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The contribution of latent inhibition to reduced generalization after pre-exposure to the test stimulus

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Abstract

Two experiments assessed the contribution of latent inhibition to the generalization-reducing effects of pre-exposure to the test stimulus using a taste aversion procedure in rats. In both experiments, lithium chloride induced illness was paired with a flavor compound (AX) of either salt or sugar (A or B) and hydrochloric acid (X). Generalization of the resulting aversion to a test compound (BX), was assessed after varying pre-exposure to BX, X, and B. Experiment 1 showed that generalization to BX was less when BX itself had been exposed than equivalent pre-exposure to either B and X separately or to B and a new compound (CX). Experiment 2 showed that levels of generalization varied directly as a function of the amount of pre-exposure to BX. The findings show that latent inhibition alone cannot account for the generalization-reducing effect of pre-exposure to BX. © 2005 Elsevier B.V. All rights reserved.

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1. Reduced generalization after pre-exposure to the test stimulus

The current paper presents two studies to assess the impact of pre-exposure to a test stimulus on generalization of a conditioned aversion. It is widely known that an aversion conditioned to one flavor (e.g., A) will generalize to another (e.g., B; Honey and Hall, 1989). It is also well recognized that manipulations involving pre-exposure to the stimuli used in the test and conditioning, prior to the conditioning of the aversion, tend to reduce that generalization (Hall, 1991). This latter effect is often referred to as perceptual learning. Pre-exposure to the test stimulus alone has the effect of reducing generalization as well (Bennett et al., 1994). That observation, along with the magnitude of the effect, has important implications for theories used to address issues related to perceptual learning because the effect is either not predicted, or its magnitude is underestimated.

In explaining the generalization that occurs between stimuli it has been commonly assumed that stimuli are made up of many elements. Some of these elements are unique to each stimulus,

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but some are common. These common elements are assumed to produce generalization (Estes, 1950). In the initial example, the stimuli A and B can be construed as AX and BX, where A and B refer to the unique parts of the stimuli, and X refers to those elements that they have in common. When an aversion is conditioned to AX it generalizes to the test stimulus, BX, by way of the conditioning that is accrued to the common X elements.

Another potential source of generalization is through a process referred to as mediated generalization or mediated conditioning (Bennett et al., 1999; McLaren et al., 1989). During conditioning of AX, where the stimulus compound is paired with lithium chloride (LiCl) induced illness, A and X may both become associated with the illness, and those elements may also become associated with each other. Such stimulus pairings, in the absence of any other unexpected event, are known to produce strong "within compound" associations (Rescorla and Cunningham, 1978; Tskanikos and Reed, 2002). Through these associations, presentations of X serve to theoretically retrieve a representation of A. Thus, on a generalization test with BX, the aversion potentially generalizes through two sources. First, as discussed above, the elements that constitute X will produce some aversion. Second, those elements theoretically retrieve a representation of A, which should further contribute to the aversion seen to BX.

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Given these mechanisms of generalization, its reduction can occur through many associative processes. First, pre-exposure to the conditioning and test stimuli might alter the ability of the elements of the stimuli to enter into associations as incorporated into the theory of McLaren and Mackintosh (2000). When exposed to AX and BX, the common elements X are exposed twice as often as the unique A and B elements. As simple preexposure to a stimulus is known to interfere with its ability to come to evoke a conditioned response (i.e., latent inhibition, Lubow, 1989) X is less likely to evoke a response when AX is conditioned, effectively reducing generalization to BX.

Mechanisms that affect mediated generalization should also reduce generalization and such mechanisms are provided by the model of McLaren and Mackintosh (2000). One hallmark of the perceptual learning effect is that the way the stimuli are preexposed affects the degree to which generalization is reduced. Intermixed exposures (AX, BX, AX, BX, ...) has been shown to reduce generalization more so than blocked (AX, AX, ..., BX, BX) (Symonds and Hall, 1995). According to the model of McLaren and Mackintosh (2000) this advantage results from the formation of inhibition between the unique elements A and B. A representation of an absent stimulus should be retrieved during alternated exposures to AX and BX. On a BX trial, for example, A should be retrieved by way of the within compound $X \rightarrow A$ association. However, A is physically absent, thus, the unique feature B is correlated with A's unexpected absence theoretically allowing B to become inhibitory for A (the same logic applies from A to B). The presumed mutual inhibition between A and B removes the influence of mediated generalization.

Perceptual learning at times may be a misnomer in the specific aspects of the McLaren and Mackintosh (2000) theory just discussed in that those aspects do not suggest that perception is necessarily altered to reduce generalization. Rather, those mechanisms explain perceptual learning phenomena with respect to the way that what is perceived comes to control responding. Gibson (1969), on the other hand, deals directly with perception. Gibson (1969) suggest that pre-exposure to the unique elements of stimuli serves to enhance their perceptual dissimilarity. Intermixed pre-exposure to AX and BX allows for a comparison mechanism (loosely specified) to operate which enhances the perceptual dissimilarity of the stimuli. This type of model deals directly with how the stimuli are perceived, more so than with how the stimuli might come to control responding.

Regardless of the theory, both types predict that a reduction in generalization should be optimal when the stimuli are presented in an alternated fashion. In accord with Gibson (1969), presentations of the stimuli should allow for comparison and subsequent differentiation or enhancement of their dissimilarity. In associative theories, latent inhibition to the common element and conditioned inhibition between the unique elements should reduce the number of conditioned elements present in the test stimulus. However, the theory of Gibson has little bearing on a perceptual learning effect that might occur if only one stimulus is pre-exposed. Thus, any generalization-reducing effect that might result from pre-exposure to only one of the stimuli helps to dissociate Gibson's comparison mechanism from associative mechanisms. An initial constraint arose from the work of Bennett et al. (1994). In their studies rats that received pre-exposure to only BX, followed by conditioning with AX, showed a reduction in generalization. In those studies the authors were able to show that the reduced generalization was not due to a reduction in neophobia. Thus, pre-exposure to the test stimulus alone was sufficient to produce some reduction in generalization. This particular effect is consistent with the model of McLaren and Mackintosh (2000) in that pre-exposure to BX should produce latent inhibition to X, resulting in a reduction in generalization as discussed earlier. A similar result has been obtained by Rodríguez and Alonso (2004) where pre-exposure to BX.

The work of Bennett et al. (1994) stemmed from another mechanism of generalization suggested by Best and Batson (1977). Namely, the level of familiarity obtained with a stimulus can contribute to the generalization observed to another stimulus. If a novel stimulus were conditioned, generalization to another stimulus could be observed based on its degree of novelty. Pre-exposure to the test stimulus, BX, would reduce its novelty, and reduce the extent to which an aversion to a novel AX would generalize to BX. In contrasting this idea with a latent inhibition based explanation, Bennett et al. (1994) gave separate groups of rats pre-exposure to BX, X alone, B and X separately, or to just B. The rationale was that if latent inhibition was the primary source of the reduction in generalization, then the first three groups should perform equally well. They should all show equivalent levels of generalization because all groups received equal pre-exposure to X. However, the groups that received both B and X, or just B, should be more familiar with the BX stimulus at the time of testing than the group that received only pre-exposure to X, and hence show less generalization if novelty is the main contributor. The results supported the former prediction. No differences were observed between conditions that received equal pre-exposure to X, and varying exposures to Β.

Despite the success of the experiments of Bennett et al. (1994) in implicating latent inhibition as the chief mechanism involved in reducing generalization after pre-exposure to the test stimulus, they only used one pre-exposure and one conditioning trial which they acknowledge might not be sufficient to allow a reduction in novelty to play much of a role. A recent set of studies by Sanjuan et al. (2004) suggest that multiple trials may, in fact, be necessary. Their work shows that after eight pre-exposures to BX, a robust reduction in generalization occurred. The magnitude of the reduction could not be explained simply on the basis of latent inhibition to the common element. Eight exposures to BX reduced generalization more than eight exposures to X alone.

The present experiments explore this effect in more detail by comparing the effects of extended pre-exposure to BX to the effects of pre-exposure to its elements alone, or in combination with other stimuli in the first experiment. In Experiment 2, the level of familiarity with BX was varied by pre-exposure to that compound in an attempt to see parallel variations in generalization.

Table 1 Design of experiments

Group	Exposure	Conditioning	Test
Experiment 1			
BX/C	8BX, 8C	$3AX \rightarrow LiCl$	BX
B/CX	8B, 8CX		
B/X/C	8B, 8X, 8C		
Experiment 2			
1	1BX, 7X	$3AX \rightarrow LiCl$	BX
4	4BX, 4X		
8	8BX		
W	W		

Note: W, water; A and B, sugar and salt, counterbalanced. X was a mild concentration of hydrochloric acid and C was coffee. See text for further details.

2. Experiment 1

In Experiment 1, three groups of animals received preexposure to the test stimulus, BX, but they varied with how the elements were presented. The design in shown in Table 1. Each group received three conditioning trials where AX was paired with LiCl induced illness followed by testing with BX. The groups varied with respect to the pre-exposure in the first phase. Group BX/C received eight pre-exposures to each of BX and C. Group B/CX received eight pre-exposures to B and X, but X was presented in a compound with C. Group B/X/C received eight pre-exposures to B, X and C where each element was presented separately.

In Group BX/C the actual test stimulus was exposed and it was expected that this group would show the greatest consumption of BX (least generalization of the aversion conditioned to AX) on the test. Experience with X should produce latent inhibition and attenuate any generalization that results from the conditioning of the X elements. If latent inhibition is the only mechanism operating, then Groups BX/C and B/X/C should show equal levels of generalization which would be consistent with the findings of Bennett et al. (1994).

Group B/CX was included where X was also presented in a compound to assess the contribution of configural cues. In Group BX/C it is possible that presentation of BX results in the formation of a configural cue to which the rats habituate, simply reducing neophobia on the test. If so, then a configural cue should also be generated in Group B/CX. Although a different cue than that provided by BX, habituation to such a configural cue should affect neophobia to the test stimulus BX differently this group than in Group B/X/C. If the cue generated by CX is similar to that of BX, then Group B/CX should consume more than B/X/C. If the cue generated by CX is dissimilar to that of BX, then the cue generated by BX might be relatively more surprising resulting in less consumption in this group. The most current model of generalization (Pearce, 1987, 1994) predicts that generalization from B, X and C, presented separately would be greater to BX than from B and CX. According to the equations of Pearce, BX is 50% similar to B or X, but only 25% similar to BC. If habituation generalizes as would excitation or inhibition, then there should more neophobia in Group CX/B, than B/X/C. Although the type

of contribution is determined after the fact, the main point is that if exposure to a configural cue contributes to the consumption in Group BX, consumption in Group B/CX should vary from that in Group B/X/C. The critical comparison involving B/CX is with Group B/X/C.

2.1. Method

2.1.1. Subjects and apparatus

Subjects were 24 experimentally naïve male Wistar rats (n=8) with an average weight of 420 g (range 367–505 g). All rats were housed individually with a constant temperature (23 °C) and humidity (50%) on a 12-h on light/12-h off dark cycle with the light period beginning at 8:00 a.m. The animals remained on a regime of free access to food and restriction of liquids until the end of the experiment. The experimental sessions were conducted with the animals in their home cages.

The stimuli consisted of solutions of salt 1% and sugar 10% (counterbalanced, A and B), hydrochloric acid 1 M 1% (X) and a solution of decaffeinated coffee 0.2% (Nescafe from the brand Nestle) as stimulus C. All the percentages were calculated as weight of solute/volume of water.

2.1.2. Procedure

2.1.2.1. Water deprivation. The experiment started with the bottles being removed from the cages in the morning. Along the next 4 days the access to fluids was restricted to two 30 min sessions, one in the morning at 10:30 and another in the afternoon at 16:30. Liquids were presented according to this schedule until the end of the experiment. Subjects were randomly assigned to three groups matched on the water consumption on the last day of deprivation. The experiment was conducted in three phases, pre-exposure, conditioning and test.

2.1.2.2. Pre-exposure. This phase lasted for 12 days. All the subjects received the treatment in both of the two daily drinking sessions described above. On each session, 10 ml of liquid was available to the subjects during 30 min. Three different solutions in every group were alternated across the 24 total sessions. Each group, thus, received eight presentations of each solution. Group BX/C received the compound BX, the flavor C, and water while Group B/CX received the flavor B, the compound CX, and water, and Group B/X/C the flavors B, C and X.

2.1.2.3. Conditioning. After the end of pre-exposure conditioning started. Three trials were conducted in the morning session over 6 days, with water available in the afternoon. All subjects received a 10 ml presentation of AX for during a 30 min session followed by an intraperitoneal injection of lithium chloride (LiCl) 0.3 M at 1% body weight. Each conditioning day was followed by a recovery day where subjects had free access to water in both sessions.

2.1.2.4. Generalization test. Following the last recovery day, a test of generalization of the conditioned aversion was conducted. All the subjects had free access to BX during 30 min in the morning session.

2.1.3. Data analysis

Data consisted of the amount (ml) of fluid consumed during conditioning and testing by the subjects. The data were analyzed with analysis of variance (ANOVA). Pair-wise comparisons were conducted with analysis of variance using error terms appropriately pooled from the overall analysis following standard procedures (e.g., Howell, 1987). In such cases, degrees of freedom were reduced using the Welch–Satterhwaite procedure to compensate for the potential pooling of heterogeneous variances. Exact probabilities of results for which the null hypothesis was rejected are reported.

2.2. Results

2.2.1. Pre-exposure

All animals consumed all 10 ml of the available liquids on each session.

2.2.2. Conditioning of AX

A Group by Trials ANOVA showed an effect of Trials, F(2,42) = 689.75, as drinking generally decreased. There was no effect of Group, F(2,21) = 2, and no interaction, F(2,42) = 1.97. Consumption of AX decreased from an initial average of 9.30 to 0.11 ml. Simple effect tests confirmed the groups did not differ on any trial.

2.2.3. Generalization test with BX

Consumption of BX on the test is shown in Fig. 1. Group BX/C showed more consumption, i.e., less generalization, than the other two groups which did not differ. To assess the level of generalization from AX a generalization (last AX conditioning trial \times BX test) by Group mixed-ANOVA was conducted.



Consumption of BX

Fig. 1. Consumption of a flavor compound BX after pairings of AX with LiCl in Experiment 1. Prior to conditioning groups received exposure to BX and C, B and CX, or the flavor elements B, X and C. Error bars represent the standard-error of the mean. See text for details.

Although the animals had only 10 ml of fluid to consume during the 30 min conditioning trial with AX, the maximum consumption (0.2 ml) was well below the 10 ml available, thus, the amount of fluid available is not a confound in the analysis. The analysis revealed effects of generalization, F(1,21) = 83.65, $p = 9^{-9}$, Group, F(2,21) = 4.47, p = 0.024, and a generalization × Group interaction, F(2,21) = 4.49, p = 0.024. Simple effect tests showed no differences in consumption of AX on the final conditioning trial, Fs < 1. On the test of BX, consumption in group BX/C was higher than that of Groups B/X/C and B/CX, F(1,41) = 11.20 and 15.37, respectively, $p \le 0.002$. In the important comparison involving Group B/CX, it did not differ from Group B/X/C, F < 1.

2.3. Discussion

The present experiment shows that repeated pre-exposure to the test stimulus reduces generalization to that stimulus. The reduction in generalization cannot be wholly attributed to latent inhibition of the common X elements. Animals that received preexposure to BX (Group BX/C) showed less generalization than animals that received equal pre-exposure to X (Groups B/X/C and B/CX). Furthermore, the reduction was not a function of pre-exposure to B. Group BX/C received equal pre-exposure to both B and X as did Group B/X/C, and still showed less generalization.

It is unlikely, though not impossible, that configural cues played a strong role in the results. A configural cue should have been generated during pre-exposure in Group B/CX, which, if effective, could have had either of two effects. First, there could have been similarity between the BC and BX configural cues, thus the effects of pre-exposing CX would have generalized better to BX on test than in Group B/X/C in which no such cue was pre-exposed. Second, there could have been dissimilarity between the configural cues. The cue generated by CX could have been substantially different from that of BX, enhancing surprise generated by the BX cue (because X is associated with a different configural cue) and leading to less consumption on test. The generalization model of Pearce (1987) predicts less generalization of any learning about the CX and B stimuli to BX than such learning about B, X and C separately. Thus, if applied to the transfer of habituation of neophobia, it would predict less consumption in BC/X than in B/X/C. There was no difference between these latter two groups, in either direction, with clear room on both sides of the consumption scale to see an effect. This lack of difference suggests that configural cues, as currently understood, played no role in the consumption of BX except in the unlikely event that such cues were sufficiently different as to allow absolutely no generalization between them.

The finding of most importance is that some process, perhaps in addition to latent inhibition, was contributing to the decrease in generalization. The next experiment directly manipulated the number of exposures to the test stimulus BX between groups while controlling for the number of exposures to X. Based on the present findings it was expected that generalization would be reduced as exposures to BX increased.

3. Experiment 2

The design of Experiment 2 is shown in the bottom of Table 1. Three experimental groups of animals were contrasted against a water control. Group 1 received one pre-exposure to the test stimulus BX, and seven exposures to X. Group 4 received four exposures to BX, and four exposures to X. Group 8 received eight exposures to BX. Thus, all groups received the same amount of pre-exposure to X, but varied in their pre-exposure to the test stimulus. The groups did vary in terms of their pre-exposure to B. However, the results from the previous study indicate that this presents no problem as pre-exposure to BX was more effective than pre-exposure to B and X separately. Pre-exposure to B produced no more of an effect than pre-exposure to X alone. Thus, simple pre-exposure to B does not necessarily produce detectable reductions in generalization with the present parameters. Each group subsequently received three conditioning trials with AX followed by successive test trials with BX.

During pre-exposure, the rats had free access to the solutions. This free access allowed us to assess whether or not habituation of neophobia to the test solution, BX, could contribute to the test results. Neophobia would present itself during pre-exposure as reduced consumption in the groups receiving flavors compared to the group receiving water on the same days.

3.1. Method

3.1.1. Subjects and apparatus

Subjects were 32 (n=8) experimentally naïve Wistar male rats with a average weight of 329.5 g (range 298–365 g) at the start of the experiment. The animals were housed individually and were given free access to food and restricted access to water, under the same conditions as in the previous experiment. The stimuli employed as AX, BX and X were the same as the previous study.

3.1.2. Procedure

The experiment started with the deprivation of liquids. After retiring the bottles from the cages the subjects received water during 7 days in two 30 min sessions, one in the morning at 11:00 and the other in the afternoon at 17:00 h. This schedule lasted until the end of the experiment. The experimental sessions were conducted in the morning session. In the afternoon session all subjects received water.

3.1.2.1. Pre-exposure. This phase lasted 8 days. Every morning the subjects received 30 min access to the corresponding flavor and water in the afternoon. In this experiment, the subjects had free access to the liquids during the 30 min session. The subjects, randomly assigned to four groups received, 1 presentation of BX and 7 of X in consecutive days (Group 1), 4 presentations of BX and 4 of X (Group 4), 8 presentations of BX (Group 8) or water every day (Group W). Groups 1 and 4 received all of the respective exposures to BX consecutively followed by X.

3.1.2.2. Conditioning. At the end of pre-exposure three conditioning trials were conducted where the subjects were allowed

to drink 10 ml of AX during 30 min in the morning session. After this period of time all the subjects received an injection of LiCl 0.3 M at 1% of body weight. Each conditioning day was followed by a recovery day as in the previous experiment.

3.1.2.3. Generalization test. After the last day of recovery one test trial with BX was conducted to assess the generalization of the conditioned response to AX. On the test all the subjects were allowed to drink an unlimited amount of BX during 30 min on the morning session.

3.2. Results

3.2.1. Pre-exposure and assessment of neophobia

In Group W, consumption of water reliably increased from 9.2 to 15.93 ml F(7,97) = 12.27, p < 0.001 over the 8 days of pre-exposure simply reflecting further adaptation to the drinking procedure that was present in all the groups. Any lack of differences between consumption of BX and water, especially on early pre-exposures, cannot be due to a ceiling on consumption. There was room on both ends of the response scale to observes differences.

Consumption of BX during each pre-exposure for each group was compared to the corresponding consumption on the same day(s) in Group W. In Group 8 there were no differences from Group W on any of the eight exposures to BX, $Fs \leq 2.91$, p > 0.11. Consumption of BX averaged 11.08 (S.D. = 3.75) and consumption of water averaged 10.99, (S.D. = 1.31). Likewise, in Group 4 consumption of BX did not differ from the corresponding 4 days of water consumption in Group W, $F \leq 2.54$, $p \ge 0.13$. Consumption of BX on the first four trials averaged 10.27 ml (S.D. = 2.55) and consumption of water averaged 9.33 (S.D. = 1.38). Finally, in Group 1, the single consumption of BX did not differ from consumption of water, F < 1. Consumption of BX averaged 9.01 (S.D. = 1.81) and consumption of water averaged 9.2, (S.D. = 2.37), on this trial. In this study, there was no evidence of neophobia to BX, leaving different levels of neophobia as an implausible explanation for any group differences on test.

3.2.2. Conditioning

Data from conditioning are shown at left in Fig. 2. A Trials × Group analysis of the consumption of AX during conditioning showed an effect of Trial, F(2,56) = 225.36. There was a near effect of Group, F(3,28) = 2.629, p = 0.065, and no interaction between the factors, F < 1, (pooled MSE = 2.57). The lack of an interaction is surprising given that the near-effect of group largely occurred due to the second trial. There were no group differences, near or otherwise, on the first and last trials, Fs < 1. An analysis of trial two revealed that Groups 8 and W did not differ from each other and Groups 1 and 4 likewise did not differ from each other. Combined, (and individually) Groups 8 and W both differed from Groups 1 and 4, F(1,83) = 20.80, p < 0.001.

3.2.3. Generalization test with BX

Data from the generalization test are presented in Fig. 2 at right. As pre-exposure to BX increased, generalization



Fig. 2. Consumption of BX (right) after pairings of AX with LiCl (left) in Experiment 2. Prior to conditioning groups received one pre-exposure to BX and seven exposures to X, four pre-exposures to BX and four to X, eight pre-exposures to BX and none to X, or no pre-exposures. Error bars represent the standard-error of the mean. See text for details.

decreased. A Generalization (last AX trial versus BX test) by Group ANOVA on the mean amount (ml) consumed was conducted. Although animals had only access to 10 ml of the compound on the last conditioning day, the maximum consumption on this day for any animal was again 0.2 ml making the different amounts of fluid available on the 2 days of no consequence. The analysis showed effects of generalization, F(1,28) = 221.83, p < 0.001, Group, F(3,28) = 6.29, p = 0.002, and a Generalization by Group interaction, F(3,28) = 6.3, p = 0.004. Simple effect tests confirmed the earlier analysis of the conditioning data showing no differences in consumption of AX on the final conditioning trial. On the test with BX, consumption of BX in Group W was less than that of Groups 1, 4 and 8, *Fs*(1,55) = 9.74, 21.68, and 30.62, for each comparison respective, $p \le 0.002$. Consumption of BX in Group 1 differed from Group 8, F(1,55) = 5.82, p = 0.02, but not from Group 4, F(1,55) = 2.43. Groups 8 and 4 did not differ, F < 1.

As reflected by the analysis of group differences above, the number of exposures to BX, (0, 1, 4 or 8) produced a linear trend among the means of consumption of BX, F(1,28) = 16.48, accounting for 38% of the variance ($\dot{\eta}^2$). There was no significant deviation from linearity, F(2,28) < 1.

3.3. Discussion

This study shows that among groups receiving equivalent pre-exposure to the common element X, generalization to BX varied directly as a function of pre-exposure to BX. As in the previous experiment, latent inhibition alone cannot account for the reduction in generalization observed after multiple exposures to the test stimulus. This conclusion is strengthened by the analysis of the data from conditioning. In Group W, there was no opportunity for latent inhibition as this group did not receive pre-exposure to any of the stimuli. The analysis of trial two from conditioning suggests that this group conditioned more rapidly than Groups 1 and 4 which each received seven and four exposures to X alone, respectively. Group 8 did not differ in the rate of conditioning from Group W, and differed from both Groups 1 and 4. This pattern suggests that either latent inhibition to BX did not generalize to AX, supporting that pre-exposure to BX enhances its ability to be discriminated, or no latent inhibition to X developed in this condition and thus could not contribute to the test performance.

It is also unlikely that different levels of neophobia to the test stimulus can explain the present findings. All groups increased their consumption across the pre-exposure phase, including Group W, reflecting an equal adaptation to the drinking procedure in all groups. Furthermore, consumption of the acidic BX never differed from consumption of water on any day, suggesting that there was no neophobia to the BX compound in this procedure.

One possibility in the current study is that the order in which the stimuli were exposed prior to conditioning might make a difference. In the groups receiving pre-exposure to BX and X, they received exposures to BX followed by exposures to X. As such, the group receiving eight exposures to BX had recently experienced BX, the group receiving four exposures had less recent experience, and the group receiving one pre-exposure had an even more distant experience. For the time differences between pre-exposure to BX and testing to account for the findings, one would need to appeal to forgetting. Hence, the more distal preexposure to BX might lead to it being forgotten, and thus less familiar while the more proximal experiences would provide for less forgetting, leaving the stimulus more familiar. Regardless of whether the generalization-reducing effects of the pre-exposure were due to the extended pre-exposure to the test stimulus, or the relative time that elapsed between pre-exposure and testing, both should theoretically be related to the same construct in that both could affect memory for the stimulus.

4. General discussion

The experiments reported in this paper demonstrate that repeated exposures to the test stimulus reduce generalization more so than would be expected on the basis of latent inhibition alone. In Experiment 1, pre-exposure to BX reduced generalization more than pre-exposure to B and X in isolation. On the basis of latent inhibition to X, these conditions would have produced equal levels of generalization. In Experiment 2, when pre-exposure to X was equal, increasing pre-exposure to BX linearly decreased generalization.

Reduced novelty as discussed by Best and Batson (1977) is unlikely to fully explain the current findings. Presentations of B and X in Experiment 1 would reduce the novelty of B and X, and hence the novelty of BX. Yet, generalization to BX was reduced the most when BX itself was pre-exposed. One might assume that the stimuli in compound produce a configural cue (Pearce, 1987; Rescorla and Wagner, 1972) whose novelty is not reduced by presentations of B and X separately, making pre-exposure to BX more effective than pre-exposure to the elements. The group receiving pre-exposure to B and CX helps to rule out this interpretation. Pre-exposure to CX should produce a configural cue with some similarity to that produced by BX affecting its novelty. This group received the same pre-exposure to X as did the group receiving pre-exposure to B, X and C separately, and should show a different level of generalization if familiarity with some configural cue is necessary. No such difference was detected.

Although typically applied to simple habituation, Sokolov (1963) offers an idea that is relevant to the effects presented here. Pre-exposure to stimuli are supposed to allow the perceptual mechanism to form better and more accurate representations of those stimuli. Thus, after these representations are formed through pre-exposure, organisms should be better able to discriminate stimuli as a comparator mechanism will be able to detect differences between stimuli. When the comparator detects a mismatch between the present stimulus and the previous representation that is stored, it generates an orienting response (i.e., dishabituation). Sokolov (1963) assumes that conditioned responding is also affected by difference between the stimulus and the neuronal model. When a mismatch is detected between the neuronal model of the CS and the actual stimulus being presented, an orienting response is generated and the conditioned response is "arrested" (Sokolov, 1963, p. 292).

Representations of the test stimulus, BX, would be formed by its actual presentation, and those representations would become more accurate with the amount of pre-exposure to BX. Thus, the comparator mechanism would be more likely to detect the differences between the conditioned stimulus, AX, and the test stimulus BX, and produce less generalized conditioned responding. The neuronal model is a supposed "polyvalent model" of the stimulus representing "all, or a considerable group of its components" (Sokolov, 1963, p. 287). The neuronal model resulting from compound presentations of B and X should contain both stimuli. In the present designs, such a model of BX would be affected when one of these stimuli are removed. When applied to the control conditions where B and X are presented separately, B and X would not serve to form the same neuronal model as presentations of B and X in compound. When BX is presented in these conditions the presence of X would be a feature not included in the neuronal representation of B, and vice versa. In

the absence of a clear neuronal model of BX, the comparator mechanism should be less able to detect differences between AX and BX, perhaps resulting in more generalization.

Recently, (Hall, 2003; Blair and Hall, 2003a,b; Blair et al., 2004; Mondragon and Hall, 2002) has suggested an analysis of perceptual learning that, in essence, combines aspects of associative (McLaren and Mackintosh, 2000) and non-associative accounts (Gibson, 1969) discussed in the introduction. Both associative and non-associative accounts assume common and unique elements among the stimuli. They both agree that the pre-exposure to the common elements, in some way, reduces their effectiveness as stimuli. For the model of McLaren and Mackintosh (2000), that reduced effectiveness is manifest as latent inhibition. For Gibson's theory, it might be assumed to be a reduction in salience manifest in its ability to distract. The theories differ in how they treat the unique elements. Recall from the introduction that, according to associative theories, generalization occurs from AX to BX because of conditioning of X, and because of mediated generalization. Associations between A and X may be formed during conditioning so that when BX is presented, X can retrieve a representation of A, which should theoretically contribute to the conditioned response. According to associative theories, pre-exposure to AX and BX prior to conditioning may allow the formation of inhibition between A and B, thus, on test, that inhibition eliminates the contribution of mediated generalization from the unique elements. According to Gibson (1969), these unique elements become more perceptually effective. That is, on a test with BX the compound is perhaps likely to be perceived more so as B than as X or BX.

How this increased perceptual effectiveness might be achieved has been somewhat unspecified until recently. Hall (2003) has suggested, in accord with McLaren and Mackintosh (2000), that when an association is formed between the common and unique elements the common element is able to evoke representations of the unique elements. Here, Hall (2003), suggests that when these representations are evoked, in the absence of the stimulus itself, the ordinarily decreased perceptual effectiveness of the unique stimulus is restored. To illustrate, during exposures to AX and BX in a typical perceptual learning study, one would expect latent inhibition to A and B, and more to X. The double exposures (and perhaps double latent inhibition to X) should result in a perceptual learning effect. When AX is presented, the representation of B should be retrieved, yet the actual stimulus is absent. According to Hall (2003) this restores the effectiveness of B as a stimulus, in essence, making it more distracting on the test. When tested with BX after conditioning with AX, a reduction in generalization might be observed in part because of some latent inhibition to X, but also because B is more distracting that it ordinarily would be after pre-exposure.

This idea might be considered to be inapplicable to the current study because AX was not exposed prior to conditioning. However, exposures to BX should still theoretically allow associations to form between B and X. Thus, during conditioning of AX, B should still be retrieved and the perceptual effectiveness of B should be restored. This would not occur in conditions where B and X are presented separately. There are, of course, challenges to this explanation. For example, one could argue that because the representation of B should be present during conditioning of AX, its image should be conditioned as well (e.g., Ward-Robinson and Hall, 1996) and provide an additional source of conditioned aversion. It may be possible that the distracting effects of B are independent of the associations it controls and, depending on the relative strengths of the two processes, either could manifest itself. Future work might uncover the conditions where these two processes could be dissociated.

The results of the present experiments make a relatively obvious point that is not so easily explained by associative theories of perceptual learning: pre-exposure to the test compound BX is not the same as pre-exposure to its elements alone. The results of the present experiments show that the reduced generalization which occurs as the result of pre-exposure to the test stimulus is due to more processes than the operation of latent inhibition.

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References

- Bennett, C.H., Scahill, V.L., Griffiths, D.P., Mackintosh, N.J., 1999. The role of inhibitory associations in perceptual learning. Anim. Learn. Behav. 27, 333–345.
- Bennett, C.H., Wills, S.J., Wells, J.O., Mackintosh, N.J., 1994. Reduced generalization following preexposure: latent inhibition of common elements or a difference in familiarity. J. Exp. Psychol. Anim. Behav. Process. 20, 232–239.
- Best, M.R., Batson, J.D., 1977. Enhancing the expression of flavor neophobia: some effects of the ingestion-illness contingency. J. Exp. Psychol. Anim. Behav. Process. 3, 132–143.
- Blair, C.A.J., Hall, G., 2003a. Changes in stimulus salience as a result of stimulus preexposure: evidence from aversive and appetitive testing procedures. Learn. Behav. 31, 185–191.

- Blair, C.A.J., Hall, G., 2003b. Perceptual learning in flavor aversion: evidence for learned changes in stimulus effectiveness. J. Exp. Psychol. Anim. Behav. Process. 29, 39–48.
- Blair, C.A.J., Wilkinson, A., Hall, G., 2004. Assessments of changes in the effective salience of stimulus elements as a result of stimulus preexposure. J. Exp. Psychol. Anim. Behav. Process. 30, 317–324.
- Estes, W.K., 1950. Toward a statistical theory of learning. Psychol. Rev. 57, 94–107.
- Gibson, E.J., 1969. Principles of Perceptual Learning and Development. Appleton-Century-Crofts, New York.
- Hall, G., 1991. Perceptual and Associative Learning. Clarendon Press, Oxford, UK.
- Hall, G., 2003. Learned changes in the sensitivity of stimulus representations: associative and nonassociative mechanisms. Q. J. Exp. Psychol. 56B, 43–55.
- Honey, R.C., Hall, G., 1989. Enhanced discriminability and reduced associability following flavor preexposure. Learn. Motiv. 20, 262–277.
- Howell, D.C., 1987. Statistical Methods for Psychology, second ed. PWS-KENT, Boston.
- Lubow, R.E., 1989. Latent Inhibition and Conditioned Attention Theory. Cambridge University Press, Canada.
- McLaren, I.P.L., Mackintosh, N.J., 2000. An elemental model of associative learning: I. Latent inhibition and perceptual learning. Anim. Learn. Behav. 28, 211–246.
- McLaren, I.P.L., Kaye, H., Mackintosh, N.J., 1989. An associative theory of the representation of stimuli: applications to perceptual learning and latent inhibition. In: Morris, R.G.M. (Ed.), Parallel Distributed Processing: Implications for Psychology and Neurobiology. Clarendon, Oxford, UK, pp. 102–130.
- Mondragon, E., Hall, G., 2002. Analysis of the perceptual learning effect in flavour aversion learning: evidence for stimulus differentiation. Q. J. Exp. Psychol. 55B (2), 153–169.
- Pearce, J.M., 1987. A model for stimulus generalization in Pavlovian Conditioning. Psychol. Rev. 94, 61–73.
- Pearce, J.M., 1994. Similarity and discrimination: a selective review and a connectionist model. Psychol. Rev. 94, 61–73.
- Rescorla, R.A., Cunningham, C.L., 1978. Within-compound flavor associations. J. Exp. Psychol. Anim. Behav. Process. 4, 267–275.
- Rescorla, R.A., Wagner, A.R., 1972. A theory of Pavlovian conditioning: variations in effectiveness of reinforcement and nonreinforcement. In: Black y, A.H., Prokasy, W.F. (Eds.), Classical Conditioning II: Current Research and Theory. Appleton-Century-Crofts, New York, pp. 64–99.
- Rodríguez, G., Alonso, G., 2004. Perceptual learning in flavor aversion learning: Alternating and blocked exposure to a compound of flavors and to an element of that compound. Learn. Motiv. 35, 208–220.
- Sanjuan, M.C., Alonso, G., Nelson, J.B., 2004. Blocked and test-stimulus exposure effects in perceptual learning re-examined. Behav. Process. 66, 22–33.
- Sokolov, E.N., 1963. Perception and the Conditioned Reflex. Pergamon Press, New York.
- Symonds, M., Hall, G., 1995. Perceptual learning in flavor aversion conditioning: roles of stimulus comparison and latent inhibition of common elements. Learn. Motiv. 26, 203–219.
- Tskanikos, E., Reed, P., 2002. The influence of a distractor during compound preexposure on latent inhibition. Anim. Learn. Behav. 30, 121–131.
- Ward-Robinson, J., Hall, G., 1996. Backward sensory preconditioning. J. Exp. Psychol. Anim. Behav. Process. 22, 395–404.