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Differences in taste-potentiated odor aversions with O+/OT+ versus OT+/O+ conditioning: Implications for configural associations

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The present research demonstrates a conditioning order effect difference: Odor-aversion conditioning is stronger following OT+/O+ conditioning than following O+/OT+ conditioning with specific odor (O) and taste (T) cues. When a weak odor cue was used in Experiments 1A and 1B, OT+/O+ conditioning produced significantly stronger odor aversions than did either O+/OT+ or O+/O+ conditioning, which did not differ. The same design was used in Experiment 2 with a strong odor, but the order effect difference was not replicated, suggesting that the order effect difference is specific to conditions that produce taste-potentiated odor aversions. The interpretation that O+/OT+ conditioning is weaker because of the absence of a taste–odor within-compound association was not supported in Experiments 3 and 4. Notably, using stimuli that supported potentiation in earlier experiments, in Experiment 4, we found evidence of a taste–odor within-compound association in the absence of potentiation. These results confirm that previous theories of potentiation (within-compound association model, sensory-and-gate channeling model) are not sufficient to produce potentiation. Instead, these results are interpreted in terms of taste–odor configural associations.

Conditioned flavor aversion is a form of classical conditioning in which an organism experiences a neutral taste or odor conditioned stimulus (CS) prior to an illness-producing unconditioned stimulus (US). As a result, the organism shows an aversion to the CS on subsequent occasions. *Taste-potentiated odor-aversion* (TPOA) learning refers to the significantly stronger odor aversion demonstrated by organisms that have experienced taste+odor compound aversion conditioning relative to those that have experienced odor-aversion conditioning only (e.g., Durlach & Rescorla, 1980; Rusiniak, Hankins, Garcia, & Brett, 1979). The phenomenon of TPOA has been of theoretical interest since its initial report because it represents an example of synergistic conditioning, whereas most compound conditioning designs in classical conditioning result in competitive conditioning. For example, the typical finding of a two-element compound conditioning design (AX+) is that the more intense CS A will decrease or overshadow conditioning to the less intense CS X in comparison with conditioning of the weak CS X alone. In contrast, in TPOA, the taste CS A strengthens aversion conditioning to the weaker odor CS X relative to X-alone conditioning. Because TPOA could not be incorporated into existing formal models of associative learning (e.g., Pearce & Hall, 1980; Rescorla & Wagner, 1972), over the past 25 years, three prominent theoretical accounts have been proposed to explain TPOA.

The first formal account, the within-compound association model, was proposed by Durlach and Rescorla (1980). In this model, three associations that form during conditioning mediate TPOA: (1) a taste–illness association, (2) an odor–illness association, and (3) a taste–odor within-compound association. During subsequent odor testing, the odor can activate the US representation both through the direct odor–illness association and via the indirect odor–taste–illness association. In contrast, the significantly weaker odor aversion observed in the odor-alone control group occurs because this group has only the odor–illness association.

Garcia, Lasiter, Bermudez-Rattoni, and Deems (1985) offered a second theoretical account. The sensory-and-gate channeling model explains TPOA through the activation of two defense systems. First, the internal or gut defense system processes threats with ingestive consequences, and taste cues are selectively processed within this system. Second, the external defense system processes threats to the periphery of the organism (i.e., visual cues and auditory cues would be processed via the external defense system). Odor cues are unique in that they can be processed by either the internal or the external

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defense system. If the odor occurs alone, it will be processed within the external defense system, but if the odor is presented in conjunction with a taste, it will be gated into the internal defense system. Once the odor has been admitted into the internal defense system, it will be processed like a taste cue, which could conceivably increase the associability of the odor and result in the significantly stronger odor–illness association.

Following a series of taste–taste experiments, Kucharski and Spear (1985) offered a configural association account of potentiation that can be extrapolated to TPOA. According to their configural model, an organism like the rat would perceive the taste+odor compound as a single, salient stimulus rather than as a combination of two, separable elements. As a result, during subsequent odor testing, the rat would confuse the odor alone with the more salient taste+odor compound, and if the enhanced conditioning to the salient compound was greater than the generalization decrement from the compound to the odor alone, a significantly stronger conditioned response to the odor would be observed. On the other hand, during taste testing, if the generalization decrement from the odor+taste compound to the taste alone was too great, an overshadowed taste aversion would be recorded. In fact, many investigators have reported the overshadowing of the taste following odor+taste compound conditioning (e.g., Bowman, Batsell, & Best, 1992; Westbrook, Homewood, Horn, & Clarke, 1983).

Over the past 10 years, our labs have conducted numerous flavor-aversion experiments using variations of the blocking or O+/OT+ design (O, odor; T, taste) to investigate the mechanism of synergistic conditioning. For example, in 2003, we reported the results of postconditioning inflation experiments on potentiated odor aversions and overshadowed taste aversions (Batsell, Trost, Cochran, Blankenship, & Batson, 2003). Experiment 3 of that report was designed to examine the effects of postconditioning odor inflation (OT+/O+) on an overshadowed taste aversion. In that experiment, both OT+/O+ conditioning and the control O+/OT+ conditioning resulted in taste aversions of equal strength. An incidental but interesting finding was that following the four taste tests, a separate test revealed that the odor aversion following OT+/O+ conditioning was significantly stronger than the odor aversion following O+/OT+ conditioning. Although a clear explanation of this difference is not possible because these results were obtained following multiple taste tests and in the absence of proper controls, this difference may provide insight into the mechanism of TPOA. In other words, an understanding of the conditions that prevent TPOA should elucidate the factors that are required for the phenomenon to occur.

The present report contains five flavor-conditioning experiments that were conducted to compare O+/OT+ conditioning and OT+/O+ conditioning on odor-aversion learning. Experiments 1A and 1B were designed to confirm the difference between O+/OT+ and OT+/O+ conditioning that was suggested in Batsell et al.'s (2003) report. The next experiment was conducted in order to determine whether OT+/O+ conditioning would produce a stronger CR when a strong odor was the odor stimulus. The postconditioning taste-extinction procedure was employed in Experiments 3 and 4 in order to compare predictions based on the different theoretical accounts of TPOA.

EXPERIMENT 1A

There were two aims for Experiment 1A. One was to determine whether OT+/O+ conditioning would produce a stronger odor aversion than O+/OT+ conditioning, and the second was to evaluate the strength of O+/OT+ and OT+/O+ conditioning relative to a traditional compound conditioning group (OT+).

Method

Subjects. Subjects were 29 experimentally naive male Sprague Dawley rats (Hilltop Labs, Scottdale, PA), housed individually in standard stainless steel hanging cages on a 12:12-h light:dark cycle. Food (Rat Lab Diet, PMI Nutrition International) was available ad lib throughout the study. Water was available ad lib for 12 days before a water-deprivation schedule was begun, which remained in effect throughout the study, with rats having ad lib access for 20 min daily at approximately 1500 h. One day before the study began, rats were randomly assigned to three groups. Mean body weights were equivalent (range, 312.1–319.9 g). All animals were treated in accordance with American Psychological Association Guidelines, and the research was approved by the Institutional Animal Care and Use Committees of our respective institutions.

Materials. All fluids were presented in 50-ml plastic drinking tubes fitted with rubber stoppers and ball bearing spouts. Liquid consumption was measured by comparing the weights of tubes before and after drinking. Amounts consumed are reported in milliliters, with the assumption that 1 g = 1 ml.

The taste cue, odor cue, and lithium chloride (LiCl) concentration were those used in previous potentiation experiments from our labs (Batsell et al., 2003; Trost & Batsell, 2004). The odor cue was a 0.02% almond odor solution (AL, 0.2 cc extract per liter of room-temperature tap water; McCormick Pure Almond Extract, Hunt Valley, MD). Previous research has confirmed that a 2% AL solution is mediated by its odor properties, not by its taste properties (Rusiniak et al., 1979); a weaker AL solution can therefore be assumed to have little taste. The taste cue was 0.01% solution of denatonium saccharide (DEN; 0.1 g dissolved in 1 L of room temperature tap water; Sigma Chemical Co., St. Louis). The compound conditioning fluid was a mixture of DEN+AL (0.1 g of denatonium saccharide and 0.2 cc of almond extract mixed in 1 L of water). Toxicosis was induced via an intraperitoneal (i.p.) injection of an isotonic 0.15 M solution of LiCl (12 ml/kg of body weight).

Procedure. To allow for comparison with previous experiments from our labs, all experimental procedures occurred in the familiar home cages. This experiment used three groups, and their treatments are summarized in Table 1A. The groups were labeled according to their conditioning experiences. Group O+/OT+ (n = 10) first received an AL–LiCl pairing and then an AL+DEN–LiCl pairing. In contrast, Group OT+/O+ (n = 9) first received the AL+DEN–LiCl

Table 1A
Design of Experiment 1A

Group	Condition 1	Condition 2	Testing
OT+	AL+DEN–LiCl	–	AL
O+/OT+	AL–LiCl	AL+DEN–LiCl	AL
OT+/O+	AL+DEN–LiCl	AL–LiCl	AL

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

pairing before receiving the AL–LiCl pairing. Finally, Group OT+ (n = 10) received a single pairing of AL+DEN–LiCl. Experimental procedures were conducted at approximately 1000 h each day.

Conditioning was conducted on Days 1 and 3. On each conditioning trial, all rats were given 5-min access to 8 ml of their target fluid, and the LiCl injection was administered immediately after removal of the drinking bottles. We chose to restrict fluid presentations in both time and volume to keep the intakes at each conditioning trial as equivalent as possible; in subsequent experiments, this amount was restricted to 5 ml. Day 4 was a water recovery day. Testing of aversions to the AL solution was conducted for 20 min daily on Days 5–9. A single-bottle test was chosen because previous work has shown this testing method to be more sensitive in detecting aversions of differential strength (Batsell & Best, 1993). Access for 20 min to supplemental water was provided in the afternoons (4 h after any experimental procedures) on all days.

Data analysis. Because all groups received two conditioning trials, we predicted the presence of floor effects and the need to conduct multiple odor tests. The AL intakes were analyzed in a one-way ANOVA with groups as a between-groups factor.[1] The statistical criterion for this and all subsequent experiments was .05.

Results and Discussion

Conditioning. During conditioning, the groups drank equivalent amounts on each conditioning trial, but they drank less fluid on the second conditioning trial (the interpretational implications of this difference will be addressed in the General Discussion). The groups' mean intakes on Conditioning Trial 1 were OT+/O+ = 5.7 ml, O+/OT+ = 6.4 ml, and OT+ = 6.4 ml. Mean intakes on Conditioning Trial 2 were 3.6 ml for Groups OT+/O+ and O+/OT+; Group OT+ drank 3.3 ml of water at this time.

Testing. Figure 1 shows mean AL consumption of the three groups averaged across the 5 days of testing. A one-way ANOVA indicated significant differences among groups [$F(2,26) = 14.7$], and a post hoc Student Newman Keuls (SNK) procedure verified that Group OT+/O+ drank significantly less than the other groups, which did not differ from one another.

The AL odor aversion in Group OT+/O+ was stronger than in Group O+/OT+, and this difference, which we will refer to as the *order effect difference*, is the focus of this article. The reduced but equivalent aversions in Groups O+/OT+ and OT+ suggest that order of conditioning is an important factor in overall AL conditioning.

The differences observed after two conditioning trials can be compared with results in the more traditional one-trial conditioning paradigm, and they allow us to evaluate how the additional O+ trial increases the odor aversion relative to that for the OT+ group. On the basis of these results, Experiment 1B was designed to replicate the order effect difference. To determine the relative strengths of O+/OT+ and OT+/O+ conditioning, Experiment 1B also included two control groups: Group O+/O+ received two odor-alone conditioning trials, and Group OT+/OT+ received two taste+odor compound conditioning trials.

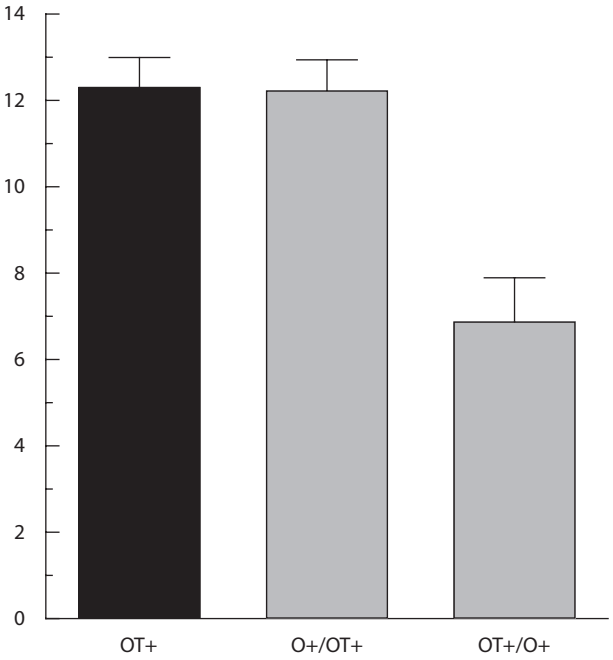

Figure 1. Mean (+*SE*) almond odor solution (AL) intake, in milliliters, averaged across odor testing in Experiment 1A. Group O+/OT+ received an AL–LiCl pairing followed by an AL+DEN–LiCl pairing. Conversely, Group OT+/O+ received an AL+DEN–LiCl pairing followed by an AL–LiCl pairing. Group OT+ received a single AL+DEN–LiCl pairing. DEN, denatonium saccharide solution.

EXPERIMENT 1B

Method

Subjects and Materials. Subjects were 38 experimentally naive albino rats (weight range, 340–420 g at conditioning) of Holtzman strain (Harlan Sprague Dawley, Indianapolis). Rats were group housed in sets of 3 animals until they each reached 250 g; then they were housed individually in standard hanging cages. They were maintained on a 12:12-h light:dark cycle beginning at 0700 h. All rats had free access to lab Rat Chow (Kaytee Forti-Diet, Chilton, WI) throughout the experiment. Two weeks prior to experimental manipulations, a water deprivation schedule was implemented as described in Experiment 1A. Intakes served to match rats to groups. The group mean water intakes ranged from 19.0 to 19.1 ml.

This experiment used four groups in a design that is depicted in Table 1B. The groups were labeled according to their conditioning experiences. Group O+/O+ (n = 9) received two pairings of AL odor solution and LiCl. Group O+/OT+ (n = 10) first received an AL–LiCl pairing and then an AL+DEN–LiCl pairing. In contrast, Group OT+/O+ (n = 10) first received the AL+DEN–LiCl pairing before receiving the AL–LiCl pairing. Finally, Group OT+/OT+ (n = 9) received two pairings of AL+DEN–LiCl. The DEN, AL, and LiCl concentrations were the same as those used in Experiment 1A.

Procedure. Conditioning Trial 1 occurred on Day 1. Groups O+/O+ and O+/OT+ received the AL odor solution, whereas Groups OT+/OT+ and OT+/O+ received the AL+DEN compound

Table 1B
Design of Experiment 1B

Group	Condition 1	Condition 2	Testing
O+/O+	AL–LiCl	AL–LiCl	AL
O+/OT+	AL–LiCl	AL+DEN–LiCl	AL
OT+/O+	AL+DEN–LiCl	AL–LiCl	AL
OT+/OT+	AL+DEN–LiCl	AL+DEN–LiCl	AL

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

solution for 5 min. All rats were injected with LiCl immediately following removal of the drinking tubes (0-min CS–US interval). All rats received 20-min access to water 4 h later. Day 2 was a recovery day, in which all rats received 20-min access to water at 1000 h.

Conditioning Trial 2 occurred on Day 3. Groups O+/O+ and OT+/O+ received the AL odor solution, whereas Groups OT+/OT+ and O+/OT+ received the AL+DEN compound solution. LiCl injections were administered at the completion of the 5-min drinking period.

Six AL odor tests were conducted (Days 5–10). During testing, all rats received a one-bottle test, in which they were given 20-min access to the AL solution.

Data analysis. At first glance, this design may appear to be a 2 × 2 factorial because of the combination of O+ and OT+ conditioning experiences. Yet this approach assumes that these events are independent and can be combined in any fashion. Instead, the main point of this research is that the order of these experiences is crucial to determining behavior, and thus each conditioning sequence should be regarded as a separate treatment. For this reason, the AL test data were averaged across the six tests and analyzed in a one-way ANOVA with groups as the between-groups factor. In addition, two planned comparisons were designated on the basis of our predictions. A comparison of Groups O+/O+ and OT+/OT+ was conducted to determine whether TPOA occurred, and a comparison of Groups O+/OT+ and OT+/O+ was conducted to detect the order effect observed in Experiment 1A.

Results and Discussion

Conditioning. During conditioning, the groups drank equivalent amounts on each conditioning trial, but they drank less fluid on the second conditioning trial. The groups' mean intakes on Conditioning Trial 1 were O+/O+ = 2.8 ml, O+/OT+ = 2.7 ml, OT+/O+ = 2.9 ml, and OT+/OT+ = 2.8 ml. The groups' mean intakes on Conditioning Trial 2 were O+/O+ = 0.5 ml, O+/OT+ = 0.4 ml, OT+/O+ = 0.4 ml, and OT+/OT+ = 0.4 ml.

Testing. Figure 2 displays the mean AL odor solution of the four groups averaged across 6 days of testing. It can be seen that Groups OT+/O+ and OT+/OT+ drank less of the AL solution than did Groups O+/OT+ and O+/O+.

A one-way ANOVA conducted over the averaged AL intakes revealed a significant group effect [$F(3,34) = 4.3$]. There were two notable comparisons in Experiment 1B. First, we observed TPOA; Group OT+/OT+ drank significantly less AL odor solution than did Group O+/O+ according to post hoc SNK tests. Second, we replicated the order effect difference observed in Experiment 1A; post hoc SNK tests revealed that Group O+/OT+ drank significantly more than Groups OT+/O+ and OT+/OT+. To restate, OT+/O+ conditioning produced a significantly stronger AL odor aversion than did O+/OT+ conditioning.

Experiments 1A and 1B are the first studies to provide an unadulterated and reliable demonstration of the order effect difference, but could the effect be produced with *any* odor or was the effect dependent on an odor that could be potentiated? In other words, would OT+/O+ conditioning produce a stronger odor aversion than would O+/OT+ conditioning if we used a taste+odor combination that would *not* produce TPOA? As has been noted previously (e.g., Bouton, Jones, McPhillips, & Swartzentruber, 1986), TPOA appears to be dependent on the relative concentrations of a taste and a weak odor.

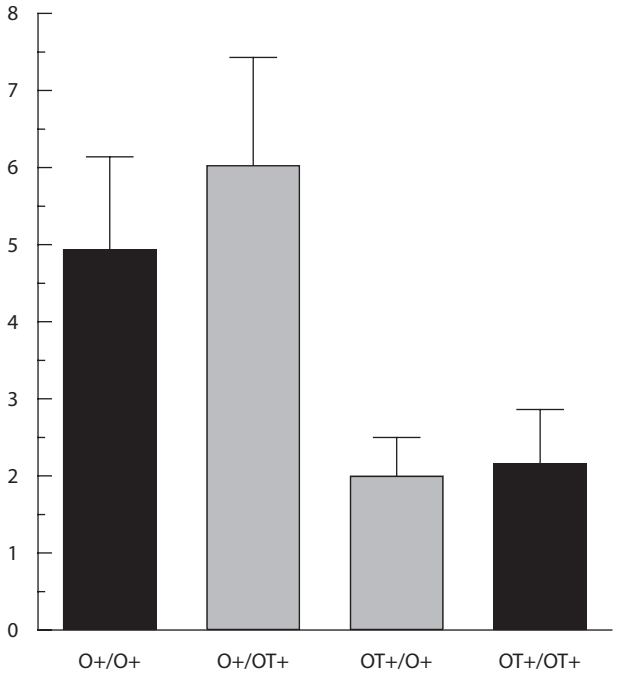

Figure 2. Mean (+*SE*) almond odor solution (AL) intake, in milliliters, averaged across six odor tests in Experiment 1B. Group O+/OT+ received an AL–LiCl pairing followed by an AL+DEN–LiCl pairing. Conversely, Group OT+/O+ received an AL+DEN–LiCl pairing followed by an AL–LiCl pairing. Group O+/O+ received two AL–LiCl pairings. Group OT+/OT+ received two AL+DEN–LiCl pairings. DEN, denatonium saccharide solution.

EXPERIMENT 2

Because previous work from our labs had shown that specific odors can interact with DEN to affect the strength of TPOA (Trost & Batsell, 2004), we conducted a pilot study in which various odors (almond, anise, chocolate, coffee, and lemon) were presented as a 0.02% solution and conditioned alone or in combination with DEN. The trend was for TPOA, except in the case of anise (AN), which also produced the strongest odor-alone aversion. Because floor effects were observed with AN odor following a single conditioning trial with our standard LiCl concentration (0.15 M), we conducted a second pilot experiment in which we weakened the concentrations of AN (0.008%) and LiCl (0.075 M). In this study, the AN group (M = 4.8 ml) and the AN+DEN group (M = 4.7 ml) drank equivalent amounts of AN solution during testing. Therefore, in Experiment 2, we used the same DEN concentration as in the first two experiments, but it was paired with AN odor solution to determine whether OT+/O+ conditioning produced a stronger odor aversion, relative to O+/OT+ conditioning, in the absence of TPOA.

Method

Subjects, Materials, and Procedure. The subjects were 49 white, male, experimentally naive rats. The housing, feeding, and water-deprivation schedule were the same as in Experiment 1B. Rats were matched to one of five groups on the basis of their mean water

Table 2
Design of Experiment 2

Group	Condition 1	Condition 2	Testing
O−/O−	AN–4 h–LiCl	AN–4 h–LiCl	AL
O+/O+	AN–LiCl	AN–LiCl	AL
O+/OT+	AN–LiCl	AN+DEN–LiCl	AL
OT+/O+	AN+DEN–LiCl	AN–LiCl	AL
OT+/OT+	AN+DEN–LiCl	AN+DEN–LiCl	AL

Note—AN, 0.008% anise odor solution; DEN, 0.01% denatonium saccharide solution; LiCl, 0.075 M lithium chloride solution.

intake (means ranged from 19.8 to 20.1 ml). The conditioning regimens for the five groups are displayed in Table 2. Group O+/O+ received two pairings of AN–LiCl. Group OT+/OT+ received two pairings of AN+DEN–LiCl. Group O+/OT+ received an AN–LiCl pairing followed by an AN+DEN–LiCl pairing, whereas Group OT+/O+ received an AN+DEN–LiCl pairing followed by an AN–LiCl pairing. Finally, we included a fifth group to confirm that rats would readily consume the AN odor solution if it was not paired directly with illness. Group O−/O− received access to AN odor solution at the same time as Group O+/O+, but a 4-h delay was imposed between odor presentation and LiCl injections.

The odor cue was a 0.008% AN odor solution (0.08 cc extract per liter of room-temperature tap water; McCormick Pure Anise Extract, Hunt Valley, MD). Because of the higher salience of the AN odor solution, we used a weaker LiCl concentration (0.075 M LiCl at 12 ml/kg). In all other respects, the conditioning and testing procedures were the same as those used in Experiment 1B.

Results and Discussion

Conditioning. During Conditioning Trial 1, Groups O−/O− (M = 2.9 ml), O+/O+ (M = 3.1 ml), and O+/OT+ (M = 3.5 ml) drank AN solution. Groups OT+/O+ (M = 2.9 ml) and OT+/OT+ (M = 3.0 ml) drank AN+DEN solution. During Conditioning Trial 2, Groups O−/O− (M = 3.6 ml), O+/O+ (M = 0.6 ml), and OT+/O+ (M = 0.4 ml) drank AN solution. Groups O+/OT+ (M = 0.4 ml) and OT+/OT+ (M = 0.5 ml) drank AN+DEN solution. All groups were injected with LiCl immediately after drinking on both trials.

Testing. The mean AN solution intakes of the five groups averaged over the six odor tests are illustrated in Figure 3. The control group O−/O− showed no evidence of an odor aversion, since AN consumption was substantially greater than in the other groups. Also, Group O+/O+ drank the least AN solution and the other three groups drank comparable amounts.

A one-way ANOVA conducted over the averaged AN odor-test data revealed a significant group effect [$F(4,44) = 26.0$]. Post hoc SNK tests revealed that Group O−/O− drank significantly more AN solution than did the other four groups, and that Group O+/O+ drank significantly less AN solution than did the other four groups. There were no significant differences between Groups O+/OT+, OT+/O+, and OT+/OT+.

There were three comparisons of interest in Experiment 2. First, a comparison of Group O+/O+ with Group O−/O− confirmed that a significant AN odor aversion was produced in Group O+/O+ (and in the other groups as well). Second, a comparison of Groups O+/O+ and OT+/OT+ showed that Group OT+/OT+ drank significantly more of the AN odor solution than did Group O+/O+ . We predicted this difference by our choice of an odor that would not be potentiated but would instead be overshadowed. Finally, our third comparison was intended to determine whether the order effect difference occurred between Groups O+/OT+ and OT+/O+. It is clear that there was no difference between these groups. Thus, when we used a taste+odor combination that did not produce TPOA, the order effect difference was not detected.

A comparison of the results of Experiments 1B and 2 suggests that order effects are observed only when an odor+taste combination is used that produces TPOA. When an odor+taste combination that does not produce TPOA was employed, order effects were not recorded. One conclusion is that the enhanced aversion seen following OT+/O+ conditioning with AL and DEN was due to the presence of TPOA, and the weaker odor aversion seen in Group O+/OT+ was due to the absence of TPOA. Therefore, if we explored the mechanisms of TPOA with each of these groups, we could determine what conditions were necessary to produce TPOA in Group OT+/O+ or what factors prevented TPOA in Group O+/OT+.

Experiments 3 and 4 were designed to explore the mechanism of the order effect difference. Because this difference appeared to be dependent on the presence of TPOA in Group OT+/O+, we chose to use the postcon-

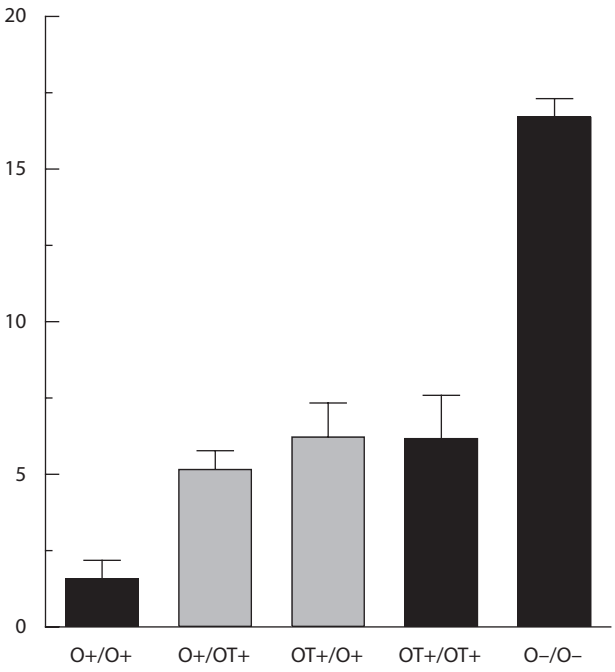

Figure 3. Mean (+*SE*) anise odor solution (AN) intake, in milliliters, averaged across six odor tests in Experiment 2. Group O+/OT+ received an AN–LiCl pairing followed by an AN+DEN–LiCl pairing. Conversely, Group OT+/O+ received an AN+DEN–LiCl pairing followed by an AN–LiCl pairing. Group O+/O+ received two AN–LiCl pairings. Group OT+/OT+ received two AN+DEN–LiCl pairings. Finally, Group O−/O− twice received AN odor solution alone, followed 4 h later by an LiCl injection. DEN, denatonium saccharide solution; AN, 0.008% anise odor solution.

Table 3
Design of Experiment 3

Group	Condition 1	Extinction	Condition 2	Testing
O+/W−/OT+	AL–LiCl	H_2O	AL+DEN–LiCl	AL
OT+/W−/O+	AL+DEN–LiCl	H_2O	AL–LiCl	AL
OT+/T−/O+	AL+DEN–LiCl	DEN	AL+–LiCl	AL

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

ditioning taste-extinction manipulation that has been used in other studies (e.g., Durlach & Rescorla, 1980; Miller, McCoy, Kelly, & Bardo, 1986). In Experiment 3, we sought to determine whether postconditioning taste extinction after the first conditioning phase would interfere with the order effect difference. In Experiment 4, we conducted the taste-extinction procedure after the second conditioning phase.

EXPERIMENT 3

Two groups in this study received treatments that were similar to those described for Groups O+/OT+ and OT+/O+ in Experiments 1A and 1B. The unique group in this study was Group OT+/T−/O+, which received taste+odor compound aversion conditioning, followed by seven taste (DEN) extinction trials, and an additional odor-alone conditioning trial. Both the within-compound association and configural association models predicted that the taste-extinction manipulation should weaken the resulting odor aversion, whereas the sensory-and-gate channeling model predicted that once the odor was gated into the internal defense system, manipulations of the taste should not alter the odor aversion.

Method

Subjects, Materials, and Procedure. Subjects were 30 rats, and their origin, housing, feeding, water-deprivation schedule, and the associated experimental procedures were the same as those described in Experiment 1A. Rats were matched to each of three groups (n = 10 in each) on the basis of their mean water (W) intake (means ranged from 18.4 to 18.8 ml). The conditioning procedures are displayed in Table 3. Groups OT+/W−/O+ and OT+/T−/O+ first received an AL+DEN–LiCl pairing, followed 10 days later by an AL–LiCl pairing. Group O+/W−/OT+ received the same pairings on the same days but in reverse order. No treatments other than the daily watering session occurred on the days immediately following the first conditioning trial or immediately preceding the second conditioning trial. On each of the 7 remaining days between the two conditioning trials, Group OT+/T−/O+ received 20-min ad lib access to DEN alone as extinction trials. Immediately after these 20-min DEN sessions, Groups OT+/W−/O+ and O+/W−/OT+ were allowed to consume water in amounts equal to the DEN consumed by Group OT+/T−/O+.

Beginning 2 days after the final conditioning trial, all groups received 20-min daily access to AL for 6 consecutive days.

Results and Discussion

Conditioning 1. During the first conditioning trial, Groups OT+/W−/O+ and OT+/T−/O+ consumed 5.2 ml and 6.3 ml, respectively, of the compound, and Group O+/W−/OT+ drank 6.6 ml of AL. These differences were not statistically different.

Extinction. During the 6 days when Group OT+/T−/O+ received access to DEN for extinction trials, their intakes were 2.8, 8.4, 10.3, 13.2, 15.2, and 14.6 ml.

Conditioning 2. During the second conditioning trial, Groups OT+/W−/O+ and OT+/T−/O+ consumed 2.1 ml and 4.5 ml, respectively, of AL, and Group O+/W−/OT+ drank 2.4 ml of the compound. These significant differences [$F(2,27) = 6.26$] suggest that the DEN extinction trials may have partially reduced the aversion to AL in Group OT+/T−/O+.

Testing. Figure 4 shows the groups' mean AL consumption averaged across the 6 test days. Group differences were significant [$F(2,27) = 16.91$]. Post hoc SNK tests revealed that Group OT+/W−/O+ drank significantly less AL odor solution than did Group O+/W−/OT+, replicating the order effect difference reported in Experiments 1A and 1B. There was also a significant and important difference between Groups OT+/W−/O+ and OT+/T−/O+, indicating that DEN extinction between

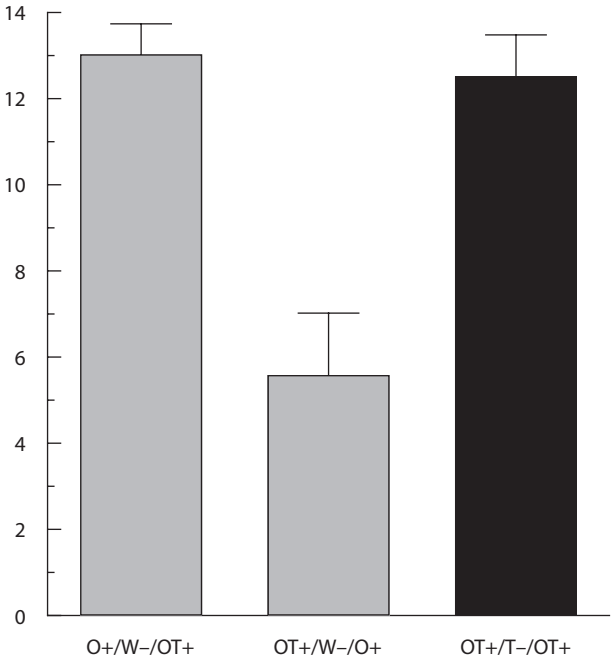

Figure 4. Mean (+*SE*) almond odor solution (AL) intake, in milliliters, of the three groups in Experiment 3. Group O+/W−/OT+ received an AL–LiCl pairing followed by an AL+DEN–LiCl pairing. Group OT+/W−/O+ received an AL+DEN–LiCl pairing followed by an AL–LiCl pairing. Group OT+/T−/O+ received an AL+DEN–LiCl pairing, four DEN extinction trials, followed by an AL–LiCl pairing. DEN, denatonium saccharide solution.

Table 4
Design of Experiment 4

Group	Condition 1	Condition 2	Extinction	Testing
O+/O+/T−	AL–LiCl	AL–LiCl	DEN	AL; DEN
O+/O+/W−	AL–LiCl	AL–LiCl	H_2O	AL; DEN
O+/OT+/T−	AL–LiCl	AL+DEN–LiCl	DEN	AL; DEN
O+/OT+/W−	AL–LiCl	AL+DEN–LiCl	H_2O	AL; DEN
OT+/O+/T−	AL+DEN–LiCl	AL–LiCl	DEN	AL; DEN
OT+/O+/W−	AL+DEN–LiCl	AL–LiCl	H_2O	AL; DEN

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

conditioning trials weakened the AL odor aversion relative to that for Group OT+/W−/O+. In fact, the AL aversion in the DEN extinction group was equivalent to the aversion in Group O+/W−/OT+. These results are problematic for the sensory-and-gate channeling model, because it predicts no weakening of the odor aversion with taste extinction. In contrast, this outcome is consistent with predictions derived from both the within-compound association model and the configural model.

Experiment 4 also included the postconditioning taste-extinction manipulation, but in this experiment, taste extinction was conducted after the second conditioning trial. This manipulation provided another means of testing the within-compound association model. To review, if the within-compound association model of potentiation was correct, TPOA would occur because a within-compound association would form between the taste and the odor during compound conditioning. If the weakened odor aversion in O+/OT+ conditioning was due to the absence of a within-compound association, postconditioning taste extinction should have no effect on the odor aversion of Group O+/OT+. In the final experiment, we tested this prediction.

EXPERIMENT 4

Method

Subjects, Materials, and Procedure. The subjects were 56 experimentally naive, white male Holtzman rats that were obtained from the Harlan Sprague Dawley company (Indianapolis). Weights ranged from 290 to 360 g at the time of conditioning. Housing, feeding, and the water-deprivation schedule were the same as those described in the previous experiments.

Table 4 shows the six groups that were designated according to their treatments. Groups O+/O+/T− (n = 7 rats) and O+/O+/W− (n = 7 rats) received AL–LiCl conditioning on both conditioning trials. Groups O+/OT+/T− (n = 11 rats) and O+/OT+/W− (n = 11 rats) received AL–LiCl conditioning on Conditioning Trial 1 and AL+DEN–LiCl conditioning on Conditioning Trial 2. Groups OT+/O+/T− (n = 10 rats) and OT+/O+/W− (n = 10 rats) received AL+DEN–LiCl conditioning on Conditioning Trial 1 and AL–LiCl conditioning on Conditioning Trial 2. During the four nonreinforced DEN trials, Groups O+/O+/T−, O+/OT+/T−, and OT+/O+/T− received DEN, whereas Groups O+/O+/W−, O+/OT+/W−, and OT+/O+/W− received water. The AL, DEN, and LiCl concentrations were the same as those in Experiments 1A, 1B, and 3. Rats were assigned to groups on the basis of their water intakes over a 7-day period before conditioning. The group mean water intakes ranged from 20.0 to 20.3 ml.

Conditioning Trials 1 and 2 were conducted in the same manner as in Experiment 1B. The DEN extinction/exposure procedure occurred across 4 consecutive days (Days 4–7). During this time, Groups O+/O+/T−, O+/OT+/T−, and OT+/O+/T− received ad lib access to DEN for 20 min in their home cage at 1000 h. The other groups received water at this time. To prevent any dehydration due to low DEN consumption across these trials, all rats were given their daily water access 4 h after each DEN exposure on Days 4, 5, and 6. Because fluid intakes were equivalent on Day 7, no replacement fluids were given.

Odor testing occurred across 4 consecutive days (Days 8–11). On each test, rats were given 20-min ad lib access to AL odor solution in a one-bottle test. Daily water maintenance was provided at 1400 h. To ensure that the DEN extinction was effective, a single DEN test was conducted on Day 13. On this test, rats received ad lib access to DEN for 20 min.

Results and Discussion

Conditioning. On Conditioning Trial 1, Groups O+/O+/T− (M = 3.4 ml), O+/O+/W− (M = 3.6 ml), O+/OT+/T− (M = 3.3 ml), and O+/OT+/W− (M = 3.5 ml) drank similar amounts of AL solution. Also, Groups OT+/O+/T− and OT+/O+/W− drank equivalent amounts of the AL+DEN mixture, 3.3 ml and 3.6 ml, respectively. The intakes on Conditioning Trial 2 varied somewhat because of conditioning history. Groups O+/O+/T− (M = 3.2 ml) and O+/O+/W− (M = 2.4 ml) drank equivalent amounts of AL solution. The AL+DEN solution consumption of Group O+/OT+/T− (M = 1.5 ml) was similar to that of Group O+/OT+/W− (M = 1.7 ml). Finally, consumption of the AL solution in Group OT+/O+/T− (M = 2.0 ml) was similar to that for Group OT+/O+/W− (M = 1.5 ml).

DEN exposure. Figure 5 shows the mean DEN intakes of the three groups that received four nonreinforced DEN trials. As expected, Group O+/OT+/T− and Group OT+/O+/T−, which experienced DEN during one of the conditioning trials, showed lower initial DEN intake than did Group O+/O+/T−, which never experienced DEN during conditioning. Yet all groups consumed equivalent amounts of DEN by the fourth DEN trial. A 3 × 4 mixed ANOVA was performed for the DEN exposure groups with groups and trials as factors. This analysis yielded a significant group effect [$F(2,25) = 7.7$], a significant trials effect [$F(3,75) = 41.3$], and a significant group × trials interaction [$F(6,75) = 2.8$]. Simple-effects analyses were conducted to explore the significant interaction. These analyses confirmed that significant group differences occurred on Trial 1 [$F(2,25) = 15.2$] and Trial 2 [$F(2,25) = 4.6$] but not on Trial 3 [$F(2,25) = 2.2$] or Trial 4 [$F(2,25) < 1$]. It is noteworthy that DEN consumption of Groups O+/OT+/T− and OT+/O+/T− did not differ on any trial.

AL odor solution testing. Figure 6 shows the groups' mean AL odor intakes averaged across the four AL tests.

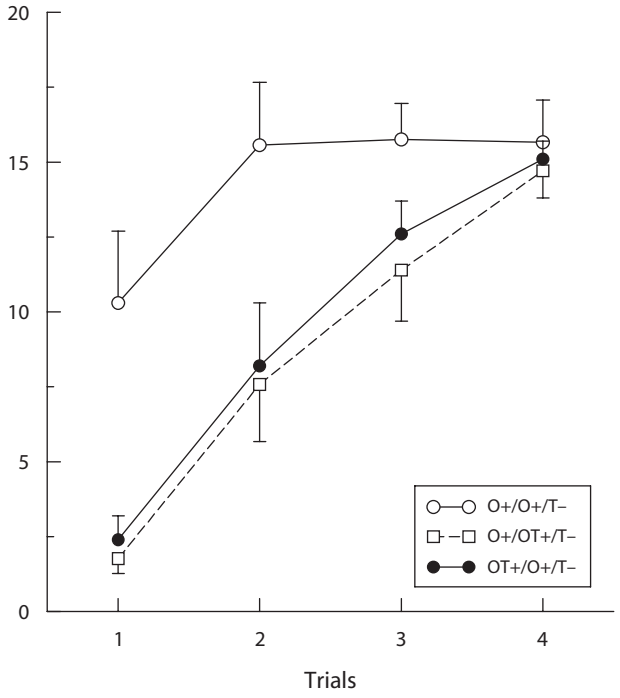

Figure 5. Mean (+*SE*) denatonium saccharide solution (DEN) intake, in milliliters, across the four extinction trials in Experiment 4. Prior to DEN extinction, Group O+/OT+ received an AL–LiCl pairing followed by an AL+DEN–LiCl pairing, Group OT+/O+ received an AL+DEN–LiCl pairing followed by an AL–LiCl pairing, and Group O+/O+ received two AL–LiCl pairings. AL, 0.02% almond odor solution.

The no-extinction groups show the characteristic order effect pattern of Group OT+/O+/W− drinking less AL solution than did Groups O+/O+/W− and O+/OT+/W−. Furthermore, the effects of DEN extinction are seen within the pairs of groups that received O+/OT+ conditioning and OT+/O+ conditioning, but not within the pair of control groups that received O+/O+ conditioning. The following statistical analyses support these conclusions.

A 3 × 2 ANOVA was conducted with conditioning (O+/O+, O+/OT+, OT+/O+) and extinction (DEN extinction, no extinction) as factors. This analysis yielded significant effects for extinction [$F(1,47) = 21.6$] and conditioning [$F(2,47) = 11.4$]. Post hoc SNK tests confirmed that the pair of groups that received OT+/O+ conditioning drank significantly less than the pairs of groups that received O+/OT+ and O+/O+ conditioning, replicating the order effect difference. Moreover, the conditioning × extinction interaction was significant [$F(2,47) = 3.3$]. Simple-effects analyses were used to further explore this significant interaction. Significant effects of DEN extinction were seen within the pair of groups that received OT+/O+ conditioning [$F(1,47) = 13.2$] and within the pair of groups that received O+/OT+ conditioning [$F(1,47) = 18.3$], but, as expected, no significant effect of DEN extinction was seen in the pair of control groups that received O+/O+ conditioning [$F(1,47) < 1$]. It is important to note that DEN extinction weakened the response to AL solution in both Groups O+/OT+/T− and OT+/T+/T−, a result that suggests that within-compound associations formed in both of these groups. This pattern of results is noteworthy, because differential responding was seen between the O+/OT+/W− group and the OT+/O+/W− group. Therefore,

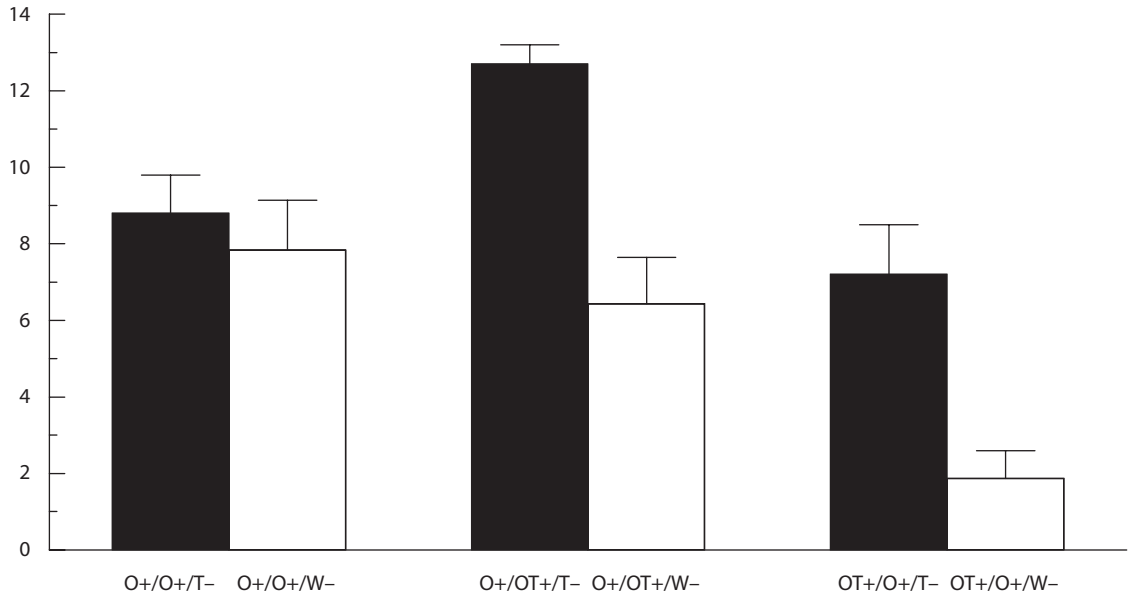

Figure 6. Mean (+*SE*) almond odor solution (AL) intake, in milliliters, of the six groups averaged across four odor tests in Experiment 4. Group O+/O+/W− received two AL–LiCl pairings. Group O+/O+/T− received two AL–LiCl pairings followed by four DEN extinction trials. Group O+/OT+/W− received an AL–LiCl pairing followed by an AL+DEN–LiCl pairing. Group O+/OT+/T− received an AL–LiCl pairing, an AL+DEN–LiCl pairing, and four DEN extinction trials. Group OT+/O+/W− received an AL+DEN–LiCl pairing followed by an AL–LiCl pairing. Group OT+/O+/T− received an AL+DEN–LiCl pairing, an AL–LiCl pairing, and four DEN extinction trials. DEN, denatonium saccharide solution.

the differences between these groups cannot be attributable to the absence of a taste+odor within-compound association in Group O+/OT+/W−.

DEN testing. The mean DEN intakes of the six groups are displayed in Figure 7. A 3 × 2 ANOVA with conditioning (O+/O+, O+/OT+, OT+/O+) and extinction (DEN extinction, no extinction) as factors yielded significant effects for conditioning [$F(2,50) = 17.5$] and extinction [$F(1,50) = 137.1$] and a significant conditioning × extinction interaction [$F(2,50) = 5.6$]. As expected, at all conditioning levels, the groups that received four nonreinforced DEN exposures drank substantially more than the groups that did not. Furthermore, there was no difference in DEN consumption between Groups O+/OT+/W− and OT+/O+/W−. This outcome is noteworthy for two reasons. First, these DEN aversions replicate the results reported by Batsell et al. (2003, Experiment 3) of OT+/O+ and O+/OT+ conditioning and the results seen on the initial DEN extinction trial here by Groups OT+/O+/T− and O+/OT+/T− (cf. Figure 5). Second, this outcome confirms that the stronger AL aversion seen following OT+/O+ conditioning cannot be due to the contribution of a stronger DEN aversion in this procedure. Third, the lower DEN intake of Group O+/O+/W− relative to Group O+/O+/T− might seem surprising, but this is a typical neophobia response to DEN seen after O+ conditioning (cf. Group O+/O+/T−, Trial 1, Figure 5).

GENERAL DISCUSSION

The present series of five flavor-aversion experiments is a continuation of our intermixing of compound conditioning (AX+) and single-element conditioning (A+) to understand the mechanisms of synergistic conditioning. The main focus in this series was to explore the differences in OT+/O+ conditioning versus O+/OT+ conditioning. Experiments 1A, 1B, 3, and 4 demonstrated that OT+/O+ conditioning produced a significantly stronger odor aversion than did O+/OT+ conditioning. Furthermore, the results of Experiments 1B and 2 suggested that the enhanced conditioning produced by OT+/O+ conditioning is present only with stimuli that yield TPOA. Finally, the postconditioning taste-extinction manipulation employed in Experiments 3 and 4 showed that neither the sensory-and-gate channeling model nor the within-compound association model could adequately account for the effects of OT+/O+ conditioning. Thus, the present experiments provided new information on the conditions necessary to produce TPOA and new evidence of the mechanism of this phenomenon.

Source of the Order Effect Difference

There are some alternative explanations for the weakened aversions produced by O+/OT+ conditioning, but they do not appear to be as valid as the absence of TPOA. For example, one alternative is that the weakened odor aversion produced by O+/OT+ conditioning is due to the lowered exposure to the taste+odor compound during the second conditioning phase. Because the initial O+ trial has suppressed the approach and sampling of the taste+odor compound, Group O+/OT+ has less exposure to the compound. Indeed, in the present experiments, Group O+/OT+ always consumed less of the taste+odor compound during conditioning than did Group OT+/O+.

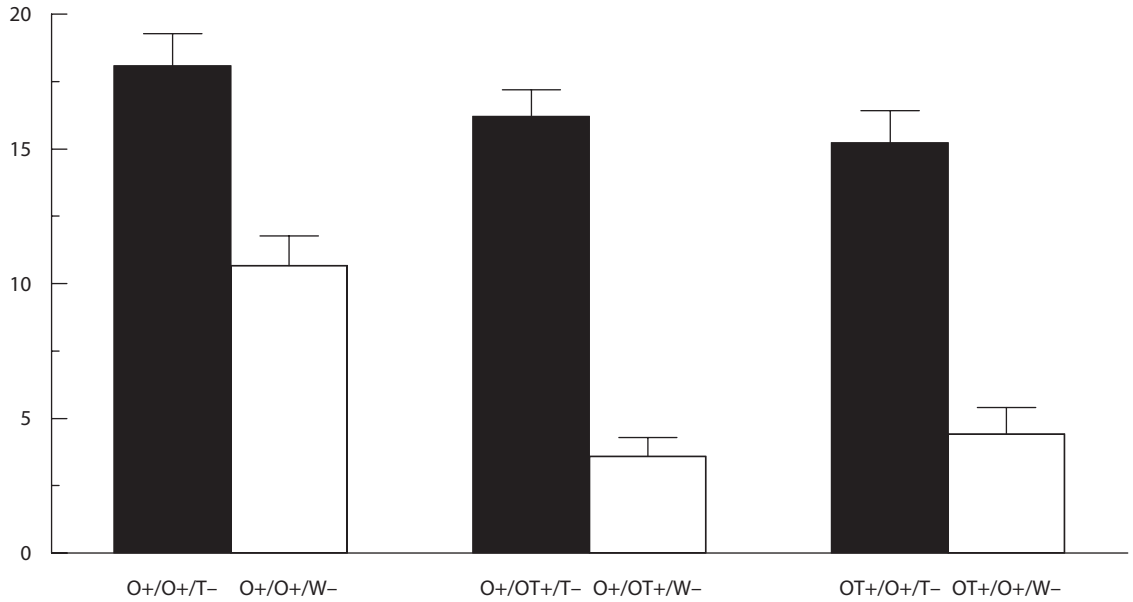

Figure 7. Mean (+*SE*) denatonium saccharide solution (DEN) intake, in milliliters, during DEN tests in Experiment 4. Group O+/O+/W− received two AL–LiCl pairings. Group O+/O+/T− received two AL–LiCl pairings followed by four DEN extinction trials. Group O+/OT+/W− received an AL–LiCl pairing followed by an AL+DEN–LiCl pairing. Group O+/OT+/T− received an AL–LiCl pairing, an AL+DEN–LiCl pairing, and four DEN extinction trials. Group OT+/O+/W− received an AL+DEN–LiCl pairing followed by an AL–LiCl pairing. Group OT+/O+/T− received an AL+DEN–LiCl pairing, an AL–LiCl pairing, and four DEN extinction trials. AL, 0.02% almond odor solution.

Yet several reasons suggest that this factor is not the source of the order effect difference. First, if the reduced sampling of the compound in the second phase of O+/OT+ conditioning was responsible for weaker conditioning, one would expect to have found significantly greater overshadowing of the AN aversion in Group OT+/O+ in Experiment 2, yet this group did not differ from their O+/OT+ counterpart. Second, another argument could be based on the logic that the reduced sampling of the compound by Group O+/OT+ interfered with the formation of a taste–odor within-compound association, but the results of Experiment 4 refute this argument as well. Third, if the reduced sampling of the AL+DEN compound during Conditioning Trial 2 is responsible for the weaker AL aversion, one would predict a negative correlation between the DEN+AL conditioning intakes and the average AL test intake for the O+/OT+ experiments in this report. To test this prediction, we analyzed the Conditioning Trial 2 data and AL test data for Group O+/OT+ for the four experiments that demonstrated the order effect difference (Experiments 1A, 1B, 3, and 4). This analysis yielded a significant positive correlation [$r(39) = .574$, $p < .01$], indicating that the rats that consumed less on the compound conditioning trial actually had stronger AL odor aversions on test. Therefore, although the taste+odor compound intakes during O+/OT+ conditioning deserve consideration, they do not appear to be the source of the order effect difference.

A second alternative explanation for the source of the order effect difference is enhanced taste-aversion conditioning in Group OT+/O+ via mediated conditioning (see, e.g., Holland, 1983). In this approach, the association of taste and odor during OT+ conditioning elicits a representation of the taste during O+ conditioning, and this produces mediated conditioning of the taste aversion. Then this mediated taste conditioning enhances the contribution of the taste–illness association following OT+/O+ conditioning. There are at least two reasons, however, why this explanation does not appear to be viable. First, there is little evidence that the taste aversion produced by OT+/O+ conditioning is stronger than the taste aversion produced by O+/OT+ conditioning (cf. Figures 5 and 7). Second, another relevant finding comes from Holland's work examining the role of mediated conditioning in TPOA. In the fourth experiment of that report, one odor (X) was paired with the taste and a second odor (Y) was presented alone during the preexposure (nonconditioning) stage. During the second conditioning stage, there was a single presentation of both Odors X and Y followed by lithium. During odor testing, the aversion to Odor Y was stronger than that to Odor X. Holland's explanation was that during the second conditioning phase, Odor X elicited a representation of the taste, which then potentiated responding to Odor Y, but this taste representation could not potentiate responding to its associate Odor X during this trial. This outcome may be relevant to the present experiments, because it suggests that once two cues have been paired (O and T), a subsequent presentation of one of these cues (O) may elicit its associate (T), but the discrepancy between the two phases will not permit the taste representation to potentiate the odor. This interpretation appears capable of addressing the present experiments and those of Holland, especially because in both cases there was only a single opportunity for mediated conditioning.

Instead, the present results suggest that the initial O+ phase in O+/OT+ conditioning disrupts some process that is necessary for TPOA to occur. This outcome is similar to that of other experiments that have shown that a sequential presentation (rather than a simultaneous presentation) of the taste and odor is sufficient to interfere with TPOA (see, e.g., Batsell, Paschall, Gleason, & Batson, 2001; Holder & Garcia, 1987). Different reports have confirmed that preexposure to the odor alone (Droungas & LoLordo, 1991) or to the taste alone (Holder, Leon, Yirmiya, & Garcia, 1987) prevents TPOA. It should be noted that some studies have preexposed the taste+odor compound and still have reported TPOA (e.g., Durlach & Rescorla, 1980), but in these cases the integrity of the compound was maintained throughout the preexposure and conditioning phases. Although the single-element preexposure studies have shown that interrupting the integrity of the compound will eliminate TPOA, one drawback of the preexposure manipulation is a subsequent weakening of the associability of the cue with the emetic US. In contrast, a distinct advantage of the O+/OT+ design used in the present experiments is that it allows for a separate presentation of the odor during Conditioning Trial 1 without a loss in associative strength. As stated above, the most parsimonious explanation of the weaker odor aversion following O+/OT+ conditioning is the absence of TPOA, and this conclusion has implications for the various theoretical models of TPOA.

Theoretical Mechanisms of TPOA

The present results provide insight into the viability of different theoretical models of TPOA—specifically, the limitations of the sensory-and-gate channeling model and the within-compound association model. According to the sensory-and-gate channeling model of TPOA, an odor is processed via the external defense system unless it is presented along with a taste. The presence of the taste gates the odor into the gut defense system, at which point it is processed like a taste, which strengthens the odor–US association. This strengthened odor–US association gives rise to the significantly stronger odor aversion relative to a group that only received odor-alone conditioning. The key experimental prediction derived from this account is that once the odor is gated into the internal defense system, it is independent of the current value of the taste. Therefore, manipulations that decrease (postconditioning taste extinction) or increase (postconditioning taste inflation) the taste aversion should have no influence on the potentiated odor aversion. In both Experiments 3 and 4, after odor+taste compound conditioning, a group that received postconditioning taste extinction showed significant weakening of the odor aversion, an outcome that is inconsistent with the prediction above of the sensory-and-gate channeling model. The present demonstration that postconditioning taste extinction decreases TPOA is consonant with previous examples of this result from

our lab (Batsell et al., 2001; Trost & Batsell, 2004) and other labs (Durlach & Rescorla, 1980; Miller et al., 1986; von Kluge, Perkey, & Peregord, 1996; Westbrook et al., 1983). Furthermore, the evidence from our postconditioning taste-inflation experiments also refuted the prediction that postconditioning manipulations of the taste aversion would not alter a potentiated odor aversion (Batsell et al., 2003). Thus, even though two reports have not found that postconditioning taste extinction alters TPOA (Droungas & LoLordo, 1991; Lett, 1984), the majority of the experiments have refuted this prediction of the sensory-and-gate channeling model.

Although it has often been argued that the results from postconditioning taste-extinction manipulations support the within-compound association account of TPOA offered by Durlach and Rescorla (1980), our recent experiments reveal limitations of this account. For example, Trost and Batsell (2004) reported that odors (orange or almond) of the same concentration that produced odor aversions of similar strengths could interact with the same taste (denatonium) to produce potentiated odor aversions of differential strengths. The within-compound association account of TPOA offers no mechanism by which odors of similar strength would be differentially affected by the formation of a within-compound association. Subsequent studies suggested that the rats' differential potentiated odor aversions resulted from the perceived relative similarity of the odors alone and unique taste+odor compounds. Furthermore, Schnelker and Batsell (2006) have shown the presence of within-compound associations with a taste+odor compound that does not produce TPOA. In this report, the odor was a strong concentration of AL odor, whereas the taste was a weaker concentration of DEN. These concentrations were chosen on the basis of previous work that had shown that the salience ratio of a strong taste and a weak odor was necessary for TPOA (Bouton et al., 1986). In Experiment 1, following taste+odor compound conditioning, postconditioning taste extinction weakened the odor aversion, even though there was no evidence of TPOA. In Experiment 2, following taste+odor compound conditioning, postconditioning taste inflation strengthened the odor aversion, even though there was no evidence of TPOA. Thus, we demonstrated in these experiments that a taste–odor within-compound association was present but that it was not sufficient to produce TPOA. Similarly, in Experiment 4 of this article, we demonstrated a taste–odor within-compound association in the absence of TPOA. The noteworthy aspect of this outcome is that these concentrations of DEN taste and AL odor can clearly support TPOA, as evidenced in this article and in other experiments (see, e.g., Batsell et al., 2003; Trost & Batsell, 2004). In sum, a number of studies have shown that a taste–odor within-compound association is not sufficient for TPOA, and thus, despite many years of support, the within-compound association model of TPOA is inaccurate. Note, however, that the role of within-compound associations in mediating other forms of synergistic conditioning, such as augmentation, remains to be determined.

As noted elsewhere (Batsell & Blankenship, 2003; Trost & Batsell, 2004), the configural interpretation of TPOA offered separately by Rescorla (1981) and Kucharski and Spear (1985) has received little investigation, partly because Kucharski and Spear discredited their prediction that postconditioning exposure to the elements of the compound would enhance responding to the compound itself. In fact, our recent investigations have also failed to support this specific prediction (Trost & Batsell, 2004); we also observed that responding to the compound was no stronger following separate extinction of taste and odor than following extinction of the compound itself (cf. Experiments 2 and 3). Instead, Trost and Batsell proposed a revision of the configural account of TPOA, the configural–elemental approach, to accommodate responding following postconditioning presentations of either element.

In the configural–elemental approach, depending on the relative salience of the taste and odor cues, the initial presentation of the taste+odor compound provides the opportunity for the formation of (1) a configural representation of these cues and (2) a latent within-compound association between these cues. Even though the exact mechanism of the configuration process has yet to be empirically verified, it is speculated to be similar to the process proposed by Rescorla (1981). Advancing an argument proposed by James and by Robbinson, Rescorla suggested that the organism perceives the compound cue as a unitary stimulus, rather than as two separable elements. Subsequent testing of an element of the compound (i.e., the odor) may elicit confusion in the organism, and the organism may respond to the odor as it would to the more salient taste+odor compound. If the odor cue is perceived to be similar to the taste+odor compound, a strong CR will be recorded (i.e., odor potentiation), but if the odor alone is perceived to be quite different from the taste+odor compound, a weaker CR will be observed. This description of responding is consistent with the pattern reported by Trost and Batsell (2004). However, following compound conditioning, if the configural representation is disrupted by postconditioning extinction or inflation, the latent elemental association between these cues can be activated. Once the configuration representation is broken, the organism would not be able to reconfigure the cues, and responding to each would follow the predictions from the within-compound association model. Finally, if the configuration process is prevented, as by preconditioning of the odor in the present experiments, the within-compound association would still form between taste and odor if they were presented simultaneously.

In closing, our experiments have provided additional evidence of the shortcomings of two long-standing theories of TPOA, the sensory-and-gate model and the within-compound association model. The present results, however, are consistent with a variation of a configural interpretation of TPOA, the configural–elemental model. Clearly, more direct tests of the configural–elemental model are required, but at present, it provides a viable explanation of much of the TPOA literature.

AUTHOR NOTE

Portions of this research were presented at the Annual Meeting of the Psychonomic Society (New Orleans, November 2001), the meeting of the Eastern Psychological Association (Boston, March 2005), the meeting of the Southwestern Comparative Psychological Association (Memphis, March 2005), and the third Magnetic Island Conference (Magnetic Island, Australia, July 2006). The authors thank Christina Trost, Stephanie Cochran, and especially Joaquin Lugo, for their contributions to this research. Correspondence concerning this article should be addressed to J. D. Batson, Department of Psychology, Furman University, Greenville, SC 29613 (e-mail: batson@furman.edu) or to W. R. Batsell, Jr., Department of Psychology, Kalamazoo College, Kalamazoo, MI 49006 (e-mail: rbatsell@kzoo.edu).

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NOTE

1. The experiments in this report were conducted in different labs, and the levels of conditioning differed across institutions. Specifically, conditioning was always more robust in the Kalamazoo College lab than in the Furman lab, but as described in this report, the pattern of results during testing was consistent across all experiments at both institutions. We initially conducted all statistical analyses using test trials as a within-subjects factor, but determined that when individual test data were displayed in a graph, floor effects obscured the primary comparisons of interest. Instead, a presentation of the data averaged across all tests yielded the best approach to showing the consistent pattern of results across studies. Finally, to ensure that the statistical analyses mirrored the data presented in the figures, we reanalyzed the data averaged across the test trials. Removing the within-subjects factor of trials eliminated in each study the significant trials effect (i.e., extinction) and the significant trials × group effect, which reflected the differential extinction across studies. In all other comparisons, the two statistical approaches yielded the same statistical effects and significant differences.

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