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Within-compound associations mediate augmented flavor aversions

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ABSTRACT

Five experiments with rat subjects explored flavor-aversion conditioning in the A+/AX+ design. In Experiment 1, odor preconditioning prior to taste + odor compound conditioning significantly strengthened a taste aversion, and taste preconditioning prior to taste + odor conditioning significantly augmented an odor aversion. Experiments 2A and 2B eliminated the alternative explanation that the augmentation effect was produced by differential exposure to the compound during conditioning. Next, we examined a possible mechanism of these augmentation effects by employing post-conditioning extinction of the augmenting stimulus (CS A); previous research had also used this technique to explore augmentation, but those studies yielded conflicting results. In both Experiments 3A and 3B, post-conditioning extinction of CS A led to a significant decrease in the strength of the augmented aversion to CS X, regardless of stimulus modality or stimulus salience. Collectively, these results suggest augmented flavor aversions are produced via within-compound associations between CS A and CS X.

In classical conditioning, when two or more conditioned stimuli (e.g., CS A and CS X) are paired with an unconditioned stimulus (US), cue competition between the CSs is frequently observed. Two notable examples of this cue competition are overshadowing and blocking. First, when CS A and CS X are followed by a US, the cues appear to compete for associative strength and subsequent responding to the weaker CS is less than if that CS had been paired alone with the US; this phenomenon was termed overshadowing by Pavlov (1927, pp. 269–270). Similarly, Kamin (1969) introduced the concept of blocking with the use of the A+/AX+ design where preconditioning of CS A prior to compound conditioning of CS A and CS X resulted in decreased or "blocked" learning to CS X. Although most formal models of associative learning predict cue competition in these situations (e.g., Pearce & Hall, 1980; Rescorla & Wagner, 1972), sometimes these designs yield outcomes that suggest synergistic conditioning rather than competitive conditioning. For example, in flavor-aversion learning, the pairing of a taste and an odor prior to an illness episode can result in a stronger taste aversion to the weak flavor cue; a phenomenon labeled potentiation (e.g., Rusiniak, Hankins, Garcia, & Brett, 1979). Likewise, when flavor CS A is preconditioned with an illness-producing US, and that preconditioned CS is next conditioned in compound with a new flavor cue (X), the subsequent aversion to X is not blocked, but instead, is augmented (e.g., Batson & Batsell, 2000). It is still unclear why the A+/AX+ conditioning paradigm can yield both competitive and synergistic outcomes, so identification of the mechanisms of the various phenomena may help resolve this question. The present studies were designed to clarify the mechanism of augmentation.

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The first two investigations of augmentation demonstrated the ability of a preconditioned almond odor to augment responding to the bitter taste denatonium saccharide (Batsell & Batson, 1999; Batson & Batsell, 2000) whereas a later report showed that preconditioned denatonium could subsequently augment an almond odor aversion (Batsell, Paschall, Gleason, & Batson, 2001). In almost every respect, the results from these two investigations paralleled each other. For example, neither phenomenon was attributable to generalization, and both phenomena required a simultaneous presentation of the flavor cues during compound conditioning. Moreover, the strength of the augmented aversion to CS X appeared dependent on the strength of CS A. In some experiments this was demonstrated by showing that extinction of CS A between the A+ and A+/AX+ phases eliminated augmentation of CS X (Experiment 4, Batsell et al., 2001; Experiment 3, Batsell & Batson, 1999); in another study (Experiment 2, Batsell & Batson, 1999), it was shown that preexposure to CS A prior to A+/AX+ conditioning effectively diminished the augmentation of CS X. Collectively, these results are consistent with an interpretation of augmentation in terms of the formation of within-compound associations. In the within-compound association model (e.g., Durlach & Rescorla, 1980), three associations form during compound conditioning. These associations are: 1) A-US, 2) X- US, and 3) A-X. During testing of CS X, X is able to activate the US representation directly through the A-US association and indirectly through the associative chain of X → A → US. In the case of augmentation, the significantly stronger aversion to CS X is due to its own association with the US summating with the robust A-US association formed during preconditioning. The critical test of the within-compound association approach is to employ post-conditioning extinction of CS A and measure responding to CS X (cf., Durlach & Rescorla, 1980). If the X–A within-compound association exists, post-conditioning extinction of CS A should break the indirect association chain, and significantly weaken the aversion to CS X relative to a similarly trained group that did not undergo extinction of CS A.

To date, only two augmentation studies have used the post-conditioning extinction procedure to explore within-compound associations, but they yielded conflicting results. Batsell and Batson (1999; Experiment 5) did not find any effect of post-conditioning almond odor extinction on the augmented denatonium aversion whereas Batsell et al. (2001; Experiment 6) found that post-conditioning taste extinction significantly weakened the augmented odor aversion relative to controls. The asymmetry observed from these two post-conditioning extinction studies is at odds with the symmetry from the other augmentation studies, and this discrepancy in the nature of the phenomenon needs to be resolved to determine augmentation's mechanism. Based on the two post-conditioning extinction studies, augmentation may be an asymmetrical phenomenon whereby taste extinction alters an augmented odor aversion, but odor extinction does not change an augmented taste aversion. A variation of this approach is that the asymmetry may not be due to stimulus modality, but instead, it may be due to stimulus salience. For example, when exploring retrospective revaluation (AX+/A−) in an appetitive conditioning task, Liljeholm and Balleine (2006) reported that extinction of the more salient CS led to increased responding to the less salient stimulus, but extinction of the less salient CS did not reliably alter responding to the more salient CS. Many previous studies have confirmed that taste aversions tend to be stronger than odor aversions (e.g., Rusiniak et al., 1979), so it may only be that extinction of the more salient augmenting stimulus (taste) can weaken responding to the less salient augmented stimulus (odor), but the converse is not true. Alternatively, augmentation may be a symmetrical phenomenon mediated via within-compound associations, so that extinction of the augmenting CS will produce a weakening of the aversion to the augmented CS, regardless of stimulus modality or stimulus salience. Considering that much augmentation research (Batsell & Batson, 1999; Batsell et al., 2001) is best accommodated by the within-compound association entailed by this third possibility, we predicted this outcome was most likely.

The present research was initiated to clarify the mechanism of flavor augmentation. The initial experiment was necessary to demonstrate the complimentary augmentation effects with almond odor and saccharin (Sigma Chemical Corp. has recently discontinued production of denatonium saccharide, so we used a sodium saccharin solution in the present experiments). Experiments 3A and 3B were designed to determine the effects of post-conditioning extinction of the augmenting stimulus (CS A) on the strength of the augmented stimulus (CS X). Experiment 3A tested the effects of taste extinction on odor responding and Experiment 3B tested the effects of odor extinction on taste responding. If evidence of a common mechanism of augmentation can be obtained, it would yield a more parsimonious account of the phenomenon, and it may provide insight into why A+/AX+ conditioning yields augmentation in some situations, but blocking in others.

Experiment 1

There were 6 groups in Experiment 1. Two control groups received single-element conditioning (X+), two groups received compound conditioning (AX+), and two groups received augmentation training (A+/AX+). For half of the groups, almond odor solution was CS A while saccharin was CS X; for the other 3 groups, saccharin was CS A while almond odor was CS X. Based on past experiments (e.g., Batsell et al., 2001; Batson & Batsell, 2000), we predicted preconditioning of CS A would augment the aversion to the second flavor or odor (CS X), regardless of stimulus modality or salience.

Method

Subjects

Sixty experimentally naïve, male Holtzman rats, purchased from the Harlan Sprague-Dawley Corporation (Indianapolis, IN) were subjects in this experiment. Rats were purchased when they were between 100 and 125 g, and they were