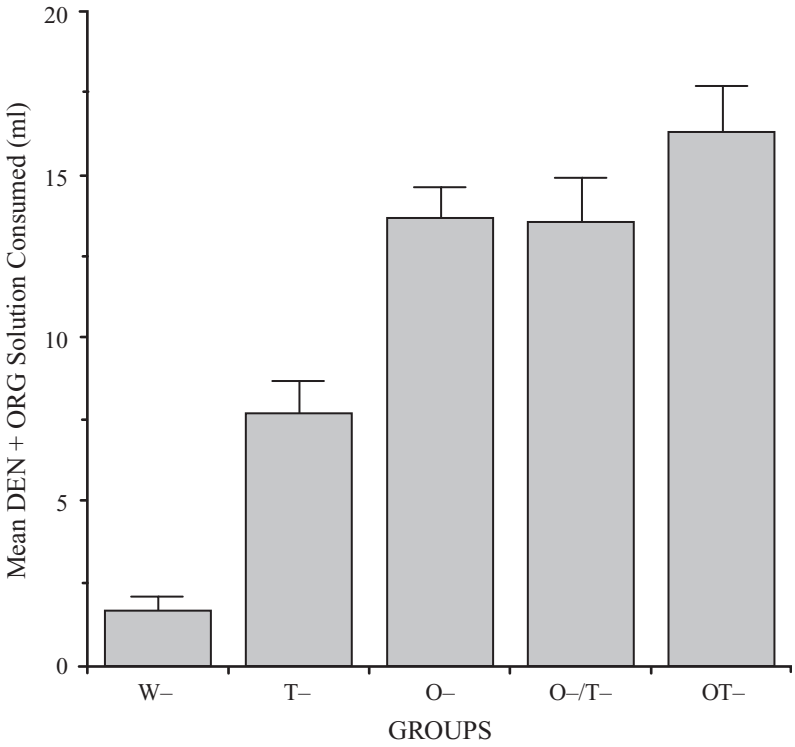

Figure 5. Mean (+*SE*) ORG + DEN compound solution intake in milliliters in Experiment 2. All the groups received an ORG + DEN–LiCl pairing before extinction. During extinction, Group W− received water, Group O− received ORG odor solution, Group T− received DEN solution, and Group OT− received the ORG + DEN compound solution. Group O−/T− received counterbalanced presentations of ORG odor solution and DEN solution. DEN, denatonium saccharide solution; ORG, 0.02% orange odor solution.

EXPERIMENT 3

Method

Subjects, Materials, and Procedure. Fifty experimentally naive male rats (weight range, 300–385 g) of the same strain and supplier as those in Experiment 1 served as subjects. Feeding, housing, and the water deprivation schedule were the same as those in the previous experiments. The stimuli (DEN, AL, DEN + AL, and LiCl) were the same concentrations as those used in Experiment 1. The subjects were matched into one of five groups based on 7 days of water consumption during a water deprivation schedule consisting of 20-min access to 20 ml daily. Each group consisted of 10 rats. The group means ranged from 18.8 to 18.9 ml.

The design was the same as that used in Experiment 2 (see Table 2); however, 0.02% AL was used in place of 0.02% ORG. On Day 1, all the groups received compound conditioning of the AL + DEN compound. Extinction trials were the same as those in Experiment 2, with the exception of the fifth extinction trial for Group O−/T− on Day 7. Because differences in fluid intake were not evident in Group O−/T− across the first four extinction trials, counterbalancing of the odor and the taste occurred on Extinction Trial 5 for Group O−/T−. Testing consisted of 20-min access to 30 ml of the AL + DEN compound solution on Day 8.

Results and Discussion

Conditioning. During conditioning, all the groups drank similar amounts of the AL + DEN compound. Mean intakes were as follows: Group OT drank 5.9 ml, Group O− drank 5.9 ml, Group T− drank 6.6 ml, Group O−/T− drank 6.5 ml, and Group W− drank 6.3 ml.

Extinction. Figure 6 shows the mean fluid intakes over the five extinction trials. As was expected, Group W− showed high consumption across all the trials, whereas the other groups showed a gradual increase in consumption over the first three trials and leveled off by Trial 5. In order to determine the effects of extinction, a 5 × 5 mixed ANOVA was performed with groups and trials as factors. This ANOVA yielded a significant group effect [$F(4,45) = 13.4$], a significant trials effect [$F(4,180) = 108.6$], and a significant groups × trials interaction [$F(16,180) = 8.9$]. Thus, separate one-way ANOVAs were conducted for each extinction trial in order to determine relative differences in consumption between groups on each trial.

On Trial 1 the group effect was significant [$F(4,45) = 35$]. A SNK test revealed that only Group W− differed from the other groups. On Trials 2 and 3, the group effect was significant [$F(4,44) = 10.1$ and $F(4,45) = 4.7$, respectively]. SNK tests revealed that only Group OT− differed from all the other groups on Trials 2 and 3. The group effects on Trial 4 and Trial 5 were not significant [$F(4,45) = 2.4$ and $F(4,45) = 1.2$, respectively].

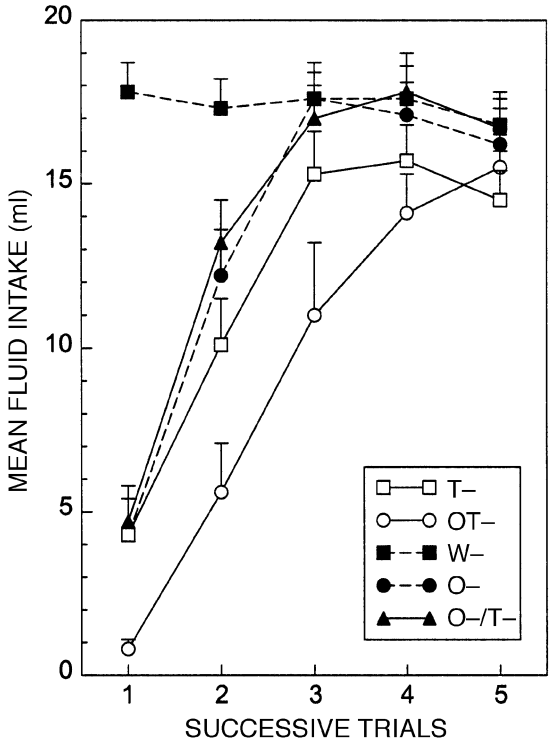

Figure 6. Mean (+*SE*) fluid intake in milliliters across the five extinction trials in Experiment 3. All the groups received an AL + DEN–LiCl pairing before extinction. During extinction, Group W− received water, Group O− received AL odor solution, Group T− received DEN solution, and Group OT− received the AL + DEN compound solution. Group O−/T− received counterbalanced presentations of AL odor solution and DEN solution. DEN, denatonium saccharide solution; AL, 0.02% almond odor solution.

Similar to Experiment 2, a 2 × 5 ANOVA with stimulus (DEN vs. AL) and trials as factors was conducted on the extinction data of Group O−/T−. There was the expected significant trials effect [$F(4,36) = 23$], but the stimulus effect [$F(1,9) < 1$], and the stimulus × trials interaction [$F(4,36) < 1$] were not statistically significant. When AL and DEN made up the compound, generalization to each element of the compound was equivalent (AL, mean = 7.1 ml; DEN, mean = 6.7 ml).

Testing. Figure 7 shows the mean AL + DEN intakes during testing. Group W− consumed the least, Groups O− and T− drank moderate amounts, and Groups O−/T− and OT− drank large amounts of the AL + DEN compound. A one-way ANOVA yielded a significant group effect [$F(4,45) = 31.6$]. As was expected, SNK tests showed that Group W− was statistically different from all the other groups. In regard to Group T− and Group O−, consumption levels were similar and were significantly less than those for Group OT− and Group O−/T−. In contrast to Experiment 2, it appears that extinguishing AL produced an aversion to the compound that was similar in strength to that produced by extinguishing DEN and that the effects of AL extinction were less than the effects of extinction of the compound. Also, the extinction data of Group O−/T− showed that AL and DEN produced similar decrements in consumption across the extinction trials. Thus, it can be inferred that the AL + DEN compound appears to be made up equally of AL and DEN components.

Post hoc SNK tests also showed that Group OT− and Group O−/T− were statistically different from all the other groups except each other, an outcome similar to that with DEN and ORG in Experiment 2. Thus, in neither Experiment 2 nor 3 was there any evidence that separate extinction of the elements of the compound produced a weaker CR to the compound, relative to extinction of the compound itself. In fact, these outcomes are consistent with those reported with adult rats by Kucharski and Spear (1985), who found no differences in consumption of a two-taste compound following compound extinction or separate extinction.

GENERAL DISCUSSION

The results of three experiments provided evidence that unique taste + odor interactions influence the strength of potentiated odor aversions. Experiment 1 demonstrated that single-element AL and ORG odor aversions were of similar strength but that, when each odor was conditioned in compound with DEN, a potentiated ORG odor aversion was significantly stronger than a potentiated AL odor aversion. Furthermore, the results of Experiment 1 showed that following compound conditioning, taste extinction weakened both the potentiated AL odor aversion and the potentiated ORG odor aversion. The effects of compound extinction or element extinction on compound conditioning were assessed in Experiments 2 and 3. Experiment 2 showed that following ORG + DEN compound conditioning, ORG odor extinction weakened the CR to the compound more so than extinction of DEN did. In contrast, Experiment 3 showed that following AL + DEN compound conditioning, AL extinction and DEN extinction equally decremented the aversion to the compound. Finally, in both Experiments 2 and 3, there were no differences in the resulting compound aversions following extinction of the compound or separate extinction of the elements of the compound. The present results suggest that even when taste concentration (and conditionability) is equivalent, how the rat perceives unique taste + odor compounds can influence the strength of potentiated odor aversions, and this has implications for theoretical accounts of potentiation.

The collective results of these experiments suggest how the ORG + DEN compound and the AL + DEN compound influence responding. It appears that when ORG odor and DEN are conditioned in compound, the compound stimulus is relatively similar to the ORG solution alone. Therefore, when ORG odor is tested alone (Group DO+ in Experiment 1), there is a substantial amount of generalization from the compound to the odor, and a strong CR is recorded. In contrast, when the taste

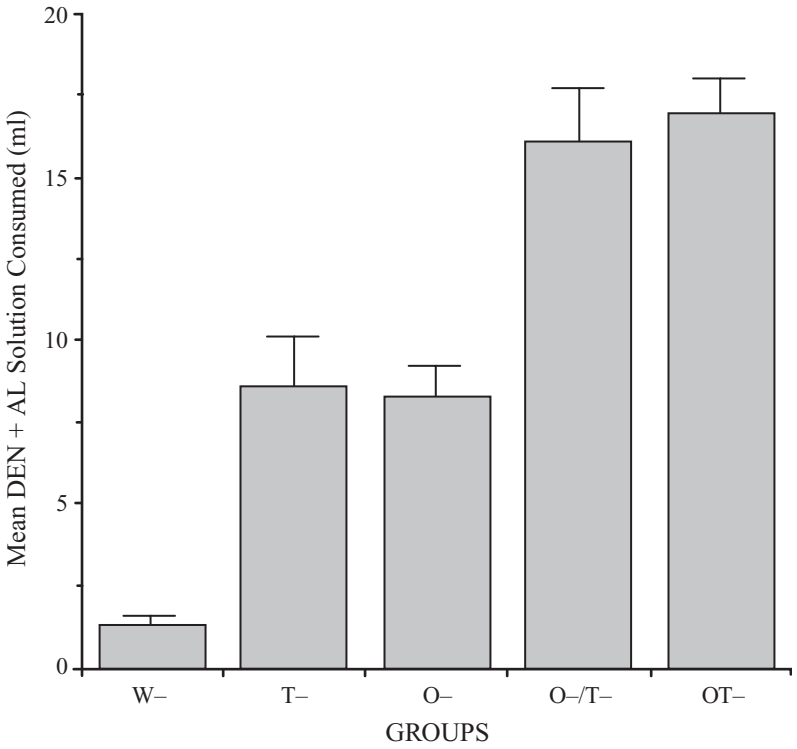

Figure 7. Mean (+*SE*) AL + DEN compound solution intake in milliliters in Experiment 3. All the groups received an AL + DEN–LiCl pairing before extinction. During extinction, Group W− received water, Group O− received AL odor solution, Group T− received DEN solution, and Group OT− received the AL + DEN compound solution. Group O−/T− received counterbalanced presentations of AL odor solution and DEN solution. DEN, denatonium saccharide solution; AL, 0.02% almond odor solution.

component is tested, because there is considerably less generalization from the ORG + DEN compound to DEN, the resulting CR is relatively weak (taste testing of Group DO+ in Experiment 1; extinction data of Group O−/T− in Experiment 2). Further evidence to support the conclusion that the ORG + DEN compound is more similar to ORG than to DEN was seen by the CR to the compound following ORG extinction or DEN extinction (Group O− vs. T−). In contrast, it appears that the perceptual unit produced by combining AL odor and DEN is different from the perceptual unit produced by combining ORG odor and DEN. This conclusion is based on the result that following AL + DEN conditioning, responding to each element was similar (extinction data of Group O−/T− in Experiment 3) and on the result that DEN extinction and AL extinction produced similar effects on the compound aversion (test data of Experiment 3), relative to Group OT−. Indeed, the conclusion that the AL + DEN compound appears to represent both elements somewhat equally, relative to the ORG + DEN compound, is supported by the weaker CR to AL than to ORG (odor testing of Groups DA+ and DO+) and the stronger CR to DEN by these groups (taste testing of Groups DA+ and DO+), as was seen in Experiment 1. In sum, it appears that even though ORG odor and AL odor are quite similar when conditioned alone, combining ORG + DEN versus combining AL + DEN creates unique perceptual units that produce different patterns. Subsequent testing of ORG versus AL produces a CR to ORG that is stronger than the CR to AL, because the ORG odor is perceived to make up a greater part of the ORG + DEN compound than is the AL in the AL + DEN compound.

It is difficult to conceive how the within-compound association model could accommodate this interpretation. The relative salience of each odor suggests that both ORG and AL should be equally associated with DEN. Furthermore, according to the within-compound association account, the CR would be stronger to ORG if the DEN → US association is stronger. Yet the taste test of Experiment 1 showed that the CR to DEN was weaker after ORG + DEN conditioning, as compared with the CR to DEN after AL + DEN conditioning. Instead, the account above is consistent with a configural account of potentiation adapted from Pierce (2002) and Kucharski and Spear (1985). In a configural account of

potentiation, the potentiated CR is produced by generalization decrement from the salient compound stimulus to its component parts. In fact, the hypothesis that the taste and the odor are combined into a unique perceptual cue is consistent with other factors that influence potentiation. For example, as has been described earlier, many studies have manipulated odor/taste concentration to show that potentiation follows a salience rule in which a stronger stimulus potentiates responding to a weaker stimulus (e.g., Bouton et al., 1986; Slotnick et al., 1997). This salience rule suggests that potentiation occurs because the relative concentrations of the taste and the odor allow for configuring of the two cues. If the concentrations are altered (i.e., both stimuli are presented in a high concentration), the animal is not able to configure the two cues, and potentiation is not observed.

The idea that stimulus concentration and stimulus interactions can be a determinant of configural processing or elemental processing of odor mixtures has been a topic of interest in recent physiological investigations (Kay, Lowry, & Jacobs, 2003; Wiltrout, Dogra, & Linster, 2003). For example, in the case of odor mixtures, Kay et al. have shown that mixing odors (citronellal and octanal) that have the same chemical structure (and therefore operate on the same receptors in the olfactory epithelium) produces discrimination responses that are consistent with a configural interpretation (i.e., rats responded only to the compound, but not to the elements of the compound). On the other hand, when odorants of different chemical structure (citral and octanal) were mixed, the responses were consistent with an elemental interpretation (i.e., rats responded both to the elements of the mixture and to the compound). It is important to note that in the citronellal and octanol mixture, the concentration ratio of the odorants was a crucial determinant of whether the odorants exhibited configural or elemental properties; parametric shifts in the concentration ratio changed configural responding to elemental responding. Thus, research from other paradigms provides converging evidence that stimulus interactions and concentrations can produce responses that suggest configural representation of compound stimuli.

Although a configural account of potentiation is consistent with many of the results in the present investigation, a configural approach cannot accommodate all of the present findings. First, Kucharski and Spear (1985) hypothesized that if the elements of the compound constitute a unique percept, separate extinction of the elements should reduce responding to the compound less than extinction of the compound does. As was detailed earlier, the results of Groups OT− and O−/T− in both Experiments 2 and 3 are inconsistent with the first prediction. In fact, Kucharski and Spear were unable to find support for this prediction when they tested adult rats. Even though the present experiments and the work of Kucharski and Spear differed in a number of procedural details, the comparison of separate, elemental extinction versus compound extinction in adult rats has yet to produce results that are entirely consistent with a configural interpretation.

Second, another prediction based on the formation of configural associations pertains to the effects of presentation of one of the elements following compound conditioning. Kucharski and Spear (1985) hypothesized that if the taste + odor compound is perceived as a unitary percept, presentation of one of the elements of the compound would strengthen the discrimination between the elements and the compound. If this was successful, testing the nonextinguished element would result in a weakened CR. In regard to this prediction, the odor results following taste extinction in Experiment 1 are consistent with this discrimination prediction (they are also consistent with the within-compound association model). Yet if this hypothesis is correct, any presentation of an element of the compound, either nonreinforced or reinforced, should enhance the discrimination between the compound and its elements and, therefore, decrease responding to both elements. In the case of our recent inflation studies (Batsell et al., 2003), we demonstrated that postconditioning inflation of one element of the compound *increased* responding to the other element of the compound. Clearly, the results of the inflation experiments are in opposition to the configural account of potentiations, but are in accord with the within-compound association approach.

Even though the present data coupled with the inflation data appear to support different explanations of potentiation, there is a possible resolution to this apparent discrepancy. A review of these experiments suggests that the configural account of potentiation is valid when one of the elements of the taste + odor compound is tested following conditioning. In other words, the results of potentiation experiments that mix the stimuli in solution may be accommodated according to generalization from a unique compound, depending on the relative salience of the cues and their ability to interact with one another. However, if compound conditioning is followed by a manipulation that involves changing the value of one of the elements of the compound (extinction or inflation), the results are consistent with the within-compound approach. A very tentative proposal is that both configural and elemental associations are operating in concert following taste + odor compound conditioning. Initial conditioning and testing reflect the animal's response to the unique perceptual qualities of the taste + odor compound, but if the animal receives experience with one of the elements, this experience elicits the within-compound association that exists between the taste and the odor.

In closing, these experiments indicate that taste + odor interactions need to be included as a factor that influences potentiation. As has been demonstrated, some combinations of taste and odor favor generalization to the odor component (producing the behavioral outcome of stronger potentiation), whereas other combinations produce less generalization to the odor component (producing a weaker manifestation of potentiation). Although it was not tested in the present series of experiments, it

is conceivable that another combination of odor and taste (or different concentrations of the present stimuli) would obscure the odor relative to the taste, thus producing a behavioral outcome similar to overshadowing. Even though these results do not collectively support any of the aforementioned models of potentiation, they suggest that future models may need to include both configural and within-compound associations.

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NOTE

1. Even though the AL and the ORG odors are of equal concentration, it is impossible to determine whether the rat perceives the odors to be of equal salience. For our purposes, we used the single-element odor aversion conditioning task, followed by a 20-min odor consumption task, as our test of salience. With this task, we did not find differences in odor aversion strength. It remains possible that a more sensitive task might detect differences in salience between AL and ORG odor solutions.

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