AN ABSTRACT FOR THE THESIS OF

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Title: TOXICOSIS - MEDIATED POTENTIATION OCCURS IN A TASTE/TASTE COMPOUND

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The phenomenon known as taste-mediated potentiation is typically defined as an enhanced conditioned aversion to a target element of a compound CS relative to that element conditioned singly. Many of the initial potentiation studies examined the associations of compounds consisting of a taste and a non-taste element such as a visual cue (Galef & Osbborne, 1978), color cue (Lett, 1980), auditory stimuli (Ellins, Cramer, & Whitmore, 1985), environmental element (Best, Brown, & Sowell, 1984) or odor (Durlach & Rescorla, 1980). This phenomenon has not been so apparent when the compound CS has consisted of two tastes (Bouton & Whiting, 1982). However, recently Bouton, Dunlap, and Swartzentruber (1987) have reported successful potentiation of a taste by another taste. In the present two studies a taste-taste compound CS, comprised of denatonium saccharide and saccharin, was presented to rats prior to lithium chloride-induced toxicosis. It is evident from both experiments that these two tastes can form an effective

compound CS. While a preexposure phase was conducted in Experiment 1, this phase was omitted in Experiment 2 to address the concern that the association interpreted as potentiation may have been formed during Preexposure and not during Conditioning. As the results of Experiment 2 mirrored those of Experiment 1, the enhanced aversion (i.e., potentiation) to the saccharin was a result of the association formed between the compound (denatonium + saccharin) and the lithium chloride-induced illness on Conditioning.

TOXICOSIS - MEDIATED POTENTIATION OCCURS IN A TASTE/TASTE COMPOUND

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Finally, I wish to express my deepest gratitude for the unconditional support of my parents. Their immeasurable pride in my achievements has continued to provide me with the necessary impetus to pursue my education and strive to be the best I can be.

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CHAPTER 1

INTRODUCTION

One of the most thoroughly studied phenomena in animal psychology is the learned taste-aversion paradigm. This phenomenon is based upon Pavlovian conditioning. Classical or Pavlovian conditioning is a form of learning in which novel, neutral stimuli come to elicit responses similar to exisiting reflexive responses. A neutral conditioned stimulus (CS) is paired with an unconditioned stimulus (US) that naturally elicits a reflexive response (unconditioned response, UR). After several pairings with the US, the CS is capable of eliciting a conditioned response (CR) which is similar to the initial reflexive UR. For example, a classical conditioning arrangement might consist of pairing a tone (CS) with a puff of air (US) and observing the eyeblink (UR) as the reflexive response. After several pairings the subject will blink its eye (CR) when just the tone (CS) is presented, i.e., as a result of associative learning (see Tarpy, 1982).

In the conditioned taste-aversion paradigm, the subject develops an aversion to a novel taste. Typically, a novel flavor (CS) is paired with a toxicosis-inducing agent (US), such as radiation (Garcia & Koelling, 1966, 1967), lithium chloride (LiCl)

(Nachman & Ashe, 1973), morphine (Miller, McCoy, Kelly & Bardo, 1986), apomorphine (Parker, 1986), cyclophosphamide (Elkins, 1974), or rotation (Green & Rachlin, 1976). Subsequently the subject decreases consumption of the conditioned flavor. Many of the earlier studies of taste-aversion learning employed a single element CS, for example saccharin or plain water (e.g., Garcia & Koelling, 1966; Nachman, 1970).

More recent studies have utilzed compound CSs in an attempt to examine associations that might occur between two flavors (Fanselow & Birk, 1982; Galef & Osborne, 1978; Klein, Freda & Mikulka, 1985; Miller, McCoy, Kelly & Bardo, 1986). It is apparent from these conditioning studies that the associative strength the CS acquires is not related solely to the US with which it has been conditioned. In fact, the strength of the aversion can depend upon the other stimuli present at the time of conditioning. The degree to which one stimulus affects another depends upon their relative associative strengths. When a target stimulus, that has been presented in compound, subsequently elicits a decreased conditioned response as compared to the response elicited when it has been conditioned singly, the second stimulus in the compound is credited with effecting the conditioning of the target stimulus. Pavlov (1927, p.269) called this particular form of associative interference overshadowing. Kamin (1969) and Revusky (1971) also have reported the occurrence of overshadowing. Overshadowing occurs in such diverse situations that it is considered to be an important general rule of conditioning (Lett, 1982).

Recently an exception to overshadowing has been observed by numerous researchers in poison-avoidance learning (Brett, Hankins & Garcia, 1976; Durlach & Rescorla, 1980; Rusiniak, Hankins, Garcia & Brett, 1979). Under some conditions an enhanced conditioning or associability has been shown to be the result of employing a compound CS. To demonstrate such enhanced conditioning or potentiation a weak cue is paired with a strong cue, usually a taste, as a compound CS and then followed by presentation of the US which induces illness. The strong cue enhances the conditioning of the weak cue rather than attenuating it as would be the case with overshadowing. Therefore, potentiation can be viewed as the opposite of overshadowing (Lett, 1982) and as such deserves much attention (see Durlach & Rescorla, 1980).

Many of the initial potentiation studies examined the associations of compounds consisting of a taste and a non-taste element such as a visual cue, color cue, environmental element, or odor. For example, Galef and Osborne (1978) found that when a specific visual cue, a colored capsule, was presented in compound with a novel taste an aversion to the visual cue developed. No aversion to the capsule was exhibited by those rats that had received the capsules containing unflavored food. Thus, the flavor enhanced the conditioned aversion to the visual property of the compound. Similar results were found in studies examining color cues in compound with tastes.

Lett (1980) administered flavored or unflavored and colored or uncolored water as the compound CS, with LiCl to induce toxicosis, to pigeons and quail. For both species, the subjects that received the color in compound with the flavor during conditioning exhibited aversions to the unflavored colored water during testing. However, those subjects conditioned to the colored unflavored water did not exhibit color aversions during testing. In those studies the presence of the flavor served to enhance the aversion to the color element of the compound stimulus providing further evidence for taste-nontaste associations.

In addition to the visual- and color-taste potentiation research, there is evidence that, at least for rats, an aversion to an auditory stimulus can be potentiated by a taste. During conditioning Ellins, Cramer, and Whitmore (1985) presented sweet food with a tone at various locations to three groups of rats and just the tone without food to another group of rats. It was discovered that spatial contiguity of the tone and the food was necessary for conditioning a taste-potentiated aversion to the auditory component. The importance of this finding is that the nontaste element of the compound CS need not be one that is typically considered a food cue. Perhaps a stimulus of any modality can be aversively conditioned provided it is spatially and temporally presented in compound with a taste and paired with toxicosis.

In 1984 Best, Brown, and Sowell investigated the ability of non-ingestive environmental stimuli to become the target of taste-mediated potentiation. Subjects received a sodium saccharin fluid in either a standard operant chamber or in a polypropylene, mouse-breeding cage lined with a plastic bag. Immediately following fluid consumption in the respective container the rats received a LiCl injection. Testing for environmental aversion consisted of presenting the subjects with either water or saline in the respective environment. Subjects that had been conditioned with the saccharin in their distinctive environment subsequently drank less water or saline than those subjects that had received water in the environmental chamber prior to toxicosis. The pairing of the compound stimulus (taste and a specific environment) with LiCl resulted in a potentiated aversion to the environment as evidenced by their unwillingness to consume a familiar, nonaversive flavor in the environment. Additional research also has shown that a novel taste consumed in a distinct environment, conditions enhanced LiCl-mediated aversions to the environment more strongly than does consumption of either water or a familiar taste in that same environment during conditioning (see Best, Batson, Meachum, Brown & Ringer, 1985).

It should be noted that not all researchers have observed potentiation when environmental cues are presented as one element of a compound CS. When Taukulis and St. George (1982) presented rats with an odor (oil of eucalyptus) in a distinctive environment (black compartment) the rats exhibited no decreased consumption of water when they were subsequently tested in the compartment. Rats that had been conditioned in the same black compartment without the odor subsequently reduced water consumption in the distinct environment during testing. The odor appeared to be an effective overshadowing stimulus, not a potentiator, when paired with the environment.

Klein, Freda, and Mikulka (1985) reported mixed results when they studied the influence of taste stimuli on environmental aversion conditioning. They poisoned their experimental rats in the distinctive black chamber of a shuttlebox partitioned into two compartments (one black and one white) while allowing the control animals to experience the black compartment without illness. Counterbalanced presentations of a salient sucrose solution or water were made in both compartments to both experimental and control animals. The experimental groups demonstrated strong aversions to the black compartment, measured by both fluid intake in the compartment and time spent in the chamber. However, only the animals allowed access to the sucrose in the black chamber and water in the white chamber exhibited stronger environmental aversions than the animals given water in the black chamber. These results indicate that potentiation can be demonstrated when employing an environmental-taste compound paired with illness, but not under all cirumstances.

In two similar experiments, Klein and Elder (1987) examined whether the place (home cage versus black chamber) where toxicosis occurred enhanced the reliability of the potentiation effect. The presence of the sucrose solution resulted in stronger aversions to the black chamber than did the water. However, it was reported that potentiation was observed only when toxicosis took place in the black chamber and not when it occurred in the home cage. Clearly, while potentiation has been difficult to produce in certain situations, its existence has nevertheless been verified and because of its relationship to overshadowing, a major learning phenomenom, it is worthy of continued examination.

It has been demonstrated that odor is an important distal cue that guides approach responses in laboratory rats (Rusiniak, Gustavson, Hankins & Garcia, 1976; Westbrook, Bond & Feyer, 1981) and that taste is the optimal proximal cue that influences ingestion (e.g., Garcia & Koelling, 1966). Furthermore, research has revealed that odor cues are more effective than taste cues in shock-avoidance learning (see Hankins, Rusiniak & Garcia, 1976; Rusiniak, Palmerino, Rice, Forthman & Garcia, 1982) but taste cues are more effective than odor cues in the case of flavor-aversion learning (Hankins, Garcia & Rusiniak, 1973). Because proximal taste cues control ingestive behaviors and distal odor cues influence approach behaviors to food sources, then an enhanced aversion to the latter due to the former would be functionally adaptive by preventing the organism from expending energy approaching and consuming a potentially toxic food. Hence, due to their influences upon ingestion, it seems reasonable that the area of potentiation that has received the most attention has been that of taste-potentiated odor aversion (Durlach & Rescorla, 1980; Palmerino, Rusiniak & Garcia, 1980; Rusiniak, Hankins, Garcia & Brett, 1979). These studies typically involve presenting an odor in compound with a taste and pairing it with illness. The taste component is usually presented as a fluid solution while the odor has been presented in numerous ways. For example, Rusiniak, Gustavson, Hankins, and Garcia (1976) presented the odor mixed with an odorless fluid like tap water. Other researchers have placed the odor on a filter paper located immediately near the drinking spout (Bouton, Jones, McPhillips & Swartzentruber, 1986). Another method has been to deliver the odor via an air stream near the drinking tube (Westbrook, Homewood, Horn & Clarke, 1983). Potentiation has then been identified when the subject conditioned to the odor-taste compound drank even less of a neutral taste in the presence of the conditioned odor than those animals that had been conditioned to the odor alone.

Along these lines, Rusiniak, Hankins, Garcia, and Brett (1979) used the typical taste-aversion procedure, CS followed by the US which elicits the UR, to establish that almond-scented water served as a weak cue for toxicosis relative to saccharin water. Then, they demonstrated that when the weak almond odor was presented in compound with the salient saccharin taste and followed by LiCl-induced illness, rats subsequently displayed a taste-potentiated odor aversion. They also used the same elements, almond odor and saccharin taste, in a second-order conditioning paradigm. In other words, they initially presented the first-order CS, paired with lithium, then presented the second-order CS paired with the aversive first-order CS without a US pairing. Finally, consumption of the second-order cue was tested. When the second-order procedure was employed rats did not use the odor to avoid the aversive taste. Furthermore, the rats did not learn a taste-aversion for the saccharin when paired with the aversive almond odor. Clearly, as indicated in this research, the potentiated aversion using the odor and taste cues results from the simultaneous pairings of the cues as a compound CS and does not occur using a second-order conditioning procedure.

In 1984 Coburn, Garcia, Kiefer, and Rusiniak published a study in which they further examined the temporal interval between the odor and taste in compound aversion conditioning. In Experiment 1 they presented the taste, sodium saccharin solution, at time 0 and presented the odor, almond extract, at intervals of either -10, -1, 0, or 10 minutes in a simple compartment that did not allow for strict control of odor diffusion. In Experiment 2, while using a "wind tunnel" apparutus to provide better control of both odor presentation and odor diffusion into the surrounding environment, they used odor intervals of -5, -2, and 0 minutes. Results indicated that while using their (Coburn, Garcia, Keifer & Rusiniak, 1984) procedure, odor by itself was not an effective CS. However, when the odor was presented simultaneously (i.e., 0 minutes) with the taste cue, the taste cue potentiated the odor cue. Furthermore, the two-minute interval between the odor and taste components served to attenuate the potentiation and the five-minute interval disrupted the effect.

Holder and Garcia (1987) used a more sophisticated "wind tunnel" apparatus than Coburn, Garcia, Keifer, and Rusiniak (1984) and also looked at the effects upon potentiation of various intervals between presentation of the odor (almond extract) and the taste (saccharin solution) elements. They found that when using their conditions the rats did not associate the odor presented alone with illness. When the taste and odor elements were provided in compound at the same time and followed by LiCl-induced illness, illness associated with the odor was potentiated. However, when 45 and 90 second intervals between the CSs were provided the potentiation failed to be exhibited, further strengthening the idea that if potentiation were to occur the elements must be provided simultaneously. In addition to these findings, Holder and Garcia (1987), discovered that as the intensity of the odor increased the aversion also increased, provided the two were presented simultaneously.

Bouton and Whiting (1982), Mikulka, Pitts, and Philput (1982), Rosellini and Lashley (1986) have all published studies that have failed to demonstrate potentiation when using odor-taste compounds. While none of their procedures have been exact replicas of studies that have reported potentiation, they have been extremely similar. For example, Bouton and Whiting (1982) used almond extract and saccharin solution as their odor and taste, respectively. While these reports do cast a shadow of doubt upon the phenomenon of potentiation, they do serve to encourage further probing into the effects of employing a compound-stimulus in taste-aversion learning.

Although flavor associations have been of interest to researchers for quite some time, the most elusive area of potentiation to be studied has been that of taste-taste compound conditioning. In an attempt to detect the association between one flavor and another when the two are presented as a compound, Brogden (1939) developed a sensory preconditioning paradigm. The procedure used for this paradigm was to initially present two stimuli together, later present one of the two stimuli with a US, and then test the second stimulus. If the second stimulus elicits a response similar to that of the conditioned stimulus then it is evidence that the two elements became associated when they were presented in compound.

More recently, Lavin (1976) used this sensory preconditioning procedure and added to the evidence that two flavors of a compound stimulus can establish flavor-flavor associations. In Experiment 1 Lavin presented the two flavors, CS1 and CS2, in sequence during a Sensory Preconditioning phase. During conditioning CS2 was paired with toxicosis. Subsequent testing consisted of a preference test between distilled water and CS1. Experiments 2 and 3 examined the effects of various interstimulus intervals upon flavor-flavor associations. The results of these studies revealed that flavor associations can occur when the flavors are sequentially paired with each other in close temporal contiguity.

Others have concentrated efforts on examining compound elements presented simultaneously rather than sequentially. Rescorla and Cunningham (1978) conducted two experiments to examine possible associations formed within a compound of two simultaneously presented flavors. In Experiment 1, compound flavor solutions were presented, then one of the flavors was paired with a toxin, and finally the rat's consumption of the other flavor was measured. Results from that experiment provided evidence that the subjects formed associations between the flavors that had been presented in compound. Furthermore, conditioning of one element of a compound resulted in increased aversion to the second flavor element of the compound. Additionally, the second experiment also demonstrated the development of within-compound flavor associations by showing that the extinction of one element resulted in a decreased aversion to the other flavor.

Given the strong associations that are readily formed between tastes and illness, one would have anticipated that a compound CS composed of two tastes would also condition quite readily. Surprisingly, it has proven quite difficult to obtain potentiation when two tastes have comprised the compound stimulus. The present experiments were designed to further investigate this phenomenon.

CHAPTER 2

EXPERIMENT 1

As can be seen from the previous discussion (see Chapter 1), taste-potentiated aversions to nontaste elements of a compound CS have been readily demonstrated. This phenomenon has not been so apparent when the compound CS consists of two tastes. For example, Bouton and Whiting (1982) have reported several failures to obtain potentiation when using a compound CS comprised of two tastes. This type of result would be expected if, as suggested by Palmerino et al. (1980), Rusiniak, Hankins, Garcia, and Brett (1979), it were true that potentiation is a special property of distal-proximal cue compounds. However, if the phenomenon were merely dependent upon the formation of a within-compound association as proposed by Durlach and Rescorla (1980), one would expect to observe taste-taste potentiation. In a recent publication, Kucharski and Spear (1985) have reported demonstrating potentiation using a compound of the two flavors coffee and sucrose. Clearly, more research is necessary to determine the extent to which taste-taste potentiation will occur.

More specifically, the purpose of the present study was to assess taste-taste compound conditioning in relation to single-element taste-aversion learning. The present experiment sought to determine whether potentiation would be demonstrated when using the two tastes denatonium saccharide and saccharin. Denatonium saccharide, hence forth to be referred to as denatonium, was selected because it is an odorless, colorless bitter that is readily consumed in concentrations of 1 part per 10,000 parts water (see Davis et al., 1986). Saccharin was choosen as the second element of the compound because of its prevalent use in taste-aversion conditioning.

Four groups were tested in the initial experiment. During Preexposure and Conditioning, two groups received a single-element CS, saccharin (SA) or denatonium (DE). The remaining two groups received the saccharin-denatonium compound stimulus (MX). A two-bottle preference test followed Conditioning. During this test the preference for saccharin versus water was assessed for group DE and one of the MX groups. The preference of the remaining two groups, SA and the other MX, for denatonium versus water was assessed. Depressed saccharin or denatonium consumption on the part of the respective MX groups would reflect the occurrence of enhanced conditioning (i.e., potentiation), while increased consumption of these elements would reflect overshadowing.

Method

Subjects and apparatus. The subjects were 32, 150-day-old male Holtzman rats. All subjects were individually housed in standard wire-mesh cages and were given free access to food throughout the experiment. All testing took place in the home cage.

Procedure. Four equal-sized groups were randomly formed at the start of the experiment. Specific group designations were: SA-SA, MX-SA, DE-DE, and MX-DE. The SA, DE and MX designations refer to a 0.15% saccharin solution, a 1 part denatonium per 10,000 parts water solution, and the compound (MX) composed of these two elements, respectively. The first portion of the group label designates the fluid received during Preexposure and Conditioning. The second designation refers to the fluid presented with water during the two-bottle Preference Test. For example, Group MX-SA received access to the compound stimulus (MX) during Preexposure and Conditioning, and a choice between saccharin (SA) and water during Preference Testing.

The experimental phases, in order of administration, were Baseline (5 days), Preexposure (2 days), Conditioning (1 day), and Preference Testing (1 day). During all phases, experimental sessions were conducted at 0800 hours. During experimental sessions all fluids were presented in 50-ml polypropylene centrifuge tubes having spill-resistant sipper tubes. On all days 10 minutes supplemental access to water was provided to each subject at 1400 hours. No experimental manipulations were carried out at that time.

During Baseline testing, each subject received 10 minutes access to water daily during the experimental session in order to establish a consumption baseline and determine group equivalence. Ten minutes access to the designated fluid (SA, DE, or MX) was administered on each day of Preexposure. Conditioning consisted of 10 minutes exposure to the designated fluid followed 5 minutes later by an intraperitoneal (ip) injection of LiCl (12mg/kg of 0.30M). Preference Testing, conducted 24 hours following Conditioning, consisted of the placement of two centrifuge tubes, one containing SA or DE, one containing tap water, on the home cage for 10 min. The amount (mls) of each fluid consumed by each subject was recorded for each daily session.

<u>Results and Discussion</u>

As analysis of variance of the consumption scores for Baseline and Conditioning failed to yield statistically reliable effects, the groups were deemed equivalent prior to the start of Preexposure and on the day preceding Preference Testing. The results of the two-bottle preference test, presented as consumption ratios, are depicted in Figure 1 on the following page. The consumption ratios were calculated by dividing the amount of saccharin consumed (Groups SA-SA and MX-SA) or the amount of denatonium consumed (Groups DE-DE and MX-DE) by the total amount of fluid consumed. Thus, a ratio of .50 would reflect equal consumption of the test fluid and water, while a ratio lower than .50 would reflect less consumption of the test fluid. Analysis of those data yielded significance for the Type of Fluid (SA vs DE), $\underline{F}(1, 28) = 5.72$, $\underline{p} < .05$, and Type of Fluid x Type of CS (single vs multiple element), $\underline{F}(1,28) = 7.98$, $\underline{p} < .01$, effects [1]. Newman-Keuls tests, employed to evaluate the significant interaction, indicated that the consumption ratios of Group MX-SA were significantly ($\underline{p} < .05$) lower than those of all other groups, while those of Group MX-DE were significantly ($\underline{p} < .05$) higher than those of all other groups. Finally, the consumption ratios of Group SA-SA were significantly ($\underline{p} < .05$) higher than those of Group DE-DE.

One thing is clear from these data, saccharin and denatonium can form an effective compound CS. If this were not the case, the differential performance shown by the MX groups should not have occurred. Even though the significantly depressed saccharin consumption displayed

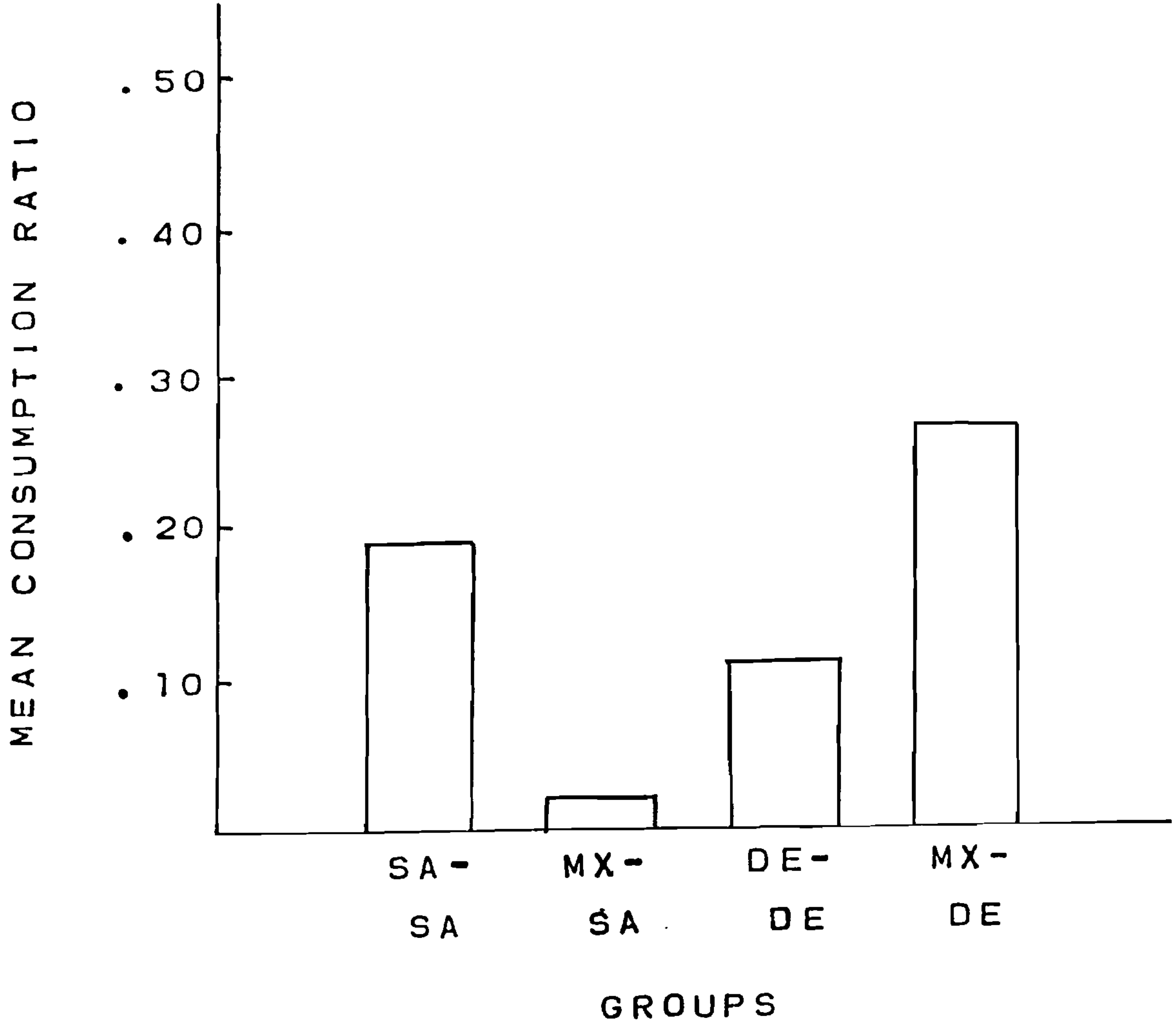

FIGURE 1: Mean consumption ratio (test fluid/test fluid + water) for the four groups during Preference Testing. Specific labels and the corresponding fluids were: SA = saccharin, DE = denatonium, and MX = saccharin + denatonium. The first portion of the group label designates the Preexposure and Conditioning fluid, while the second designation refers to the target fluid presented with water during Preference Testing. Experiment 1.

by Group MX-SA may well be characterized as potentiation, there is a potential interpretaion difficulty. The main problem facing such an interpretation concerns the preexposure period that was employed to avoid "floor" effects. It might be argued that the two flavors became associated during Preexposure, rather than on Conditioning when LiCl was administered. Thus, the results of Experiment 1, while clearly demonstrating that these two tastes can form an effective compound CS, do not unequivocally demonstrate that the occurrence of taste-taste potentiation was occasioned by LiCl-induced illness.

CHAPTER 3

EXPERIMENT 2

Several researchers have reported that preexposure to the CS can have a significant effect upon subsequent conditioning (see Domjan, 1972; Fenwick, Mikulka & Klein, 1975; Riley, Jacobs & Mastropaolo, 1983). Therefore, one might argue that the enhanced aversion observed in the previous experiment may have been the product of an association between the two elements of the CS formed during Preexposure. On the other hand, it may be proposed that the observed effects upon consumption resulted from a specific association formed between the two elements of the compound when paired with the LiCl US during Conditioning. Unfortunately Experiment 1 was not able to clearly distinguish which of these alternatives serves to best explain the results. Experiment 2 was designed to address this issue by comparing groups receiving preexposure (as in Experiment 1) and groups not receiving preexposure, as well as providing a partial replication of the first experiment.

Method

Subjects and apparatus. Thirty-six, 150-day-old male Holtzman rats, housed as in Experiment 1, served as subjects. Testing was conducted in the home cage.

Procedures. The subjects were randomly distributed across four equal-sized (n=9) groups: WAT-SAC, WAT-MIX, SAC-SAC, and MIX-MIX. The WAT, SAC, and MIX designations refer to water, saccharin, and saccharin + denatonium solutions, respectively. As in Experiment 1, SAC was a 0.15% saccharin solution and MIX was a compound composed of 0.15% saccharin + 1 part denatonium per 10,000 parts water solution. The first label of each group designation refers to the fluid received during Preexposure, while the second label refers to the fluid administered on Conditioning. For example, Group WAT-SAC received water on each of the two days of Preexposure and saccharin on Conditioning.

The length of Baseline, Preexposure, Conditioning, and Preference Testing phases of Experiment 2 was the same as the first experiment. Likewise, supplemental waterings were conducted in the same manner as in the first study. Consistent with the procedures in Experiment 1, each animal received 10-minutes access to water during daily Baseline sessions. On each day of Preexposure the subjects were allowed 10-minutes access to the appropriate solution. Identical to the manipulations employed in Experiment 1, Conditioning consisted of 10-minutes exposure to the designated fluid followed 5 minutes later by an intraperitoneal injection of LiCl (12mg/kg of 0.30M). Preference Testing, as in the first experiment, was conducted 24 hours after Conditioning and consisted of the placement of two centrifuge tubes on the home cage for 10 minutes. The only exception was that all groups received access to saccharin and water during Preference Testing in the present experiment, i.e., no denatonium vs. water tests were conducted.

Results and Discussion

Figure 2, on the following page, depicts the mean consumption ratio for each of the groups on the day of Preference Testing. Analysis of the data yeilded significance only for the Type of CS (single vs. multiple element), $\underline{F}(1, 32) = 8.35$, $\underline{p} < .01$, effect. Clearly, those subjects receiving taste-aversion conditioning to the compound (MIX) CS displayed significantly lower consumption ratios. This effect occurred whether or not the subjects had experienced preexposure to the compound CS. These results corroborate those of Experiment 1 and indicate that preexposure to the denatonium/saccharin mixture was not

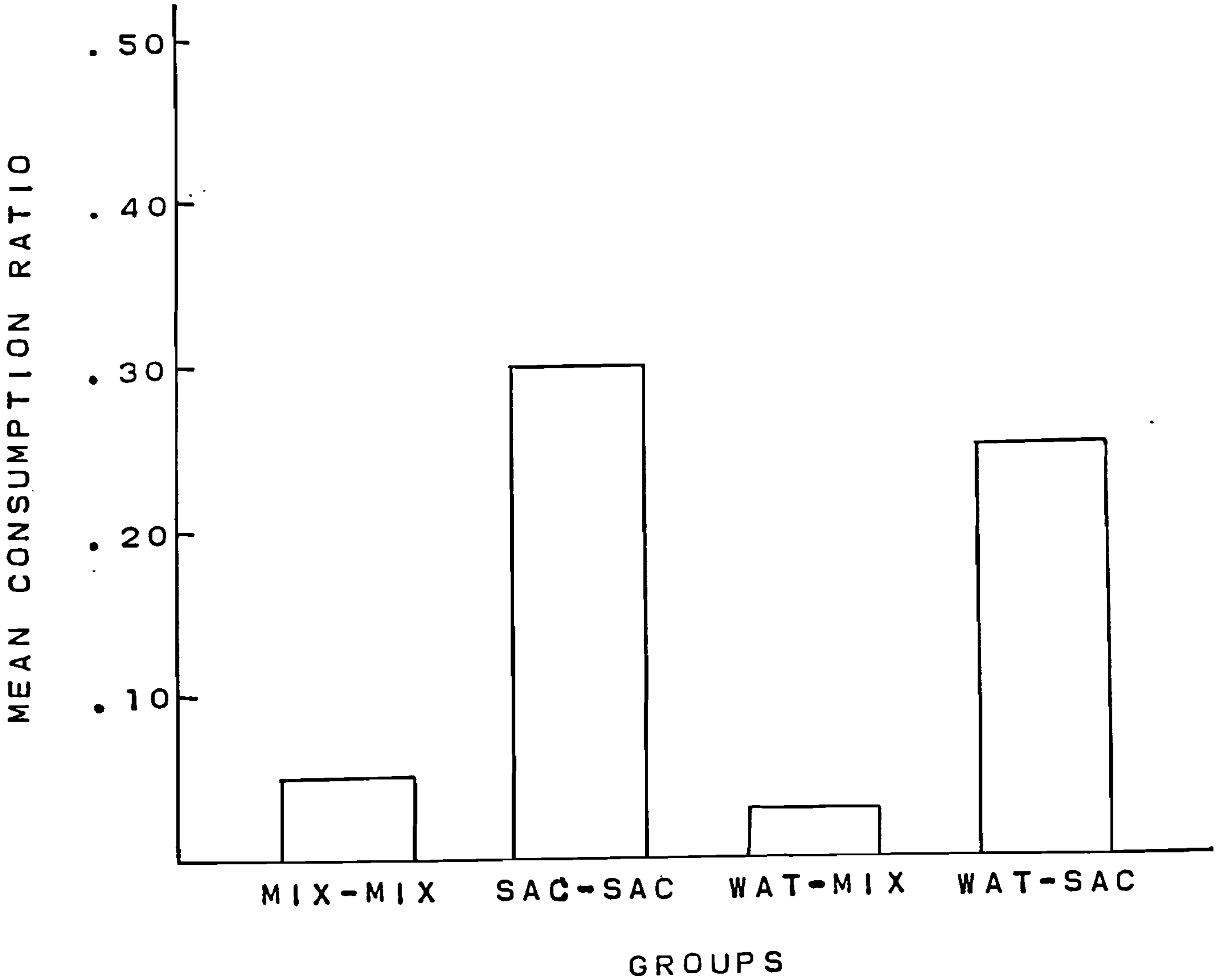

FIGURE 2: Mean consumption ratio (saccharin/saccharin + water) for the four groups during Preference Testing. Specific labels and corresponding fluids were: WAT = water, SAC = saccharin, MIX = saccharin + denatonium. The first label of each group designation refers to the fluid received during Preexposure, while the second label refers to the fluid administered on Conditioning. Experiment 2.

necessary to obtain denatonium-mediated potentiation of saccharin.

CHAPTER 4

GENERAL DISCUSSION

Experiments 1 and 2 investigated the effects of presenting two tastes, denatonium and saccharin, as a compound CS in a taste-aversion procedure. Both experiments consistently demonstrated that animals receiving the compound CS on the Conditioning trial consumed significantly different amounts of the test fluid relative to those animals that received the single element CS. Therefore, it can be concluded that the these two taste components, denatonium and saccharin, can form an effective compound. Had the consumption of the two single element groups not differed from that of the compound groups, one could not deduce that such an association had been established.

In Experiment 1 subjects conditioned to the mixture (i.e., Group MX) consumed greater quantities of the denatonium test fluid than the single element group. These findings are consitent with the prediction of "overshadowing" reported by Kamin (1969) and Revusky (1971). However, an evaluation of the second element of the compound, saccharin, revealed findings similar to taste-nontaste potentiation (e.g., Best, Brown & Sowell, 1984; Lett, 1980; Rusiniak, Hankins, Garcia & Brett, 1979). When saccharin was employed as the test fluid, subjects conditioned to the single element drank larger amounts than did the compound-CS animals. This pattern of results suggests that when those two tastes are presented in compound during taste-aversion conditioning, denatonium may enhance or potentiate the conditionability of saccharin. This demonstration of taste-taste potentiation discredits the claim that taste-mediated potentiation can be evidenced <u>only</u> in aversion-learning studies using taste-nontaste compounds (see Garcia, Lasiter, Bermudez-Rattoni & Deems, 1985; Garcia & Rusiniak, 1980; Palmerino, Rusiniak & Garcia, 1980).

While Experiment 1 demonstrated a potentiated aversion to one element of a compound CS, it did not determine whether the association responsible for those results occurred on conditioning or preexposure. As mentioned earlier, it is possible that the association between the denatonium and the saccharin may have been formed during preexposure. However, in Experiment 2, group WAT-MIX displayed potentiation to the target element even though there had been no preexposure to the compound CS. Clearly, Group WAT-MIX's enhanced aversion to the saccharin was a result of the association between the compound (denatonium + saccharin) and the LiCl-induced toxicosis on conditioning. These results suggest that preexposure is not necessary for the development of potentiation.

In attempting to explain the taste/taste potentiation observed in their experiment, Bouton, Dunlap, and Swartzentruber (1987) suggest that the potentiated target taste is weakly conditionable relative to the potentiating taste. Those authors speculate that the rat perceives the weak taste as a "feature" of the more intense conditionable taste. The target taste, which has become a "feature" of the compound, is then more readily associated with the toxicosis on conditioning. Thus, taste-taste potentiation would be predicted when the compound CS is composed of a strong (potentiating) taste and a weak (target) taste.

This theory suggests that further investigation of the comparative conditionability of denatonium versus saccharin as single elements might be warranted. If, in fact, denatonium is demonstrated to be a more conditionable taste than saccharin, then such findings would lend support to Bouton, Dunlap, and Swartzentruber's (1987) explanation of taste-taste potentiation. Given such positive results, one might be able to more readily predict the occurrence of taste-taste potentiation on the basis of the relative strength/saliency of the elements forming the compound CS.

Finally, it should be noted that while the present experiments clearly document the occurrence of taste-taste potentiation, they do not establish that this effect is attributable to within-compound associations between denatonium and saccharin. For example, it may be argued that the effects observed in Experiment 1 and 2 are due to some sort of generalization between the two tastes employed. If the effects demonstrated in these two experiments are merely the results of generalization, studies employing sequential, as opposed to simultaneous, presentation of the elements should yield the same effects because both CS elements would be presented to the subjects, just not together. However, if the potentiation is due to a within-compound association, then presenting the CS elements sequentially rather than simultaneously (as in the present studies) should result in inferior conditioning. Similarly, it might be argued that an experiment in which one of the CS elements is extinguished prior to Preference testing would shed light on the nature of the effective association. Extinction of one of the CS elements should have a pronounced effect on potentiation, particularly if this effect is attributable to a summated within-compound association that is established on the day of conditioning.

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